Measuring and Monitoring Biodiversity in Tropical and Temperate Forests

Edited by Timothy J. B. Boyle and Boonchoob Boontawee

CIFOR
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MEASURING AND MONITORING BIODIVERSITY IN TROPICAL AND TEMPERATE FORESTS

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Proceedings of a IUFRO Symposium held at Chiang Mai, Thailand August 27th - September 2nd, 1994

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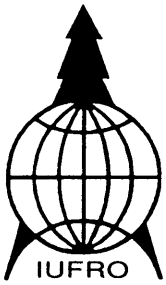

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Center for International Forestry Research
Bogor, Indonesia

Mailing Address: PO Box 6596 JKPWB, Jakarta 10065, Indonesia

Preface

This book contains 24 papers selected from among those presented at an international symposium on *Measuring and Monitoring Biodivcrsity in Tropical and Temperate Forests* , held in Chiang Mai, Thailand, between the 27th of August and 2nd of September, 1994. The symposium was attended by over 240 scientists from more than 40 countries from around the world. In addition to four days of paper presentations, there was also a one-day field trip, and a continuous poster session, with more than 35 posters, as well as computer demonstrations of software packages for identifying and measuring biodiversity.

Biodiversity is an immense subject, and as tropical and temperate forests are home to a large proportion of the earth s terrestrial biodiversity, it is obviously very difficult to cover the topic comprehensively in a single volume. The papers included in this book were selected to give as broad a coverage as possible of key topics under the general title, including *Principles of Measuring and Monitoring Biodiversity* (8 papers), *Genetic Diversity* (6 papers), *Species and Ecosystem Diversity* (5 papers), and *Methodology* (5 papers). Inevitably, forest trees are the theme of many papers, but also included are papers dealing with diversity of arthropods, microfungi, birds and butterflies, and gibbons, as well as many papers dealing with the entire range of biodiversity.

We would like to thank many people who helped to make the symposium and this book possible. Among these are the sponsors of the symposium, the Royal Forest Department of Thailand, the Commission of the European Communities, the Canadian International Development Agency (including the ASEAN Forest Tree Seed Centre and SADCC Tree Seed Centre Network), the Canadian Forest Service, the U.S. Forest Service, the Center for International Forestry Research, and the International Plant Genetic Resources Institute.

We would also like to acknowledge the contribution of the entire Organizing Committee in Thailand, and particularly the assistance of Ms. Rosita Go of CIFOR, for her work before, during, and after the symposium, especially in arranging financial support for developing country scientists, and preparing the manuscripts for publication.

Finally, we would like to thank reviewers of the manuscripts: Md. K. Alam, S. Appanah, P. Ashton, K. Bawa, K. Boonpragob, W. Brockelman, J. Brouard, N. Byron, K. Chaisurisri, J. Coles, M. Collins, J. Cornelius, C. Cossalter, J. Davie, L. Duchesne, Y. El-Kassaby, R Finkeldey, A. Gillison, M. Green, P. Hall, S. Harris, O. Hendrickson, M. Hossain, M. Ibach, H. Joly, P. Kanowski, M. Kariuki-Larsen, R Leakey, S. Magnussen, E. McKenzie, J. McNeely, D. Meidinger, C. Nair, F. Ng, I. Nielsen, T. Nieman, M. van Noordwijk, H. Offerman, A.S. Ouedraogo, C.

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T.J.B. Boyle
B. Boontawee

This book is Dedicated to the Memory of

Professor Dr. Tem Smitinand, 1920-1995

Born on 27th June 1920, Professor Dr. Tem Smitinand was educated at Depthsirin College, Bangkok, before continuing his studies at Phrae Forestry School, from where he obtained a Certificate in Forestry in 1939. He then joined the Royal Forest Department of Thailand, and started his career in forest botany.

Professor Dr. Tem Smitinand was, until his death, Senior Expert in Botany at the Royal Forest Department, and a fellow of the Royal Institute. He was one of the most famous botanists of the Asia-Pacific region, and was also widely respected around the world. He received Honorary Doctorate degrees from Kasetsart University, Srinakarintaraviroj University, and Silpakorn University. He was a member of many botanical societies in Thailand and overseas, and was chair of the Natural History Division of the Siam Society.

He was a prodigious author and editor of many books and periodicals, including *The Vanasarn, The Thai Forest Bulletin (Botany), Flora of Thailand*, produced by the Royal Forest Department, and *The Natural History Bulletin* of the Siam Society. He was also a consultant to the Board of Editors of the English edition of the Sciences Society of Thailand. Some of his principal works included *Thai Flora* in the Thai Encyclopedia of the Royal Institute, *Cycadaceae Family* in the Flora of Thailand, *Orchids of Thailand*

(with Dr. Gunnar Seidenfadon), *Edible and Poisonous Plants in Thailand,* produced by the Military Research and Development Centre of the Ministry of Defense, and *Wild Plants of Thailand,* in the Thai Encyclopedia for Youths, initiated by H.M. King Bhumipol Adulyadej .

Professor Tern had been working on wild flowers and wild plants from the very beginning of his career until the end of his life. He acquired an enormous depth of experience in botany, on his own, by trekking through all the forests and regions of Thailand. His worldwide reputation meant that any visiting botanist or forest scientist were always recommended to see him when they visited Thailand.

At the end of his life, he contributed actively to the debate on forest biodiversity. He was a member of the organizing committee for the IUFRO Symposium on *"Measuring and Monitoring Biodiversity in Tropical and Temperate Forests",* held in Chiang Mai, August 27 - September 2, 1994. He presented the keynote speech at the Symposium, which is included in these Proceedings, and led participants on a field trip to examine forest biodiversity at Doi Inthanon National Park.

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OVERVIEW OF THE STATUS OF BIODIVERSITY IN TROPICALAND TEMPERATE FORESTS

KEYNOTE ADDRESS
Prof. Dr. Tern Smitinand

Ladies and gentlemen, since the Director General of the Royal Forest Department has an urgent commitment elsewhere, the organising committee has asked me to deliver the keynote address in his stead. I will try my best to make it as brief as possible.

CONCEPT OF BIODIVERSITY

Biodiversity is a term that has recently been widely used. It is the variety and variability among living organisms and the ecological complexes in which they occur. It can be defined as the number of different items and their relative frequency, For biological diversity, these items are organised at many levels, ranging from DNA sequences that are the molecular basis of heredity to complete ecosystems. Thus, the term encompasses genes, species, ecosystems and their relative abundance.

Biodiversity can be divided into three hierarchical categories:

- Genetic diversity refers to the variation of genes within species covering distinct populations of the same species or genetic variation within a population.
- Species diversity refers to the variety of living organisms on earth.
- Ecosystem diversity refers to the variability of habitats and biotic communities including the variety of ecological processes within ecosystems.

VALUE OF BIODIVERSITY

The diversity manifested by the countless kinds of genetic materials, varied species and ecosystem types has enormous value. The variety of distinct micro-organisms, plants, animals and habitats can influence the productivity and services derived from the ecosystems.

Biodiversity provides direct economic benefits in terms of food, medicine and industrial raw materials, and supplies the functional ingredients for natural ecosystems to provide an array of essential services to man (photosynthesis, regulation of absorption and breakdown of the hydrologic cycle and climate, absorption and breakdown of pollutants and many others). Plants and animals, like human beings, have an established right to existence, therefore we should be concerned with their value and conserve their diversity.

LOSS OF BIODIVERSITY AND ITS CAUSES

Our biological resources are being overused, hampering their regenerative capacity. The crucible of extinction is already threatening our natural environment. In order to save our remaining forests from ultimate destruction, a clear understanding of the major causes of biodiversity losses is needed. The known manifestations of the loss of biodiversity are: habitat loss and fragmentation, overharvesting, introduced species, chemical pollution, global climatic changes, and agricultural and forest industries. The decline of biodiversity is caused by direct and indirect factors. It is the consequence of use or misuse of the environment by man for his own purposes.

The loss of tropical forests can have far-reaching effects, including changes in regional climate, especially rainfall pattern, and biological productivity; acceleration of soil erosion, disruption of watershed stability, and an increase in the global atmospheric temperature, as well as further impacts on global climate dynamics.

In terms of biological diversity, the destruction of primary tropical and temperate forests threatens quite a number of species with extinction. Their inherent and aesthetic value, and their potential agricultural, pharmaceutical, and silvicultural values vanish with them.

GENETIC DIVERSITY

At present the research in genetic diversity of tropical and temperate forests is carrying on at an accelerating rate, resulting in genetic conservation of economic species.

SPECIES DIVERSITY

Plants

It is estimated that some 248,000 species of plants have been described world-wide, with increasing numbers where the current exploration in the tropics is still being undertaken.

Animals

It is estimated that some 1.4 million animal species have been described world-wide and follows the same trend as plant species. The diversity of animals is higher than that of plants, and yet many more are awaiting further study.

ECOSYSTEM DIVERSITY

Terrestrial ecosystems

Terrestrial ecosystems consist of seven main categories, namely: temperate and tropical evergreen forests, dry and moist mixed deciduous forests, scrub forest, savana and agricultural land.

Freshwater ecosystem

Freshwater ecosystems can be defined into three major habitats, namely: lakes, ponds/reservoirs, flood plains.

Marine ecosystems

Marine ecosystems consist of mangrove forests, saline lakes, coral reefs, seagrass

beds, and off-shore ecosystems. These ecosystems play important roles in fisheries as spawning grounds for marine life and in coastal protection. They are facing the same trends as freshwater ecosystems.

FUTURE PLANS

Our understanding of the Earth's biological diversity has significant gaps. The lack of information hampers our ability to comprehend the magnitude of the loss of biodiversity and to formulate sustainable alternatives to resource depletion.

To achieve good conservation and management of our natural resources, we should know the status of our genetic and biological resources. Thus continuous work and intensive research in the fields of genetic diversity, species diversity and ecosystem diversity are urgently needed. It is indeed a time to instigate international collaboration in education, technology transfer, research and last, but not least, financial support.

This symposium will certainly provide a good opportunity to learn and exchange ideas and expertise with experts and researchers from different countries and contribute to international collaboration in measuring and monitoring forest biodiversity in an effective way in the near future. Thank you.

Chapter

2

BIODIVERSITY VERSUS OLD-STYLE DIVERSITY MEASURING. BIODIVERSITY FOR CONSERVATION

E. C. Pielou[1]

INTRODUCTION

This Symposium is about biodiversity. Right at the outset, it is worthwhile pondering the difference between two words frequently used by ecologists nowadays: diversity and biodiversity. This is the distinction, as I see it, between the meanings of the two words:

Diversity is a concept that was introduced into ecology more than 50 years ago, and it has been a central topic in theoretical ecology ever since. It is at the heart of several fundamental problems ecologists are still wrestling with, for example: does competitive exclusion limit the number of related taxa that can coexist in a given environment? Is there a limit to the similarity between coexisting species? And, how finely can "niche-space" be subdivided?

Investigators of these and related problems are usually concerned with communities that are fairly narrowly defined (in the taxonomic sense), and which are confined to fairly restricted spaces. For instance, one might want to compare

[1] **Denman Island, British Columbia, Canada VOR 1TO.**

communities of cavity-nesting birds in deciduous forest with those in evergreen forest, or the communities of benthic organisms in flowing water with those in still water. To facilitate comparisons it is desirable to measure quantitatively an attribute of each community that can be called its diversity index. The index is analogous to a variance, it measures the "qualitative variability" of a collection of objects (e.g., organisms belonging to several species) in the same way that variance measures the "quantitative variability" of a collection of magnitudes (e.g., the heights of the trees in a forest).

Biodiversity is an altogether different topic. Though diversity and biodiversity both deal with variability in a general sense, the scales of variability concerned, and the reasons for studying it differ enormously. Biodiversity is concerned with the biota as a whole, and the reason for investigating it is in order to conserve it as it is in nature, by maintaining extant species in their natural habitats.

The distinction between the two concepts can be summarized thus:

Diversity is a theoretical topic, biodiversity is part of applied ecology. Note, however, that biodiversity is an attribute of the natural world, one that applied ecologists are seeking to conserve. To attempt this by artificially increasing the diversity in local patches of forest (Namkoong 1991) is an aberration.

Diversity is value-neutral, whereas biodiversity weights (or values) different items according to their rarity. For example, consider two cavity nesting birds of the forests of northeastern North America: the eastern bluebird, an indigenous rarity, and the starling, an introduced pest that excludes other birds from many of the available nesting cavities. A student of diversity would treat these species as equal. A student of biodiversity, concerned to conserve species and prevent extinctions, would attach a high value to bluebirds, and a very low, possibly negative, value to starlings.

Diversity is a property of taxonomically narrowly defined groups of organisms, biodiversity is a property of the whole biosphere. For example, a student of the diversity of shorebirds and their diets would not put several species of birds and the organisms they eat (insects, crustaceans, and the like) all on a single list to be treated as a unit. But a conservationist wishes to treat the whole biosphere as a unit and finds it an unfortunate necessity, not a theoretically desirable simplification that, for practical reasons, the biosphere has to be studied piecemeal, generally one ecosystem at a time.

MEASURES OF DIVERSITY AND BIODIVERSITY: THE CONTRASTS

Species Richness

The simplest measure of both diversity and biodiversity, in spite of the great conceptual contrast between them, is S, the number of species in the community or ecosystem concerned. This is the species richness. Its value is arrived at merely by counting. Admittedly, statistical problems arise when the community of interest is too large to census in its entirety; then S must be estimated by extrapolation.

For a student of biodiversity, concerned with all the organisms existing in an ecosystem, the counting of species is wholly impossible. It is often useful to treat some well-defined, manageable taxon, for instance all vascular plants, as a surrogate for "all life." In such a case, one often wishes to do more than merely count species. It may be desirable to weight them, or equivalently, attach values to them. In the context of plant biodiversity, Usher and Pineda (1991) have recommended giving greatest weight to native species growing in their characteristic habitats, or "quality species". Lower weights are given to native species not in their characteristic habitats, and still lower weights (zero, perhaps) to introduced species. Alternatively, in a region with a well-known flora, species' weights could be made inversely proportional to some measure of their rarity, or of the extent of their geographic ranges. Many possible weighting schemes can be devised, and the whole topic deserves the attention of research workers.

It is worth noting, and dismissing, the criticism sometimes made that weighting species is somehow "unscientific" (Walters and Ramsay 1992). The criticism applies to theoretical studies of diversity, but is wholly inappropriate in the context of biodiversity and its conservation.

Conservation of Species-poor Ecosys terns

All ecologists are aware of the urgent need to conserve the world's natural biodiversity. It should not be necessary (though unfortunately it is) to emphasize an obvious fact: that the concern is, or should be, with biodiversity as opposed to diversity. The "worthiness" of a tract of land from the conservation point of view cannot be judged by considering the tract in isolation and comparing its species richness with that of other tracts. Such an approach leads to absurd consequences, such as the protection of tracts rich with ubiquitous species at the expense of species-

poor tracts where uncommon species of limited range or unusual habitat requirements are found.

Magurran (1988) has rightly argued that in choosing lands to protect, "[a]ssessing sites by diversity alone can be misleading." It is worse than misleading - it is counterproductive. Biodiversity, not diversity, is the point at issue. Colwell and Coddington (1994) likewise emphasize the distinction, they discuss measures of complementarity - the degree to which a tract being considered for preservation complements other tracts instead of merely duplicating them.

Diversity Indices

Numerous diversity indices based on measures (or estimates) of the quantities of the different species in each sample plot have been devised. The two best known are Shannon's Index, and various inverse functions of Simpson's Index of Concentration (the converse of diversity). They are wholly unsuitable for measuring biodiversity. This becomes clear from consideration of the following points:

- Biodiversity studies need rapidly gathered data from as many plots as possible, over large areas. This requires presence/absence (binary) data, not detailed, time-consuming measures of quantity.
- Biodiversity deals with organisms ranging in size from trees to bacteria, making comparable quantitative measurements on such different scales is impracticable.
- Use of binary data overcomes difficulties with quantitative data, such as the size of herbaceous plants changing rapidly with the seasons.
- In many animals (e.g., insects), population sizes fluctuate enormously from year to year. Binary data are much less affected than quantitative data by such quantitative variability.

SPECIES LISTS AND CHECK LISTS: THE PROBLEM OF MONITORING

Check lists

This Symposium is about "measuring and monitoring biodiversity." In my opinion, these activities are separate: measuring is not a necessary preliminary to monitoring. This is fortunate, considering the tremendous disagreements among ecolo-

gists on how measuring should be done. Some ecologists believe that the overriding criterion for a biodiversity measure is that it be quick, cheap and easy to obtain. Certainly monitoring should be quick, cheap and easy, but measuring need not be. Keeping monitoring separate from measuring makes our problems much easier to solve.

In exploited forests, the components of biodiversity most at risk are those species (of all taxa) characteristic of late successional forests, in a word, old growth. Conservation can be called successful if it ensures the survival of old growth species. Species associated with earlier successional stages are at much less risk, and are rarely in need of special protection. It is nonsense to suppose that biodiversity benefits from converting a natural forest to a patchwork of plantations of different ages; or that removing old growth and then tinkering with the genetic diversities of the replacement trees, as can easily be done, is an exercise in conservation (Namkoong 1991).

Monitoring should therefore be based on an assessment of the degree to which old growth attributes are retained in an exploited forest. This is readily done by drawing up a check list of species and objects typical of old-growth forest. In the context of the temperate rainforest of British Columbia, the species listed might be a few herbaceous angiosperms and a larger number of bryophytes associated with old growth, several lichen species, some cavity-nesting bird species, and several amphibians (mostly salamanders). The objects would be such things as standing dead trees ("snags"), which are known to provide habitats for many specialist species, logs in different stages of decay, upturned root discs of fallen trees, streams with deep, shady pools overhung by tree roots, and so on.

It would be straightforward to train people to inspect forest plots and check off the items on the check list. The items chosen should be easy to identify, and most of them should be fairly common. Rarities should not be omitted, but they cannot be depended upon to appear. Checking would be done before and after commercial forest operations. It would be the responsibility of trained ecologists in charge of a monitoring program to compile a suitable check list, assign scores to the items listed, and decide how large a drop between "before" and "after" scores would be permissible without penalty.

Biodiversity measures

Whereas a check list approach yields both names and a number (the "score"), a

biodiversity measure by itself is merely a number. It cannot be too strongly emphasized that a comparison of biodiversity indices, however computed, is altogether useless without lists of the species concerned.

This obvious fact is often overlooked, because species lists may not be needed when diversity comparisons are made in theoretical work. For instance, a student of niche widths in wood-boring insects might be interested in comparing the wood-borers of deciduous forests in Europe with those of eucalypt forests in Australia. Knowledge of the respective diversity indices would be relevant, since the interest lies in the way each group of insects partitions the available microhabitats within and between trees. The specific identity of the insects from the two regions would be of comparatively minor interest in this context.

In the context of conservation, however, species lists are obviously necessary. To compare indices derived from two species lists without naming the species makes as much sense as comparing the weights of two locked boxes without noting that one contains diamonds, the other firewood.

MEASURING BIODIVERSITY

It is unreasonable to search for one single index to measure as complicated a property of the biosphere as its biodiversity. Consider a parallel - Physicists describing a mechanical system's properties define and measure several separate attributes of each component:mass, velocity, acceleration, force, work, momentum, and the like. An ecosystem is many times more complicated than a mechanical system. To summarize its properties quantitatively will surely require the definition and measurement of several different aspects of the system. Attempts to single out one measure as paramount in some way seem doomed to failure. The following paragraphs describe two of the many measures that may be useful in particular contexts.

Biodiversity as Species Richness

To recapitulate: comparisons between diversity indices are meaningful only when the communities being compared are closely similar in a qualitative sense. The same is true for any biodiversity "indices" that may be proposed, when whole ecosystems

are being compared. That said, the problem remains: how can biodiversity be measured. To estimate S, the number of species, is obviously the first thing to do. It is seldom possible to determine S from an exhaustive census: communities of concern in conservation contexts are usually far too big for this to be possible, and estimation by extrapolating a cumulative "collector's curve" is unavoidable. The topic has recently been reviewed by Colwell and Coddington (1994).

Biodiversity as Qualitative Variance

Another measure of biodiversity is the following (Pielou and Fenger 1993). It arises from considering biodiversity as analogous to the variance of a body of data. Suppose plants are used as a surrogate for all living things, and that a species list is made for each of a sample of plots. Construct an s x n data matrix, where n is the number of sample plots and s the number of species observed in all plots combined (note that s is the number of species sampled, and will normally be less than S, the number in the whole population). The (i, j)th element in the matrix is 0 or 1 according to whether species i did or did not occur in plot j. Obtain the SSCP matrix of the data (sum of squares and cross products) and compute its trace, Tr(SSCP). This is the within-group dispersion, i.e. the sum of squared distances between every data point and the centroid of the whole swarm of points or, equivalently, n times the sum of the variances of the s species' binary scores. As has already been noted, biodiversity (and also diversity) could be described as "qualitative variances."

The value of Tr(SSCP) depends on s and n. To standardize the measure, bringing it into the range [0,l], it should be divided by its maximum possible value, which is ns/4 (proof in Appendix). Then the (estimated) index, denoted by c, becomes

$$c = 4\,\mathrm{Tr}(\mathrm{SSCP})/ns.$$

Estimation of C, the population value of c, is discussed below, as also is the reason for choosing C and c as appropriate symbols.

C as an Index of "Internal Complementarity"

The index C is comprehensible to laymen because it can be derived by a different method, without considering variances. Thus, let every possible pair of plots be compared; denote by M the "mismatch" between each pair, that is, the number of species present in only one (not both) of the plots. Obviously, some function of ΣM is an appropriate measure of the "diversity" (in a nontechnical sense) of the plots. It is easy to prove (Pielou 1977, p.320, and Pielou 1984, p.55) that

$$\mathrm{Tr(SSCP)} = (\Sigma M)/n.$$

The term on the left is familiar to statisticians, while that on the right has meaning for non-mathematical ecologists.

Note also that each of the $n(n-1)/2$ values of M can be regarded as a measure of the complementarity of the pair of plots being compared, in the senses that their species lists complement, rather than duplicate, each other; hence the appropriateness of the symbols c (for an estimate) and C (for the population value) of the standardized form of the index proposed. That is

$$c = 4\,\mathrm{Tr(SSCP)}/ns = 4\,((M)/n \leq s. \quad (1)$$

C as an Index of Habitat Diversity

C is also an index of habitat diversity, the name most appropriate for it . Clearly, the greater the habitat contrast between a pair of plots, the greater will be the mismatch, M, between their species-lists. Loss of habitat is one of the chief causes of extinctions, conversely, preservation of habitats, in other words maintenance of habitat diversity, is a prerequisite for conservation.

Other advantages of C, and a disadvantage

Use of C as a measure of biodiversity (in addition to species richness, S) has two

further advantages. First, the only data required for its calculation are lists of the species observed in a number of sample plots. But these are the data already collected, for estimating S. No additional observations are needed.

Second, the measure can be used at any scale. For example, if the area of interest is small (say 10 ha or less), one might use sampling plots (quadrats) of 1 or 4 m^2 and list all species of vascular plants and bryophytes in each plot; the data would allow estimation of a "high resolution" value of C. Given an area of 100 ha, one might sample with plots of 16 to 25 m^2 and list either the genus of all sampled plants, or else all woody plants identified to species. Given an area of 1000 ha, one could aim for even lower "resolution," by using 100 m^2 plots and listing trees and tall shrubs only; at 10000 ha one might list life forms rather than taxonomic units. And so on. For a given geographic region, it would be worthwhile to standardize the plot sizes and taxa to be used in estimating C for areas of different extent. The principle is the same whatever the area, only the degree of resolution changes.

The disadvantage of C, shared by all conceivable measures of complementarity, is that a large sample of plots is needed for its estimation. This is illustrated below, in the context of an example.

AN EXAMPLE

Studies are in progress on the biodiversity of the forests of Quadra Island, in the Strait of Georgia, British Columbia. The island is in the Coastal Western Hemlock Zone (Meidinger and Pojar 1991). Three contrasted sites (Sites 1, 2, and 3), each of 20 ha, have so far been studied. A sample of 50 plots, each of 25 m^2 was examined at each site, and vascular plants species in each plot were listed.

The population value of S (species richness) for each site was estimated using Chao's method (Chao 1987 and see Colwell and Coddington 1994). The observed numbers of species, s, and the 95% confidence intervals for S were:

Site 1: s = 60; S = 59 to 102.
Site 2: s = 58; S = 60 to 128.
Site 3: s = 46; S = 46 to 78.

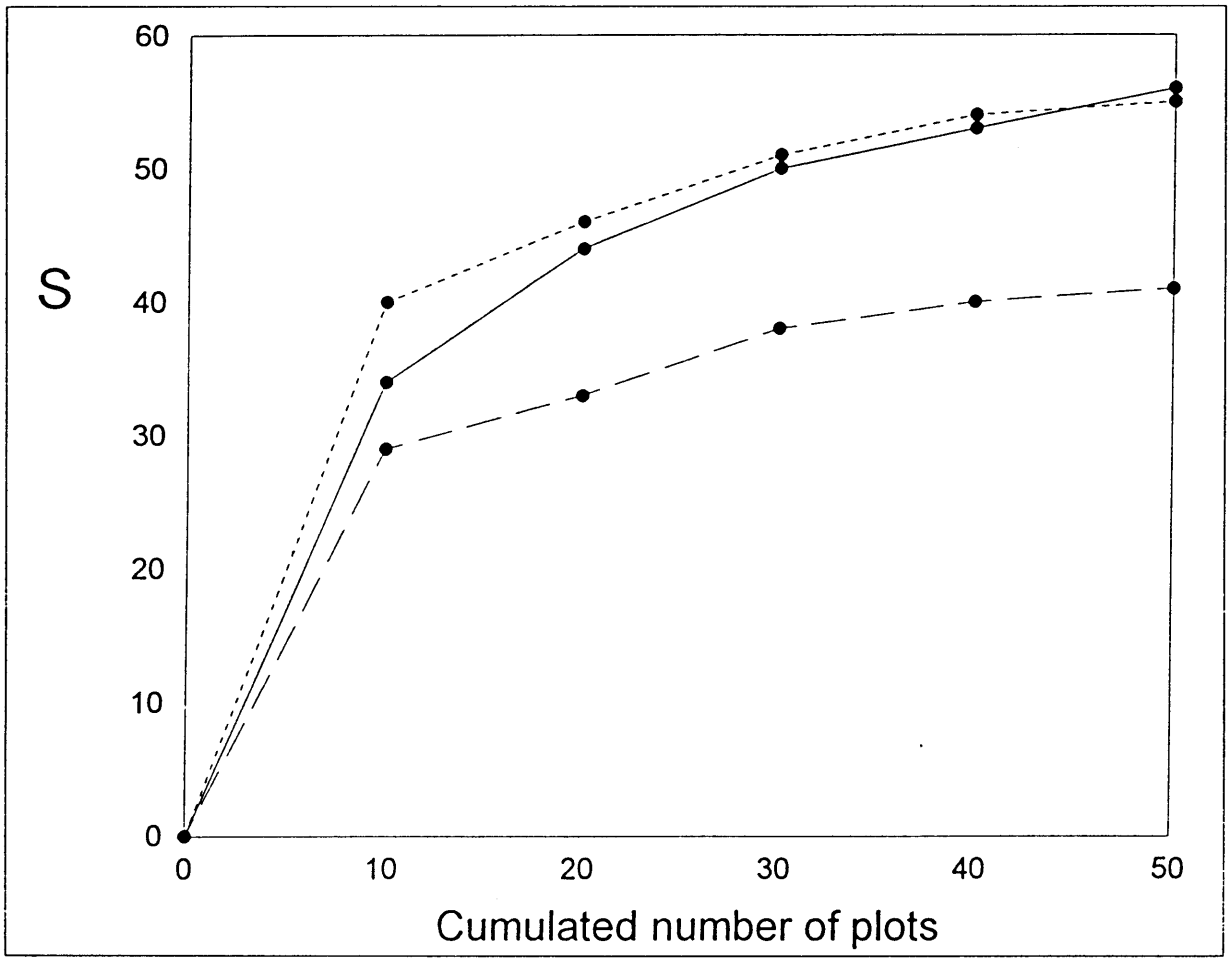

Figure 1: Collector's curves showing s, the number of vascular plant species, in cumulated samples of 10, 20, ..., 50 plots from three forest sites. Site 1, solid line. Site 2, dashed line. Site 3, dash-dot-dot line.

The imprecision of the estimates shows that additional sampling is desirable to ensure that a larger fraction of the S species at each site are captured in the sample. Figure 1 shows a "collector's curve" of s for each site. Each curve was constructed by counting s for an initial batch of 10 plots. The batch was then augmented by an additional 10 plots, and s counted again, this was repeated until the whole sample of 50 plots had been added in.

Estimates, c, of each site's index of biodiversity C were then computed from (1).

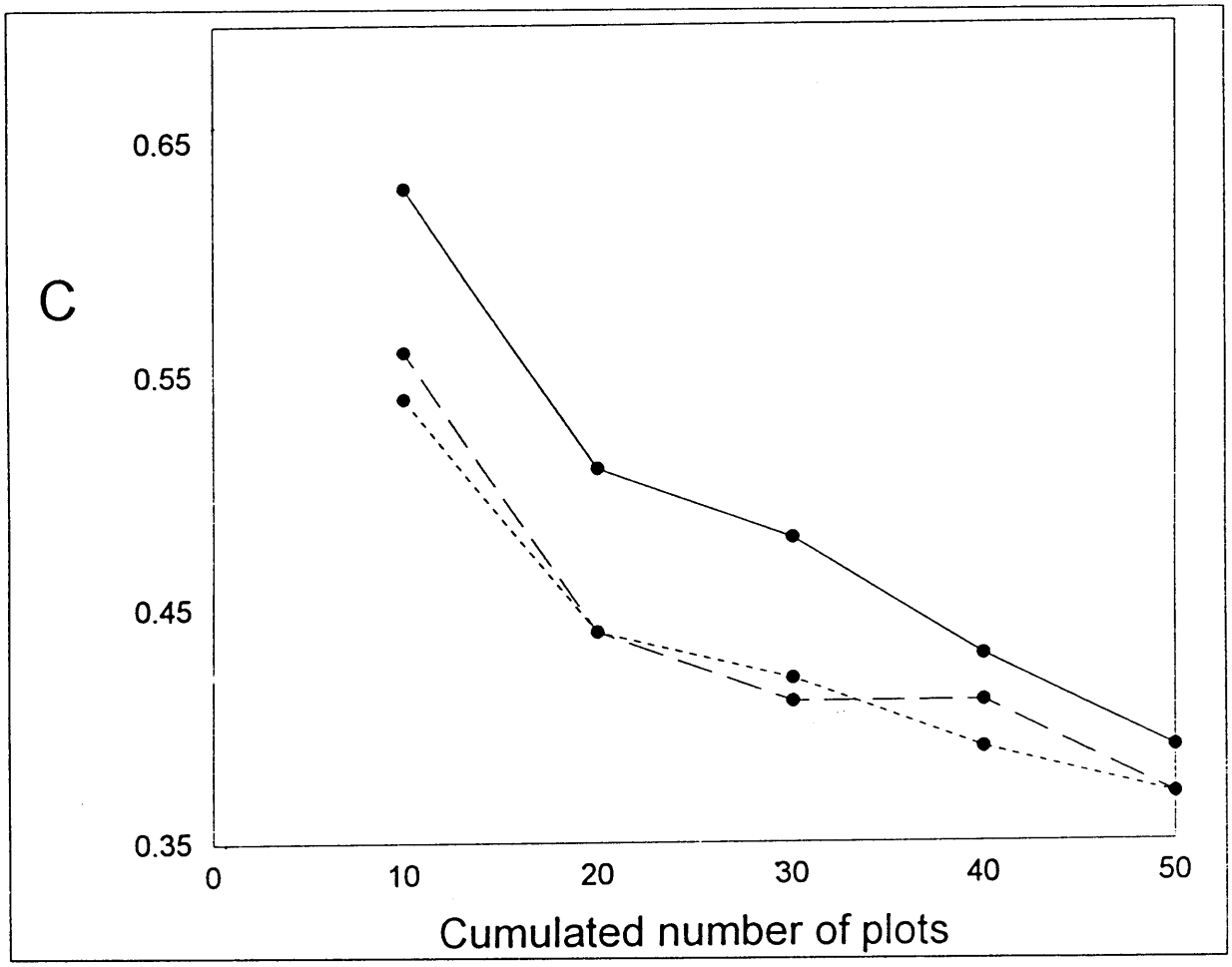

Figure 2: Curves showing the values of c, the index of habitat diversity, for the same cumulated samples of plots as shown in Figure 1.

They were:

Site 1: c = 0.38; site 2: c = 0.36; site 3: c = 0.36.

Collector's curves of c were obtained for each site in the same manner as the collector's curves of s just described. The results are shown in Figure 2. It is evident that c decreases with sample size and that procedures are needed for estimating C by extrapolation, and for finding the variance of the estimate. Work on the problem remains to be done.

ACKNOWLEDGEMENT
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APPENDIX

Proof that Max[Tr(SSCP)] = ns/4

The s x n data matrix can be represented as a scatter diagram of n points in s-space. Because the data are binary, the points must be concentrated at the comers of an s-dimensional hypercube.

Tr(SSCP) is the sum of the distances^2 of the data points from their centroid. Its

maximum value is attained when the n points are arranged in any of the several possible symmetrical patterns that have the centroid (centre of gravity) of the points at the centre of the hypercube. This is possible only when n is even.

Assume n is even and that the centroid of the data points is at the centre of the hypercube. Then each point's distance from the centroid is equal to $\sqrt{s/2}$, that is, one-half the longest diagonal of the hypercube. The sum of the distances^2 is therefore ns/4.

When n is odd, the pattern of the data points is necessarily asymmetrical, and their centroid cannot be at the centre of the hypercube. The maximum sum of distances$\leq$ is then approximately, but not exactly, ns/4. The inexactitude is negligible in ecological contexts.

Chapter

3

MEASURING AND MONITORING FOREST BIODIVERSITY

A Commentary

J. Burley[1] and I. Gauld[2]

INTRODUCTION

In this joint presentation we review briefly the theory of biodiversity and the general principles and problems of its measurement and monitoring. We identify immediate assessment needs, new research requirements and possible rapid monitoring methods, illustrating some of these with entomological examples from tropical forests, especially examples from collaborative research between our own institutions and several in tropical countries with which we have inter-governmental agreements. This should set the scene for the remainder of the symposium in which a large number of exciting papers will address many of these scientific topics in detail.

It is not possible in this conference to detail the many benefits obtained from forests. One of us reviewed these at a previous symposium in this room (Burley 1993); in summary, renewable natural resources, especially forests, are conserved

1 Oxford Forestry Institute, South Parks Road, Oxford, UK.

2 Natural History Museum, Cromwell Road, London, UK.

for three major sets of purposes: the maintenance of ecological processes and life support systems; the sustained use of the resources for consumptive and social benefits; and the conservation of biodiversity in its own right for ethical, moral, aesthetic and evolutionary reasons. Only if all three of these can be met and integrated into the socio-political process will true sustainable development be achieved; to meet them requires quantification of the current status and of changes in the resources. To ensure political and public support for conservation and wise use of such resources may require economic evaluation also (see e.g. Flint 1991) and the various values and benefits of presenting biodiversity were summarized by Pitelka (1993).

The focus of this symposium is *"Measuring and monitoring biodiversity in tropical and temperate forests"* but in this overview we shall concentrate primarily on tropical forests although we acknowledge that, in temperate countries, many of the rarest and most endangered species are those that are restricted to mature forests - such as some large wood-boring beetles and, amongst the Hymenoptera, the wood-feeding sawflies and the guild of parasitoids associated with them. It is these cerambycids, orussids and acaenitine ichneumonids that are amongst the most extinction-prone of all British insects. Indeed orussids, a taxonomically isolated and evolutionarily bizarre group of parasitic sawflies, have not been found in the British Isles for more than 140 years (Gauld and Bolton 1988). However, only a small proportion of the British fauna is restricted to forests and conservation efforts are focused on species-rich anthropogenic habitats such as wetlands, chalk grasslands, heathlands and highland moor areas maintained for hundreds of years as subclimactic non-forest communities by human intervention. In many tropical countries a very much larger proportion of the biodiversity is restricted to forests. Both these are strong arguments for the urgent assessment of biodiversity from a landscape or "forested lands" viewpoint.

Comparisons of all but a few groups are difficult but, as one of us (I. Gauld) has been involved with the arthropod inventory of parts of the Costa Rica biota for a decade, preliminary comparison can be made. In Britain (area 24.2 million hectares) there are approximately 6500 species in the insect order Hymenoptera, and less than 500 of these seem to be restricted to forest areas (Gauld, unpubl.). Indeed more than one third occur in suburban gardens miles from any significant area of forest (Owen *et al.* 1981). In Costa Rica (area 5.1 million hectares) the situation is apparently rather different, for although many species have been collected in highly disturbed areas, over 12,000 of the 20,000 hymenopterans have only ever been found in afforested areas.

Whilst we should not ignore temperate forests, it is tropical forests, on a global scale, that are home for the great majority of our planet's species of plants and animals, and it is for this reason that interest in their conservation is so great. Loss of extensive areas of tropical forest (currently approaching 20 million hectares annually) will undoubtedly cause the loss of innumerable species and populations of plants and animals and thus will impoverish the global species and genetic diversity. This in turn will restrict the standard use of resources and the application of the emerging gene technologies to an ever-decreasing resource base. Paradoxically, it is the immense species-richness of tropical forests that severely complicates any attempt to measure and monitor their biodiversity.

Socioeconomic development, population pressure and an almost insatiable demand by developed nations for wood products mean that tropical forests will continue to diminish. As so-called wilderness areas vanish an increasing proportion of the Earth's plant and animal species will survive only in managed forests. Successful conservation will depend on balancing many conflicting interests but it will be important to have both quantitative information about biodiversity and methods for monitoring changes.

Tropical forests are lost or degraded for several reasons including the following (Evans 1982): clearance for agriculture; intensive logging; production of firewood and charcoal; shifting cultivation; urban and industrial expansion; over-grazing and fodder collection; accidental or deliberate burning; and war damage. In addition to these, the constituent biodiversity may be decreased as a consequence of the following (Burley 1994): over-exploitation; fragmentation of habitats; climate change; pollution; introduction of exotics, some of which may become invasive; and widespread application of artificially bred material.

Knowledge of the political issues and constraints underlying these reasons is necessary in allocating research resources and it is vital to define clearly the objects of biodiversity assessment. We recognize that biodiversity may be assessed for four reasons:

(a) comprehending ecosystem structure and function (for scientific understanding of ecosystems and evolution and as a basis for managing resources for their life support functions and productivity)

(b) conserving and developing germplasm for breeding and genetic improvement of planted forests

(c) monitoring the impact of land management interventions and both natural and anthropogenic environmental changes on biodiversity

(d) deciding areas of priority for conservation of biodiversity in its own right for reasons of ethics, aesthetics, religion, culture, scientific enquiry, or future production including "biodiversity prospecting" for foods, drugs, pharmaceuticals, other chemical products and biological control agents.

For such conservation, comparative information between sites will be essential for allocating priorities to sites for planning new conservation areas and, more depressingly, for advising land-use planners which areas of forest can be converted to other uses with least impact on biodiversity. Preliminary baseline assessment followed by monitoring will be necessary to assess the impact of forest management practices on biodiversity (with a view to finding an optimum practice that results in both timber and non-timber commodity production and the conservation of biodiversity); it will also be necessary to assess other effects on biodiversity through time such as global climate change or pollution.

TYPES OF BIODIVERSITY AND CAUSES OF CHANGE

The first two plenary sessions of this symposium will deal with the general concepts of measuring biodiversity and it will become apparent that, historically, several schools of thought have been interested in different concepts and have developed different indicators of biodiversity. Taxonomists have been responsible for inventories of biota in the sense that they are responsible for formally describing the species present. Ecologists and taxonomists have been concerned mostly with diversity of both plants and animals and their interactions within and between ecosystems and landscapes (e.g. *alpha-, beta-,* and *gamma*-diversity; Whittaker 1975, Magurran 1988). For species diversity itself, ecologists, taxonomists and evolutionists share interest in the number of taxonomic groups within a habitat, species-richness, relative abundance or rarity, the degree of endemism, size and form classes and trophic levels.

Measures and derived indices for these purposes have been based largely on species counts or relative abundances and are "value-neutral" (i.e. they do not give special weightings to rarity or endemicity, for example) so that they have questionable value for conservation prioritization. The United States Nature Conservancy, in its National Heritage Programme, while essentially undertaking inventories of State biological resources, has identified global, regional and local values for conservation through coarse screening based on rarity of ecosystem types initially, later progressing to individual species. An outstanding example of the

development of conservation prioritization that includes taxonomic, ecological, biogeographic and socio-economic knowledge is the ranking of all forest reserves in Ghana by Hawthorne and Musah (1993), to be published also by the International Union for the Conservation of Nature and Natural Resources, IUCN, in 1994; see in addition Hawthorne (1995); the "genetic heat index" revealed subtle variation within and across "hot-spots" and showed that subtle and fine-grained exploitation has little or no negative influence on those aspects of biodiversity measured.

Forest geneticists and tree breeders, on the other hand, have been more concerned with the infra-specific genetic variation between and within populations of the tree species themselves. Their concern is for the conservation and use of gene complexes, genes, alleles and DNA sequences for current or potential future use and this often includes the need to determine natural breeding systems, including pollinators and gene flows.

Specialist authors later in the symposium will tend to take a species or species group approach but we stress the inter-dependence of organisms in an ecosystem and thus emphasize the ecosystem approach. Further, we emphasize the need to define precisely the objectives of measuring and monitoring such biodiversity whether it is to determine responses to human intervention or environmental change, or to evaluate resources in land use decisions.

The major, potential, environmental changes are global and local climate change (whether natural or caused by mans activities) and pollution of soil, air and water. There is considerable evidence on the effect of these factors on individual plant growth and on the genetic variation within some species; in addition there is some evidence for their effects on the species composition of ecosystems. However, more information is required to be collected in a planned, systematic and comparative manner that will provide greater visibility of the data, facilitate comparable analyses, permit widely applicable conclusions, and support the planning of remedial or conservation efforts.

For forests there is a continuous spectrum of managerial interventions that have known or hypothetical effects on biodiversity. These include the selective management of natural forest with thinnings at various intensities, enrichment of natural forest with desirable species, fragmentation of forest through partial clearance, total clearance of forest (with natural or artificial regeneration), and the establishment of plantations and agroforestry combinations. In addition to the obvious effects of these on the constituent tree species, they have significant implications for the diversity of other organisms.

Simply counting numbers of species present in an area (always assuming the

taxonomy is robust) may give surprising results. Several studies have shown that the species-richness of some groups of organisms (such as butterflies) increases following disturbance in an area. This increase is the result of increasing heterogeneity of the forest area, permitting the immigration of species characteristic of disturbed habitats. However, the species that are characteristic of disturbed habitats generally are widespread and opportunistic generalists that may have potential for utilization but that are in little danger of extinction and thus may not be of great conservation interest; it is the species characteristic of closed canopy forests that are usually of higher conservation interest. Thus simply counting the number of taxa present is not a useful measure of biodiversity for conservation prioritization. A pristine forest and a seriously degraded site may have identical numbers of species present but the composition of those species may be quite different, and the degraded site may have lost many of the rarer, highly restricted species. This was demonstrated by Daniels *et al.* (1992) in peninsular India, where they found that in evergreen forests 77 percent of the 200 bird species present were closed forest specialists but in teak plantations this percentage had decreased to 37 and in eucalypt plantations to 5. This type of evidence emphasizes the need to consider functional groups as well as taxic groupings to discriminate better between otherwise misleading or uninformative species richness alone.

Working with the leaf litter ant fauna, Belshaw and Bolton (1993) demonstrated that there was no significant difference in species-richness between the faunas of primary forest, secondary forest and cocoa plantation. Thus differences in the species-richness of the ground ant faunas are not necessarily indicative of differences in woody plant species-richness, nor are they likely to be of much use in monitoring the effects of human impact on forest ecosystems.

In addition the ownership or tenure of forested land has a potentially important impact on the likelihood of sustainable management and the conservation of biodiversity. Different managers will have varying concepts of the importance and valuation of diversity. Tropical forest management may be conducted by governments (with or without external donor agency support), by joint ventures between government and industrial companies, by commercial companies or individual entrepreneurs, by community forestry activities, or by individual smallholders. These are compared in Table 1 (from Burley 1994) on the basis of system complexity, inputs, level of biodiversity, non-market benefits obtained and the commitment to such benefits, time horizon, and institutional and human resource needs.

PROBLEMS OF EXISTING DATA AND SAMPLING

For the assessment of biodiversity at the ecosystem and species level for conservation, there are several sources of variation that must be considered in designing sampling procedures for measurement and monitoring.

Temporal effects

Historical data. A great deal of verifiable, specimen-based data about the distribution of forest biodiversity are available in or from museum or herbarium collections. Although these collections and published data derived from them are potentially valuable sources of information, care is needed in interpretation for several reasons.

First, the actual geographical range of many of the organisms is likely to be seriously under-represented. This is because, at least in the tropics, most small species, such as insects and other invertebrates, are described from single individuals or small samples made at one favoured site, and few have subsequently been recorded from elsewhere. A clear example of this can be seen by comparing two quite closely related groups of South American parasitic wasps, the Mesosteninae and the Ophioninae. The former is a group that has been studied in the traditional way, by taxonomists working with small samples (Townes and Townes 1966), whilst the latter group has been collected more systematically in very large numbers (Gauld 1988). Only 114 (21 percent) of the 543 described species of mesostenines are known to occur in more than one country, whilst 91 (76 percent) of the 120 ophionines occur in two or more countries. Given the general similarity of these two groups of organisms, there is no reason to believe their species should show any great differences in range size, and to some extent this is confirmed by the fact that only 39 percent of the ophionines had been recorded from more than one country prior to Gauld (1988) by Townes and Townes (1966). High levels of endemicity may thus simply reflect taxonomists' predilections to visit certain areas.

Second, the specimens on which the information is based are not usually a random sample of the biota of a region. Taxonomists' "sampling" of tropical biodiversity is highly selective, and there is a general tendency to maximise the species-richness obtained in a collecting foray, favouring rarity or scarcity, rather than to attempt to sample in any ecologically meaningful way. Thus common widespread organisms or physically very similar species are usually under-represented in collections, whilst uncommon organisms are highly sought after, and thus exceptionally well-represented.

Third, there have been strong biases towards collecting and describing large

	Government (± donor support)			Joint venture project			Commercial company project			Individual entrepreneurial project			Community forestry activity			Substantial farmer activity		
	N	P	A	N	P	A	N	P	A	N	P	A	N	P	A	N	P	A
1. System complexity	H	L	M	H	L	M	H	L	M	M	L	M	M	L	-	-	L	M
2. Artificial and human inputs	L	M	H	L	H	M	L	H	M	L	M	M	L	L	L	L	L	L
3. Level of biodiversity	H	L	M	H	L	M	H	L	M	M	L	M	M	L	_	_	L	M
4. Level of non-market benefits possible	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M
5. Commitment to non-market benefits	H	L	M	H	M	L	M	L	L	L	L	L	M	L	M	L	L	H
6. Time horizon	L	L	L	M	M	M	M	M	M	S	S	S	M	M	M	S	S	S
7. Institutional/ human resource needs and potential for training	H	H	H	H	H	H	M	M	M	H	H	H	M	L	M	L	L	L

Table 1 : Managerial and Technical Aspects of Biodiversity within Projects under Different Management (Rating by organization and characteristics).

H = High M = Medium L = Low; except in 6, where: S = Short M = Medium L = Long

N = Natural forest P = Plantation A = Agroforestry

Source: Burley, J. (1994). Biodiversity in development and conservation. Invited paper, British Council/ODA Seminar on *"Forest land use options: conflicts and solutions"*, Kumasi, Ghana.

and showy organisms, such as butterflies and dragonflies whilst, much more numerous smaller and less attractive species are both undersampled and have escaped the attention of many taxonomists (Gaston 1991). Any attempt to assess patterns of biodiversity from taxonomic literature must consider such biases.

Individual growth stage. The numbers, abundance and rarity of individual species change throughout their life span from plant seed through germinant, seedling, juvenile, mature and senescent stages (with corresponding phases for animals). Knowledge of the changes in frequency with age and of general population dynamics is needed ideally to determine optimum conservation management strategies for any one species within an ecosystem; however, in real field situations, it is often difficult to disentangle confounded effects such as inherent seral developmental growth stage from the results of progressive environmental change. Further, the time and resources required for such dynamic studies preclude rapid assessment and monitoring.

Seasonal and annual scale. In addition to these effects of growth time within the life of one organism, there is a major series of time effects on the presence and sampling of biodiversity; these include the it-&a-annual seasonal change and the natural variation between years caused largely by differences in climate and ontogeny but also, in some areas, by pollution. Further, human decisions on land use rotations or multiple rotations obviously have major impacts on biodiversity over time; in most tropical regions there are examples of the human introduction of fruit trees that subsequently spread naturally into forests. The entire question of invasiveness is of current concern.

Reproduction in rainforest species is nearly exclusively sexual, yet this process is greatly influenced by life stage and by environment, flowering con-specifics and flowering heterospecifics in ways that are little understood. Furthermore, any measure of biodiversity at a single point in time must take into account problems of sampling within and between years. Through a collaborative project with the Oxford Forestry Institute (OFI) and Centro de Pesquisa Agropecuaria do Tropical Umido (CPATU), Empresa Brasileira de Pesquisa Agropecuaria (EMBRAPA), the dynamics of reproduction of Amazonian trees is being investigated in order to provide information for conservation initiatives, representative sampling of intraspecific genetic variations and sustainable management of natural forests. Analysis of floral phenology data for 50 species over a ten year period reveals an array of flowering

syndromes, including: synchronous annual flowering, supra-annual flowering (masting), asynchronous supra-annual flowering and bi-annual flowering. Clearly, one definition of reproduction is not applicable and attempts at modelling regeneration will need to take into account species differences in density of flowering individuals, pollen dispersal distances, functional gender of individuals, synchronicity of flowering and alternate food sources (i.e. other species flowering at the same time) for the generalist biotic pollen vectors.

In lowland tropical habitats with rather little seasonal change in weather pattern, there may be marked differences in the abundance of many insect species (Wolda and Roubik 1986; Hanson and Gauld, in press). In habitats with pronounced seasonality, there may be very pronounced differences in abundance of any given species between one year and the next. This may present a particular problem in tropical forests where some species of insects exist at levels of abundance that are so low they are virtually undetectable by a variety of well-established sampling procedures, then have a large population in a single year. In this situation, if sampling is restricted to one technique, such a species may only "appear" in a habitat in an outbreak year. A good example of this was observed recently in Central American dry forest. Sustained light-trapping over a number of years has shown that the ichneumonid *Enicospilus madrigalae* seems to be present in Santa Rosa most years (Gauld 1988; unpubl.), but more than 80 percent of individuals collected over a decade were taken in a single year. Although light trapping is a highly efficient method of collecting nocturnally active wasps, flight interception traps are more generally used to trap wasps as they are less labour-intensive to use, and require only about one hour's attention every fortnight instead of several hours every night. Examination of interception trap catches in the same area reveals that *E. madrigalae* was only taken in the outbreak year, and has never been found either before or since.

Mobility. A further problem with sampling of highly mobile organisms, and one that, of course, does not occur for sedentary species, is what does an occurrence at a site mean? It may be part of a viable population occurring in a particular habitat, or it may be simply a vagrant that chanced to be caught. Gauld (unpubl.) recently found a female of the ant *Atta cephalotes* in a flight interception trap catch from 3100 metres on the Cerro de la Muerte in Costa Rica. Because attine (leafcutter) ants are such a conspicuous part of the fauna of tropical America it is well known that they almost never nest above 1500 metres, and certainly will not do so above 3000 metres.

Thus it is obvious that the single female encountered is a vagrant, probably blown up by wind from lower altitudes. Such vagrancy might not be appreciated for decades if the insect involved were one of the more cryptic, little-studied denizens of the lowlands. It is interesting to note, that in Costa Rica, the most species-rich site for Hymenoptera (Hanson and Gauld, in press) is the garden of a roadside restaurant on Cerro Zurqui! We consider it unlikely that the restaurant garden supports such diversity; it is more likely that its high species richness is due to large numbers of species moving up an adjacent gully that runs through a large national park. Clearly very mobile species may not be reliable for site biodiversity assessment but this may vary with species and sampling method.

Community seral stage. There has always been debate about the static and dynamic aspects of conservation of resources, particularly genetic resources in which evolutionary change is a natural phenomenon. Whatever the reasons for conservation, natural vegetation commonly progresses through stages from cleared land through pioneers to "climax" populations in the current environmental conditions although some fluctuations in composition still occur. Most of the associated species change as this process occurs and thus sampling methods for monitoring must take this into account. The poster displayed by one of our colleagues (D. Sheil) at this symposium illustrates such changes with time over half a century in the Budongo Forest, Uganda.

Locational scale

Physical position. Different organisms obviously occur in different locations within the ecosystem from the soil/root interface through the stem to the crown of mature trees. The sampling procedures must clearly differ between these even for similar groups of organisms (particularly insects). This seems to be the case for ants, a group that is particularly suitable for biodiversity studies as they are both abundant and diverse in most tropical habitats. They may comprise up to a third of the arboreal arthropod biomass (Fittkau and Klinge 1973) and nearly 90 percent of the individual insects encountered in a tropical ecosystem (see e.g. Majer 1993), and there may be as many as 43 different species in a single tree (Wilson 1987). Sampling of ants can be undertaken by various means which can be grouped into two methods - extraction from litter samples using a process involving gradual drying, and extraction from vegetation by sweep netting, insecticidal fogging (Paarmann and

Stork 1987), hand picking, etc. These two types of methods may yield quite different results. As we have already mentioned, little change was observed in the composition of leaf litter ant communities in variously disturbed afforested areas in West Africa (Belshaw and Bolton 1993) but Dejean *et al.* (1994), also working in West Africa, observed considerable differences between the arboreal ant mosaics in old secondary forest and a forest edge composed of fast growing colonizing species.

Geographic scale. The different concepts of *alpha-, beta-,* and gamma-diversity and of abundance, rarity and endemicity were referred to above but, even at the ecosystem level, these indices differ and have different implications for sampling and conserving biodiversity at the global, regional, national and ecosystem/habitat/patch levels. What is abundant or apparently stable at one location may be rare or threatened at a global scale.

In Costa Rica, the Osa peninsula in the extreme southwest is notable in that it supports small populations of lowland rainforest bird species that are otherwise only known to occur in the Amazon basin (Stiles and Skutch 1989). Such species may be very local, scarce and probably endangered on the Osa, and thus in Costa Rica they may be a major focus of conservation effort, although further south in the Amazon Basin, such species may be very common. These endangered peripheral populations may reflect incipient speciation and they may also detract conservation effort from other areas, such as the rather less exotic high altitude fauna of the Cordillera de Talamancas, an area of exceptional endemism straddling the Costa Rican/Panamanian border (Gauld 1988, 1991, Hanson and Gauld, in press).

Interactions between species

Links in the food or pollinator chain. The links in the food chain range from the primary producers and saprophytes through herbivores and predators to decomposing micro-organisms. As individual size and/or natural range area increase, so do the public recognition and valuation of particular species. Concurrently, the scientist specializing in one species or related group tends to develop intensive recurrent sampling systems to obtain adequate precision for the group but these may not be applicable to other species. The inter-dependencies and other inter-actions between species must be understood to obtain adequate overall sampling to support the objective of ecosystem maintenance.

BIODIVERSITY INDICATORS

It is clear from the above that there is an urgent need for collaboration between scientists who study many different disciplines and who work on different groups of species, firstly to seek consensus on the concepts and priorities for biodiversity assessment, and secondly to identify means of linking disparate assessments or initiating joint studies.

In addition to direct total or sample counts of species or individuals in a given area and an understanding of population dynamics, there are six sets of information that facilitate or add to biodiversity indicators in support of decisions on biodiversity conservation:

Species-urea relationships. These are commonly used by ecologists to determine, describe or predict species richness within an area and by conservationists to help estimate minimum population sizes in reserves (see e.g. Soulé 1986, Simberloff 1992).

Keystone species. These species are recognized as playing a major role in maintaining ecosystem structure and integrity; for a classification of types of keystone species see Bond (1993). There has been considerable debate about the concept and reality of keystone species but there seems little doubt that in some cases a species or species group may have a major role in the survival of the ecosystem as currently recognized, e.g. the fruits of figs are a fundamental resource for primates and many frugivorous birds that themselves ensure the perpetuation of the Budongo Forest (yet for decades foresters wished to eradicate figs for silvicultural reasons).

Ecological indicator species. These species are adapted to (or react characteristically to) changes in specific environmental factors, or their diversity appears to be correlated with that of several or many other species. The nymphs of some groups of aquatic arthropods (e.g. Plecoptera and Odonata) are used for river water quality assessment in the UK. Some authors (e.g. Kremen *et al.* 1993) have advocated using terrestrial arthropods as an easily sampled "indicator" group and, although some groups of arthropods do seem to be useful indicator groups (Klein 1989, Brown 1991), one common problem with measuring or monitoring such speciose taxa is obtaining representative samples. Samples collected over fairly short periods often comprise very large numbers of individuals with few represented by more than one or two specimens. Longer term sampling, such as has been undertaken in Costa Rica as part of the fauna1 survey of Costa Rican Hymenoptera (Hanson and Gauld 1995), shows that in the short term samples of arthropods from sites can be very

different, but species-accumulation curves at these sites continue to rise very steeply, and over a period of two years the species-composition of the sites becomes increasingly similar. Comparison of species-accumulation curves for individual sites and for the region show, at the regional level an asymptote being approached after about 18 months malaise trap continuous sampling, while at any one site the species accumulation curve continues to rise steeply, suggesting increasing sampling effort at any one site will yield an ever greater proportion of a regional fauna at that site. Thus more intensive sampling will result in the samples from the sites having an ever more similar species composition, and apparent differences in species composition between sites, revealed by short term sampling, are perhaps only artefacts resulting from insufficient sampling effort.

Another strategy for measuring and monitoring biodiversity involves working with very well-known and well-characterized groups of organisms such as birds or mammals. With such well-known groups areas of endemicity can easily be recognized as can areas of high species richness. Obviously, for conservation planning to be most easy and effective, it would be convenient if two postulates were true - i.e. habitats that are species-rich for one taxon are species-rich for other taxa; and rare species occur in species-rich habitats. These postulates have often been assumed by conservationists working in tropical habitats but have rarely been tested. One of the most detailed studies on this question was conducted in a temperate country, the UK, by Prendergast *et al.* (1993) looking at the distribution of birds, butterflies, dragon flies, liverworts and aquatic angiosperms. They found little support for either proposition: species-rich areas (so-called hotspots) frequently do not coincide for different taxa, and many rare species do not occur in the most species-rich sample areas.

Few comparable analyses have been undertaken in the tropics, although in India it has been shown that high bird species-richness does not necessarily correlate with high species-richness in other fairly well-known groups (although it frequently correlates well with ecosystem structural diversity). For example, Daniels *et al.* (1992) demonstrated that, in the Uttara Kannada district of southern India, bird species-richness is inversely correlated with woody plant species diversity. In this particular case Daniels *et al.* were able to suggest plausible reasons for such an apparent anomaly; they suggested that this inverse relationship may be explained by the fact that although the peninsular Indian evergreen forests are rich in woody plant species when compared with drier surrounding areas, they harbour an impoverished bird fauna due to their small overall extent and great isolation from other extensive tracts of wet forests. Thus the evergreen forests rich in plant species

have a smaller pool of potential colonizing species than the relatively plant species-poor dry forests. Whatever the causes of this avian impoverishment, it is well established that it is erroneous to assume simply that maximum bird species richness is indicative of maximum richness in biodiversity; in such comparisons it is axiomatic that niche size is important. Ecologists are seeking better indicators; for example, four Danish institutions are working on montane biota in southern Africa and South America using DNA-based population phylogenies to supplement traditional biogeographic methods for detailed interpretation of the diversity in selected groups and the age of endemicity (Fjeldsa 1992).

The distribution of few tropical species is well enough known to allow comparison of species-richness with rarity. However, two observations are pertinent here. First, whilst there is a general decline in species-richness in most insect groups above about 1000 metres in tropical habitats, there is a general increase in endemicity with altitude. Gauld and Mitchell (1981) observed that whilst less than 30 percent of a sample of ichneumonids collected in lowland forests in New Guinea were endemic to the island, at high altitudes (above about 2000m) more than 90 percent of the species were endemics.

Second, the intensive Hymenoptera survey of Costa Rica, carried out over the past decade (see Hanson and Gauld, in press) has clearly shown that some of the very rarest of all Hymenoptera occur in rather species-poor areas - areas that are very seldom collected in because they are regarded as unproductive. The most striking examples of this include members of the extraordinarily rare Hymenoptera groups Bradynobaenidae, Scolebythidae, Sierolomorphidae and brachycistidine Tiphiidae, all of which are found in species-poor, open, dry areas during the dry season.

Taxicgroups. Groups of species and/or higher taxa, as accepted by current taxonomic agreement, offer a straightforward method of comparing sites and ecosystems for their diversity and conservation status. More recently methods have been developed for assigning conservation priorities not just on species richness but by incorporating measures of taxonomic distinctness of the species concerned (e.g. Vane-Wright *et al.* 1991, Faith 1992, 1994). Areas inhabited by groups of phylogenetically distantly related species have been accorded higher conservation priority than similar areas occupied by an approximately equal number of phylogenetically very closely related species.

Functional groups. These comprise groups of species fulfilling the same function

and having similar morphological structure within a ecosystem; for example, lianes may be assessed as a group without identification of individual species.

Economic valuation species. While ecologists, taxonomists and geneticists have a range of indicators and assessment methods for biodiversity, land use or conservation decisions are commonly based on over-riding economic valuations. These are species of known or potential economic value *per* se or that occur in assemblages that have other individually valuable species. In the Budongo Forest of Uganda *Khaya* and other mahogany timbers in the Meliaceae are found in the same formations and have similar ecological requirements. The economic weighting of such productive species, or of habitats that have non-wood products, amenity and touristic value (such as drug plants, gorilla forests), frequently over-ride ecological and genetic weightings in current political and financial climates.

ASSESSMENT METHODS

Whatever the index or indicator desired, and whatever scale or sampling intensity is sought, a range of methods may be more or less applicable and more or less expensive:

Traditional forest inventory and vegetation analysis. Foresters have historically developed the science of forest inventory, principally for estimates of standing volumes of wood in forests and for recurrent measurements to indicate changes with time or management; the numbers and densities of non-wood plant species are occasionally recorded but not as a principal object of the survey nor in an internationally comparable standard system. Systems of permanent and temporary sample plots in forests have sometimes been established for these forestry purposes (see e.g. Adlard 1990, Husch 1971). Substantial work in Australia by the Commonwealth Scientific and Industrial Research Organization (CSIRO) has expanded such traditional forest inventories into multi-taxa surveys. There has also been considerable international activity recently to establish biodiversity monitoring plots e.g. United Nations Educational, Scientific and Cultural Organization (UNESCO) Man and the Biosphere Programme; Smithsonian Institution, Washington; and the Food and Agriculture Organization of the United Nations (FAO).

Several standard textbooks of vegetation analysis exist and one of our Oxford colleagues (D. Sheil) is currently preparing a guide to field assessment for conservation and biodiversity research in East Africa; he will also be presenting a poster

in this symposium on the evaluation of long-term change in permanent plots within the Budongo Forest of Uganda. Ideally insect and other animal assessments should be undertaken in such plots and another Oxford colleague, A. Plumptre, has shown that primate densities increase in Budongo after selective logging.

A large number of quantitative biodiversity indices have been developed based on counts or measurements of standing trees or trap samples of animals (see e.g. Magurran 1988, Pielou 1975, Solbrig 1991, or Whittaker 1975) and many of these will be reviewed or used during this symposium. (Pielou prefers to use *diversity indices* to *biodiversity indices* and stresses that these are not suited for monitoring.) Many of the published indices do not specifically value rarity and may thus have less significance for conservation; the National Heritage Program of the United States Nature Conservancy identifies areas of vulnerable and rare species to maximize biodiversity on a global as well as a local scale. On a different level, Reid *et al.* (1993) have shown the applicability of these and other measures as indicators of biodiversity conservation that would have political and administrative applications (summarized in Table 2) while the Danish studies referred to above seek to identify major locations of species endemism.

Molecular methods. The last decade has seen an increasing use of high profile molecular genetic techniques to study genetic diversity, systematics and population genetics at the DNA and protein levels. These technologies have included isozyme, restriction fragment length polymorphism (RFLPs), randomly amplified polymorphic DNA (RAPD), DNA fingerprinting and, more recently micro-satellites. These, and the techniques of secondary product analysis (e.g. Hanover 1992), are now relatively commonplace and have been tested in a wide range of taxa, providing powerful methods for: (i) the inference of phylogenies (e.g. Harris *et al.* 1994); (ii) the identification of hybridisation (e.g. Carr *et al.* 1986, Keim *et al.* 1989); (iii) the assessment of genetic diversity (e.g. Lavin *et al.* 1991, Chalmers *et al.* 1992, Loveless 1992, Bardakci and Skibinski 1994) and (iv) the potential to explore the interaction between genome adaptation and ecotypic variation (e.g. Rieseberg *et al.* 1993).

Remote sensing. A large array of technologies now exists for examination of terrestrial resources including aerial photography and satellite imagery in various electromagnetic wavebands. Their scales and precision differ but the locations and changes in forest or ecosystem boundaries can be identified easily and the stand-

Indicator	Biodiversity Conservation Concerns		
	Genetic Diversity	Species Diversity	Community Diversity
Wild Species' and Genetic Diversity			
1. Species richness (number per unit area, number per habitat type)	X	X	
2. Species threatened with extinction (number or percent)	X	X	
3. Species threatened with extirpation (number or percent)	X	X	
4. Endemic species (number or percent)	X	X	
5. Endemic species threatened with extinction (number or percent)	X	X	
6. Species risk index	X	X	
7. Species with stable or increasing populations (number or percent)	X	X	
8. Species with decreasing populations (number or percent)	X	X	
9. Threatened species in protected areas (number or percent)	X	X	
10. Endemic species in protected areas (number or percent)	X	X	
11. Threatened species in *ex-situ* collections (number or percent)	X	X	
12. Threatened species with viable *ex-situ* populations (number or percent)	X	X	
13. Species used by loçal residents (number or percent)	X	X	
Community Diversity			
14. Percentage of area dominated by nondomesticated species		X	X
15. Rate of change from dominance of nondomesticated species to domesticated species		X	X
16. Percentage of area dominated by nondomesticated species occurring in patches greater than 1,000 sq km		X	X
17. Percentage of area in strictly protected status		X	X
Domesticated Species Diversity			
18. Accessions of crops and livestock in *ex-situ* storage (number or percent)	X		
19. Accessions of crops regenerated in the past decade (percent)	X		
20. Crops (livestock) grown as a percentage of number 30 years before	X		
21. Varieties of crops/livestock grown as a percentage of number 30 years before	X		
22. Coefficient of kinship or parentage of crops	X		

Table 2: Indicators of Biodiversity Conservation

Reid, W.V., J.A. McNeely, D.B. Tunstall, D.A. Bryant and M. Winograd, 1993. Biodiversity indicators for policy-makers. World Resources Institute, Washington, USA, 42p.

ing volume of wood in some forest types can be estimated reasonably precisely. If coupled to appropriately detailed ground truthing, the techniques are applicable to identifying rare communities and vulnerable remnants, for mapping vegetation and for zonation and land use planning (e.g. Mount Elgon, Uganda). However, none of these techniques are yet refined sufficiently to identify individual plants unequivocally at a scale and precision that would permit biodiversity monitoring within ecosystems.

Databases and geographic information systems. All of the historical and current data collected by any of these technologies may now be combined into electronic databases and portrayed by a large number of geographic information systems that are commercially available. A session of this symposium will hear of applications of several of these. Together with the growth in databases, there is a need to develop analytical techniques to highlight areas of high species richness or high conservation priority (see e.g. ICBP 1992, WCMC 1992). Amongst the techniques currently being developed are the WORLDMAP programme (Vane-Wright *et al.* 1991, Williams *et al.* 1993) currently under development at the Natural History Museum.

One of the most intensive and extensive database systems now available appears to be the Biological and Conservation Database (BCD), of the United States Nature Conservancy (see Carr 1988); this allows rare taxa to be identified and critical sites to be recognized. An excellent example of a currently operational management tool is "FROGGIE", the database-GIS system developed by Hawthorne and Musah (1993) for the forest reserves of Ghana; this allows forest managers to act upon research data with all knowledge of the distribution of all species in the forest area (and it is now being linked to other OFI software including "BRAHMS" and "SISTEM+" for the incorporation of data from herbaria and field experiments). It must be recognized continually that the success of such research is dependent on the careful, repetitive and tedious recording and management of essentially simple, primary, "key" data; standardization and agreement on parameters to measure must not preclude the addition of other observations for specific purposes.

CURRENT NEEDS

There appear to be three main groups of requirements relating to current knowledge, policies and practices for biodiversity assessment and conservation. These

are immediate assessment needs, new research required, and evaluation or implementation of rapid monitoring techniques; they are summarized below. Underlying all of them is a great need for unequivocal taxonomies and for guides to species identification (see e.g. the field guide to trees of Ghana by Hawthorne 1990).

Immediate assessment needs

Methods

- define key data
- develop standardized sampling protocols for baseline studies and later monitoring for defined objectives

Organisms

- agree internationally on focal groups of organisms (whether taxonomic, locational or service groups) that can be assessed easily and relatively cheaply, and that can indicate biodiversity in other organisms for stated objectives
- resolve current taxonomic uncertainties in these groups and establish adequate reference material
- produce simple taxonomic/identification manuals and computer-based identification systems
- undertake baseline studies for the focal groups nationally

Data management

- develop database and information systems to accept and process information from a wide range of historical and current sources, including knowledge of generalist and specialist species derived from earlier ecological research
- review the holdings of herbaria and museums
- review and interpret significance of historical records of forest management
- review value of existing permanent forest sample plots and long-term ecological monitoring plots; establish new plots or transects if required

New research requirements

- prioritize the information required for the four major objectives and at the three main geographic levels

- refine and validate baseline surveys of focal groups and extend to other groups to begin development of monitoring models
- determine which groups are sensitive to environmental and managerial change; consider them for use as indicators; check the rarity of species and ecosystems
- conduct ecological studies to understand principal linkages and propagation systems, and to determine whether keystone species exist
- use molecular methods on samples from the extensive networks of international population (provenance) trials of forest trees to examine intra-specific diversity, provided that adequate information is available on the original source and subsequent management; if possible these should be compared with samples from the original natural populations to detect change following transfer to exotic conditions. It is critical that material from the whole range be analysed (for example, the OFI study of the isozymes of *Faidherbia albida)*
- determine the correlation between conservation of species richness, species rarity and intra-specific variation within given species and the correlation between different species (in the different regions of the world)
- establish regional and national databases and geographic information systems to summarize, display, digest and interpret information on national biodiversity for land use managers and policy makers

Rapid monitoring methods

- define and justify what is to be monitored
- involve local human populations and indigenous knowledge in recording of species occurrence, distribution and use
- progressively increase sampling proportion among permanent sample plots until acceptable accuracy is achieved
- use molecular sampling methods to determine intra-specific variation of focal groups; this will require resolution of the debate over the best method
- use remote sensing to detect ecosystem boundary changes and some structural changes, plus geographic information systems to portray all levels of biodiversity currently known
- link monitoring data to forest management and to subsequent model building.

EXAMPLES FROM THE UK-MALAYSIA COLLABORATIVE PROJECT

Confronted by the problem of designing a project to measure the impact on biodiversity of intervention practices one thus has to address the question "what should be monitored?" with some caution, as it is obviously possible to register loss, gain or no change in biodiversity depending on what group is monitored, or to fail to obtain a sample of sufficient size to have any meaning whatsoever. This dilemma had to be addressed when, under two recent Intergovernmental Memoranda of Understanding, organizations in Malaysia (including the Forest Research Institute of Malaysia and several Universities) and the United Kingdom (the Natural History Museum, the Natural Resources Institute, the Oxford Forestry Institute and several Universities) agreed to collaborate in undertaking programmes to study the effects of human intervention practices on biodiversity. Experimental sites were selected with good historical records of site factors and management, particularly the Pasoh Forest Reserve in Peninsular Malaysia.

To address the question of what to monitor, it was decided to try and encompass some of the biotic variation present in the site. To help achieve this we looked at components of this variation and recognized several including taxic, genetic, trophic and positional variation together with some that reflected variation in economic importance.

Taxic variation. This refers to the entire taxonomic spectrum of variation present in the biota. It focuses on the variation of species richness within taxonomic rank (e.g. monotypic or polytypic) and is used to weight species sets when assigning conservation priorities. This encompasses a broad spectrum from prokaryotes to higher plants and the charismatic megavertebrate fauna. It was felt that different components of the taxic spectrum might respond in different ways and, because of their different mean generational times, with different speed. We hoped that by using a range of organisms it would prove possible to identify groups that have. different degrees of sensitivity to a range of human interventions such as logging. The groups included mycorrhizal fungi, epiphytic cryptogams including lichens, climbing plants, shrubs, palms, Zingiberaceae (for their chemical interest), Dipterocarpaceae (for their commercial wood interest), ants, birds and small mammals; these mixed (a) taxonomic groups with functional groups and (b) individual with community indicators.

Genetic variation. This implies the level of genetic variation within a particular species. In practice this is both more expensive and labour intensive to monitor than some

other axes of variation, but it is both interesting and important to address questions concerning the change in genetic diversity occurring in a population of forest trees following selective logging. For example, does this select against characteristics desirable in timber yielding trees (as these are the ones removed) or does it favour them (as they have already seeded, are present in the understorey and grow immediately to fill gaps created by logging)?

Trophic variation. It is well known in temperate ecosystems that perturbations may affect organisms higher in the food chain more severely than the more numerous organisms lower in the food chain. Thus we attempted to select organisms with different positions in the food chain, primary producers, herbivores, carnivores, parasites, saprophytes and so on in an attempt to embrace this spectrum and to cover other levels of functional variation, guilds etc.

Positional variation. Many organisms are normally restricted to a certain position or site in an ecosystem and intervention may have a greater impact on some of these. For example, the high degree of similarity between leaf litter ant communities in pristine habitats and in a range of progressively increasingly disturbed habitats suggested that leaf litter communities may not be very sensitive to perturbation (Belshaw and Bolton, 1993). However, as intervention involves removal of many large trees it may significantly reduce the canopy, and consequently have a deleterious effect on the canopy community of ants. By monitoring a range of organisms occurring in the soil, leaf-litter, under bark and in the canopy it was hoped that variation in this spectrum could be accommodated although it was recognized that this was difficult to test.

Other axes of variation relating to different aspects of behaviour and/or habitat requirement could have been addressed, but in the budgetary constraints of the programme it was only possible to select groups of organisms that embraced the variation outlined. This then is one attempt to answer the question of what should be monitored. We hope that the discussions at this symposium will provide some insights into the broad range of problems of measuring and monitoring forest biodiversity.

CONCLUSION

It is somewhat difficult to preview the results of a symposium without having seen

all the contributed papers and without having heard all the discussions. However, we hope that the symposium will result in some approach towards consensus on the needs for future research at a time when financial resources are limited and competition is increasing. Biodiversity clearly means different things to different people and it is affected in various ways by the several purposes for which resources are managed and at different scales from local to global.

Knowledge of taxonomy, reproductive biology and genetic systems is clearly fundamental. We need to determine how conservation values should be assessed and to identify what types of information are required at the different geographic scales. We must also agree on the types of indicators that may be appropriate to determine adequate biodiversity conservation and management (e.g. trees, vascular plants, habitat varieties, viable habitat sizes, level of habitat protection, or existence of corridors to other sites).

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Chapter

4

LANDSCAPE CHARACTERIZATION AND BIODIVERSITY RESEARCH

Virginia H. Dale[1], Holly Offerrnan[2], Robert Frohn[3] and Robert H. Gardner[4]

INTRODUCTION

Rapid deforestation often produces landscape-level changes in forest characteristics and structure, including area, distribution, and forest habitat types. Changes in landscape pattern through fragmentation or aggregation of natural habitats can alter patterns of abundance for single species and entire communities (Quinn and Harrison 1988). Examples of single-species effects include increased predation along the forest edge (Andrean and Angelstam 1988), the decline in the number of species with poor dispersal mechanisms, and the spread of exotic species that have deleterious effects (e.g., gypsy moth). A decrease in the size and number of natural

1 **Environmental Sciences Division, Oak Ridge National Laboratory[5], P. 0. Box 2008, Oak Ridge, Tennessee 378316035.**

2 **Geography Department, 1113 LeFrak Hall, University of Maryland, College Park, Maryland 20742.**

3 **Department of Geography, Remote Sensing Unit, University of California, Santa Barbara, California 93106.**

4 **Appalachian Environmental Laboratory, Gunter Hall, Frostburg, Maryland 21532.**

5 **Managed by Martin Marietta Energy Systems, Inc. for the U.S. Department of Energy, under contract DE-AC05840R214OO.**

habitat patches increases the probability of local extirpation and loss of diversity of native species, whereas a decline in connectivity between habitat patches can negatively affect regional species persistence (Fahrig and Merriam 1985). Thus, there is empirical justification for managing entire landscapes, not just individual habitat types, in order to ensure that native plant and animal diversity is maintained (McGarigal and Marks 1993).

A landscape can be defined as an area composed of a mosaic of interacting ecosystems, or patches (Forman and Godron 1986), with the heterogeneity among the patches significantly affecting biotic and abiotic processes in the landscape (Turner 1989). Patches comprising a landscape are usually composed of discrete areas of relatively homogeneous environmental conditions (McGarigal and Marks 1993) and must be defined in terms of the organisms of interest. For example, in a landscape composed of equal parts of forest and pasture, a photophilic butterfly species would perceive the pasture areas as suitable habitat whereas a shade-tolerant species would prefer the forest. In addition, both landscapes and patches are dynamic and occur on a variety of spatial and temporal scales that vary as a function of each animal's perceptions (McGarigal and Marks 1993). For instance, a long-lived and far-ranging bird will view its environment at broader spatial and temporal scales than a short-lived, wingless insect (Allen and Starr 1982, Urban *et al.* 1987). These differences must be incorporated and used in landscape analysis by changing the spatial or temporal resolution of a database or simulation model.

Species with different life-history characteristics have been used in simulation models (Gardner *et al.* 1993) which show that the interaction of natural and anthropogenic disturbance with existing landscape pattern may dramatically affect the risk of species loss. Those species which are most vulnerable are ones that become isolated as a result of landscape fragmentation and are also restricted to specific habitat types. These simulation results have also shown that policies for land management that change the degree of landscape fragmentation will result in a change in the competitive balance between species, further jeopardizing the maintenance of native species diversity (Gardner *et al.* 1993).

Theoretical work in landscape ecology has provided a wealth of methods for quantifying fragmentation and other spatial characteristics of landscapes (e.g., Baker and Cai 1992, Gardner and O'Neill 1991, Gustafson and Parker 1992, Krummel *et al.* 1987, ONeill *et al.* 1988, Plotnick *et al.* 1993, Loehle and Wien 1994). Recent advances in remote sensing and geographic information systems (GIS) allow these methods to be readily applied over large areas. One of today's challenges is to relate quantitative measures of landscape characteristics to

changes in biodiversity of animals dependent on the landscape structure. The current paucity of spatially-explicit ecological field data makes exploring this relationship difficult.

The objectives of this paper are to present a brief overview of common measures of landscape characteristics, to explore the new technology available for their calculation, to provide examples of their application and to call attention to the need for collection of spatially-explicit field data. The paper focuses on spatial issues related to macroscopic tropical fauna, although the ideas are, in theory, applicable to temporal analysis and other biotic groups.

MEASURES OF LANDSCAPE CHARACTERISTICS

Landscapes can be quantified in terms of area, diversity, and pattern. Area measures such as total area of habitat suitable for a particular species, maximum patch size, and mean patch size are often the simplest to calculate and interpret. For instance, a decrease in the total area of habitat available often correlates with species decline (Wilson 1988, Saunders *et al.* 1991). Similarly, information on maximum patch size may provide insight into long-term population viability because populations are unlikely to persist in landscapes where the largest patch is smaller than that species' home range.

Traditional diversity indices such as the Shannon Index and Simpson Index quantify diversity rather than pattern. These indices first gained popularity as measures of plant and animal diversity and are easily applied to landscape diversity (O'Neill *et al.* 1988). Unfortunately, these indices convey no information about the structure and arrangement of patches within the landscape. For instance, a landscape composed of 90% forest and 10% pasture would yield the same diversity index value as a landscape of 10% forest and 90% pasture. In addition, these diversity indices combine patch richness and evenness information, although these components are often more useful when considered separately. Richness refers to the number of patch types present; because many organisms are associated with a single type, patch richness may correlate well with species richness (McGarigal and Marks 1993). Following this line of reasoning, Stoms and Estes (1993) outline a remote sensing agenda for mapping and monitoring biodiversity which focuses almost exclusively on species richness. Evenness, on the other hand, refers to the distribution of area or abundance among patch types.

Indices which represent the spatial arrangement of landscapes have been developed from theoretical work in landscape ecology. Because no single index

can capture the full complexity of the spatial arrangement of patches, a set of indices are frequently evaluated. Three of the more common indices are dominance, contagion, and fractal dimension (O'neill *et al.* 1988). Dominance, which is the complement of evenness, provides a measure of how common one land cover is over the landscape (Figure 1). Its value indicates the degree to which species dependent on a single habitat can pervade the landscape (e.g., koalas dependent on eucalyptus groves). The contagion index measures the extent to which land covers are clumped or aggregated (Figure 2). Contagion is a useful metric for those species which require large contiguous areas of a particular land cover (e.g., carrion beetles unwilling to cross deforested gaps between forest patches, Klein 1989). Fractal dimension uses perimeter-to-area calculations to provide a measure of complexity of patch shape (Figure 3). Natural areas tend to have a more complex shape and a higher fractal value, whereas human-altered landscapes have more regular patch structure and a lower fractal dimension (Krummel *et al.* 1987). This difference can influence the diversity of species which inhabit edges or require multiple habitats (e.g., large herbivores requiring both forests for cover and open fields for forage, Senft *et al.* 1987).

INDICES: DOMINANCE

- degree to which one land cover type dominates the landscape.

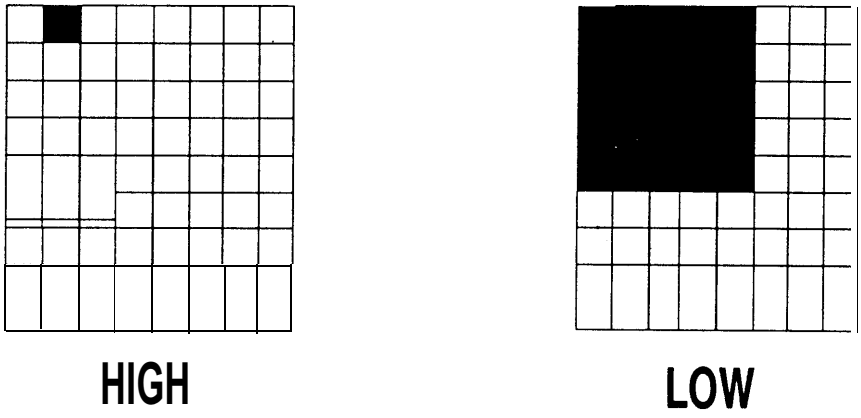

Figure 1: Examples of dominance.

INDICES: CONTAGION

- extent to which one land cover types are aggregated or clumped.

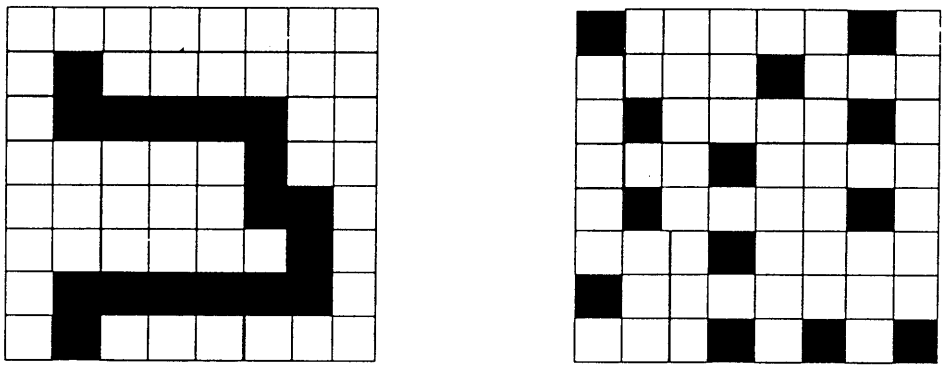

Figure 2: Examples of contagion.

INDICES: FRACTAL DIMENSION

- a measurement of the complexity of patch shape.

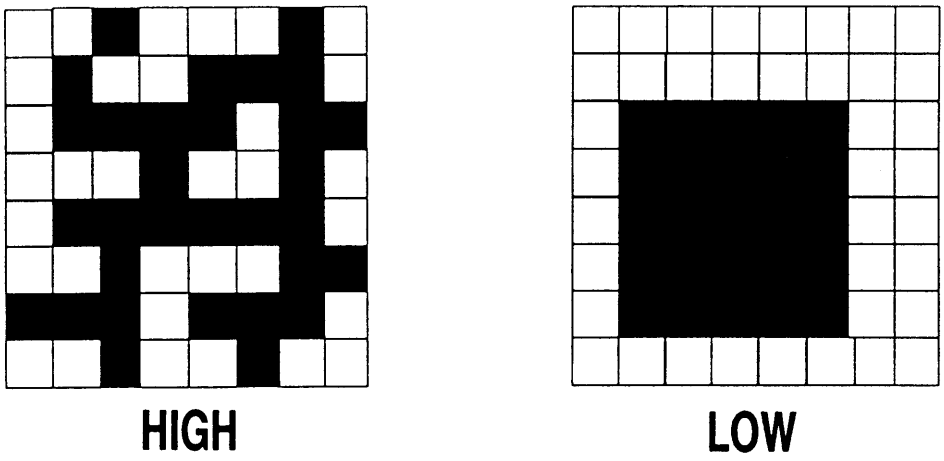

Figure 3: Examples of fractal dimension.

RECENT APPROACHES FOR QUANTIFYING LANDSCAPE PATTERN

Spatial indices and other landscape-level measures can be painstakingly calculated by hand from maps but are typically calculated digitally by computer from a grid of numeric values which represent those maps. Both field work and aerial photography can provide mapping data, but satellite-borne sensors automatically collect and store such data in a digital grid-cell format. This format is ideal for quantifying spatial characteristics of landscapes or as input to geographic information systems (GIS) and computer simulation models.

Satellite remote sensing offers several other advantages over traditional field work. First, data can be collected simultaneously over large areas. Whereas it might take two years of field work to map the vegetation over a 1000 km^2 area, a satellite can obtain an image of the same area in a few seconds. In addition, satellites collect data for multiple time periods and at multiple spatial and spectral resolutions using a repeatable and non-destructive sampling method. Finally, satellite images have a very high information content, and the prices for both images and computer equipment are dropping rapidly. Free public domain software is available for image analysis and the quantification of the results maps (McGarigal and Marks 1993). These features combine to make remote sensing, and satellite imagery in particular, an important tool for ecological monitoring and quantitative assessment of landscape pattern.

The utility of remotely sensed data is increased by integration with computerized geographic information systems (GIS) and simulation models that project changes in spatial cover under specific scenarios. GIS allows the efficient layering of many types of data (e.g., vegetation, hydrology, elevation) by referen-cing all data to a common denominator: geographic location. This multilayered data set can be used to drive spatially-explicit simulation models which examine causes and effects of changes in the spatial arrangement of each layer. Existing biodiversity data can be stored as one of these layers, or biodiversity information can be inferred from other layers (e.g., fauna1 biodiversity may be associated with structural diversity of the vegetation layer).

The theoretical and technical groundwork has been laid to allow efficient quantification of GIS landscape layers for biodiversity research. Nevertheless, the ties between theory, technology, and reality are tenuous at best. Dale *et al.* (1994) used the Dynamic Ecological-Land Tenure Analysis (DELTA) model to explore the implications of various land management alternatives on Amazonian biodiversity as discussed below. This case study demonstrates how spatially-explicit ecological data can be used to strengthen the ties between theory, technology and reality.

CASE STUDY: LINKING LANDSCAPE MEASURES WITH ECOLOGICAL DATA

Background

Amazonian biodiversity is being negatively impacted by large scale forest clearing. The case study focuses on the Brazilian state of Rondônia which is located in the central Amazon Basin (Figure 4) and is dominated by mature neotropical forests. Government initiatives produced an 18-fold increase in the total length of roads

Figure 4: Location of case study area in Rondônia, Brazil.

between 1979 and 1988 (Frohn *et al.* 1990) which opened the interior forest areas to colonization. Colonists used slash and burn techniques to clear the forest for agriculture, producing a dynamic mosaic of agricultural fields, pasture, regrowth, and mature forest, with most of the clearing originating near roads. Between 1978 and 1988, 17,717 km^2 of Rondonia's forest were cleared, and an additional 1,417 km^2 of forest were isolated from the contiguous forest into small (<l00km^2) patches (Skole and Tucker 1993).

Changing patterns of forest clearance and isolation can be simulated by the Dynamic Ecological-Land Tenure Analysis (DELTA) model (Southworth *et al.* 1991, Dale *et al.* 1993, 1994). DELTA is a stochastic spatially-explicit model which combines a decision model of farmers' land-use choices with ecological information about changes in biomass. The model uses side-looking radar imagery, GIS, field estimates of biomass in forests, and socio-economic data to produce statistics and maps of the simulated changes in the area, biomass, and pattern of land-cover types.

Quantifying modelled landscapes

DELTA model simulations suggest that different scenarios of land management result in unique land-cover patterns (Dale *et al* .1994) (Figure 5). Simulating the best, typical, and worst-case scenarios permits evaluation of the causes of specific land-cover changes. Land-use activities that are typical for colonists in Rondonia (Coy 1987, Dale and Pedlowski 1992, Leite and Furley 1985) involve rapid clearing of the forest and almost complete deforestation within 18 years. The worst case scenario (taken from the extreme of the Transamazon Highway experience as reported by Moran 1981 and Fearnside 1980, 1984, and 1986) results in total clearance in the first 10 years. On the other hand, a best case scenario can be simulated in which forest clearance stabilizes at about 40% by year 20. The best case scenario involves some clearing, but no burning, of the virgin forest and planting of perennial trees. The worst and best case model projections are hypothetical, but the typical model scenario is meant to replicate recent land management activities in central Rondonia.

Comparing model projections to satellite imagery over recent years is a way to verify the modeled projections. Frohn *et al.* (in prep.) compare the percent of forest cleared, contagion and fractal indices from the three model scenarios to those values obtained from classified Landsat imagery for 1978, 1980 and 1986 (Figure 6). The clearing pattern for 1978 and 1980 are similar to the typical simulation projections (Figure 6a). However, the model overestimates the amount of clearing for the 1986 scene. Initially, contagion is high for both the simulation and the Landsat estimate

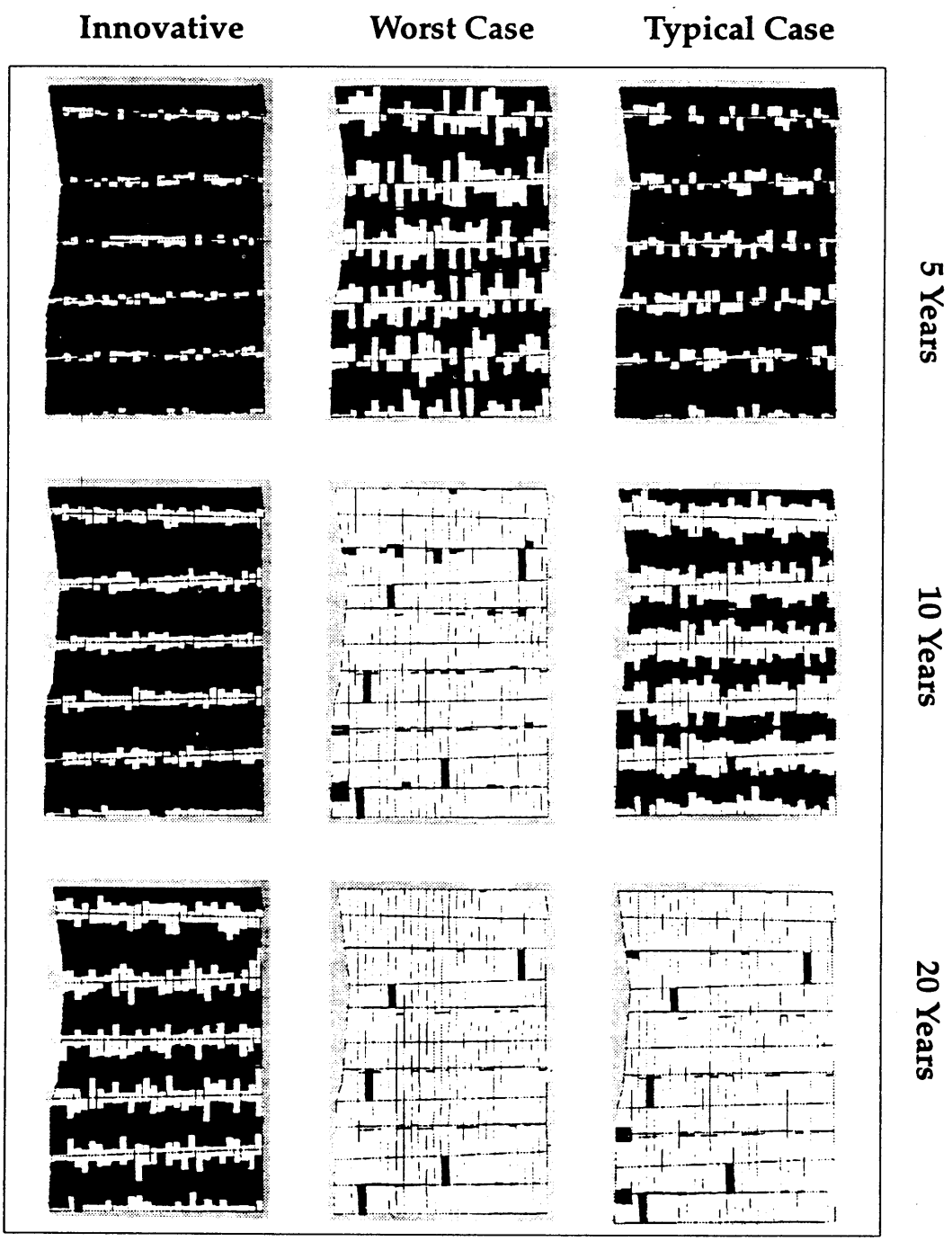

Figure 5: Simulated landscape pattern: years 5, 10 and 20 for typical, worst case, and sustainable agricultural management scenarios. The dark areas are undisturbed tropical forest and the light areas have been cleared for agriculture.

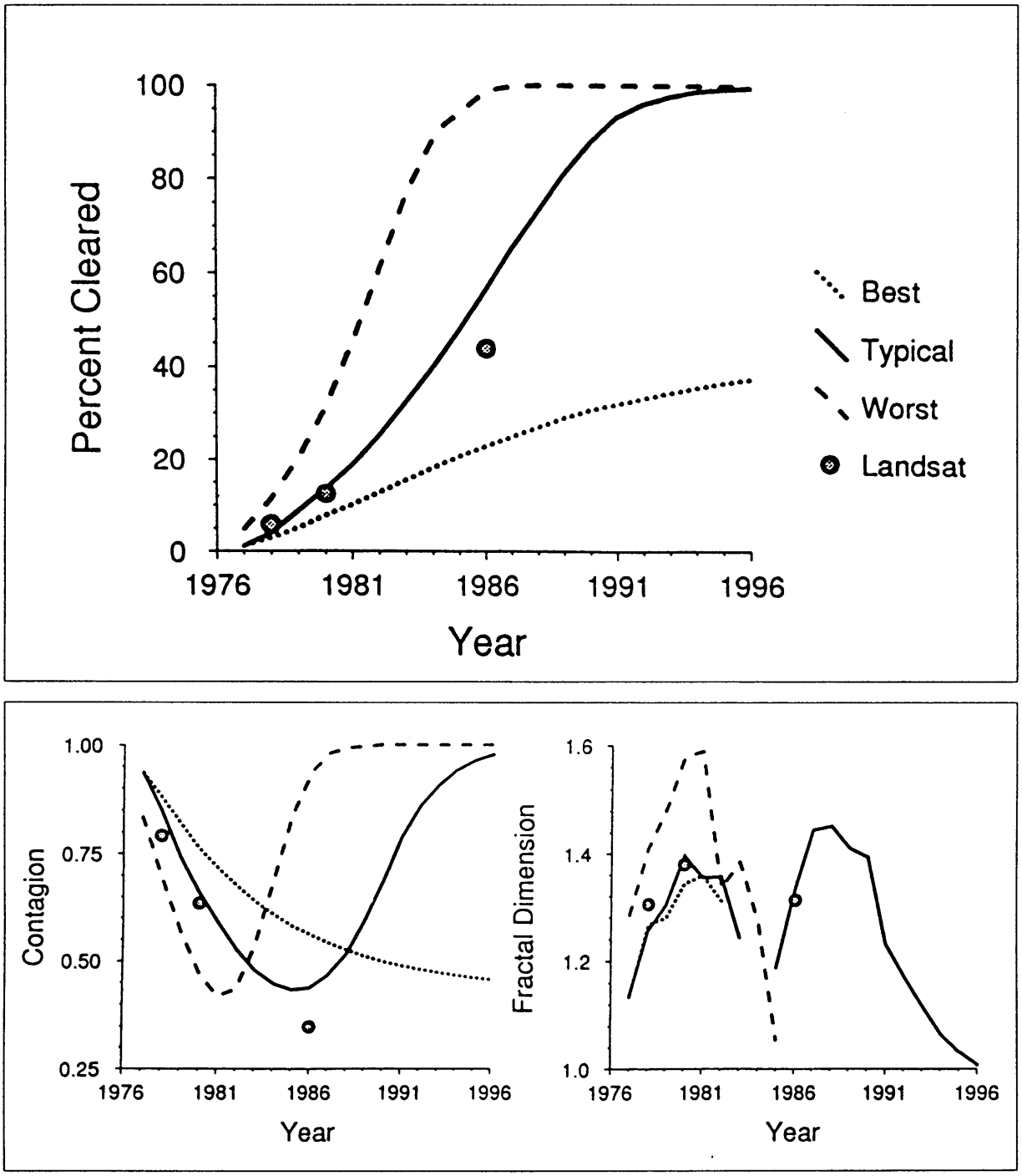

Figure 6: Comparison of the total area, contagion and fractal values of model projection under three management scenarios to Landsat imagery data for 1978, 1980 and 1986.

(Figure 6b) because the landscape consists primarily of large contiguous patches of forest. Contagion decreases in both estimates as the number of small forest clearings increases and the landscape is less dominated by large patches of forest. In the simulations, contagion increases as larger patches of cleared forest dominate the landscape. However, this pattern has not been verified by Landsat data. The fractal dimension (Figure 6c) values for the typical simulation and the Landsat estimate show similar patterns, indicating that the model predicts land-scape patch complexity similarly to that determined from remote sensing.

These comparisons show that the typical scenario simulation is consistent with both the amounts and patterns of forest clearing for central Rondonia for the years tested. Model estimates can therefore be used with greater confidence to predict landscape changes in later years and the response of biodiversity to those changes.

Modelling faunal response to landscape pattern

In order to relate landscape-level changes to changes in fauna1 abundance and distribution, spatially-explicit data were collated for 9 taxonomically diverse groups of neotropical forest animals and summarized in Table 1 (as discussed by Dale *et al* 1994). Examples of spatially-explicit data include the maximum gap width between habitat patches that an animal is likely to cross; the minimum patch area required to maintain normal behavioral patterns; the spatial distribution of rare or patchily distributed resources vital to a particular species' survival (e.g., special habitats for breeding); and the width of the "buffer zone" at a forest edge where climatic or ecological edge effects render the area uninhabitable for a particular species. These data were collated from a literature search and studies of animal activity subsequent to experimental manipulation of intact forests into patches of 1, 10, 100 and 1000 km^2 (the manipulation and full data sets are discussed by Bierregaard *et al.* 1992 and Offerman *et al.* in press).

The landscape scale and patch characteristics were defined based on the animals' perception of their environment. DELTA typically runs on an area of -3000 km^2 this scale represents an intermediate landscape size for the macroscopic, mobile fauna selected. Model output data was stored in a grid with 37.5 m resolution, because field observations of maximum gap width crossed between habitat patches was most easily divided into multiples of 37.5. In other words, those animals that could not cross a distance greater than 37.5 m were assigned a low gap-crossing ability. Patches were defined simply as areas covered by forest, because the 9 selected groups of animals were all primarily forest-dwellers.

For each model year, the area of forest habitat suitable for each animal group

Species or species groups	Gap-crossing ability[a]	Area requirement[b]	Source of information
Jaguar (*Felis onca*)	High	High Parker 1990	Emmons, pers. commun.,
Bare-tailed woolly opossum (*Caluromys philander*)	Moderate	Moderate	Bierregaard *et al.* 1992, Malcolm 1990 and 1991
Mixed-species bird flock	Moderate	Moderate	Bierregaard *et al.* 1992, Bierregaard and Lovejoy 1989
Ant-following bird flock	Moderate	Moderate	Bierregaard 1990
Tropical frog (*Chiasmocleis shudikarensis*)	Moderate	Moderate	Zimmerman and Bierregaard 1986, Zimmerman pers. commun.
Black and white saki monkey (*Pithecia pithecia*)	Low	Low	Schwarzkopf and Rylands 1989, Rylands and Keuroghlian 1988
Three-toed sloth (*Bradypus variegatus*)	Low	Low	Montgomery and Sunquist 1974 and 1978
Scarab beetles	Low	High	Klein 1989, Howden pers. commun.
Euglossine bees	Low	High	Becker *et al.* 1991, Powell and Powell 1987

Table 1: Relative gap-crossing ability and area requirements for selected tropical fauna (modified from Dale *et al.* in press). The first seven species have their gap-crossing ability proportional to area requirements; the last two species have low gap-crossing ability and large area requirements.

[a] Width of pasture which begins to inhibit movement between forest fragments: high is greater than 500 m, medium is 50 to 500 m, and low is less than 50 m.

[b] Area requirement: high is greater than 1000 ha, medium is 10 to 1000 ha, and low is less than 10 ha.

was measured. First, "connected" clusters of habitat cells were identified. A cluster is connected if an animal in one cell can move to any other cell in that cluster (i.e., gaps between cells in a cluster are not wider than the maximum gap width that animal is able to cross). Next, clusters with areas less than the minimum area required by an individual or group (for those that only occur in groups) were discarded. Further discussion of this technique can be found in Pearson *et al.* (in press).

The result of this analysis is that changes in available habitat are similar for animals that have their gap-crossing ability proportional to area requirements (Figure 7a), regardless of taxonomic affiliation (Dale *et al.* 1994). For instance, the model suggests that species with large gap-crossing abilities and large area requirements (e.g., jaguars) respond in a similar fashion as species with small gap-crossing abilities and smaller area requirements (e.g., sloths). In contrast, animals with gap-crossing ability disproportionately small in comparison to their area requirements (e.g., scarab beetles) decline more rapidly (Figure 7b). Few animals larger than insects seem to fall into this latter group; therefore landscape-level analysis using simply gap-crossing ability and area requirements may provide a swift preliminary identification of the animals most susceptible to rapid decline and possible extirpation, assuming that fragmentation does not induce behavioral changes.

Once sensitive species have been identified, additional spatially-explicit life history data may be incorporated to improve the accuracy of the assessment. For example, when possible edge effects and breeding habitat requirements are included in the assessment of suitable habitat available for the tropical frog *(Chiasmocleis shudikarensis),* the amount of suitable habitat is decreased to 39% of the original area defined by gap-crossing and area requirements alone (Dale *et al. 1994).*

Case study results

Spatially-explicit land-cover and fauna1 life-history data are both vital for assessing the impact of landscape change on biodiversity. These data can be derived from remote sensing and from *in situ* ecological studies, and integrated with models which simulate the cause and effect of changes in spatial pattern. Maps produced from the model simulations can be quantified using spatial indices; these indices can then be used to represent the changes in land-cover patterns to which species respond.

Combining spatial indices with species-specific ecological data provides a useful method for identifying species sensitive to landscape-level habitat modifica-

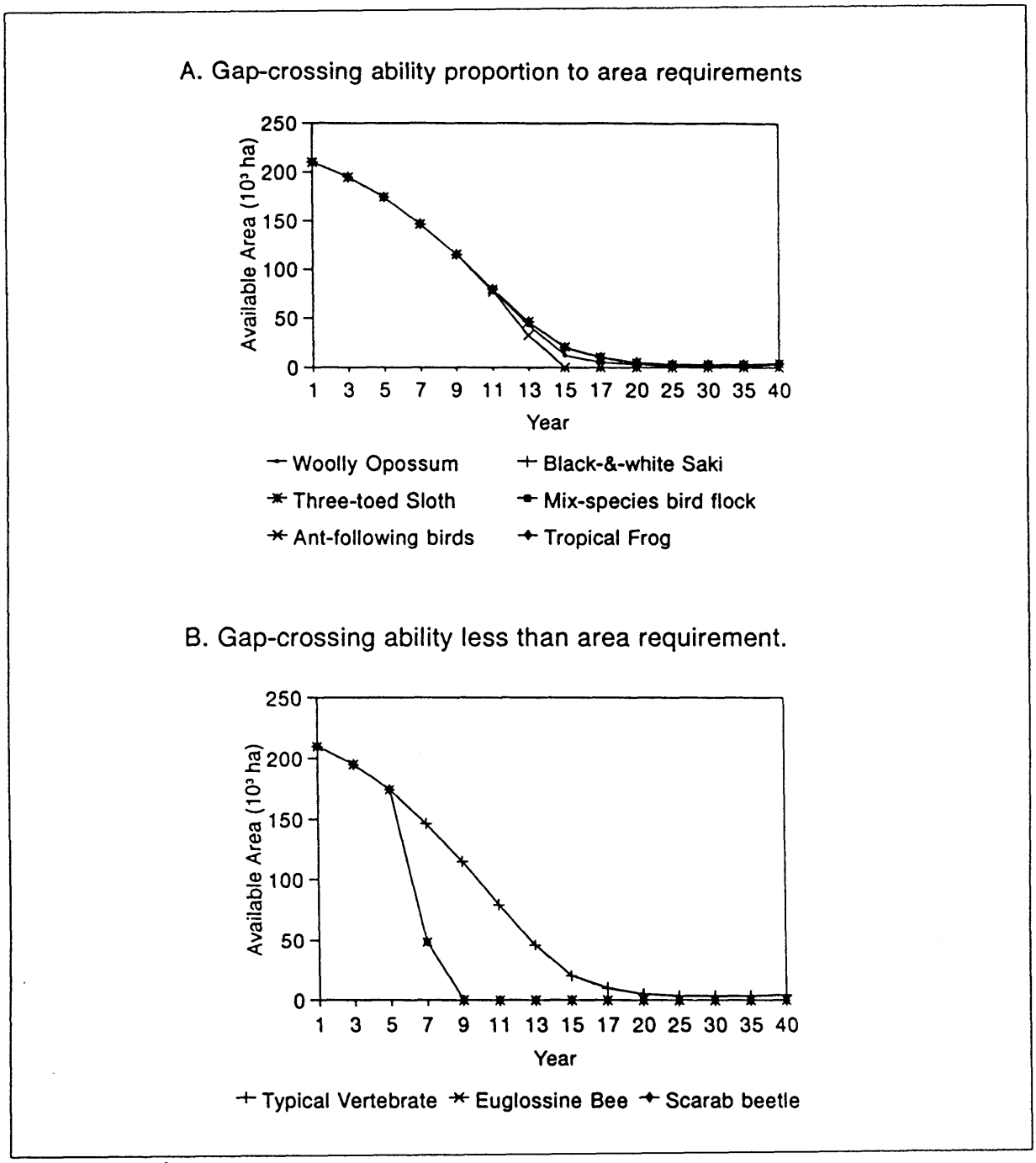

Figure 7: Simulated changes in area of suitable habitat for two groups of species: (a) animals with their gap-crossing ability proportional to their area requirements, and (b) animals with their gap-crossing ability less than their area requirements.

tions. Species response to these modifications may be based on spatial-explicit behavioral characteristics rather than taxonomic classification. The major implication of the Rondonia study is that a "balance" between gap-crossing ability and minimum area requirements allows species to maintain themselves under varied land cover conditions.

CONCLUSIONS AND FUTURE RESEARCH OPPORTUNITIES

The theory and technology currently exist to perform rapid, large-scale quantitative analysis of biodiversity in real and modelled landscapes. Policymakers request this type of analysis before making high-profile, million-dollar decisions (e.g., the issue of harvesting old-growth forests of the United States' Pacific Northwest while protecting the spotted owl). However, the current paucity of spatially-explicit fauna1 life-history data makes it difficult to verify the link between real-world phenomena and the statistical phenomena seen in the landscape indices.

Policymakers require the linkage between indices and biodiversity be firmly established before the indices can be used to define policy. The urgency of biodiversity conservation issues, therefore, suggests first that field-based research agendas should focus less on taxonomy and morphological description, and more on collection of spatial data; and second, that researchers with remote sensing, GIS, and modelling capabilities should quantify the link between measures of landscape characteristics and the observed ecology of species occupying those landscapes.

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Chapter

5

COMPARATIVE PARADIGMS FOR BIODIVERSITY ASSESSMENT

W. L. Myers[1], G. P. Patil[2] and C. Taillie[2]

INTRODUCTION

Formulation and comparison of diversity measures has such extensive precedent as to be considered an integral domain of classical statistical ecology (Grassle *et al.* 1979, Hurlbert 1971, MacArthur and MacArthur 1961, Magurran 1988, Patil and Taillie 1982, Pielou 1975, 1977). Such work, however, has mostly cast the several measures as competitors rather than-being complementary. The case basis for conventional diversity work lies primarily in local intensive studies, with recorded occurrence of taxa being considered definite, and relative abundance estimates considered as quasi-ratio information. Issues of uncertainty, such as mis-identification and differential detection, have been largely relegated to the background. Increasing representation of taxa with expanding area of observation has been extensively studied, but issues of appropriate plot size and configuration have overshadowed the more fundamental implication that any

1 School of Forest Resources; Environmental Resources Research Institute, Pennsylvania, State University, University Park, PA 16802, USA.
2 Center for Statistical Ecology and Environmental Statistics, Department of Statistics.

diversity determination is relative to its area basis. Temporal gap dynamics of forested landscapes are well-documented, but not explicitly recognized as a scale consideration in diversity assessments. Recognition of need for regional diversity investigations, as evidenced by actual funding of operations, is relatively recent.

The classical view of diversity remains important for intensive studies of particular ecological communities and forest stands (Gove *et al.* 1994, Hunter 1990, Swindel *et al.* 1984, Swindel *et al.* 1987, Swindel *et al.* 1991). However, the emerging sciences of landscape ecology and conservation biology have made evident the logistical and economical impracticality of such intensive observational coverage for regions on the order of square kilometers and larger (Scott *et al.* 1989). Such spatial scales are necessarily encompassed by contemporary ecosystem-oriented resource management and design of regional/national networks of biodiversity reserves. Furthermore, species/area and minimum viable population issues become fundamental in these latter contexts.

Turner provides an overview of these scale, observation, and measurement issues (Chapter 7, this volume). Lund *et al.* (Chapter 25, this volume) likewise provide an overview of contemporary broad-area observational technology, but do not emphasize the important consideration that the informational outputs of these technologies must be interpreted either manually or algorithmically relative to diversity factors. Available evidence regarding diversity at landscape and regional scales is thus substantially indirect. Our focus is on possible approaches to determination of patterns having probable relevance to diversity. Patterns constitute second-order information, subject to analysis with respect to diversity, and refinement by further collection of additional information. Patterns likewise provide a basis for designing acquisition strategies for obtaining further information that addresses unresolved questions. Any particular pattern, however, often has several potential implications.

We first consider patterns of different diversity indices that are subject to joint interpretation as diversity profiles. We then turn to spatial patterns derived from broad-area observational technologies and knowledge-based models.

PROFILES OF DIVERSITY INDICES

Diversity is generally described as a composite property that reflects both the number of species *(richness)* in a biological community and the *evenness* with which abundance is distributed among the different species. A wealth of indices have been proposed for measuring diversity; the most popular appear to be (i) the number

of species *s* in the community, (ii) the Simpson index,

$$\sum_{i=1}^{s} \pi_i (1 - \pi_i) = 1 - \sum_{i=1}^{s} \pi_i^2,$$

where (π_i is the *relative* abundance of the *i*th species, and (iii) the Shannon information index,

$$-\sum_{i=1}^{s} \pi_i \log(\pi_i),$$

In general, diversity indices are mathematical functions (Δ) of the relative abundances $\pi_1,\ldots,\pi_s$ that satisfy a property of *Schur concavity* (Patil and Taillie, 1982). An important limitation of the traditional diversity analysis is its dependence upon relative instead of absolute abundance. Thus, processes which change total abundance without markedly affecting the pattern of relative abundance will not be detectable by a traditional diversity analysis.

The traditional approach to site diversity obtains a random sample of n organisms from the community and these are classified to yield n_i organisms from species *i*. The relative abundance of the *i*th species is then estimated by

$$\hat{\pi}_i = n_i / n$$

Other probability sampling schemes can be employed with appropriate modification to the estimator $\hat{\pi}_i$. When interest lies in the spatial pattern of diversity across broad regions and at different geographic scales, then the foregoing sampling and classification is often impractical and one may adopt a regionalized indicator of diversity (see below).

The diversity index is often estimated by inserting. $\hat{\pi}_i$ for π_i in the formula for the index. Because of Schur concavity of the index, this leads to an underestimate of community diversity and the magnitude of the bias depends upon the sample size *n*. Jack-knifing is a useful technique for reducing the magnitude of the bias. In addition, jack-knifing provides an estimated standard error which can be used to provide an approximate confidence interval for the index. See Zahl (1977) and Patil and Taillie (1979) for details.

One of the purposes of a diversity analysis is to make comparisons among

communities at different points in time and/or space. But it is widely recognized that the use of different indices can lead to inconsistent comparisons (e.g., Hurlbert, 1971). With this in view, Patil and Taillie (1982) have formulated an intrinsic diversity ordering of communities which is only a *partial* ordering in the sense that not all communities are intrinsically comparable. They have also devised the notion of a *diversity profile* to graphically portray the diversity ordering. In general, a diversity profile is a labelled collection, Δ_t ,of diversity indices, where the labels Δ_t range over some set of real numbers. The profile is generally displayed as a graph of versus t.

A diversity comparison of two communities C_1 and C_2 is performed by superimposing their profiles. If the profile for C_2 is everywhere above that of C_1 then the second community is intrinsically more diverse. However, the profiles may intersect corresponding to the situation of different indices giving different diversity orderings.

Patil and Taillie (1979) define four different profiles, of which two will be described here. The Δ_β family of diversity indices is defined by

$$\Delta_\beta = \left(1 - \sum_{i=1}^{s} \pi_i^{\beta+1}\right) \Big/ \beta, \quad -1 \le \beta < \infty$$

The family includes as special cases the Simpson index (ß=1), the Shannon index (limit as ß→0), and species richness minus one for ß=-1.

An important property of a family of indices is its variable sensitivity to rare and abundant species. An understanding of this varying sensitivity can aid in interpreting intersections of the corresponding profiles. A precise definition of sensitivity is given by Patil and Taillie (1982) who show that, for large ß, the index Δ_β is sensitive to abundant species, whereas it is sensitive to rare species for small values of ß.

A second family of diversity indices is defined by

$$s(m) = \sum_{i=1}^{s} (1 - \pi_i)[1 - (1 - \pi_i)^m], \quad 1 \le m < \infty$$

Some special cases are the Simpson Index when m=1 and the species richness minus one as $m \to \infty$. However, this family does not include the Shannon index, even as a limiting form. When m is a positive integer, $s(m)$ is the expected number of species to be found in a hypothetical random sample of size m. This index is sensitive to abundant species for small m and to rare species for large m.

SOME EXAMPLES

Patil and Taillie (1979) have employed the s(m) profile to examine the temporal trend in avian diversity in the vicinity of Colstrip, Montana, during the 1975-1977 time period. The 1975 breeding season was taken as the baseline since several power plants had not yet gone into operation. In all, 81 bird species were recorded over the survey period. Observations were made along a number of short transects, but the data were available by transect for the Western Meadowlark species only. Annual total frequencies were available for the other species.

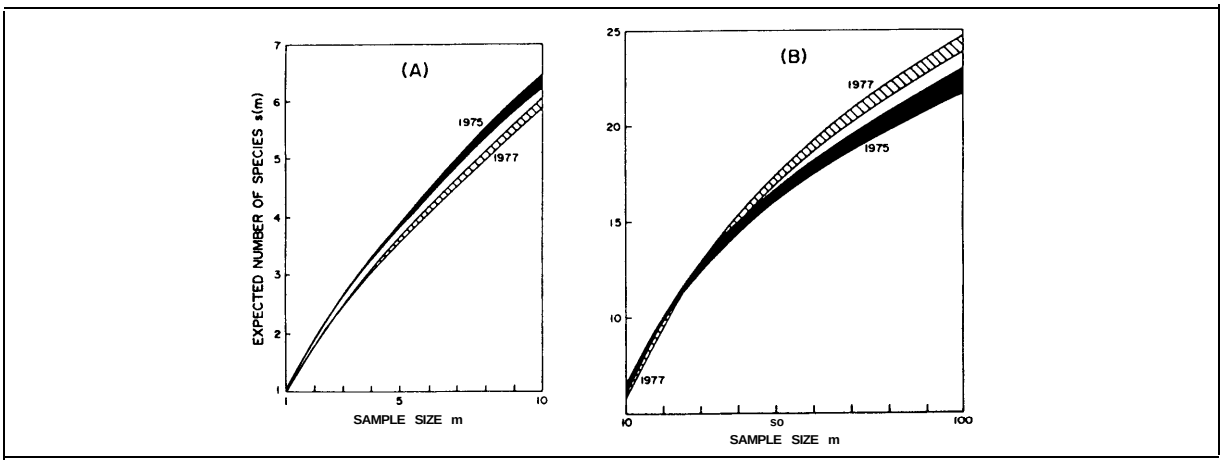

Figure 1: Ninety-five percent confidence bands for the jack-knifed estimates of the avian *s(m)* diversity profiles. (A) $1 \leq m \leq 10$ and (B) $10 \leq m \leq 100$.

The *s(m)* profiles are shown in Figure 1. The 95 percent confidence bands were obtained using the jack-knifed estimates of standard error. Jack-knifing was done by individual, although jack-knifing by transect would have been preferable if the information had been available. The profiles show that between 1975 and 1977 there was a drop in diversity for small *m* (abundant species) but an increase for large *m* (rare species). These changes correspond to a growing dominance of Western Meadowlark, on the one hand, and an increase in the number of occasional species, on the other hand. The changes are statistically significant since the confidence bands about the profiles do not overlap. But the changes are not necessarily attributable to start up of the power plants since the confidence bands reflect only within-year sampling variability and do not include between-year fluctuations in avian diversity.

Swindel *et al.* (1987) has used the Δ_β profiles to study trends in plant diversity following clearcutting of a Douglas-fir community in the Oregon Cascades. TWO

measures of abundance were considered: species plot-frequency and crown cover. When frequency was used, clear patterns emerged from the profiles. There was a sharp drop in diversity immediately after clearcutting, followed by a steady increase to levels above those that prevailed before clearcutting. Interpretation was more difficult with crown cover since the profiles displayed several intersections. Gove *et al.* (1994) uses the Δ_g profiles to examine the management issue of maximizing the diameter-class diversity in an uneven-aged northern hardwood stand.

EXTENSIVE SPATIALLY COMPARATIVE DIVERSITY

Progressive impoverishment of biota at regional and global scales has engendered a growing sense of urgency for conservation of biological diversity (Wilson and Peter, 1988) in light of which locally intensive biodiversity analysis becomes somewhat akin to making a detailed statistical inventory of a particular stand in a burning forest. The onslaught of destruction limits the value of the detailed information to documentation of impending loss. While there may be virtue in such documentation for the historical record, the more critical need is for rapid assessment over threatened regions to guide formulation of strategy for damage control and focus attention on critical areas. Quick acquisition of more approximate information over extensive areas is thus in order. When the situation becomes more stable, the approximate information can also serve to guide more rigorous characterization at the site level.

Fundamentally, diversity consists of co-occurrence of differing entities in space and time. The conventional approach to acquisition of diversity information involves observing multiple entities "simultaneously" during a time period in space partitions. An alternative is to observe different entities separately in common space partitions, and then spatially compare (overlay) the separate observations for co-occurrence. The latter approach has been promulgated for rapid assessment through GIS (geographic information systems) technology by Scott *et al.* (1987).

Apparent Diversity

Rapid diversity assessment involves synoptic recording of ordered categorical evidence for occurrence and/or expectation of taxa in spatial tessellations as GIS layers. Associations of taxa with landscape features, such as habitat, are exploited for evidential refinement and preliminary analysis. This has been characterized as

a "biodiversity filter" approach working from coarser to finer filters (Davis *et al.* 1990). Such work is inherently comparative, with a major goal of locating areas likely to have high biodiversity for further elaboration with finer (both spatial and categorical) filters.

In the USA this work is being conducted in a state-wide national program called "Gap Analysis" with the purpose of determining "gaps" in the conservation safety net of protected areas of critical habitat (Scott *et al.* 1993). The philosophy underlying Gap Analysis is essentially that protecting substantial areas of representative habitats which support complexes of species will simultaneously forestall the onset of endangerment for all members of the complex. The goal thus becomes one of identifying regional occurrences of critical habitats and then determining instances where such habitats are lacking in long-term protective management. Proponents of Gap Analysis are emphatic that it is intended to complement, not replace, the species-by-species approach to preserving biodiversity which is so critical to the survival of species now nearing extinction. The main goal of Gap Analysis is to help prevent additional species from being listed as threatened or endangered. The U.S. Environmental Protection Agency's EMAP (Environmental Monitoring and Assessment Program) includes similar components under a monitoring perspective.

While there is an ongoing evolution of Gap Analysis protocols, it typically proceeds through the following stages (Scott *et al.* 1991):

1. Derive and digitize map information on vegetation type distribution.
2. Verify the vegetation map information with field work.
3. Digitize existing species distribution maps for fauna.
4. Refine species distribution maps using digital map information relative to habitat factors.
5. Verify fauna1 distributions.
6. Input data on land ownership status.
7. Digitize current management areas according to levels of protection.
8. Generate map(s) depicting species richness and compositional variations from information of steps 1-5.
9. Generate map(s) for special-interest species such as threatened, endangered, and sensitive plants and animals; endemic taxa; or uncommon species found in fewer than three vegetation types. Information for such species comes largely from existing databases.
10. Regionalize the map information on diversity from steps 8-9, and locate centres of species richness (recognizing compositional variation).

11. Compare centers of richness regarding species representation and vegetation types to determine redundancy.
12 Prioritize centers of richness in light of their contribution to state, regional, and continental biodiversity.
13. Determine to what extent the areas of species richness and vegetation types are in protected zones, using information from steps 6-7.
14. Identify minimum and optimum areas required for protection of predetermined levels of state wide diversity.
15. Identify landscape corridors between candidate areas.

There is a good deal more parallelism and iteration in the Gap Analysis scenario than the numbering of steps might suggest. Assembly of the basic maps typically proceeds concurrently rather than sequentially. Both vegetation and species distribution maps may go through "first-cut," "second-cut," . . . , "nth-cut" versions. Idaho, as a prototype state, has had a rather complete second "go-round" of the entire Gap Analysis scenario.

Gap Analysis renditions of vegetation types and fauna1 distributions are essentially knowledge-based digital map models. Vegetation types are typically interpreted visually from small-scale satellite imagery and/or inferred by unsupervised digital analysis of the corresponding image data. Larger scale imagery and existing local maps support the interpretive and unsupervised inferences. Limited sample-based verification of vegetation types serves more as an indicator of realized classification error levels than for rigorous quality control.

Fauna1 distribution maps are effectively representations of apparent habitat, obtained by partial range deletion. Species are ascribed to vegetation types on the basis of current ecological knowledge of habitat requirements. Vegetation types that are thought to constitute unsuitable habitat are deleted from the best available range maps. Negative physiographic elements are likewise deleted using commonly available GIS layers, such as soils, geology, topography, and hydrography. Detailed habitat needs, such as dead snags and ephemeral ponds, are assumed to occur in the absence of evidence to the contrary. Verification of fauna1 occurrence is even more difficult and sparse than for vegetation. The recently completed breeding bird atlas database for Pennsylvania (Brauning 1992) is among the stronger sources of such information for verification. The breeding bird atlas database divides the state into a grid of cells, each covering one-sixth of a 7 l/2 minute topographic quadrangle map. In each cell, each observed species is designated in one of four categories as: a) confirmed breeder, b) probable breeder, c) possible breeder, or

d) observed without indication of breeding. The distinctions are based on behaviour exhibited by-birds as recorded in 19 activity types.

For most species of vertebrates, Gap Analysis synthesizes records of occurrence in terms of the 635 sq. km. hexagonal grid used by the U.S. Environmental Protection Agency for its EMAP work. Gap Analysis avoids the issue of intra-stand patch dynamics by imposing a minimum mapping area of 100 hectares. Gap Analysis presently makes the rather heroic assumption that vertebrate diversity is indicative of diversity in other major taxa. Since Gap Analysis casts its fauna1 distributions in terms of apparently suitable habitat, it seems appropriate to suggest the term apparent diversity for the corresponding patterns of spatial co-occurrence.

Gap Analysis for Pennsylvania is proceeding generally according to the foregoing regime, with the work being conducted in the spatial analysis laboratory of the Office for Remote Sensing of Earth Resources within the Environmental Resources Research Institute. Vegetation and ecological land type determination are being conducted concurrently A first-level photo-interpretive breakdown of the landscape into naturalistic and humanistic complexes is based on overall vegetation and land-use patterns. Delineation of such complexes is accomplished by on-screen digitizing. Unsupervised digital image analysis yields breakdowns of vegetation cover within each complex. Knowledge of the ecological setting for the complex is exploited in assigning attributes to cluster-based polygons. Future research will contribute additional ecological detail to the attribute information for polygons.

Ordinal Formations as Spatial Pattern Comparatives

Given the uncertain and speculative nature of Gap Analysis maps, diversity information arising therefrom is at best ordinal. Nevertheless, such maps do represent a synthesis of available ecological knowledge and advanced broad-area observational technology. In and of themselves, however, Gap Analysis species distribution maps from steps l-5 above are fundamentally just visual aids to thinking and dialogue concerning the species. If it is to move forward, such thinking and dialogue inevitably become spatially comparative among locations, landscapes, and regions.Aside from highlighting what we don't know, the utility of Gap Analysis thus rests on ability to extract coherent composite spatial patterns for comparative purposes. The composition, regionalization, and comparisons in steps l0-11 above are therefore crucial.

Humans have considerable perceptual facility for obtaining a visual sense of

pattern from maps, but such perception is unfortunately very subjective and indefinite. Different observers perceive differently, and have little ability to express a perceived sense of pattern. If discussion and debate are to transcend perceptual differences, regionalization and pattern extraction/characterization from maps must become more systematic. In what follows, we propose a systematic approach to ordinal spatial structure (pattern) that is applicable to biodiversity in the Gap Analysis context, but also extends more generally to any synoptic ordinal spatial context.

A prerequisite to systematic extraction of meaningful spatial pattern is the selection of mapping variables that are relevant to the issues and lead naturally to more specific analyses. We suggest that two classes of synoptic mapping variables are particularly relevant to the biodiversity context. One such class is species richness with possible restriction to certain taxa, guilds, functional groups, or conservation status. The second class is number of species, however restricted, that a particular spatial partition (cell or polygon) has in common with at least one of its neighbouring partitions. The first class addresses diversity in a general sense. The second class is indicative of interesting compositional regionalizations. Both classes are obviously scale dependent. The new approach we offer also provides for systematic exploration of progressively more generalized scales working upward from the base resolution of the map data source as a scale floor.

Our proposed approach addresses either smooth-surface or tessellated spatial variables of ordinal, interval, or ratio strength. Tessellations may be regular (cells) or irregular (polygons), but the tessera are viewed as flat-topped facets versus the sloping-facet elements of a TIN (triangular irregular network) model. Since our habitat mapping is still in progress at this time of writing, we cannot offer a full illustration of application to Gap Analysis. Therefore, we focus instead on conveying the concepts in terms of contrived data. The smooth-surface case provides the simplest point of departure for explanation, although it is not necessarily simple in terms of software.

Consider the stylized "contour map" of a spatial variable in Figure 2. To emphasize that we are assuming only ordinal strength of information, the contour "levels" are lettered rather than numbered. Relative to Figure 2, the letter "a" would be the base (lowest) level. The "a" level is absent from Figure 2 in analogy to the absence of mean sea level from most topographic maps. Our strategy is to provide for constructing spatial "objects" that are arranged in formations which are

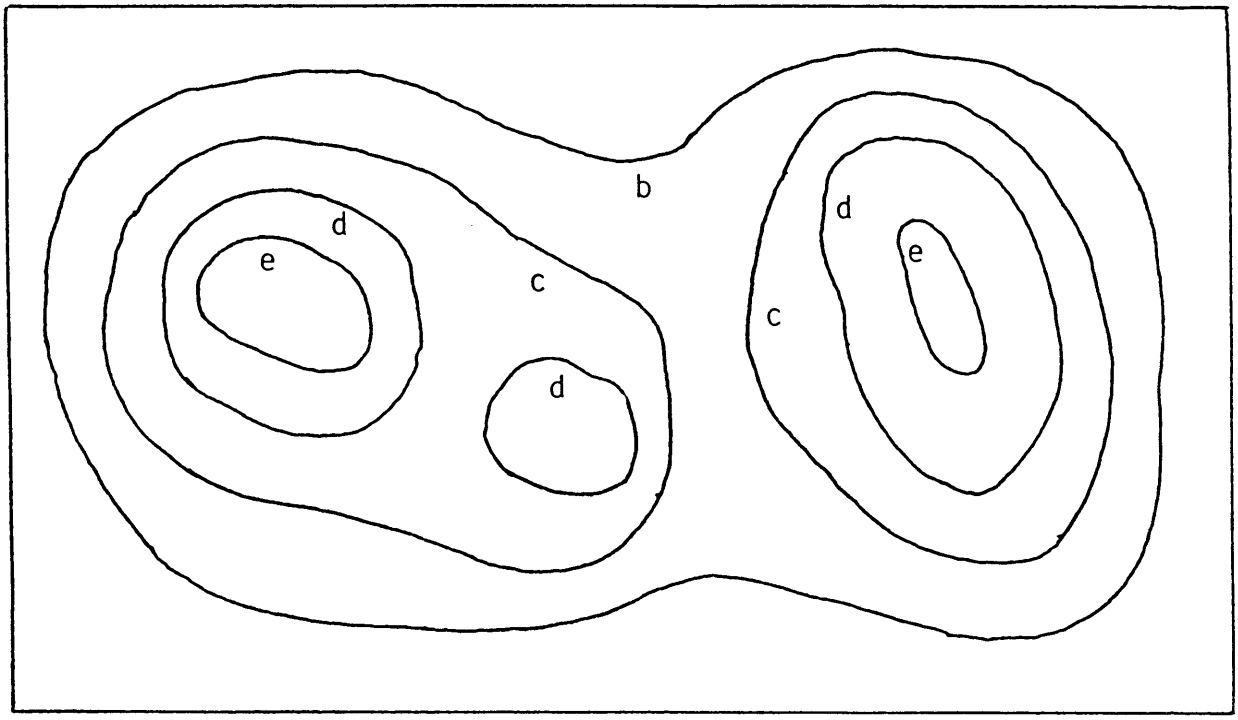

Figure 2: Contour map of hypothetical ordinal spatial variable with letters as ordinal levels.

hierarchical. A dendrogram is one way of depicting the formation domain. The leaves of the "tree" are unitary peak objects. These attach to first-order foundation objects, which attach to second-order foundation objects, and so on until the global foundation object is reached as the root of the dendrogram. Each of the formation objects is numbered, and the sub-hierarchy of objects attached to a foundation object is the "family" of that object. Other than the global foundation object, each formation object has a higher-order foundation object as its parent.

The highest contour level must be determined as a prelude to the process of recognizing and numbering formation objects, which begins with selection of an initial contour ring at top level and initiation of a number 1 object. The following "rules of the rings" then govern the process.

If the initial ring has no enclosed neighbour rings, then join the object to the inside of the initial ring and progress to exterior neighbour rings. If the initial ring has an interior neighbour ring, then join the object between the rings, add the interior ring(s) to a "ringlet" list, and progress to exterior neighbour rings.

If any exterior neighbour ring is at a higher level, then truncate the exterior

progression and process any ringlets.

If there is a single (enclosing) exterior neighbour ring at equal or lower level, then join the object between the rings and progress to the exterior of the neighbour.

If there are any non-enclosing exterior neighbour rings at equal or higher level, then truncate the exterior progression and process any ringlets.

If all exterior neighbour rings are at lower level, then join the object between the rings, add non-enclosing neighbour rings to the ringlet list, and progress to the enclosing neighbour.

If exterior progress reaches an enclosing ring that is already joined to an object, then truncate exterior progress, attach the current object to the exterior object, and process any ringlets.

Ringlets are processed similarly with interior replacing exterior. If inward progress meets an existing object, that object is attached to the current object. When all ringlets have been processed, then object number is incremented with a new initial ring being selected. Initial rings are selected from high to low, with rings already joined on both sides being ineligible. When the formation is complete, any object attached to an object of the same order is merged with its parent object.

Figure 3 shows the result of the process for Figure 2 in terms of object numbers. Objects numbered 1, 2, and 3 are first-order. Object 4 is second-order, and object 5 is third-order. Object 4 has objects 1 and 3 as children. Object 5 has objects 2 and 4 as children, with objects 1, 2, 3 and 4 all being its descendants.

Geometrically, the object structuring is motivated by "peaks and saddles". A complete intuitive understanding can be obtained by constructing a clay model and then "slicing" it into objects. "Hillocks" will be sliced off first, then hills, then foundations of entire "ranges" of hills. Depressions that "hold water" are ignored in the slicing process.

The dashed line in Figure 3 is a course that transects elements which decide objects. Figure 4 is a "vertical profile" along this course showing the formation of the associated dendrogram. The solid descending arrows indicate "centers" of first-order objects. The dashed descending arrows indicate nodal features.

With this relatively graphic introduction to the formation domain as background, consider next the cellular equivalent which is easier to manage with respect to software but more difficult to grasp visually. For purposes of illustration, consider Figure 5 to be a cellular array (raster grid) of species richness. To elaborate the formation domain of nested objects from such a cellular grid, begin at the highest cell and assign object number 1, as long as "outward" movement would be only

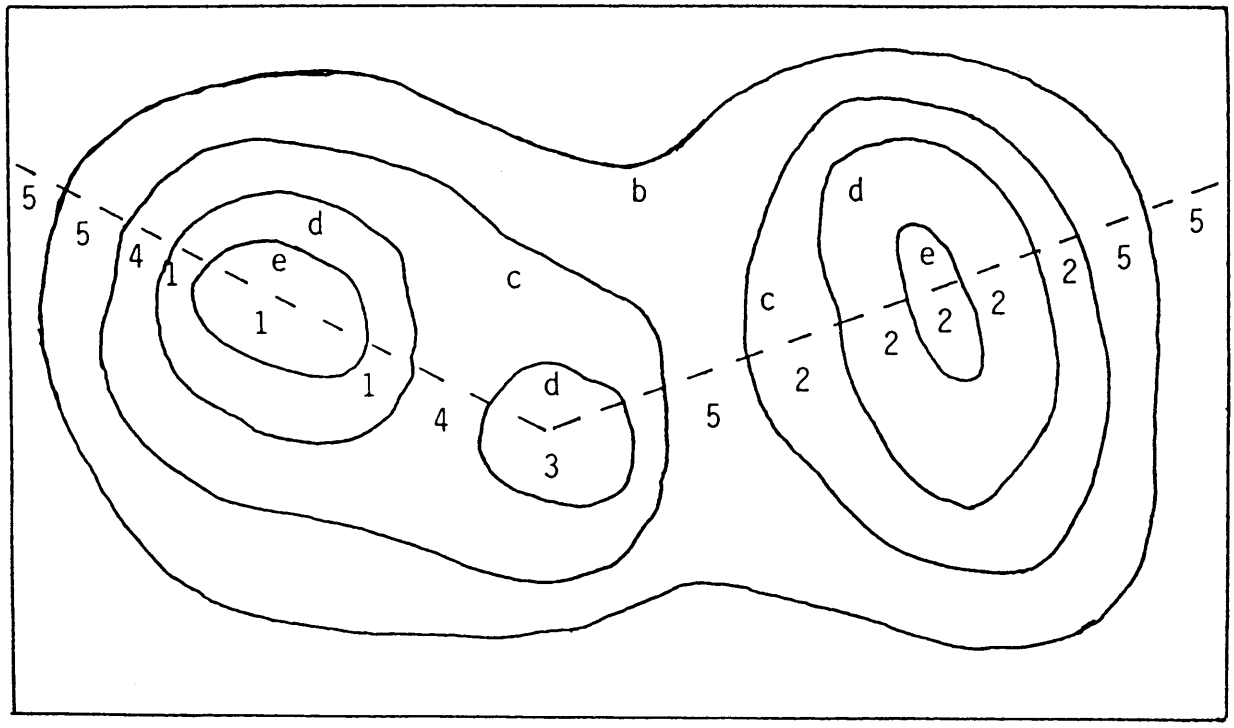

Figure 3: Contour map of hypothetical ordinal spatial variable with letters as ordinal levels and numbered formation objects. Dashed line is profile line for Figure 4.

downhill. "Flats" must be explored to their edges in developing an object. If a flat falls off in all directions along its edges, then the flat is included in the developing object. Otherwise it will become part of a subsequent foundation object. Depressions are included in a developing object. That is, the possibility of upward movement does not "count" if the "climb" is back into the current object.

When a first-order object (peak) is complete, select the next highest cell to begin development of the next first-order object. When all first-order objects are developed, proceed to second-order objects (foundations for peak objects). Flats between existing objects are included in their foundations. In all other respects, development of foundation objects proceeds as for peak objects. Always work globally downward in selecting the next object for development.

The result of applying this process to Figure 5 is shown in Figure 6 using symbols

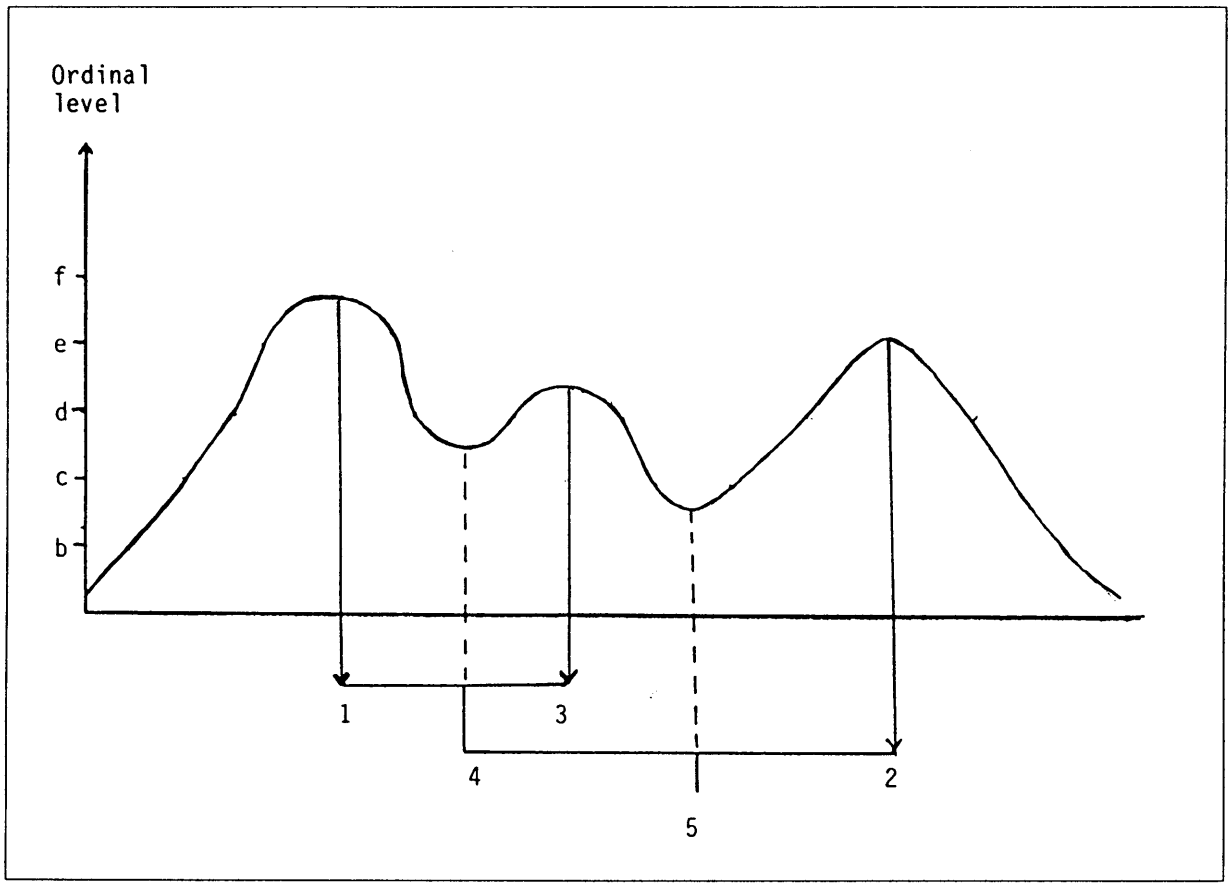

Figure 4: Profile along dashed line of Figure 3 showing formation dendrogram with object numbers.

	1	2	3	4	5	6	7	8	9	10
1	58	65	70	60	50	55	70	80	75	60
2	60	82	85	75	70	75	85	95	90	70
3	60	87	89	81	80	82	90	99	85	75
4	50	65	75	70	65	67	69	75	60	55
5	30	35	40	46	48	52	50	45	40	35
6	50	60	65	60	58	53	55	54	53	50
7	56	63	69	65	60	62	70	79	67	60
8	50	60	65	60	56	58	63	68	62	58
9	45	56	60	56	45	47	51	56	52	48
10	40	45	55	50	40	45	48	50	50	45

Figure 5: Cellular grid of hypothetical species richness data.

	1	2	3	4	5	6	7	8	9	10
1	+58+	+65+	+70+	+60+	:50:	+55+	+70+	+80+	+75+	+60+
2	+60+	<82>	<85>	+75+	+70+	+75+	[85]	[95]	[90]	+70+
3	+60+	<87>	<89>	<81>	+80+	[82]	[90]	[99]	[85]	+75+
4	:50:	+65+	+75+	+70+	+65+	+67+	+69+	+75+	+60+	+55+
5	:30:	:35:	:40:	:46:	:48:	:52:	:50:	:45:	:40:	:35:
6	:50:	−60−	(65)	−60−	−58−	−53−	−55−	−54−	−53−	:50:
7	−56−	(63)	(69)	(65)	−60−	{62}	{70}	{79}	{67}	−60−
8	:50:	−60−	(65)	−60−	−56−	−58−	{63}	{68}	{62}	−58−
9	:45:	−56−	−60−	−56−	:45:	:47:	:51:	−56−	:52:	:48:
10	:40:	:45:	−55−	:50:	:40:	:45:	:48:	:50:	:50:	:45:

Figure 6: Formation objects for data of Figure 5. Object symbology is 1=[], 2=<>, 3={}, 4=(), 5=++, 6=--, 7=::

as aliases for object numbers in the interest of better visual comprehension. If depressions are thought to be important formation features, a complementary bottom-up formation process can be used to develop a "hollows" tree as the negative of the "hills" tree. The process extends to vector polygons by treating them as irregular cells.

As recompense for the computational effort, there emerges new capability for extracting well-defined and perception-free spatial structure (pattern) from ordinal maps. The formation domain provides a new database schema and casts the map as a formal communication system subject to signal processing in an engineering sense. If there was no advantage in objective treatment of "poor" data, engineers would not bother to design and install filters for electronic communication systems.

With respect to the new database schema, the "objects" of the formation domain become database entities with suites of properties such as order, areal extent, local relief, number of children for given order, ordinal gradient, etc. These database entities can be readily indexed back to the spatial domain so that interesting occurrences in the formation domain may be located and displayed in map coordinate space. It thus becomes possible to conduct criterion searches on the attributes of objects and then transpose findings into the spatial domain.

General utility is perhaps best appreciated in terms of "prospecting." Consider the "contours" of Figures 2 and 3 as representing "ore deposit" information interpolated from borings. In deciding what areas to lease for mineral explora-

tion, our interest extends from local concentrations, to ranges of deposits, to the "mother lode." Our context is one of prospecting for particular aspects of biodiversity.

The tree structures of the formation domain place it within the purview of mathematical graph theory for tree metrics. Formation domains for a given area at different times can be compared quantitatively in these terms, as can formation subdomains. Formation domains for different areas are likewise comparable in terms of structural parameters.

With regard to signal processing, the formation objects become signals modulated at different orders by their families. High-pass filters will direct attention to the "busy" areas for further investigation and more intensive data collection to determine whether the business constitutes signal or noise. Conversely, low-pass filters will direct attention to the "quiet" areas having low orders of spatial variance. It thus becomes possible to explore the spatial variance properties of the data systematically in a manner that should serve to guide further data collection and suggest appropriate resurvey intervals and sampling intensities for monitoring. Such exploration requires no prior assumptions beyond that of at least ordinal strength for the data.

Scale and spatial modulation are intimately intertwined. While it is impossible to go below the scale floor corresponding to the spatial resolution of the data, one can study modulation at coarser scales by pruning the formation trees downward from the leaves toward the root. This is accomplished by suppressing objects through assigning the parent object number to them and their descendants. Mapping of pruned objects can serve for such generalizing exploration of the scale spectrum.

Whereas fractal dimension is only indicative of pattern over scale, the formation domain expresses pattern as structure while defining the elements of structure. Stated differently, fractal dimension indicates the nature of pattern whereas the formation domain elaborates the pattern.

Because of their binary nature, formation analysis cannot be applied directly to Gap Analysis apparent habitat maps for individual species. Mapping a habitat suitability index for each species would, however, provide an ordinal spatial variable appropriate to formation analysis.

SUMMARY

Diversity is intrinsically relative since data are necessarily acquired in time and space. Patterns and comparatives are thus fundamental to diversity questions.

Perceptual heuristics have dominated approaches to pattern and comparison with respect to biodiversity, usually generating more heat than light. We outline systematic approaches to pattern and comparatives that are independent of perception. Diversity profiles address patterns of different indices. The spatially-based formation domain approach is object-oriented as well as perceptually objective.

Data of ordinal strength can convey spatial pattern. Both informational strength of data and spatial resolution will, however, affect coherence of patterns and definitiveness of interpretation. Even vague patterns at broad scales can be useful in focusing further data collection effort. Gap Analysis and apparent diversity exemplify such broad-scale to fine-scale progression of pattern analysis.

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Chapter

6

WHAT DO MEASURES OF BIODIVERSITY TELL US?

Gene Namkoong[1]

As stated in the background document for this meeting, there is a need to quickly and accurately measure and monitor biodiversity on an operational scale as a first step towards effective conservation. It is implicitly assumed in this statement that if these measures are embodied in operational plans and manuals, the policy objectives will be achieved if the measures are satisfied. The need to quickly develop operational scale measures underlines a sense of urgency since forests are being harvested and otherwise changed so rapidly that any measure that would help target monitoring, management, or rescue efforts would be useful. Therefore, estimates of summary statistics are reasonable candidates for use as measures and one of the questions we have to ask is whether there are conditions which limit the utility of those measures to guide management.

From an operational perspective, simple measures or summary statistics are often desirable since they encapsulate considerable information in a few numbers. They are necessary because decisions must be made before much research on possibly relevant factors can be conducted. From a biological perspective, the organisms and the interactions that determine the efficacy of management seldom lend themselves to reduction to easily measured features. Biologists who understand the complexity of forests are loath to admit that biological processes can be

[1] U.S. Forest Service and University of British Columbia, Faculty of Forestry.

summarized in simple statistics. They also believe that the complexity of forests is due to complex interactions, and are not emergent properties of simple and easily controlled factors. The problem for biologists is that if the processes are so complex that only vast amounts of detailed research can yield useful guidelines, or if the processes are so simple that they can be summarized in a few simple statistics, then either way, biology is irrelevant to conservation management. Particularly when different measures of biodiversity at different scales are to be used and integrated, biological detail at any one level will be suppressed, possibly to the vanishing point. Therefore, a task for this conference is to assess the extent to which simple measures of biodiversity can tell us enough about its present biological structure and dynamics that some management can be effectively targeted. If we conclude that biodiversity is so complex and unknowable that no targeting is possible, then biology will be largely irrelevant to conservation.

MEASURES OF DIVERSITY

In general, measures are intended to tell us something about things that we think we can know. Formally, measures are often numbers that indicate size, distance, extent, or other features of objects. The objects are usually assumed to be known items, and these quantities describe important features of those objects or the relationships between them. In fact, there is a whole section of mathematics that deals with the theory of measures and their features and properties (Doob 1994). While I will not discuss these concepts, I introduce the topic to indicate that we are talking about abstractions of the physical world and as such, we must necessarily have a concept in mind about what is a significant and abstractable feature. Thus, when we measure weight, we think that mass is a significant feature of the object of interest and that a single number representing one of the features of mass is useful for comparing the object to another, or that it has something to do with other properties of the object, such as how easy it is to lift or move.

When applied to biodiversity, we are dealing with a collective measure of something that has many parts and different distinctive features, is evaluated in many different value systems, and is already an abstraction. Therefore, its measure cannot be simple. Nevertheless, we can use features of individuals, populations, species, etc., their spatial patterns and frequency distributions, to tell us something about those distributions and about what we think those measures imply about things we cannot see. While not diminishing the importance of understanding and describing the features of diversity that we can state with given probabilities, I

would like to focus attention on those features of biodiversity that we cannot see, but about which we would like to make inferences. Among the features that forest managers may find useful for delimiting areas for sampling and intervention are the presence or absence of environmental factors associated with diversity; or whether the taxa are randomly distributed, and diversity is uniform.

To begin with, the simplest features of biodiversity or of any feature of a biological assemblage, are its average levels and variability over an area of concern such as a state forest. Just a broad statement of total variability however, is seldom sufficient, just as average size or stocking density and a variance is insufficient to tell us much about tree structure. The measures described by Magurran and Pielou in this conference and elsewhere (Magurran 1988, Pielou 1969) substantially refine our ideas of total variability and allow us to compare groups or areas with respect to the frequency distributions of organisms or features of sets of entities. Ever since early observations of the distribution of species showed that different sites have characteristically different curves relating species abundance to sample area, random models of species assembly could be fitted and parameters derived to characterize area differences. Various indices could also be derived for the number and relative frequencies of species that reflected species richness or packing that were relatively stable with respect to sample size. These indices could then be estimated and, as they varied from site to site and characteristically differed among types of organisms, inferences could be drawn about the structure of diversity.

One of the uses to which these indices have been put is to discern relationships between diversity and factors of the environment, such as nutrient or soil quality, distance from source populations of invaders, frequency and type of disturbance, etc. The attempt is often to discern causal factors by relating diversity measures to some set of physical factors, for some set of organisms. In one study conducted by the U.S. Forest Service in a 5,000 ha. forest in the southern Appalachian Mountains, some fifty plots were simultaneously surveyed for trees, shrubs and low vegetation, herbaceous vegetation, birds, reptiles and amphibians. In this study, we found good agreement among various simple measures of biodiversity, including Simpson's and Shannon's Indices, and species richness, and that there was substantial variation in all of these measures among plots for all types of organisms. We also found that some plots had high diversity for more than one class of organism and some were low for all classes.

In order to determine the extent to which certain ecological relationships with possible causes of diversity could be discerned, correlations of diversity with several variables were estimated. If there were site qualities that contained generally optimal

levels of available moisture or nutrients or high variation in those variables, then there should be some sites that are high in diversity for all types of organisms. High diversity might also be correlated with other measures of biomass productivity. If site quality for diversity was related to physical features of the environment, then we should be able to detect regressions with measures of independent variables, such as the mean or variance in elevation, soil moisture, stand age, etc., and may then infer some causal mechanisms. If diversity was strongly affected by biotic relationships among mutualists, competitors, symbionts, etc., then sets of species should have similar distributional attributes. Then, if relationships were relatively simple, a few guidelines might be inferred for sampling and managing diversity.

We found that some generalizations could be derived. Older stands and sites situated at lower elevations had higher diversity than comparable younger or higher elevation sites for several classes, but not for all. In general, the alpha diversity was not well focused if all types of organisms were considered. We could identify sets of plots that captured most of the alpha and beta diversity such that less than 20% of the sites contained more than 90% of the species. Also, beta diversity was related primarily to elevation gradients and hence physical variability could account for diversity only in large scales and only generally in the one factor. Nevertheless, some drainage basins that contained high alpha and beta diversity in compact areas were delineated which would be highly efficient for sampling total diversity. In general, we could find some correlation of diversity for each organism type with some site features, but the correspondence of diversity between classes of organisms was quite low.

From the preliminary analyses, it was immediately obvious that we could detect no pattern of sites that were generally rich for everything. This might be expected either because sites occupied by one species or set of species would exclude some others by chance, by preferential migrations to alternate sites, or perhaps by mechanisms of competitive exclusion. When we investigated correlations of species richness or diversity with biomass or with physical features of the sites, no general relationships were found. There were particular subsets of species within classes that had high diversity in identifiable site types such as a positive association of salamanders with moist sites, and a negative association of herbaceous vegetation with trees on most sites. Patterns could be detected, but only if finer subdivisions of site factors and species groups were used. Therefore management systems cannot simply identify rich versus poor but must specify the kinds of richness desired. Furthermore, we identified rare species of plants in the areas studied and found

that their presence or absence was not strongly correlated with either general species diversity nor with any single environmental factor. It seems that rarity is associated with different phenomena, some because certain sites are rare and others because of a general and diffuse rarity. This again may not be a surprise to the botanists and ecologists who are familiar with this vegetation, but it does imply that for these species, even finer individual species management plans have to be considered since there are no other obvious indicator variables that can be used. Some of these species may well be adapted to rarity and their rarity does not in itself pose a survival problem. However, even then, their dependence on maintaining a specific density may be critical for survival or reproduction, and detailed life histories would be needed before a rational conservation plan could be devised.

No single index is sufficient for describing the distribution of diversity. It may still be possible, though, to decompose the total set of species into subsets and to generate at least a moderately simple management plan without having to research every species and every pair of species-environment relationships. These sets may be groups of similarly behaving species of the same class that can competitively coexist, or may be members of a mutualistic association or food web of species in different classes or trophic levels. It was possible to discern some general patterns of sites and diversity for subsets of species that suggest priority areas for management programs by using correlates of diversity indices in these areas. However, there is enough variation from a broadly inclusive and uniformly useful pattern, to question the development of a conservation plan based on only this information. Further, there is no information on population dynamics, so that by sampling and conserving only the targeted areas, it is not likely that we can maintain the present diversity. This is asking diversity indices to do far more than they were intended to do. In the words of Magurr an (1988), "Diversity measures are valuable, but are only a means to an end. That end is that ecologists should be able to ask the questions and formulate the hypotheses to help them understand, and sensibly manage, the natural world. ”Since it is the ecosystem that we manage that produces diversity, we try to avoid the mistake of managing for measures of diversity that may result in poor ecosystem management and the ultimate diminution of diversity.

TAXONOMIC DIVERSITY

While questions of dynamics require other kinds of studies and surveys than can be considered here, we can consider other refinements of general diversity indices

that may assist conservationists in targeting their efforts. Since all forms of conservation management will require starting with a finite sample of forests and managing finite populations and stands, efficiency in choosing initial samples and targeting types of management activity is highly desirable. Some forms of structural diversity for example, can be managed most effectively by site or silvicultural treatments. Taxonomic diversity, on the other hand, is highly dependent on the initial sampling and slow to respond to area management. Some of the diversity indices mentioned above can be modified to include hierarchical levels of taxonomic diversity (Pielou 1969) and hence provide more refined descriptors of the richness of phylogenetic differentiation.

Phylogenetic information is often available and provides considerably more information on genetic diversity than only the number and frequency of species. When that information is available a conservation objective for diversity can be to distinguish plots that may have equivalent distributions of species but different phylogenetic diversity as represented by those species. Sampling for diversity may be considered to be inefficient if we include only a small range of taxa, such as only *Pinus* or only Compositae, but more efficient in some sense if more phylogenetically diverse taxa are sampled. Thus, the total number of species, or frequency weighted numbers, are very useful as ecological indicators but may not be as useful for conservation purposes as measures that include genera, families, orders, etc.

To construct a measure of taxonomic diversity we can consider measures that have been used for phylogenetic analysis as indicators of evolutionary relationships as well as of phenetic similarity. For purposes of this paper, I will not discriminate between phenetic versus cladistic approaches for inferring phylogeny but will instead assume that phenotypic, genetic, and historical evolutionary data are informative and any or all are used to define distances between genotypes and taxa. This is a useful, but only approximately valid, assumption that allows us to consider that distances can be estimated between taxonomic units. If the distances are metrics then various descriptions and properties of evolutionary trees can be used for phylogenetic analysis and some features can be summarized into indices of average or total similarity or dissimilarity. Several types of indices come to mind that, as far as I know, have not been explored for application to biodiversity conservation. They include total taxonomic branch length, number of cladistic nodes, or the volume and dimensionality included in a convex hull of inter-taxon distances. Recent research on phylogenetic trees and other kinds of network phylogenies (Smith 1989, Eigen *et al.* 1988) present interesting new possibilities for estimating phylogenetic topologies even when evolution has not proceeded hierarchically.

With other measures of taxonomic diversity available, it is still possible to consider which environmental variables may be associated with that diversity. A single measure of total diversity such as the volume and dimensionality measure mentioned above, could be correlated with environmental variables. There would also be several levels of diversity such as at the family or order level that could now be used. In addition, since taxonomic diversity measures often have phylogenetic distance measures associated with them, it is possible to determine whether the matrix of phylogenetic distances or their complementary similarities are associated with matrices of distances between the taxonomic units as measured by geographic or environmental similarities. By means such as described by Leduc *et al.* (1992), and testing for the consensus of distances (Lapointe and Legendre 1992) it is possible to directly examine whether patterns of taxonomic diversity are related to patterns of environmental diversity.

CONSERVING DIVERSITY

Measures of diversity can clearly help us to locate and to begin to understand the present and possible future states of its distribution. They can be more useful if the measures can be sufficiently refined as to inform us of their associations and possible causative mechanisms, but we cannot expect that these relationships will be simple or easily accommodated into forest management plans. We might be able to understand the extent to which historical events determine how species packing and assembly rules are the result of initial conditions, and how physical and biotic environmental factors control the evolution of species and communities, but these also cannot be easily translated into conservation plans. We do not derive information on evolutionary dynamics from static samples and hence cannot discern whether the sample is from a stable and strongly attracting equilibrium, or if we are in unstable and transitory phases that may have more complex dynamics. For these questions, we still, and always will need, more biology.

What the measures can do for us however, is to pinpoint our ignorance so that we can put priorities on research, and perhaps indicate whether more research will ever provide enough information, soon enough, to guide policy. On the one hand, it is conceivable that the distribution and biological dynamics of most species are so simple that forest policy and management can use one index that suffices for sampling and conserving all biodiversity in perpetuity. On the other hand, it is conceivable that the population and evolutionary dynamics of many species are so complex and intertwined with other species that no general rules or conservation

targets can be defined. Using currently available statistics and estimable parameters, initial indications are that we can derive some predictions about the present locations of diversity but that those measures and predictions require at least moderate levels of environmental and taxonomic refinement. At this point, we do not know how much more refined we have to be in order to derive feasible targets for forest management to capture the present levels of diversity. We also have no indication of how much more research is needed to define management for conserving diversity in the foreseeable future.

In this uncertain situation, a complete conservation program cannot be well described, but an adaptive program can be suggested. Most obviously, a core set of sites and areas can be delineated that would at least include a great majority of species. In the case of the sampled forests in the southern Appalachians, more than 90% of all species of all types could be included in less than 20% of the area. Rare or sparsely distributed species could be specially treated in designated areas that would require only small additions to the core. Below the species level, further genetic sampling may be required, but in most cases can probably be best done by sampling different areas for species with genetic variation that is widely distributed. Above the species level, the sampling would not necessarily include the same levels of structural or community diversity, but once designated, additional areas can be designated as increments to a core structure. If this kind of an incremental designation can form a plan for conservation, then the measures of diversity already available can be used to design a programme, even if they are not as refined as they can be nor as refined as biologists would like them to be. It can also be expected that further developments in diversity measures and their analyses will make them even more useful.

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Chapter

7

SCALE, OBSERVATION AND MEASUREMENT: CRITICAL CHOICES FOR BIODIVERSITY RESEARCH

Sandra J. Turner[1]

INTRODUCTION

Biodiversity has taken on a meaning in the consciousness of the world's societies that goes far beyond the original definition known to science. Biodiversity has become a mantra and a rallying cry for maintaining ecosystem functions which have been identified as socially important for many reasons. Biodiversity has become the focus of ecosystem management and a great deal of political debate.

In addition "diversity" now has considerably more meaning to scientists than it did in the last century. The fact that species diversity is not a steadily increasing historical trend such as. Wallace (1876) and Willis (1922 citation in Ricklefs and Schluter 1993) suggested has been brought home to us rather dramatically with the loss of species after species; the result of human manipulation of ecosystems. Early scientists thought that diversity was an artefact of time and that the amount of diversity measured was related to the age of the community which was being

1 **Biology Department, University of New Mexico, Albuquerque, NM 87131, USA.**

investigated. These assumptions may be true for some communities but importantly, science has moved well beyond this notion of diversity. Diversity is dynamic in space and time; both upward and downward fluctuations occur. Membership in a community is a function of the spatial and temporal dynamics of the community in which it is embedded. As Ricklefs and Schluter (1993) suggest, it is necessary to recognize that ecology, evolution, geography, and history are different facets of a single set of processes and the patterns they generate. One cannot isolate one system, of a particular dimension, from processes and structures at a smaller scale embedded within it, or from those at a larger scale containing it.

Species diversity is the type of diversity which springs most quickly to the mind of both scientists and lay people whenever diversity is mentioned. However, it is not the only level of diversity important for modern investigation and for measurement and monitoring of resources. Allele diversity, genetic diversity, polygenic genetic diversity, species diversity, patch diversity, habitat diversity, community diversity, landscape diversity, regional diversity: at every scale within the biotic system diversity is under investigation. Each scale has its own describable dynamics and, in addition, many features of diversity are common to all scales.

In some cases the diversity at one scale can be shown to relate to diversity at another scale (Franklin 1993). This relationship may provide a method for associating diversity at a scale which is easily measured (e.g., vegetation structure measured from remotely sensed data) with diversity at a scale which is more difficult to measure (e.g., diversity of the animal community living in that vegetation).

This paper addresses the problem of identifying the appropriate observation and measurement criteria, and the appropriate time and space scales for measurements. It is also about the dynamics of change - how can we find out how diversity may be altered with time? I am going to begin with landscape ecology and hierarchy theory and use that as a backdrop for making these critical choices about measurement and monitoring. My examples will be from measurement but the application is the same for monitoring.

LANDSCAPE ECOLOGY

Landscape ecology is an integrative science that focuses on the way ecological systems are arrayed in space and through time. Landscape ecology covers such diverse topics as: (1) elements in a park created for recreation; (2) the functional analysis of agricultural landscapes; (3) analysis of human flow through park and wilderness areas; (4) analysis of beetle eye view of the world to understand fractal

patterns (Wiens and Milne 1989; Johnson *et al*. 1992); (5) understanding what reserve size means for maintaining species diversity (Margule *et al*. 1988; Nicholls and Margules 1993; and others); (6) how fire influences forest landscapes (Turner and Romme 1994); and (7) the integration of human values into long term monitoring of ecological processes, such as the U.S. Environmental Monitoring and Assessment Program - Landscape Ecology Resource Group (EMAP-LE) seeks to accomplish.

Although landscape ecology usually involves temporal considerations, the unifying theme is that landscape ecology always involves space. For instance, Whittaker's (1972) work which treated large spatial scales is an example of landscape ecology, even though it ignored temporal considerations. In contrast, the work of Lotka (1925) and of Volterra (1926), cannot be considered landscape ecology because, while it considered the temporal dynamic, their important work did not consider space.

Moreover, the spatial scale at which landscape ecologists work is often considerably broader than traditional ecology. Traditional plant ecology, for example, has focused inordinately on scales of $1m^2$ and one growing season. However, the distribution and abundance, and processes affecting a species at the community level is partly a function of the landscape in which it lives. By acknowledging this interaction, a landscape study adds spatial heterogeneity to a population, community, or ecosystem study.

Expanding the spatial scale and including heterogeneity can reveal how the distribution and abundance of species within a local community is influenced by the larger landscape context in which it is embedded. As larger areas are considered, longer-term temporal processes become important determinants of ecological dynamics.

Understanding phenomena within their landscape context can provide important insight for management. The original efforts to save the Northern Spotted Owl (*Strix occiden talis)* in the northwest United States focused primarily on the total amount of reserved habitat without considering the ability of juveniles to disperse to suitable habitat within the landscape. Dan Doak and colleagues (Simon Moffat 1994) found that the original patchy preserves were especially vulnerable to extinction and showed that the arrangement and size of habitat patches on the landscape was as important as the overall amount of habitat. Thus, patch level diversity at a larger scale can influence species diversity and species distributions at local and regional scales.

The landscape component of Ecological Measurement and Assessment Program of the United States Environmental Protection Agency (EMAP-LE) is

expected to tie together studies at all levels to yield a regional analysis (Figure 1). EMAP-LE is using societal values to determine the direction and focus for monitoring and measurement. Water "purity", which is valued by society for health, recreational and aesthetic reasons, is analyzed with fine scale measurements - but water quality is the integration of landscape structure and function at the regional scale.

PRINCIPLES OF LANDSCAPE ECOLOGY

The consequences of adding broad-scale spatial heterogeneity and long-term temporal dynamics are profound. The spatial dimension allows for integration across studies from studies of small organisms to regional analysis. It allows for the analysis of impacts which are at scales different from those normally incorporated into the system. Expanding the time scale of the temporal dynamics allows us to integrate history, both abiotic and biotic, and the activities and cultures of human beings into our analysis.

Three properties of landscapes form the core of the discipline. First, landscapes in general have structure. That is, there are spatial relationships between elements. The relationship may be between trees and gaps in a forest. At a broader scale there is a relationship between forest and agricultural patches in a landscape mosaic. Landscapes have spatial continuity between these elements but they are not considered to be homogenous. Landscapes exhibit pattern and internal heterogeneity. It is that heterogeneity which is of interest. The continuity of the landscape suggests that it also has boundaries where landscape elements come together. Boundaries and barriers may prevent individual species from responding to changes by shifting between habitat types or sites and that, in turn, may result in decreased diversity (Vos and Opdam 1993). Boundaries, natural and anthropogenic, are very important in designing research and monitoring for biodiversity.

Second, landscapes also have function. That is, there are interactions among spatial elements. These may be flows of energy, materials and species or even genes between component elements of the landscape. Sometimes these ecological functions become important in a societal context. For instance, a corridor may provide access between interbreeding populations of important species and so help to maintain species diversity. A wetland may function as a filter for pollutants and maintain or increase water purity within the system. These are ecological functions which are a service to society.

Patterning and patchiness of both structure and function can be recognized at virtually every scale of investigation. Thus landscapes may be of any size. In fact,

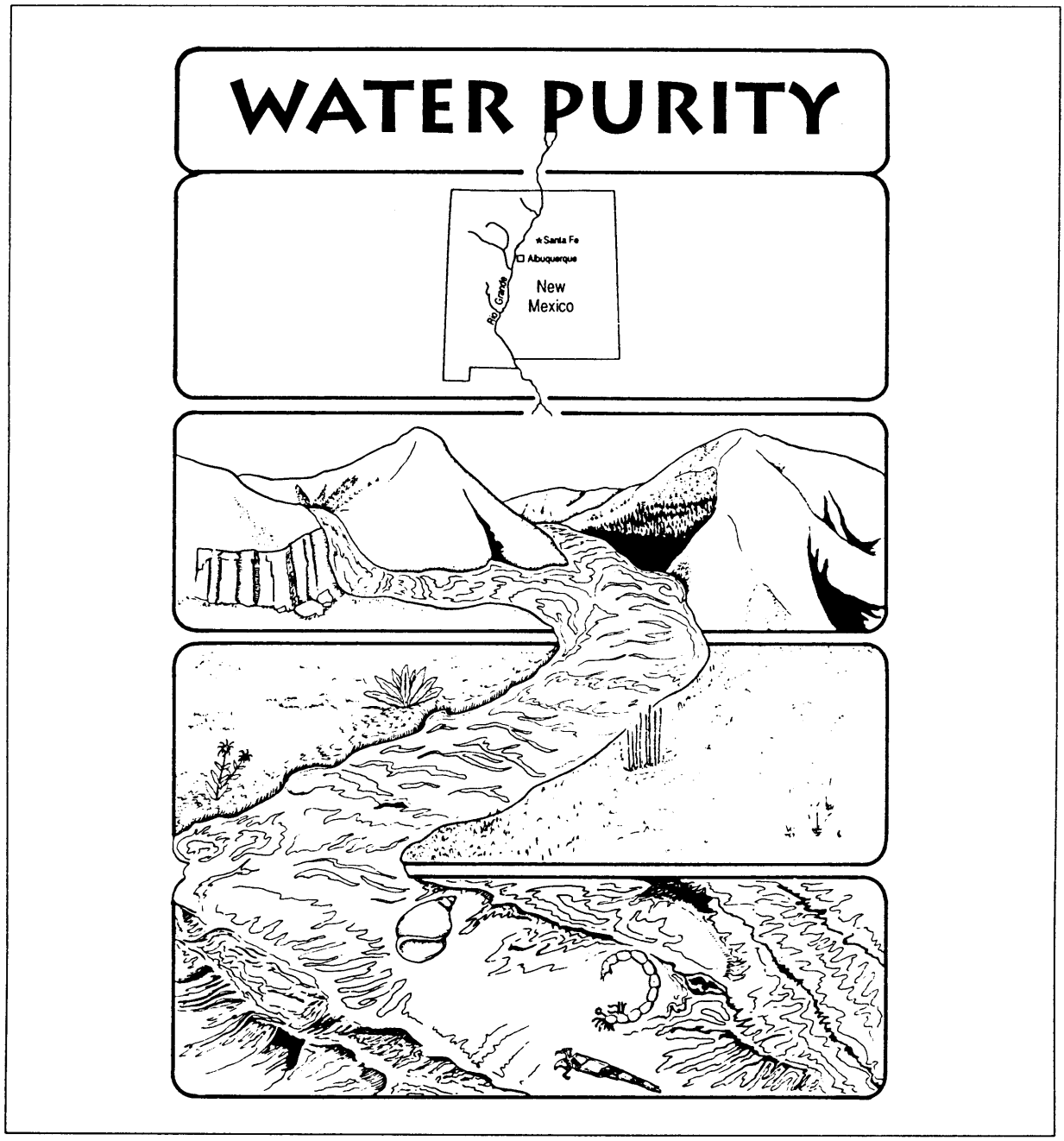

Figure 1: Landscapes may be of any size: a riffle in a stream, the whole stream, the watershed, or the region containing the watershed. Water purity is a societal value which is measured at the smallest scale but which actually integrates landscape structure and function at all scales.

I suggest that the notion of landscape is scale independent in the same sense as ecosystem is scale independent. This is a widely held view (Allen and Hoekstra 1992 and others). However, some researchers, among them Richard Forman (Forman and Godron 1986), hold that landscapes occupy a definable and limited portion of the spectrum of ecological scales. They view landscapes as occupying the scale that incorporates a number of ecosystems and is yet smaller than regional. I do not view that scale as definitive. It is very useful and practical to view the landscape concept as scale independent because it can then be easily applied to such notions as diversity. Diversity occurs at many different spatio-temporal scales.

Third, landscapes change. There is an alteration of structure and function of the ecological mosaic (the elements arrayed in space) over time. Landscape change may result in, or conversely be the result of, changes in species frequencies or abundances or even of local extinctions. Clearly change is a natural process and natural changes in dynamical ecological systems are integrated from the smallest organisms in a stream to the watershed and regional levels (Figure 1). Change may be the normal turnover in species in a forest which varies in time or in space with the formation of gaps and the resulting successional dynamics. Alternatively, change may be anthropogenically induced, such as by the clearing of an agricultural field or the harvesting of timber from a forest.

HIERARCHY THEORY

Landscapes can also be profitably viewed as hierarchical in organization. The landscape is a hierarchy of differently scaled structures and functions (Figure 2). The structure and function at a particular level which we choose to observe, say a forest, has a particular time and space scale. This is the "N" level. The lower level (N-l) is composed of sub-systems of the forest. These may be patches or gaps or soil differences, or individual species which have smaller and quicker spatio-temporal dynamics and provide the mechanism for creation and maintenance of the forest. The next level (N+l) is larger in space but changes more slowly. The larger slower level may be the region which exerts control on the forest.

Hierarchy theory (O'Neill et al. 1986) applied to landscapes implies this upper level control and lower level mechanisms and provides an epistemology for measurement based on the scale of observation and level of analysis. For instance, growth of a plant (N) is controlled by physiological processes which are N-l. Of course, the level of interest (N) and the N-l, N+l levels are set by the problem which is being investigated and may not be the same hierarchy for all problems.

Depending upon the criterion employed, there can be defined many subsystems (N-1) for any one level (N) (Figure 2). Observer perception determines the relevant levels (MacMahon *et al.* 1978). At any scale one can observe many different types of things. What is included for analysis depends upon what is important for the study. The description of the system as a hierarchy of mechanisms

(N-1), phenomena (N) and controls (N+1), helps in sorting though the complexity by isolating the dynamics which are of interest and structuring the research

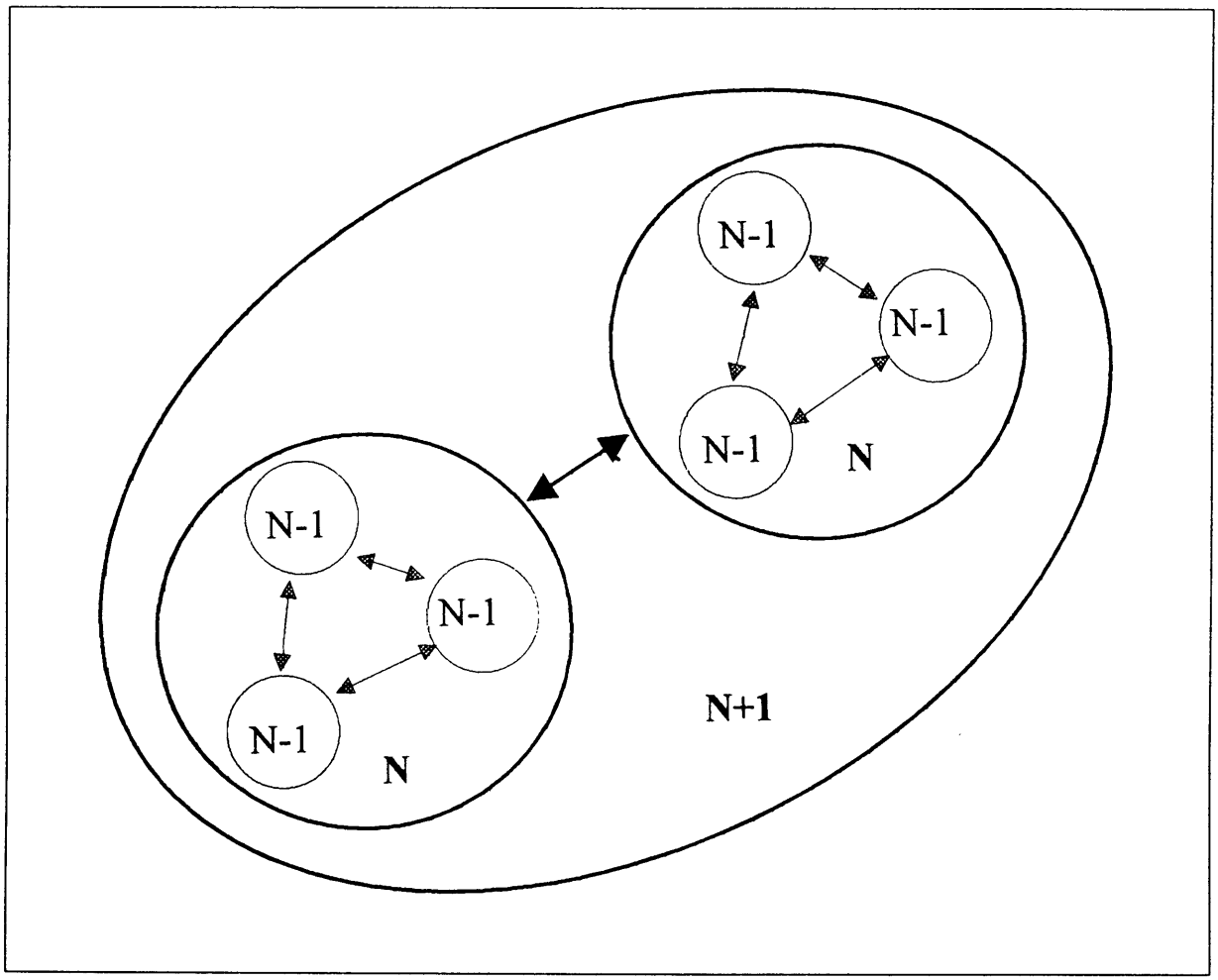

Figure 2: The hierarchical approach to landscape analysis suggests that the phenomena of interest, level N, is created and maintained by mechanisms which are subsystems, level N-1, of the system (N). The level N+1 is the context of the level of interest and provides higher order control of the system. Redrawn from Allen and Hoekstra 1992.

around important interactions. This is the art. Leave out everything that is unimportant in sorting through the complexity. Find the correct criteria to address the problem. The hard part is to determine the correct level in the system, that which is truly important to the observer. It may be a single species, a biotic community or an ecosystem type. Choose the important level N. Then carefully, remaining within the same hierarchy, identify the N+l level of control and the N-l level of mechanisms. These drive landscape investigations whether they are field tests, modelling, applied or theoretical.

WHAT CAN LANDSCAPE ECOLOGY DO FOR DIVERSITY RESEARCH?

What can landscape ecology and the concept of ecological hierarchies contribute to measuring and monitoring forest biodiversity? Classical diversity theory considers population processes and ecological interactions at a local scale in small uniform habitats. But these small time and space scales are not sufficient to understand diversity patterns (Schluter and Ricklefs 1993), particularly at larger scales.

Patterns of diversity, whether we are interested in genetic, species, habitat, ecosystem or landscape diversity are arrayed in space. The measure which we define as diversity is in part a function of the size, shape and temporal dynamics of the area considered and of our observational protocols. Many researchers have included spatio-temporal dynamics in diversity research and have found that the landscape perspective often provides considerable explanatory power.

Species-area curves clearly indicate that diversity has a spatial component. More than just the extent of space occupied by species, structure, function and change of landscapes are also implicated.

Two decades ago Pianka (1974 and others), and more recently Franklin (1993 and others), have shown that species diversity is related to the structure of the forest. Genetic diversity may be maintained by the structural array of refugia for some populations according to Shepherd and Brown (1993). There is evidence that variability in polygenic genetic diversity within salmon populations is partitioned temporally and spatially (Gharrett and Smoker 1993). Rosenberg and Raphael (1986) have show that abundance is associated with patch size. Rey-Benayas and Scheiner (1993) show that biodiversity at the mosaic and community levels and landscape complexity respond to geochemical function of the landscape at those scales. Pearson (1993) found that variation in bird species richness and diversity was explained solely by landscape variables, structure and function. Franklin's (1993), work suggests that "structural complexity offers the abundance of habitats that in turn

support a large array of specialized species. Directly and indirectly the structural complexity provides biological and functional diversity". And of course, anyone who is familiar with the monsoon and fire driven forest of Kakadu (Woinarski 1993) and northern Australia are fully aware that change is paramount. If you are not there at the correct time, or many times, all measures of diversity will be suspect. Spatio-temporal effects on diversities are the results of events ranging from those that occur over very long evolutionary scales of time to recent events (Blonde1 and Vigne 1993), such as the last bulldozer.

Thus landscape ecology provides the tools to describe and understand how the diversity of species, alleles or habitats are arrayed in space and though time. Hierarchy theory within this context suggests methodology for making decisions about observation scales and measurement.

WHAT CAN HIERARCHY THEORY DO FOR DIVERSITY RESEARCH?

Figure 2 suggests that there is a focal level "N" to which research, measurement and monitoring should be directed. It also suggests that the research, whether modelling of ecological systems or field based research, need only account for three levels as suggested by Johnson (1995). Remember that functions at one level produce the structure of the next (i.e., physiological processes grow and maintain the trees). Often we find that it is change or variability at the higher level which controls or constrains the system (i.e., abiotic processes constrain forest expansion). Diversity fits this pattern. Landscape diversity is at least in part the result of the structure of vegetation. Population processes are the mechanism which create diverse communities.

The level at which the inquiry begins is arbitrary (Allen *et al.* 1987). This decision sets the answers to the questions of observations, scales and measurements. "N" is defined uniquely for the question at hand."N" may be defined by purely scientific interest or in response to ecological crisis or by societal concerns as is happening more frequently in North America. It may also be defined politically.

Figure 3 is one (far from unique) conception of a phenomena and measurement criteria hierarchy. This is a vegetation hierarchy. It could have been any set of interesting and related phenomena. More familiar are space-time diagrams in which structures, functions, systems or other lists of ecologically interesting and related things are arranged along a diagonal of their inherent time and space scales. By related, we mean that there is a connection between the processes and functioning of one level and the expression of phenomena at a higher level. In this figure

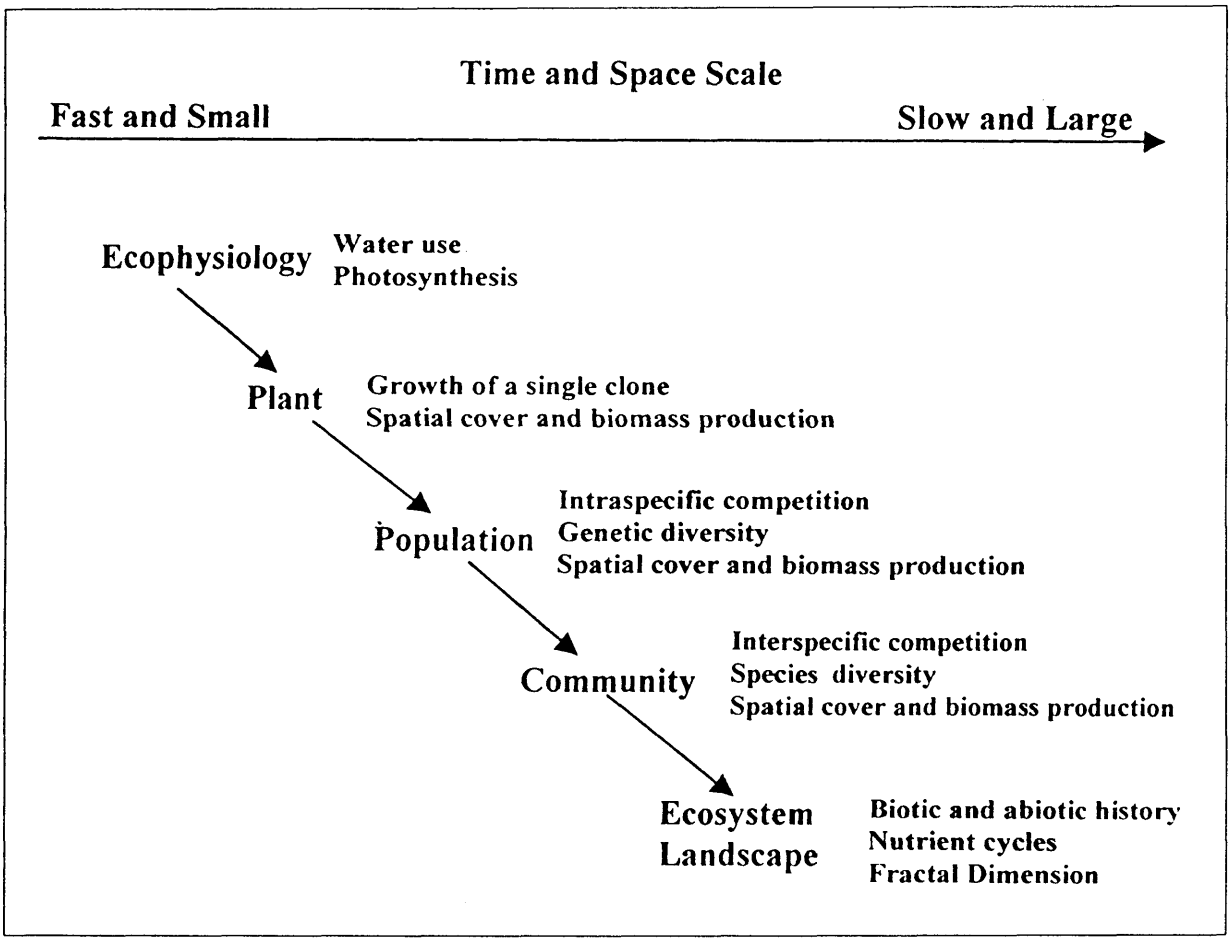

Figure 3: A hierarchy of phenomena and some of their associated measurement criteria. Intraspecific competition, genetic diversity, spatial cover and biomass production are measurements which are appropriate for investigations at the population level.

the time-space dynamics are combined in one line across the top and the phenomena are arranged so that some of the possible measurement criteria can be associated with each phenomenon. Note that I have defined a large/slow level which I am calling landscape. This is arbitrary. Note too, that there are spatially arrayed processes which are appropriate criteria at most scales. Measurement of spatial cover produced by a population of plants is amenable to landscape analytical techniques.

The phenomena along the diagonal (ecophysiology, plant, population, community and ecosystem/landscape) may each be considered as a focal level N. If the population level is chosen as the level of investigative focus then the

level of the plant is the N-l level of mechanisms and community is the N+l control level. Among the criteria which could be chosen to describe the population level are intraspecific competition effects, genetic diversity, and the spatial dispersion and biomass production of the population, and dispersal or invasion rate of propagules. Understanding of the mechanisms which create and maintain the population would come from the lower level of the single plant (N-l) where reproduction and growth potential are important. The limits and context of the population will be found in the community (N+l) interactions of interspecific competition, for instance, between various populations.

Measurement of species diversity, a criterion at the community level, is straightforward in this context. The number and spatial extent of populations are the N-l metrics which are important if all you want is a one time answer to the question: how many species are there out there right now?

Understanding the dynamics of species diversity is a different question and it is paramount for monitoring. Certainly counting populations remains important, however it is necessary to understand how those populations are likely to change in the future. In this context the population will be profitably understood both as the mechanism which creates the community and as controlled by the community.

The controls upon species diversity dynamics may be very complex and involve all the factors that have been discussed including structural and functional components, current and past history of the region under investigation and, most likely, the variability at which controlling functions and structures can be expected to change. It may well also include some measure of society's value of that particular community and the probability that anthropogenic influences will affect species diversity.

ARE DIVERSITY INDICES AT ONE SCALE RELATED TO DIVERSITY AT ANOTHER?

The complexity of the controls of biodiversity have sent researchers scurrying to find surrogates which are easy to measure and which integrate all the processes which control diversity (much as water quality is an integration of regional scale structure and function) or which change in the same way as biodiversity but are easier to monitor. Of particular interest to monitoring is the question of the relationship of diversity at one level in the hierarchy of phenomena and measurement of diversity at another scale.

Regional or landscape complexity has been implicated in patterns of diversity

at these large scales. Can indices of large scale diversity be used to infer anything about diversity at different levels in the system? At the largest scale, remotely sensed image data can be analyzed to yield a metric of landscape diversity which is, in fact, a measure of variance between pixel colour values for several spectra. These are being shown to relate to large scale structure. Many researchers are using remotely sensed data to characterise natural vegetation using colour and textural measurement (Bijlsma 1993 and others). Using satellite images, B.T.T. Burns (Bums *et al*. 1994) is able to delineate old growth forest stands from a dense matrix of multiple use forests having multiple histories in northern Mexico. Low aerial reconnaissance confirms his classification. These are structural components of the landscape which are available to us from remotely sensed data.

As mentioned earlier, the structural components of a landscape do, in fact, help to structure the distribution of species at all levels. If landscape structure can be derived from satellite images and diversity can be derived from structure, then indices of landscape diversity at these largest scales can be shown to relate to species diversity. Thus, it does seem possible to make this translation across scales in some cases. Further development will add important techniques for measurement and monitoring of diversity. It remains to be seen how indices of species diversity may relate to diversity at lower levels such as genetic diversity within a population.

SUMMARY

Diversity is apparent at every scale in the ecological system. Landscape ecology and hierarchy theory provide a way to understand and sort though the complexity of the system so that investigations can focus on that information which will most clearly answer the research question. The level or levels in the system which are investigated will depend upon the nature of the question and the type of answer required. A single time answer to diversity may be found by simply counting numbers of species, but the dynamics of diversity will require the investigation of several levels in the system. At whatever the scale of investigation, genetic diversity, population, community or ecosystem, and with whatever techniques chosen to conduct the investigation, the vital research that must be done is to understand the dynamics which generate and maintain diversity. In order to do that, it is necessary to understand and investigate the lower level mechanisms which create diversity and the higher level controls upon diversity.

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Chapter

8

MONITORING AND MEASURING FOREST BIODIVERSITY IN THAILAND

B. Boontawee[1], C. Plengklai[1] and A. Kao-sa-ard[1]

INTRODUCTION

During the past decade "biological diversity" or "biodiversity" has become one of the most popular topics for discussion both as scientific and political issues and at national, regional and global levels. The main theme of the discussion is the contribution of biological diversity to social and economic development; losses of biological diversity and their causes; how to manage the remaining biological diversity for sustainable utilization; the measurement for conservation (*in situ* and *ex situ)* of biological diversity and techniques for measuring and monitoring of biological diversity.

"Biodiversity" is defined as the variety and variability among living organisms and the ecological systems in which they occur. Generally, biodiversity is divided into three components, i.e. ecosystem or ecological diversity, species diversity and genetic diversity. (Kapoor-Vijay 1992, Sandlund *et al.* 1992). It has been recognized that tropical forests are the major source of global biodiversity, and they are also great producers of biological resources for human welfare.

1 Royal Forest Department, Bankhen, Bangkok, Thailand.

Biological resources have provided tremendous benefits to human beings and McNeely *et al.* (1990) have classified their direct and indirect values. Despite this, biological resources are still being destroyed at high rates, as mentioned previously Therefore, appropriate measures are needed to conserve the existing biological resources, so as to maintain and to improve their productivity.

This paper is intended to summarize the status and activities undertaken in measuring and monitoring of biodiversity in Thailand, with particular reference to forests and forest tree species.

Thailand is located in the Southeast Asian region, covering the latitudes between 6 and 20° N. The country's area is 513,115 km^2 with a forest area of 136,698 km^2 or about 27% of the country's area (RFD 1992). The range of elevation is from sea level up to 2,200 m. Climatic conditions vary from the lowland humid tropics to alpine and/or subtropical types.

Thailand is one of the most bio-resource rich countries of the world. This is due to its biogeographical location, which is at the junction of the three main floristic regions, namely the Indo-Burmese, the Indo-Chinese and the Malesian regions (Smitinand 1994). The Indo-Burmese floristic region is in the northern, northwestern, and western parts of the country. The Indo-Chinese floristic region is found in the northeast, whereas the Malesian floristic type is found in the southern peninsular and in the eastern part of the country.

Due to population pressure, the forest area in Thailand has been depleted rapidly Both identified and unidentified ecosystems, species and their genetic resources are being eroded. There is an urgent need to explore, identify, protect, and manage the available forest biodiversity properly for future sustainable utilization.

MONITORING OF FOREST BIODIVERSITY

Assessment of Forest Area

As mentioned above the present forested area in Thailand is 136,698 km^2, which is about 27% of the country's area. Figures illustrated in Table 1 show that the rate of deforestation during the past 5 years is relatively high, about 3,000 km^2 per year. This reflects the fact that the status of forest biodiversity, in terms of habitat, forest ecosystem, species, population and genetic diversities seems to be endangered. The major causes of deforestation are due to (1) population pressure increasing the demand on land and forest products and (2) the improvement of the country's physical infrastructure, such as road and dam construction etc.

Despite a shift in government policy on environmental conservation, the rate of forest degradation and deforestation is still high. The core bio-resource and unique forest ecosystem areas have been identified and declared as biological protected areas in various forms and for various functions. These protected areas, including

national and forest parks and wildlife conservation areas, amounts to 72,020 km^2 (Table 2), which is about 53% of the country's forested area. The remaining forested areas are being explored and identified as national biological conservation areas.

In investigating the existing forest biodiversity, a long term programme of remote sensing techniques, especially satellite imagery, is being used to detect forested areas all over the country. The results will be interpreted every two years. At the ground level, permanent sample plots have also been set up at different locations in different types of forest so as to monitor species diversity. Appropriate measuring and monitoring techniques will also be used for future assessment of biodiversity, such as line-plot, strip and/or plotless systems etc., in order to obtain basic data on plant and animal distribution in the biological conservation areas.

Source : RFD 1992 Forest Statistics of Thailand.

year	Forest Area km^2	Country Area %
1976	198,417	38.67
1978	175,224	34.15
1982	156,000	30.52
1985	150,866	29.40
1988	143,803	28.03
1989	143,417	27.95
1991	136,693	26.64

Table 1: Forest area in Thailand as detected by LANSAT-TM image.

Source : RFD 1992 Forestry Statistics of Thailand.

Type of Protected Area	No. Unit	Area (km^2)
National Park	77	39,238.5
Forest Park	44	610.2
Wild Life Conservation Area	35	27,867.2
No Hunting Area	49	4,187.9
Wild Life Park	2	24.5
Botanical garden	5	15.4
Arboretum garden	44	31.9
Total		72,020.7

Table 2: Types, numbers and areas of biological conservation areas in Thailand.

Assessment of Forest Ecosystem Diversity

As stated earlier, the bio-geographical location of Thailand consists of the Indo-Burmese, the Indo-Chinese and the Malesian floristic regions. As a result, the forest ecosystems in Thailand are highly diverse and can be broadly divided into six main types (Table 3 and Figure 1). These forest types include tropical evergreen forest, mixed deciduous forest, dry dipterocarp forest, mangrove forest, pine and pine/ dipterocarp forests, and scrub forest. The area of these forest types as determined and monitored through aerial photograph interpretation are illustrated in Table 3.

Source : RFD 1992 Forestry Statistics of Thailand.

Forest Ecosystem	Area km^2	% of Country
Tropical Evergreen Forest	62,800	12.2
Mixed Deciduous Forest	31,400	6.1
Dry Dipterocarp Forest	44,900	8.8
Mangrove Forest	1,800	0.4
Pine Forest	2,000	0.4
Scrub Forest	800	0.2
Total	143,700	28.1

Table 3: Types and area of forest ecosystems in Thailand in 1988.

Within these types, sixteen sub-types or sub-ecosystems have been classified (TFSMP 1993). These sub-types or sub-ecosystems are : (1) Malayan mixed dipterocarp forest, which has the highest species diversity,(2) wet seasonal evergreen forest, which has the same level species diversity as the Malayan mixed dipterocarp forest, (3) lower montane forest, (4) upper montane forest, (5) dry evergreen forest, which is most common evergreen forest in Thailand, (6) limestone forest, which is a very unique type of forest and consists mostly of a number of endemic plant species, (7) peat swamp forest, which is also a unique type of forest and consists of a number of endemic plant species, (8) beach forest, (9) mixed deciduous with teak forest, (10) mixed deciduous without teak forest, (11) bamboo forest, (12) dry dipterocarp forest, (13) dry dipterocarp with pine forest, (14)

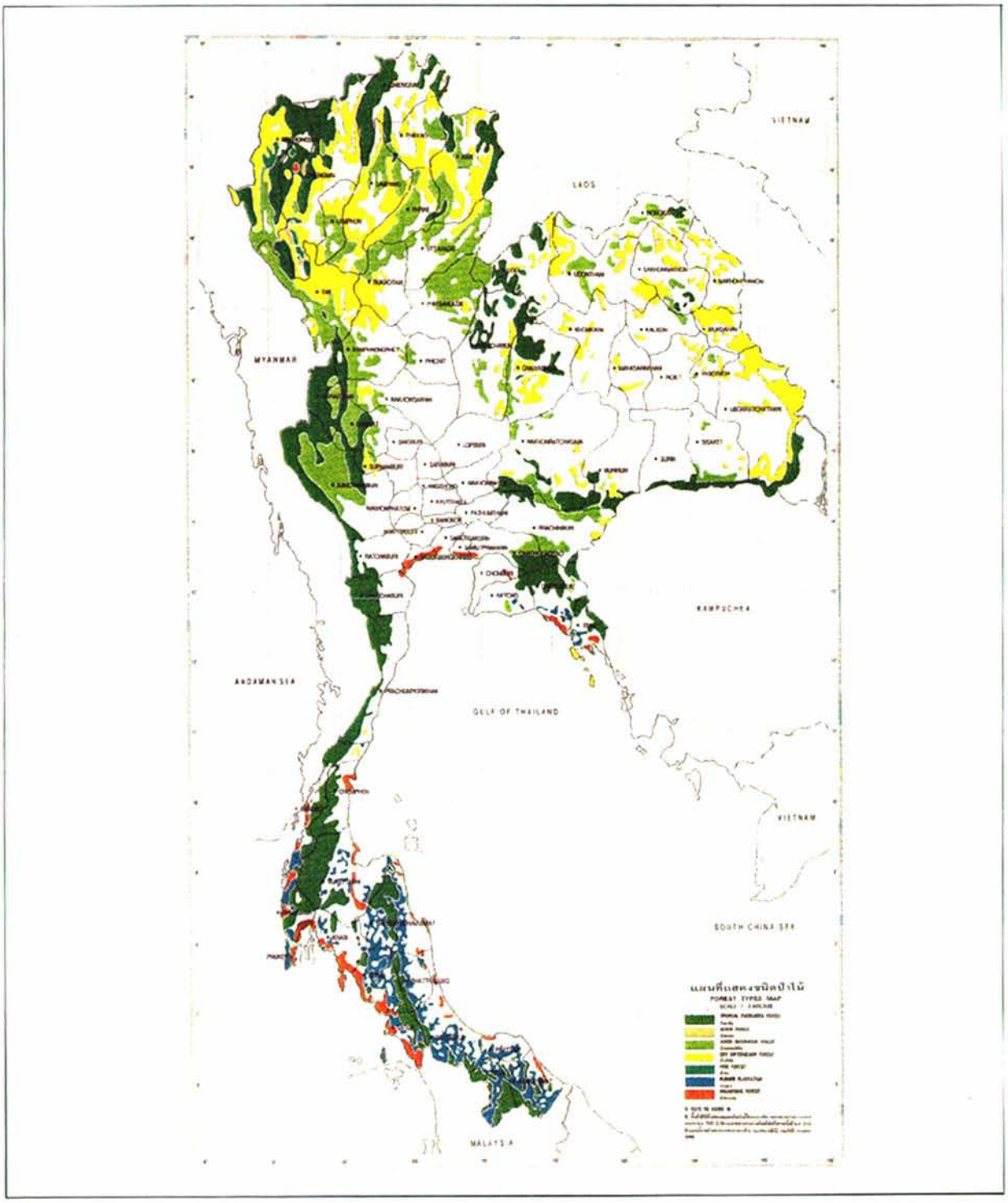

Figure 1: Forest types of Thailand.

mangrove forest, (15) pine forest, and (16) scrub forest. Among these forest types, both mangrove and peat forests, which represent the transitional zone between terrestrial and the marine/freshwater ecosystems, are seriously endangered ecosystems. The mangrove forest area declined almost 50% during the past 25 years, i.e. from 3,127 km^2 in 1975 to 1,736 km^2 in 1991 (RFD 1992). The remaining mangrove and peat forest areas are still being converted into marine (prawn) culture and agricultural land areas.

SPECIES ESTIMATION AND IDENTIFICATION

It has been estimated that there are at least 18,000 species of vascular plants, 1600 species of non-vascular plants, 86,900 species of vertebrate and invertebrate animals and 15,700 species of micro-organisms associated with both terrestrial and water (freshwater and marine) ecosystems in Thailand (NBU 1992). Within these ecosystems, only 13,200 species of vascular plants from 1,913 genera and 293 families have been studied and identified (Nanakorn 1993). Among these vascular plants, approximately 650 species of ferns, 50 species of gymnosperms, 2,500 species of monocotyledon plants and 10,000 species of dicotyledon plants have been identified (Table 4). However, a continuous survey of Thai plants has been undertaken by the Royal Forest Department (RFD) staff for years to identify the species in detail. The results have periodically been published in a series of Thai Forest Bulletin and Flora of Thailand.

Categories	Family	Genus	Species
Thallophytes	na	na	na
Bryophytes	na	na	1,000
Pteridophytes (Ferns)	34	132	650
Gymnosperms	9	14	50
Spermatophytes			
Monocotyledon	50	417	2,500
Dicotyledon	200	1,350	10,000

Table 4: Number of families, genera and species of identified plants in Thailand.

na = information not available

MEASURING FOREST BIODIVERSITY

To manage forest biodiversity for sustainable utilization, it is essential to know and/or to understand the structure and characteristics of forest ecosystems. The most commonly used method of measuring forest biodiversity is to establish sample plots replicated on a number of sites of the same, or similar forest ecosystems. Various techniques of forest inventory have been applied for assessment, measuring and monitoring of forest biodiversity in Thailand. The common techniques are the line-plot and plotless (point centred quarters) methods for large scale inventory, the block/plot with replication method for intensive study, and the establishment of permanent plots for monitoring of population dynamics in long term ecological research site studies (LTERS). Based on species-area curve studies, the plot size for measuring of forest biodiversity is between 0.1 - 1.0 hectare, depending on the forest types (Thammincha 1993); that is, the greater the stand density, the larger sample plots used. Within the sampled plots, number of species, number of individuals, trees, saplings, seedlings and undergrowth are counted to assess species richness and tree density. For species diversity, the Shannon-Wiener's species diversity index, the dominance and rarity index etc. can be calculated. In such ways, numbers of sample plots are set up and data on species diversity are also compiled. Currently, the measurement of biological diversity in Thailand has been expanded to cover gene and species levels (Changtragoon and Chaisurisri 1994). However, at the ecosystem level, measurement is still in the infancy stage.

TREE DENSITY AND SPECIES RICHNESS

Tree density and species richness have been largely studied in various forest ecosystems. It is clearly shown that the highest tree density and species richness are found in the tropical rain forest, especially the Malayan mixed dipterocarp sub-ecosystem, in the southern peninsular of Thailand (Table 5). In this ecosystem, the highest tree density and the highest number of species were recorded as 1,540 tree/ha and 109 species/ha respectively (Kiratiprayoon 1986). Among the deciduous forest ecosystems, the dry dipterocarp forest, in all cases, contains a greater number of tree species and higher plant densities than the mixed deciduous forest, both with and without teak.

Under favourable conditions, such as in the *Dipterocarpus tuberculatus* subtype, which is one of the sub-ecosystems of the dry dipterocarp forest, tree density in this forest can be as high as 789 trees/ha with 37 species/ha (Visaratana *et al* 1986).

Forest Ecosystem	Plant Density (no. tree/ha)	Species richness (no.spp/ha)	References
Dry Dipterocarp Forest	554-789	35-37	Visaratana *et al.* 1986
Mixed Deciduous Forest	253	14	Sahunalu *et al.* 1979 and Kiratiprayoon *et al.*, Chapter 16, this volume.
Teak Forest	262-395 -	- 21	Bunyavejchewin 1983 Dhanmanonda and Sahunalu 1992
Pine Forest	145-280	- 22-34	Kajornsrichon 1988 Maiman 1982
Dry Evergreen Forest	731	57	Visaratana 1983
Hill Evergreen Forest	726	56-70	Vannaprasert 1985
Tropical Rain Forest	818-1,540	69-109	Kiratiprayoon 1986

Table 5: Tree density and species richness under different forest ecosystems in Thailand. (Number of tree > 4.5 cm in DBH /ha).

GENETIC DIVERSITY

Genetic diversity of a species can be assessed either by the establishment of field trials such as provenance, progeny and clonal tests, or through genetic marker techniques, such as isozyme and DNA analysis. In the breeding programmes of teak and pines in Thailand, a number of provenance trials, progeny trials and clonal trials were extensively established during the period of 1960 - 1980. The main objectives of these trials are to study genetic variation of teak and pines at population (provenance), family/progeny and individual/clonal levels and to identify promising provenances, families and individuals/clones for forward and backward selection in the breeding programme. During the past few years, efforts were made on the development of isoenzyme gene marker techniques for population

(provenance) and clonal identification of teak, pines, neem etc. (Changtragoon and Finkeldey 1994, Changtragoon and Szmidt 1994).

Recent research on genetic diversity was also carried out in Thailand using isoenzymes as genetic markers to determine genetic diversity of some forest tree species. Some forest tree species of high economic value were assayed for allozyme variability, viz. *Dalbergia cochinchinensis* (Soonhuae *et al.* 1994), *Pterocarpus macrocarpus* (Liengsiri *et al.* 1995), *Pinus merkusii* (Changtragoon and Finkeldey 1994), *Pinus kesiya* (Boyle *et al.* 1991) and *Azadirachta* spp. Within the next three-year plan, a group of dipterocarp species will be examined for their genetic diversity, viz. *Hopea ferrea, Hopea odorata, Cotylelobium melanoxylon,* and *Dipterocarpus alatus.*

One accomplishment of these studies has been the description of population structure and patterns of genetic diversity in both leguminous species (Table 6) and tropical pines (Table 7). In all studied species the results were based on 11 - 12 enzyme systems. For leguminous species, the studies have shown high levels of population differentiation (Fst), similar to that reported for other tropical trees (Butcher *et al.* 1992, Hamrick *et al.* 1992; Joly *et al.* 1992). Possible reasons for high levels of population differentiation in tropical species may be caused by lower population densities, more widely scattered populations, reduced gene flow and increased genetic drift, and greater spatial variation in natural selection pressure (Bawa 1976). Tropical pines exhibited lower genetic differentiation (Gst) than broad-leaved species probably due to the difference in mode of pollen dispersal (Loveless and Hamrick 1987).

Species	F_{is}	F_{it}	F_{st}	Sources
D. cochinchinensis	-0.200	-0.048	0.127	Soonhuae *et al.* 1994
P. macrocarpus	0.099	0.208	0.121	Liengsiri *et al.* 1994

Table 6: Summary of F-statistics in two tropical broad-leaved forest tree species.

Species	H_t	H_s	G_{st}	Sources
P. kesiya	0.173	0.166	0.039	Boyle *et al.* 1991
P. merkusii	0.104	-	0.041	Changtragoon & Finkeldey 1994

Table 7: Summary of G-statistics in two tropical pines.

SPECIES DIVERSITY

To estimate the diversity of species, the Shannon-Wiener index method is commonly used. In this method, the proportion of number of individuals of a species to the overall number of individuals in the sampled plots is used to express the diversity of species in the studied ecosystem (Krebs 1972). A higher index value indicates higher species diversity. In Table 8, the species diversity index values measured and calculated from different forest ecosystems have been listed. It is clearly demonstrated that the highest species diversity is from the tropical rain forest in the southern peninsular. The lowest species diversity is from the dry dipterocarp forest (Table 5). When species richness values (Table 5) are taken into account, it is clearly shown that the dry dipterocarp forest (which is higher in species richness values than the mixed deciduous forests) performs relatively poorer in the distribution pattern of species than that of the mixed deciduous forests. Similarly, the mixed deciduous with teak forest has a poorer distribution of species than that of the mixed deciduous forest without teak.

In a long term programme, the RFD of Thailand has established permanent sample plots in two important forest type areas, tropical rain forest and mixed deciduous forest, in order to study species diversity. Moreover, specific assessment of species diversity has also been undertaken in a collaborative programme among the ASEAN member countries, under ASEAN Institute of Forest Management (AIFM) Project and initial results are presented in Chapter 16 of this volume.

Forest Ecosystem	Shannon - Wiener Diversity Index	References
Dry Dipterocarp Forest	1.9 - 3.0	Sahunalu *et al.* 1979
Dry Dipterocarp Forest	3.6 - 4.0	Nilroung 1986
Mixed Deciduous Forest	3.5 - 3.9	Sahunalu *et al.* 1979
Teak Forest	2.9	Dhanmanonda and Sahunalu 1992
Pine Forest	3.3 - 4.0	Kajornsrichon 1988
Dry Evergreen Forest	3.5 - 4.9	Sahunalu *et al.* 1979
Hill Evergreen Forest	5.0 - 5.1	Vannaprasert 1985
Tropical Rain Forest	5.0 - 6.2	Kiratiprayoon 1986

Table 8: Species diversity index under different forest ecosystems in Thailand. (Shannon-Wiener species diversity index value of tree > 4.5 cm in the dbh).

ECOSYSTEM DIVERSITY

Measurement of forest biodiversity at the ecosystem level has been conducted to develop the means for sustainable management of tropical forests in the country, either for optimal production of goods and services, or for conservation of biodiversity.

This study has been aimed at understanding the dynamics of interrelationships between seasonal evergreen and dry deciduous forests in order to formulate means to explain how species richness and patterns of commonness and rarity within each forest type are related to overall patterns of forest composition, and environmental factors, especially moisture.

With these questions in mind, a permanent plot of 50 ha. covering a seasonal primary evergreen forest at Huai Kha Khaeng Wildlife Sanctuary has been set up, and the methodologies used for ecosystem study are as follows.

Technical plan

Activity 1 : Permanent plot

A 500 x 1000 m permanent plot was established with a 20 m interval permanent grid. In the plot trees have been tagged for their identity. Their diameters have been measured. This activity was expected to be completed in 1995.

Enumeration of species composition was planned to include trees and climbing plants with dbh larger than 1 cm. Permanent demographic records of these plants will be kept and will be subjected to recensus after 3 years, and later every 5 years.

Activity 2 : Supplemental observation of artificial populations of seeds and seedlings

Patterns of regeneration within the studied plot will be observed by establishing artificial populations of seeds and seedlings along the moisture gradient. In this case, growth and survival will be recorded.

Activity 3 : Environmental monitoring and phenology observation

During this study, several environmental factors will be monitored.

An automated weather station has been set up to monitor rainfall, air temperature, relative humidity, wind speed (including wind direction) and solar radiation. Soil moisture will also be analyzed by appropriate techniques.

Phenology of approximately 80 tree species will be recorded biweekly in the first year using a focal tree approach, i.e. observing the activity of 5 adult individuals. When the general patterns of phenology have been discerned, the key

species will be observed with larger sample sizes in subsequent years.

When this study is completed, it is anticipated that this information will provide a guideline for proper management of these types of forest habitats on a sustainable basis. However, it is still in an initial stage. This will be the starting point for other sites.

Huai Kha Khaeng, as a World Heritage Site and considered as an important bio-resource of the country, more studies are being planned such as effects of forest fire on forest ecosystems, natural regeneration of forest tree species and their distribution, and wildlife dynamics etc.

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Chapter

9

MONITORING OF FOREST BIODIVERSITY: POLICY AND RESEARCH ISSUES

M. N. Salleh[1] and N. Manokaran[2]

INTRODUCTION

Biodiversity refers to the entire range of variation among plants, animals and microorganisms, across all levels of the biological hierarchy from genes to ecosystems (Solbrig 1991). It is usually considered in terms of numbers of species, particularly of vertebrates and higher plants but is more than that. At the species level, tropical forests are exceptionally rich, containing half of all vertebrates and vascular plant species so far documented and, allowing for the much larger numbers of invertebrate species, many yet to be discovered, possibly 90% of the world's total species (McNeely *et al.* 1991).

Environmental degradation, and with it habitat loss, has led to loss of biodiversity worldwide. There is no accurate account of the loss of species and this loss may occur even before species are discovered. An estimate indicates that since the year 1600,724 known species have become extinct (McNeely *et al.* 1991). Another

1 **Director-General, Forest Research Institute Malaysia (FRIM), Kepong, 52109 Kuala Lumpur.**

2 **Senior Research officer, Forest Research Institute Malaysia (FRIM), Kepong, 52109 Kuala Lumpur.**

estimate places the potential loss of biodiversity at 15,000 to 50,000 species per year from the 1990s onwards, due mainly to tropical deforestation (Reid and Miller 1988).

GLOBAL INITIATIVES ON BIODIVERSITY

The first steps to environmental degradation can be traced to the Industrial Revolution. Pollution of the atmosphere and the waterways began. Forests were systematically removed. Soil degradation began. The rapid economic growth following the Second World War rapidly accelerated environmental degradation. By the early second half of the twentieth century, concern for the global environment translated into the United Nations Conference on the Human Environment held in June 1972 in Stockholm, Sweden. The first ever meeting of the international community on environment addressed the relationship between environment and development at the global level. The Stockholm Declaration of the Conference addressed biodiversity concerns in three of the 26 principles enunciated. The need to safeguard flora and fauna and especially representative samples of natural ecosystems for the benefit of present and future generations through careful planning and management is stressed in one principle. The need to safeguard and wisely manage the heritage of wildlife and its habitat is stressed in another principle. The need to prevent pollution of the seas that is harmful to marine life is stressed in a third principle.

A decade after Stockholm, environmental degradation had continued unabated. Global warming, ozone layer depletion, marine pollution, acid rain, deforestation, loss of biodiversity, and soil degradation had become serious environmental issues by the early 1980s.

The United Nations General Assembly established the World Commission on Environment and Development in 1983 with the mandate to re-examine the critical environment and development issues and to formulate realistic proposals for dealing with them. The 1987 Report of the Commission, entitled *"Our Common Future"*, focused its attention on several issues, one being the loss of species and genetic resources.The Commission deemed it necessary to place this issue on political agendas as a major economic and resource issue. The Commission felt that reservoirs of biological diversity needed to be developed economically and envisaged the necessity of protecting large areas for future needs, with assistance for conservation coming from international agencies.

The 1987 Report led to preparations for holding the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in June 1992. A

series of preparatory meetings, or PREPCOM meetings, were held at governmental level, beginning in 1990, and culminating in UNCED. A voluminous 500 page, 40 chapter document, Agenda 21, an action programme for environment and development issues, was a major output at Rio. A chapter, Conservation of Biological Diversity, addresses various issues, including that of monitoring. The Conference in Rio was exactly 20 years after Stockholm.

Around the time of the Stockholm Conference, and shortly thereafter, a number of international instruments had been developed for the protection of biological diversity. The most important are:

- Convention on Wetlands of International Importance Especially as Waterfowl Habitat (RAMSAR) 1971
- Convention Concerning the Protection of World Cultural and Natural Heritage (PARIS) 1972
- Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (WASHINGTON) 1973
- Convention on the Conservation of Migratory Species of Wild Animals (CMS) (BONN) 1979

These international instruments are all, however, inherently limited in application, however liberally their texts are interpreted. RAMSAR is confined to only wetland habitats. CITES is essentially about trade in species. CMS deals only with migratory organisms, and the Convention on World Heritage natural sites is limited in scope. Collectively, the coverage of all these conventions is only sectoral in nature and none has been designed to protect biological diversity as a primary objective. A common thread in all these conventions is the element of monitoring.

In 1987, the United Nations Environment Programme (UNEP), established as a consequence of the Stockholm Conference, formally recognised the need for concerted international action to protect biodiversity. It initiated a series of intergovernmental meetings that developed a negotiated document, the Convention on Biological Diversity, that was brought to UNCED for signature by heads of governments. The ratification of the treaty by governments is in progress.

The chapter on Conservation of Biological Diversity in Agenda 21 places emphasis on monitoring of biodiversity. However Agenda 21 has no legal standing. The Convention on Biological Diversity is a legal instrument. In one article titled "Identification and Monitoring", Parties to the treaty are required to monitor components of biological diversity, especially those requiring urgent conservation measures and those which offer the greatest potential for sustainable use. Also,

effects of activities that are likely to have significant adverse impacts on the conservation and sustainable use of biological diversity are required to be monitored through sampling and other techniques.

At the governmental level, efforts are underway to put the Convention into operation. The first Conference of Parties was held in December 1994 to initiate the process of giving the Convention operational form.

THE MONITORING PROCESS

In the context of forest biodiversity, or for that matter, any form of biodiversity, what does monitoring involve? It involves the gathering of data to enable the detection of changes in the status, security and utilisation of biological diversity for the purpose of improving the effectiveness of management of that diversity (UNEP 1993).

As a condition, therefore, monitoring requires the building up of an information baseline which is practically an incremental process. Such an information baseline on forest biodiversity would allow for more enlightened resource planning. Such an information baseline of forest biodiversity would usually include habitats and species, but rarely genetic diversity.

Continuous enlargement of the information baseline, filling key gaps in the information coverage, is required for more effective planning of biodiversity management. Continuous updating of the information baseline through repeated collection of data will be part of the monitoring process.

FOREST MANAGEMENT

Before one considers the issue of monitoring of forest biodiversity, one really needs to consider the issue of what is forest management in practice at the moment. Salleh (1991, 1992) has discussed this issue at length. Are forests being managed for biodiversity at all? How are tropical forests, where much of the world's terrestrial biodiversity resides, being managed and for what? The question of policy and research issues in the context of monitoring of forest biodiversity would need to be addressed with reference to answers to the above questions.

Forests fulfil many functions. They are the source of timber and nontimber goods, and provide numerous services. Nontimber goods include rattan, bamboo, fuelwood and extractives (dyes, gums, incense, latexes, oils, resins, and including those leading to development of pharmaceuticals), and food such as fish, game,

fruits, nuts, honey and spices. Services provided by forests include soil and watershed protection, soil generation, energy supply, conservation of biological diversity, regulation of climate, recycling of nutrients, carbon sequestration, oxygen release and tourism and recreation. Interactions between a certain number of species and genetic diversity uphold the cyclical relations within the forest ecosystem, and thereby maintain ecological services.

Forests in almost all countries, whether temperate or tropical, have been utilised primarily for the production of timber as it has been considered the only option for economic growth. The sustainability of forestry practices is now being questioned, especially pertaining to the tropics. The study of the International Tropical Timber Organisation (ITTO) and the International Institute for Environment and Development (IIED) (Poore *et al.* 1989), for example, reported that less than one tenth of a percent of tropical forests are managed on a sustainable basis.

Malaysia, where forest management has been practised for nearly a century has, like most other nations, focused solely on the production of timber in forests outside of those totally protected, even though the forests produce a whole spectrum of other products. Management and harvesting plans are prepared only for logging of timber and, at most, other nontimber products such as rattan are only briefly mentioned. Management to ensure sustained supply of the multitude of other economically important products such as rattan, bamboo, fruits, wildlife, medicinal plants, resins and other products from any particular locality is difficult, if not impossible.

In the management for timber supply, the basic approach is to assess the standing stock of the forest, determine the growth rate of the forest from research plots, determine the economic yield that should be produced and thus determine the rotation or cycle to be used. The forest is then divided into blocks equivalent to the number of years in the cycle. This is a simple straightforward exercise. Timber harvesting is controlled by blocks, and after harvesting, silvicultural operations are undertaken to assist the growth of seedlings or saplings, depending upon the silvicultural system being used. Seldom, if ever, are considerations given to other resources, except for minimising damage to rivers and streams, and to soil erosion when preventive or conservation measures are put in place. Timber harvesting is also not permissible in very steep areas or environmentally sensitive areas. No attention is given to managing biodiversity, nontimber products or other environmental aspects in the timber production forest.

Clearly there has to be a policy decision taken at the highest level to shift emphasis of management from only timber production to management of the forest

for other goods and services as well. Could timber be produced in conjunction with soil and watershed protection? What technological changes in timber harvesting are required to ensure this? Would the conservation of biological diversity be compatible with sustainable production of timber? Could tropical forests be managed for multiple uses all at the same time? If not, should zoning of forests be considered for optimum utilisation, as a further refinement of the system in place in Malaysia where the Permanent Forest Estate is classified into Protective, Productive and Amenity forests?

A major problem in arriving at a reasonable valuation of multiple functions of tropical forests is that of lack of data, including monitoring systems. That is why only timber resources have been considered and nontimber goods and forest services have been ignored in national accounting systems. As tropical forests are almost all in Third World countries, international funding and collaboration is required to develop the data collecting and monitoring systems. Without such data there is every likelihood that tropical forests will continue to be viewed solely from the perspective of timber in the national accounting systems. Management for timber alone for shortterm gains would lead to disruption of the ecological processes and the complex species interactions that guarantee the sustainability of the natural forest ecosystem.

FOREST BIODIVERSITY BASELINE DATA

This then brings us back to the question of data gathering in relation to monitoring of forest biodiversity. What kind of data on biodiversity is available and what kind of data requires to be collected so that a monitoring process could be implemented, to detect changes in the status, security and utilisation of biological diversity. A discussion of this in relation to the Malaysian context may help to highlight relevant issues.

The beginning of documentation of forest biodiversity could be dated to the last couple of centuries, during the colonial period, when botanical collections were carried out leading to publications such as *The Flora of British India* by Hooker (1894) and *Palmae* by Beccari and Hooker (1894). During this period there were similar

efforts at documentation in the region, in countries now collectively known as ASEAN (Association of Southeast Asian Nations).

In the then colonial territory of Malaya, work on flora led to publications such as *Flora of the Malay Peninsula* by Ridley (192225), *Commercial Timber Trees* by Foxworthy (1927), *Wayside Trees of Malaya* by Corner *(1940), Foresters' Manual of Dipterocarps* by Symington (1943), Pocket Check List of Timber Trees by Kochummen (1979). Work on fauna, in many cases of a general nature, led to publications such as *Introduction to Malayan Birds* by Madoc (1976), *The Birds of Borneo* by Smythies (1981), *The Butterflies of the Malay Peninsula* by Corbet and Pendlebury (1978), *Moths of Borneo with Special Reference to Mt. Kinabalu* by Holloway (1976), *Poisonous Snakes of the Malay Peninsula* by Lim (1991), *Introduction to Mammals of Singapore and Malaya* by Harrison (1966), and *The Birds of the Malay Peninsula* by Medway and Wells (1976).

The tree flora of Peninsular Malaysia has been documented in four volumes, edited by Whitmore (1972, 1973) and Ng (1978-1989). This voluminous work, carried out by 15 authors over a period of about 20 years, covers all the families of flowering plant species forming trees reaching 90 cm girth (28.6 cm diameter), and covers gymnosperms as well. Herbarium collections at the Forest Research Institute Malaysia and at Singapore were the main source of the studies, with reference to collections in Europe on critical matters. A total of 99 families comprising over 3000 species were covered. Work has started, along similar lines, on the tree flora of the Malaysian states of Sabah and Sarawak in the island of Borneo. Based on both herbarium and extensive field work, the rattan flora of Malaysia has been documented by Dransfield (1979, 1984, 1992). Taxonomic accounts of the bamboos (Wong 1992) and termites (Tho 1992) of Peninsular Malaysia were completed recently.

Much is now known about the habitats, food, behaviour and distribution of large mammals such as the tiger, elephant, rhino, deer and 'seladang'. This is the result mainly of continuing studies associated with the wildlife conservation programme of the Department of Wildlife and National Parks.

Data gathering has included documentation of the forest types of Peninsular Malaysia [(see Symington (1943) and Wyatt Smith (1964)]. This broad classification,

shown in Table 1, applies to Sabah and Sarawak as well.

Climactic climax forest	Edaphic forest
Lowland dipterocarp forest	Heath (or Kerangas/Kerapah) forest
Hill dipterocarp forest	Forest over limestone
Upper dipterocarp forest	Forest over ultramfic outcrops
Montane oak forest	Beach stand vegetation
Lower ericaceous forest	Mangrove forest
Montane subalpine vegetation	Brackish-water forest
Semi-evergreen seasonal forest	Peat swamp forest
	Fresh-water swamp forest
	Seasonal swamp forest

Table 1: The Rain Forest Types of Malaysia [Adapted from Symington (1943) and Wyatt-Smith (1964)].

MONITORING OF FOREST BIODIVERSITY IN MALAYSIA

UNEP (1993) describes monitoring of biodiversity in four categories at the national level, these being monitoring of genetic diversity, species diversity, habitats and protected areas. There is virtually no baseline data in Malaysia on genetic diversity of flora and fauna of the forests, and this is generally a global phenemenon. There has been some monitoring of species and of habitats or ecosystems.

Remote sensing monitoring through aerial photography has provided information on change in the extent of forested land. Over the period 1970 to 1989, forested land for the whole of Malaysia had been reduced by 22.7%, mainly due to forest conversion to agriculture (Manokaran 1992). Almost all the forests cleared were lowland forest, with its multitude of habitats. As a result of this forest clearance, and therefore of loss of habitats, reduction in populations of wildlife such as the tiger, elephant, rhinoceros and 'seladang' (wild cattle) occurred (Anonymous 1998a, 1998b).

Monitoring of forest resources, essentially timber resources, has been, and is, an ongoing process. The Forest Resources Reconnaissance Survey (FRRS), initiated in 1962 and completed in 1969 and designed to assess the extent, distribution and

nature of the forest resource on all forested lands throughout Peninsular Malaysia, provided initial baseline data and maps for planning purposes. Up until then, a limited amount of qualitative and quantitative data did exist for some of the forest reserves. The FRRS was based on aerial photointerpretation and sufficient quantitative survey on the ground.

The FRRS led to the first national forest inventory of Peninsular Malaysia (1970-1972), a project that consisted primarily of reviewing and complementing where required, the results of the FRRS, with the purpose of preparing a forest development plan (Anonymous 1973). The inventory involved field sampling of the main commercial species and species groups. Mangrove forests were excluded from the survey. The national forest inventory was repeated in 1981-82 when the most important commercial species of rattan were included in the survey. A third inventory was carried out in 1991-92. A similar inventory of the mixed dipterocarp forests of the state of Sarawak was carried out between 1969 and 1972, and the main commercial species and species groups were enumerated (Anonymous 1974). To date the inventory has not been repeated.

Tree species diversity, and populations of these tree species have been monitored in detail for long periods of time in 2ha plots in primary lowland and hill dipterocarp forests in Peninsular Malaysia. Results of the monitoring of trees of 10 cm diameter and larger for periods of 13,36 and 38 years have been documented (see Manokaran and Kochummen 1987, Manokaran 1988), and monitoring still continues. A 50ha plot established in primary forest in Pasoh Forest Reserve, a lowland dipterocarp forest, beginning in 1985, has provided baseline data on all woody species of 1 cm diameter and larger (Manokaran *et al.* 1990, Kochummen *et al.* 1990, Kochummen *et al.* 1992, Manokaran *et al.* 1991, Manokaran *et al.* 1992a and Saw *et al.* 1991). Arecensus in 1990 (Manokaran *et al.* 1992b) and repeated monitoring at five-year intervals thereafter is expected to provide information on tree species diversity and population change over time. In the same forest, Wells (unpublished) has monitored populations of birds for about two decades, and Ratnam and Lim (unpublished) have monitored small mammal populations for several years now.

Of the total land area of Malaysia of 32.86 million hectares, 19.2 million hectares or 58.4 percent are covered with natural forest (Table 2a). National parks and wildlife sanctuaries cover an area of 2.14 million hectares. Except perhaps for certain groups of wildlife, no proper inventory has been carried out of species or habitats within these protected areas.

The National Forestry Policy 1978 and the National Forestry Act 1984 catered for the establishment of the Permanent Forest Estate (PFE). The original area of the

PFE of 12.73 million hectares is being increased to 14.05 by the gazetting of state-land forest (Table 2b). While the Productive Forest of the PFE is for timber Production in perpetuity, the Protective Forest is for the protection of watersheds and the environment. There has been no inventory of species or habitats within these protected areas.

Region	Permanent Forest Estate	National Park & Wildlife (PFE) Sanctuary	Stateland Forest	Total Natural Forest	Total land area
Peninsular Malaysia	4.70+	0.74*	0.78	5.97	13.16
Sabah	3.35	0.40*	0.93	4.54	7.37
Sarawak	6.00+	1.00	1.70	8.69	12.33
Total	14.05	2.14	3.41	19.20	32.86

Table 2a: Natural Forest Land Use Pattern in Malaysia, 1992 (million hectares).

* 0.19 and 0.14 million hectares respectively in Peninsular Malaysia and Sabah are located within the PFE

\+ 0.06 and 0.01 million hectares respectively in Peninsular Malaysia and Sabah are plantation forests within the PFE

Source: Ministry of Primary Industries, Malaysia

Region	Protection Forest	Production Forest	Total forested area under PFE
Peninsular Malaysia	1.90	2.80	4.70+
Sabah	0.25	3.10	3.35
Sarawak	1.00	5.00	6.00*
Total	3.15	10.90	14.05

Table 2b: Permanent Forest Estate in Malaysia, 1992 (million hectares).

\+ Includes 0.24 million hectares to be gazetted

* Includes 1.50 million hectares to be gazetted

Source: Ministry of Primary Industries, Malaysia

MONITORING POLICY AND RESEARCH ISSUES

In the absence of any clear policy on biological diversity, baseline information gathering would probably proceed in an uncoordinated manner. Many aspects of biological diversity may be neglected altogether. In the forestry sector, for example, only timber species may be considered to the exclusion of all other aspects of biological diversity. This is generally the case at the moment. A policy on biological diversity would help to focus on these other aspects as well as to strategise the way in which biodiversity considerations are included in planning for development. The policy would need to cover not only the question of gathering of baseline data but also that of a monitoring programme and of an information management system. In parallel with the development, signing and ratification of the Convention on Biological Diversity several nations have been developing such a policy. In Malaysia a National Policy on Biological Diversity has been developed.

Policy documents themselves would be ineffective unless they are backed by an adequate legislative framework and the necessary political commitment towards enforcement. This legislative framework should fully integrate other aspects of land use, in particular agriculture, with forestry practices since these other land use practices generally impinge on the wellbeing of forest biodiversity. Expansion of areas for agriculture (especially for cash crops) and aquaculture are almost always at the expense of forested lands, and this issue has to be properly addressed in the legislative framework.

Monitoring is the repeated standardised collection of data on certain parameters that could indicate the status and use of resources. Time-series data are nonexistent except for a few "megafauna" species, such as mammals and birds, tropical forests and the landuse estimates produced by FAO (UNEP 1993). In Peninsular Malaysia, with baseline information on tree flora available, monitoring of timber resources has been made possible. Aerial surveys have also made it possible to monitor the extent of the major forest types over time.

A focus of research in this region should be the identification of fragile or sensitive ecosystems or habitats such as steepland areas and wetlands, and subsequent monitoring of these sites. Often these are endangered or threatened by human activity. In the same vein, endangered or threatened species need to be identified and their populations and habitats monitored. In all these a multidisciplinary approach is required.

Baseline data of forest biodiversity, especially in tropical countries, is woefully inadequate, thus hindering any attempt at monitoring. This is due to a large extent on the lack of trained personnel in the field of taxonomy. For example, except for

reasonable expertise in the tree flora, local expertise on shrub, herbaceous and epiphytic flora is totally inadequate. The problem is compounded by the fact that institutional infrastructure is extremely weak or is lacking altogether. Manpower and infrastructure development is therefore an area where international funding and collaboration is required to develop data collecting and monitoring systems. Conservation International (1992) discusses aspects of these issues in its Rapid Assessment Program, a biological inventory programme designed to meet the information needs necessary to catalyse conservation action and improve biodiversity protection. UNEP (1993) devotes a whole section to these issues, and besides addressing the questions of institutional capacities and human resources, also discusses points such as national legislation, technological facilities, information resources, and data management and monitoring capacity.

In tropical countries, species richness, compounded by poorly developed manpower and infrastructure facilities, is likely to ensure that comprehensive inventories of all species in the forest ecosystem will remain a Herculean task. Not only would such inventories, if at all possible, be highly time consuming, they would also be too costly For example, Janzen (1993) estimates that an intensive all taxa biological inventory analysis would cost US $25 million over 5 years for each and every site in the tropics. Monitoring of forest biodiversity would therefore have to focus on certain key parameters.

UNEP (1993), in noting that rapid advances in remote sensing, environmental measurement techniques and information technology have greatly facilitated the monitoring of biodiversity, provides a provisional list of key parameters under four categories for monitoring biodiversity at the country level (monitoring genetic diversity, species monitoring, habitat monitoring, protected areas monitoring). Taken together with the Minimum set of indicators for monitoring biodiversity at the country level' of Reid *et al.* (1993) and the 'Parameters that an early warning network must monitor at the country level' of the Global Biodiversity Strategy of WRI/IUCN/UNEP (1992), UNEP (1993) considers that a framework is in place for determining priorities and goals for biodiversity planning, that generates the data necessary to monitor how well the country is doing in achieving its strategic planning objectives, and that supplies the early warning information necessary for the rapid response to new threats.

Genetic diversity of forest species in the tropics remains unexplored. Early studies are just beginning and it is anticipated that baseline information gathered, and any monitoring thereafter, will have implications on forest management practices.

Developing countries are gene-rich but the economic potential of forest biodiversity in these countries remains largely untapped. Developed countries are technology-rich, and efforts at baseline information gathering and monitoring should include collaboration between the North and the South in developing more economic use of components of this biodiversity. That biodiversity knows no boundary would also mean that regional cooperation is required in biodiversity prospecting.

A research issue of great importance to countries like Malaysia is whether management of forests for sustained production of timber will conflict with conservation of biological diversity, both at the gene and species levels. The few studies of timber harvesting effects on biodiversity so far carried out in Peninsular Malaysia have been limited to selected locations and concentrated particularly on the trees or other woody plants in the floral composition, and on some vertebrate groups, particularly birds, among the fauna. Vincent and Binkley (1992) argue that dominant-use management, managing some forests for timber as a dominant use, and others for nontimber values, is more efficient than multiple-use management, based on the economic theory of "comparative advantage". As Production Forests form about 57 percent of the total natural forest area in Malaysia, it would be in the best interests of forest management to monitor the effects of harvesting at a range of intensities on the inventory of species and their spectrum of distribution and activity. Ultimately guidelines could be developed on forest exploitation and management to conserve biodiversity, by the most costeffective means, in concert with sustainable production of timber and other benefits. Such guidelines should make it mandatory for Environment Impact Assessments (EIA) to be carried out before timber harvesting, and this to be complemented by environmental auditing during and after the harvesting activities. EIA and environmental auditing should be legislated to be part of timber harvesting operations.

There is also the issue of global warming and acid rain and their effects on forest biodiversity. Although uncertainties remain, there is now much broader scientific consensus that the problem of global warming is real, while increased levels of acid rain have been detected in tropical countries like Malaysia which are on the path towards industrialisation. These phenomena are expected to affect forest biodiversity in unpredictable ways over a long time frame, and some kind of monitoring process would eventually have to be set in motion.

CONCLUSIONS

Most of the world's forest biodiversity is located in tropical forests which are almost

entirely found in developing countries. Baseline information on biodiversity in these countries is woefully inadequate, other than perhaps on the extent of forested areas, timber resources and "megafauna" such as mammals and birds. Weaknesses in the field of human resources (especially of taxonomists), institutional capacities, technological facilities, information resources and data management capacities are the reasons for this state of affairs. This is compounded by the fact that in forest management, timber is the only option considered to the exclusion of all other aspects of forest biodiversity. In such a scenario, therefore, the monitoring of forest biodiversity is a most difficult task.

Policy formulation or changes are required that would shift focus to other aspects of forest biodiversity from solely timber. This would have to be supported by international funding and collaboration that would alleviate weaknesses in the baseline information gathering capacities of the countries concerned. The international support should also help to develop a monitoring system, initially making use of information available, and eventually based on the wider baseline information gathered.

The documentation of each and every species for the purpose of monitoring may be an unrealistic goal although such documentation could be an ultimate target. Nevertheless parameters or indicators that have been provisionally identified could form the database of the monitoring system.

Monitoring of forest biodiversity should not just be in protected areas but also in areas designated as permanent timber production areas. Research should therefore focus also on the effects of timber harvesting on other species diversity, and a monitoring regime should lead to developing guidelines on timber harvesting that would include conservation of biodiversity in these permanent timber production areas.

In the final analysis, only policies on biodiversity backed by legislation and political commitment, and supported by international funding and collaboration, would lead to meaningful progress in baseline data gathering and monitoring. The legislative framework should integrate other land use practices such as agriculture with forestry, as these are very closely inter-twined. Collaboration between the gene-rich countries of the South and the technology-rich countries of the North should also include efforts at greater utilisation of components of biodiversity. In all these a reasonably efficient monitoring system is essential for detecting changes in the status, security and utilisation of forest biodiversity that would allow steps to be taken to manage biodiversity effectively.

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Chapter
10

MEASUREMENT OF GENETIC DIVERSITY WITH SPECIAL REFERENCE TO THE ADAPTIVE POTENTIAL OF POPULATIONS

Hans-Rolf Gregorius[1]

INTRODUCTION

In principle, the use of any measure of biodiversity is restricted to the real or modeled biological phenomena for which it is developed. A central biological phenomenon is the capacity to persist (maintain identity) by adjusting to changing conditions (adaptation) a fundamental characteristic of life *per se.* Therefore, studies of the relationship between adaptive capacity and biodiversity represent one of the pivotal points in ecological and evolutionary research.

Elaboration of distinctive features of diversity measures that are of relevance to problems of adaptation requires a clear concept of adaptation and its basic mechanisms. In order to allow specification of the position in a broader framework that any particular measure takes, the present demonstration will be based on concepts of adaptation that apply to the level of the ecosystem just as well as to that of the individual. (The definitions of terms compiled in Table 1 sketch the con-

[1] Abteilung fur Forstgenetik und Forstpflanzenzuchtung, Universitat Göttingen, Busgenweg 2, D 37077 Göttingen.

cept applied in the present considerations; for a detailed system theoretical formulation of the concept of adaptation - see Gregorius 1993). Among these levels the smallest unit of biological organization that shows continuity in time and is capable of adaptation is to be found in the population, and the mechanisms of adaptation are part of its genetic system. In this sense the population is the smallest unit of evolution and adaptation* . At lower levels of organization, such as the individual or cell, (physiological) adaptation lacks continuity simply because of limitation of life span.

Adaptedness - adjustedness of a character to an environment in the sense that the vital functions of its carriers are not impaired in this environment.
Adaptation - (1) any process ultimately leading to a state of adaptedness (thus securing the persistence, integrity, or identity of the underlying system); (2) an adapted character.
Regulatory adaptation - adaptation not involving a change in system state (such as specified by genotype, genetic structure, species spectrum, etc.).
Structural adaptation - adaptation involving changes in system state.
Adaptability - of a system state; capacity of a system state to adapt (regulatorily or structurally) the system's response (output) to a specified environment (system input).
Adaptive potential - of a system state; set of all environmental conditions to which a system state is adaptable.

Table 1: Terminology of adaptation

While adaptive processes in populations clearly serve their physical perpetuation (genealogical continuity, see Gregorius 1994), the system identity maintained by adaptive processes at the ecosystem level is less obvious. The most appealing candidate for specification of an ecosystem's identity might be its species spectrum (including producers, consumers, and decomposers). However, changes in the species spectrum occur regularly and continuously, and it is not clear how such changes can be conceived of as a constituent of an adaptive system intrinsic to the ecosystem. Anyway, this concept would contain circular reasoning by using the species spectrum as a mechanism of maintaining the species spectrum.

On the other hand, the characteristics of the species spectrum determine the capacity of an ecosystem to sustain the nutrient cycle and to balance the nutrient

* since in asexually reproducing species no genetic recombination takes place between individuals, each individual line of descent can be conceived of as representing a separate population.

budget under the limitations set by the external (primary. mainly physical or abiotic) environment. (The book of DeAngelis, 1992, gives a review of current concepts and modelling efforts of nutrient cycling; for the hierarchical aspects of balancing nutrient budgets of ecosystems that are relevant in regulatory and structural adaptation, see e.g. Bums *et al.* 1991 or Ulrich 1993). Hence, more fundamentally, the identity of an ecosystem is definable by characteristics of its nutrient cycle, and the biological entities mediating and balancing this cycle are specified by the species spectrum. Among the most important members of this spectrum are the "key species", i.e., those species which are indispensable for sustenance of the nutrient cycle under the respective external environmental conditions (the term "key species spectrum" will be used to emphasize this fact).

From the point of view of the population or species, all higher levels of organization, including interspecific or other interactions at the ecosystem level, define environmental conditions to which the population must adapt in order to persist. These conditions can be of a *probiotic* type in the sense that they lower the adaptive pressure on the population, or they can be of an *antibiotic* type, in which case they add to the adaptive pressure. Examples of probiosis known from interactions among tree species in forest ecosystems result in reduction of rates of pest attack, improved wind protection, stabilization of water supply, or improvement of soil structure and decomposition. To a certain extent such probiotic effects are of course offset by antibiotic actions, mostly in the form of competition (for the recently revived interest in the roles of probiosis frequently referred to as "facilitation" versus competition in ecological research, see e.g. Bertness *et al.* 1993).

An ecosystem's stability is significantly determined by the strength of adaptive pressures on its populations due to the interactions inherent in the species spectrum. Probiotic interactions effectively increase the adaptive potential of the benefiting populations by providing a buffer against exogenous environmental pressures and by this stabilize the ecosystem (see Figure 1 for an illustration). Genuinely antibiotic interactions can be expected to have an adverse effect, since they introduce additional stress. Nevertheless, regulation of population size by competition, for example, may only superficially resemble antibiotic interaction, since unregulated growth could endanger the persistence of the concerned species or even its ecosystem. Moreover, different species may show both pro and antibiotic interactions, so that, in total, the pro- must at least offset the antibiotic interactions in order to have a positive effect on ecosystem stability.

This adaptability-oriented concept of ecosystem stability centers upon populations as units of adaptation. It assigns to the interactions within the species

community the role of generators of endogenous (milieu) and modifiers of exogenous environmental conditions to which the populations have to adapt. The basic determinant of the species spectrum lies in the sustenance of the nutrient cycle in the respective external environment. The species spectrum itself, however, does not constitute an adaptive system, since a species is replaceable by others as long as its function in the nutrient cycle remains unaffected. Ecosystems are resistant to environmental disturbances or fluctuations only to the degree to which their populations can adapt to them. Thus the adaptability of the population stabilizes the key species spectrum.

The intrinsic mechanisms of ecosystem stability, and thus of adaptation to varying environmental conditions, are therefore to be sought in the genetic systems and structures of the populations. Any environmental change that exhausts the adaptive capacity of a key species of the species spectrum destabilizes the ecosystem. This explains the specialization of the present paper on investigations of the relationships between adaptive potentials and a particular component of biodiversity, namely intraspecific genetic variation.

ADAPTIVE POTENTIALS OF POPULATIONS

As stated in Table 1. the specification of adaptive potentials requires definition of a system and its state. The system now comprises the population, and its state encompasses all features of its genetic system relating to physiological adaptation (where, controlled by its genotype, the individual adjusts its vital functions to its environment; regulatory adaptation) and to evolutionary adaptation (where the population adjusts its genetic structure to its environment; structural adaptation). Accordingly there are two types of adaptive potential, a physiological and an evolutionary.

Physiological adaptive potential

Physiological adaptation apparently involves two types of environment, which an individual must harmonize,

1. an *epigenetic environment,* which induces the individual's genotype to express a character which is adjusted to
2. an *adaptational environment.*

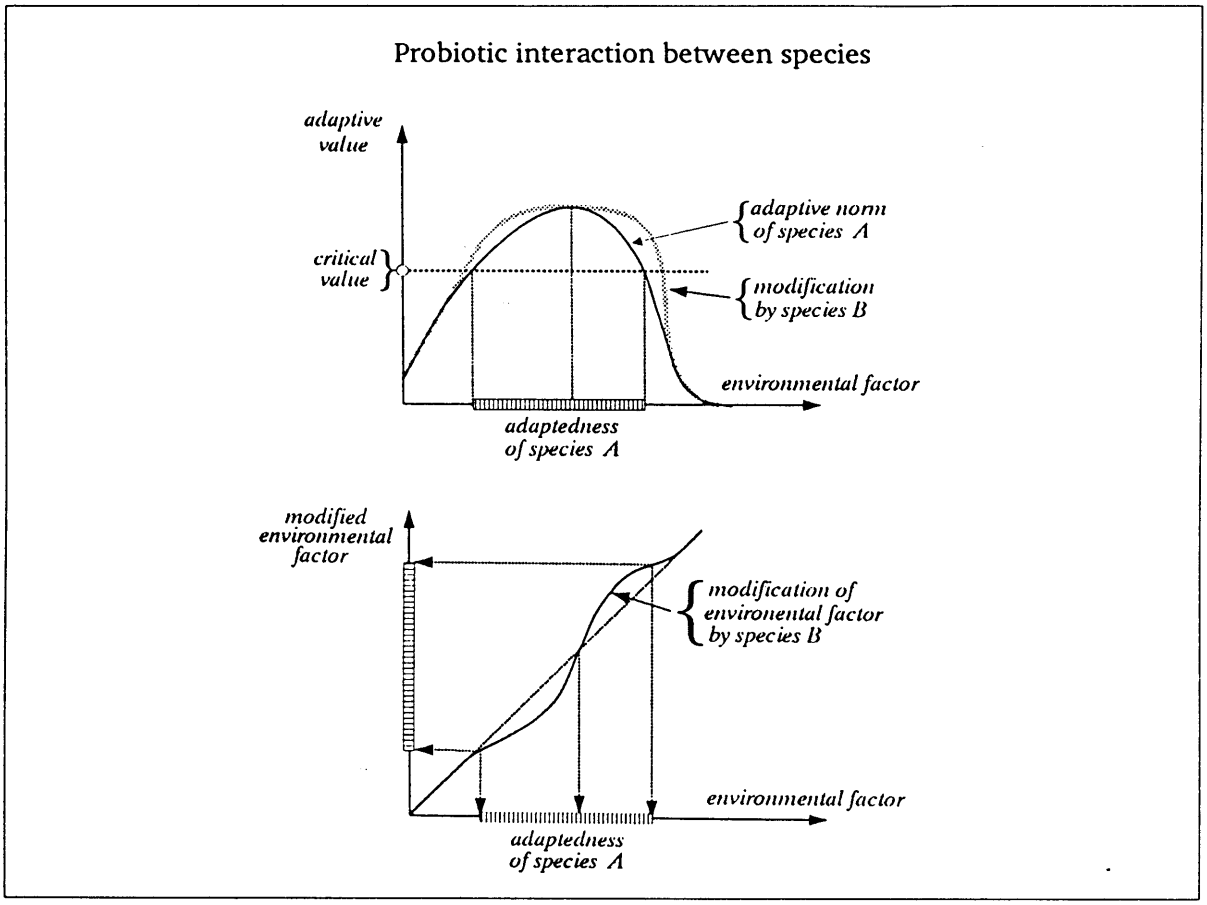

Figure 1: Graphical illustration of the probiotic effect of one species (B) on another (A) in terms of the adaptive norm (solid curve in upper part). Adaptive values above the critical value represent adaptedness as defined in Table 1. Species B facilitates adaptation of species A by increasing its adaptive value and extending its range of adaptedness (shaded curve in upper part) through positive modification of the external (primary) environmental conditions of species A (solid curve in lower part).

Adaptedness of a genotype is thus always specified with respect to *both* types of environment. If epigenetic and adaptational environments of a genotype are distinct and vary independently, physiological adaptation to changing environments is difficult, if at all, to realize. In most cases, physiological adaptedness may therefore be restricted to situations where both types of environment coincide, i.e. where the environmental factor modifying the trait is at the same time the one to which the trait is to be adapted and *vice versa*. The adaptive potential of a genotype is thus

made up of those environmental conditions for which epigenetic and adaptational effects harmonize to guarantee physiological adaptability or adaptedness.

An extension of physiological adaptive potentials of individual genotypes to the population must be based on distributions of genotypes, i.e., on the genetic structure of the population. In accordance with the above definitions, *physialogical adaptedness of a specified genetic structure* can be claimed for an environment, if this structure includes a number of individuals that is physiologically adapted to this environment and that is sufficient to maintain a viable population size.

Evolutionary adaptive potential

The establishment of genetic states of physiological adaptability or adaptedness is an evolutionary principle, and the pertaining process of harmonizing epigenetic and adaptational environments is one of the main characteristics of evolutionary adaptation. Another such characteristic consists in the capacity of providing physiologically adapted genetic structures (in the above-defined sense) under varying environmental conditions. Any of these processes is governed by the population's genetic system and is realized through changes in the genetic structure. This identifies the genetic structure as the state of the system that determines the evolutionary adaptive potential of a population. Hence, the *evolutionary adaptive potential of a specified genetic structure* of a population can be defined by all environmental conditions which, starting with the specified structure allow evolution of a physiologically adapted genetic structure. In more special situations where a population is considered at a given instant of time, the system state must be complemented by the demographic components (age class distribution, sex ratio, reproductively effective population size, etc.) in order to enable realistic specifications of evolutionary adaptive potentials.

CHARACTERIZATION OF EVOLUTIONARY ADAPTIVE POTENTIALS

In principle, all non-transient genetic types in a population may contribute to its evolutionary adaptive potential. This view gains support from the reasoning that differences in genetic structure are associated with adaptive differences for at least one environment, provided the differing genetic types are not generally malfunctioning. However, different classes of environments may make basically different adaptive demands on genetic structures.

When characterizing environments of populations, spatial distribution and dynamics (and thus change in time) have to be included as constituent parts. The

adaptive significance of an environment encompasses the proportion of the population on which it acts (its expanse), the rate at which it expands or diminishes, and possibly the speed of modification of a continuous environmental variable such as temperature. *Expanse and speed* are thus distributional and dynamic characteristics of environments of populations to which certain characteristics of their genetic structures must correspond in order to allow for evolutionary adaptation.

For example, the chance of a genetic type to contribute to the evolutionary adaptive potential for fast or wide-spread environmental changes may increase with the initial frequency of this type. Typical situations are realized in spatially adaptively differentiated plant populations in which one of the local environments expands as a consequence of some major environmental change. The genetic types adapted to the (pre-existing) local environment in principle provide adaptive potential for this change. Yet, if the expansion occurs at a high rate and if the initial frequency of the adapted types is low, the selection process might be accompanied by reductions in population size which are too drastic to allow restoration of a viable population and therefore prevents adaptation. Adaptation to such *quantitative environmental dynamics is* quite likely to depend on frequency distribution characteristics of the genetic structure in combination with the speed of environmental change.

Qualitative environmental dynamics, on the other hand, where previously largely nonexisting environmental conditions spread, are adaptively more demanding in that they may require the formation and multiplication of new gene complexes (genotypes). Adaptability to such changes is very sensitive to their rates. since for high rates the adaptive lag increases continuously and may ultimately completely obstruct adaptation. For qualitative environmental dynamics, adaptability may therefore completely depend on the presence of rare genetic variants such as can be maintained by recurrent mutation or gene flow.

In order to distinguish between the adaptive consequences of the above two classes of environments for the genetic structures of populations, the terms *operating* and *latent genetic potential* were suggested (Stebbins and Hart1 1988, Bergmann *et al.* 1990). The operating genetic potential consists of those genetic types which contribute to the adaptedness of a population to its current environmental conditions; these genetic types usually prevail. The adaptive reserve is to be found in the rarer genetic variants which form the latent genetic potential for adaptive demands of future environmental changes. Obviously the adaptive potentials for quantitative and qualitative environmental dynamics are based on the operating and latent genetic potential, respectively. The capacity to maintain latent potential

(which is adaptively inferior under the currently prevailing conditions) is a vital part of a population's capacity to preserve its adaptability and is therefore one of the most important characteristics of genetic systems.

Numbers of prevalent genetic types and the existence of rare ones are also the subject of the well established distinction between "major" and "minor" polymorphisms (Lewontin 1985), which relates these to the above two types of genetic potential. In particular, the rare types in minor polymorphisms can be considered as candidates for the latent genetic potential. However, unambiguous distinction between rare and prevalent types is only possible in the absence of types with intermediate frequency, i.e., where frequency distributions are highly concentrated. The observation of genetic types with intermediate frequencies could indicate that adaptive processes are transforming the genetic structure into a new state of adaptedness.

This line of thinking motivates consideration of characteristics of *genetics frequency profiles* (in which genetic types are ordered by decreasing frequency; Gregorius 1992, Gregorius and Bergmann 1994) as indicators of the existence of potentials for adaptation to certain classes of environmental conditions. The significance of this approach for interpretation of the majority of the common methods of measuring genetic variation will be referred to later.

Adaptive potential and phenotypes

The above considerations reflect the common approach of correlating characteristics of genetic frequency profiles with more or less well-specified classes of environments in order to analyze adaptive potentials. Phenotypes as the direct objects of adaptedness and adaptability are not explicitly regarded in this approach. Yet phenotypic variation may reflect adaptive events when observable for traits, the states of which attest adaptedness or lack of it. Traits, particular states of which represent stress symptoms, belong to this category. In fact, while transient stress symptoms may be the result of a physiological adaptation process, individually persistent or even intensifying stress symptoms indicate adaptive failure with respect to a current environmental pressure.

The latter situation calls for evolutionary adaptation, the potential for which can only be recognized as genetic differences between groups that are distinguished by the intensity of the persistent stress symptoms (Gregorius 1994). The prerequisite for existence of this potential is that the environmental factors causing the reaction are also the ones to which adaptation is required, i.e. that epigenetic and adaptational environments coincide. For stress traits this prerequisite

is realized by definition. As a consequence of this coincidence, the (evolutionary) genetic potential available for adaptation to the stressful conditions includes those genetic types that exhibit no or only minor persistent stress symptoms when subjected to the stressor.

This approach to the description of evolutionary adaptive potential provides a concrete example of the above general definition, in that it assigns to a fraction of a population's genetic structure those environments for which this fraction contains the genetic potential for adaptation. This fraction also determines the initial population size available for adaptation (the *adaptively qualified population size)* and together with the genetic variability remaining within the adaptively qualified population, the bounds for the population's future adaptability are set. It is thus important to obtain information on the degree to which adaptation to the stressing conditions reduces the genetic potential for future adaptive processes. For the experimental verification of an adaptive condition, estimations of fractions of populations containing genetic potential for adaptation to current environmental pressures as manifested in the phenotype are therefore highly desirable.

Practical problems in obtaining such estimates arise, of course, from poor suitability of the available gene markers and the fact that stressing conditions do not affect all members of the population equally Despite genetic disposition, stress symptoms may not be expressed either because not all individuals are exposed to the stressor or because the presence of other environmental conditions neutralize the stress effects. Nevertheless, based on appropriate sampling methods there is a practical solution to this problem even for studies of populations *in situ*, as will be demonstrated later.

CHARACTERIZATION OF FREQUENCY PROFILES BY MEASURES OF DIVERSITY

The common approach to the measurement of ecological or genetic diversity of a collection of organisms aims at summarizing numbers and abundances of types within the collection into a single value. In this sense, diversity represents itself as a characteristic of a frequency profile q of defined types, where such profiles are represented by vectors of relative type frequencies arranged in decreasing order (i.e. $q_1 \geq q_2 \geq ... \geq 0, \sum_i q_i = 1$). The usage of relative in place of absolute frequencies is implied by the fact that, in general, the diversity of a collection need not depend on its size. Collection size is thus considered to represent an independent quality. Yet, this does of course not exclude the possibility of strong (positive) correlations

between size and diversity.

On the other hand, the concept of diversity is largely agreed upon to reflect numbers of types or some transformation of such numbers. Representation of a type in the collection is considered to increase with its relative frequency, and equal representation of all types is equivalent to maximum diversity for a specified number of types. Therefore. with reference to differential representation of the types, diversity is often described as an "effective number", which equals the actual number only for even representation of all types in the collection. Hence, diversity, when expressed as an effective number of types, can never exceed the collection size, so that collection size indeed sets an upper limit to diversity.

With reference to the correspondence between adaptive potentials of populations and their genetic compositions, genetic diversity can be conceived of as relating ranges of environments to which adaptation is possible to numbers of genetic types, where the frequency of each type serves as a weight of the adaptive significance of the respective environment. In particular, the "effectivity" of a type can be identified with its "operativity" and thus its prevalence, so that the effective number specified by a diversity measure relates to the size of the operating genetic potential. The relation to operating potentials probably represents one of the most appealing and obvious interpretations of diversity measures.

As a consequence of unspecific use, however, the term "diversity" is also applied to measures of differentiation or concentration within collections (cf. Nei 1975, chapters 6 and 7, Pielou 1977, p. 309ff). These measures quantify variation relative to the collection size, so that minimum and maximum differentiation are reached if all members are of the same type and if each member of the collection differs from each other in type, respectively.

Collection size therefore sets no explicit bounds to differentiation. The most widely used such measure is Simpson's (1949) index, which is specified by the probability that two members of a collection sampled at random and without replacement differ in type.

Yet, at least for large collection sizes, the common (bounded) measures of differentiation can be transformed into (unbounded) measures of diversity (cf. Pielou 1975, p. 8, Pielou 1977, p. 311, Gregorius 1978) which (as do almost all of the more widely used diversity indices) belong to the family

$$v_a := \left(\sum_i q_i^a \right)^{\frac{1}{1-a}}, 0 < a \neq 1,$$

or which are one-to-one transformations of such measures (cf. Pielou 1977, p. 311, Gregorius 1978). Among the measures most widely used in ecology and genetics are $v_2 = (\Sigma_i q^2_i)^{-1}$ and $\log (\lim_{a \to 1} v_a) = -\Sigma_i q_i . \log q_i$. In fact, the indices of v mark different criteria of effectiveness. This becomes obvious from the observation that, for non-uniform distributions, v_a is a strictly decreasing function of a and v_a ranges from n (total number of types in the collection) to q^{-1}_1 as a moves from 0 to ∞ (see Gregorius 1978). Hence, for values of a close to 0, all types (including the rare ones) receive almost equal weight in v_a, while for very large values of a ultimately only the largest frequency determines the diversity v_a (for worked fictional examples see Figure 2). However. apart from this, little seems to be known about objective criteria aiding distinction between these measures for application to special problems (cf. e.g. Hennink and Zeven 1991).

As was mentioned above the *evenness* of representation of the extant types plays a crucial part in the definition of diversity, even though it is frequently considered as an independent characteristic of frequency profiles. In fact. the evenness itself can be viewed to measure the degree to which the profile is concentrated on the effective number of types specified by the diversity. It is probably this view that explains the concept of independence between evenness and diversity. Complete evenness implies the absence of more types than are specified in the diversity value, while with decreasing evenness and otherwise constant diversity, either the types contributing to the effective number gradually become less distinguishable in abundance from the rest, or additional types appear at low abundances in the collection. Hence, in combination, diversity and evenness may hint at the existence of distinctive profile characteristics, such as steep frequency declines.

Yet, considering diversity measures from among the family v_a, it is possible to vary the effective number of types of a given non-uniform profile from the total number of types in that profile to q^{-1}_1 by choosing a suitable value for a, as was noted above. Rare types may thus be given increasing weight in the measurement of diversity. This obscures an existing separation between prevalent and rare types, since the "effective" number comes very close to the actual number suggesting large evenness. The joint analysis of diversity and evenness may therefore not reliably reveal such profile characteristics, and this is even aggravated by the fact that, with only a few exceptions, the measurement of evenness is confronted with considerable conceptual and statistical problems (see e.g. Peet 1975, Pielou 1977, p. 307, or Gregorius 1990). Effective numbers as defined by diversity indices may also be difficult to interpret in terms of numbers of prevalent types.

Apparently, among the characteristics not explicitly reflected by current diversity and evenness measures are those distinguishing prevalent from rare types, as is required for the recognition of operating and latent genetic potentials and the associated states of adaptation. The following chapter will therefore be devoted to distinguishability between rare and prevalent types (provided the latter are defined) as an adaptively important characteristic of genetic frequency profiles.

DISTINGUISHABILITY BETWEEN PREVALENT AND RARE TYPES IN FREQUENCY PROFILES

Genetic frequency profiles of populations are shaped by adaptational processes. These include the possibility of temporary adaptive neutrality or quasi-neutrality of certain genetic traits (the latter leading to more or less erratic profiles). As was argued earlier in connection with operating and latent genetic potentials, states of adaptedness are likely to be characterized by a number of prevalent genetic types and a remainder of more or less rare types (for a more detailed discussion with special reference to isoenzyme data collected in forest tree populations see Gregorius and Bergmann 1994). In such genetic profiles, prevalent and rare types (i.e. operating and latent potential) are separated by a distinct step in the frequency profile, as is exemplified in the first three profiles in Figure 2. On the other hand, certain processes of adaptation progressing from one state of adaptedness to another have to pass through intermediate profile characteristics in which either no distinct frequency steps exist (such as in the rightmost profile in Figure 2) or in which several types are approximately evenly distributed.

Moreover, the above reasoning suggests that operating and latent genetic potentials correspond to evolutionary adaptive potentials for quantitative and qualitative environmental dynamics, respectively. Therefore, characteristics of' genetic frequency profiles indicating differentiation between the two forms of genetic potential and quantifying their sizes are of considerable interest in the evaluation of adaptive potentials.

With the probable exception of certain mating systems, such as gametophytic incompatibility, where large numbers of evenly distributed genetic types may stably coexist irrespective of the adaptive pressures of the external environment, the operating genetic potential for single traits can be expected to concentrate on only relatively few types. The main reason is that even with frequency-dependence the conditions for selective maintenance of large numbers of alleles are too specific to be realizable in a continually varying environment (the first three fictional profiles

in Figure 2, for example, are typical of the vast majority of profiles observed for enzyme gene loci: see Gregorius and Bergmann 1994).

There are two basic approaches to the separation of prevalent from rare types. One consists in explicitly defining two frequency levels p and r, say, such that types with frequency larger than p or smaller than r are considered prevalent or rare, respectively. Instead of relying on such levels, the other approach consists in identifying frequency steps between neighbouring types in the profile that are sufficiently large to justify division of the types to the left and right of this step into prevalent and rare. In both approaches, the representation of types with "intermediate" frequencies plays a central role for the quantification of separability of profiles.

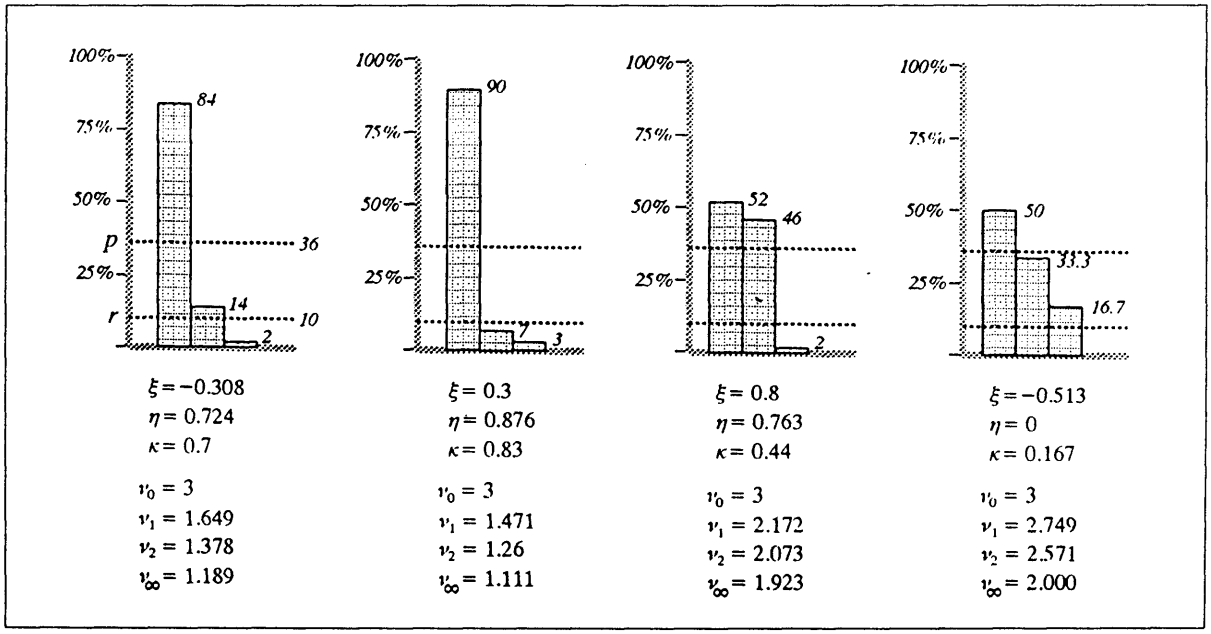

Figure 2: Examples of frequency profiles with measures (1) ξ of separation between prevalent and rare types for level $p = 0.36$ of prevalence and $r = 0.10$ of rarity, (ii) η of relative separation (or evenness), (iii) κ of concentration (maximum step size), (iv) ν_a of diversity (effective number) for $a = 0$, $a = 1$, $a = 2$, $a = \infty$.

Specified levels of prevalence and rarity in frequency profiles

In this section considerations will revolve around two frequency levels p and r ($0 < r < p < 1$), the first of which defines prevalence for a type i by $q_i > p$, and the second defines rarity by $q_i < r$. The type frequencies q_i are taken from a frequency profile $\mathbf{q}$, which implies that they are characterized by $q_1 \geq q_2 \geq \ldots \geq 0$ and $\sum_i q_i = 1$. If $q_k > p$ and

$q_{k+1} < r$ for one particular index k, the profile can be considered to be unambiguously separated into prevalent and rare types, since no "intermediate frequencies" $r \leq q_i \leq p$ exist (consult Figure 2 for an illustration). The profile thus crosses the separating interval $[r, p]$ in a single step. On the other hand, separability is absent if at least one of the profile's steps is located within the separating interval, so that $r \leq q_i \leq p$.

More generally, whenever the frequency of a type i is not located in the separating interval (i.e. $q_i > p$ or $q_i < r$), it contributes to separability according to its distance from (the nearest boundary of) this interval. Analogously, if the frequency is located within the separating interval (i.e. $r \leq q_i \leq p$), the type is "intermediate" and signifies inseparability according to the distance of its frequency from the nearest boundary of the separating interval. This concept can be simplified by considering the absolute distance of each frequency from the center of the separating interval, i.e. $| q_i - {}^1/_2(r+p) |$. If this distance is less than or equal to half the length of the separating interval (${}^1/_2-(p-r)$), the respective type belongs to the class of intermediates, while otherwise it is either prevalent or rare. In addition, the deviation $| q_i - {}^1/_2(r+p) | - {}^1/_2(p-r)$ quantifies the degree to which the type is located within or outside of the separating interval. Thus, denoting by ξ' the minimum of these deviations. i.e.

$$\xi := \min_i \left| q_i - \frac{1}{2}(r+p) \right| - \frac{1}{2}(p-r),$$

then prevalent are separated from rare types if $\xi' > 0$, and they are not if $\xi' \leq 0$. The value of ξ' indicates the (non-normalized) degree to which this is the case.

To be able to assess the completeness of separation or inseparability of a profile, consider the fact that $\xi' \geq -{}^1/_2(p-r)$. Moreover, since ${}^1/_2(p+r)$ is always among the terms over which the minimum in ξ' is to be taken (for $q_i = 0$), $\xi' \leq {}^1/_2(p+r) - {}^1/_2(p-r) = r$ specifies the upper bound for ξ'. Consequently, ξ' can be represented in the normalized form

$$\xi := \begin{cases} \frac{\xi'}{r} \text{ for } \xi' \geq 0 \\ \frac{\xi'}{1/2(p-r)} \text{ for } \xi' < 0 \end{cases}$$

in which $\xi = 1$ indicates maximum separation and $\xi = -1$ complete inseparability

of prevalent from rare types. In particular, if a profile consists of prevalent types only. i.e. if $q_i > p$ for $i = 1,...,$ n and $q_i = 0$ for $i = 1 > n$, then $\xi' = \min\{q_n - {}^1/_2(p + r), {}^1/_2(p + r)\} - {}^1/_2(p-r) = \min\{q_n - p, r\} \geq 0$, so that $\xi = \min\{q_n - p, r\}/r$. In this case $\xi = 1$ if $q_n \geq p+r$. Similarly, if all types are rare ($q_i < r$ for all i), then $\xi' = {}^1/_2(p + r) - \max_i q_i - {}^1/_2(p - r) = r - q_i \geq 0$, so that $\xi = (r - q_1)/r$. Figure 2 provides examples for ξ-vales of different frequency profiles.

Numbers of prevalent, intermediate and rare types in a frequency profile with n types are consistently defined by

$$n_+ := \max\{i \mid i \geq 1, q_i > p\}, \qquad n_0 := \max\{i \mid q_i \geq r\} - n_+, \qquad n_- := n - n_+ - n_0,$$

respectively. Among these numbers, n_+ and n_0 but not n_- can be estimated from random samples. The pertinent sample values are consistent estimators. and the probability of detecting all types with frequency $\geq p$ or $\geq r$ in the population can be specified for each sample size (Gregorius 1980).

A special case of interest arises if $p = r$, where the separating interval reduces to a single point and, consequently, prevalent types are separated from rare ones by only a single value. In this case ξ' and ξ simplify to

$$\xi' = \min_i |q_i - p|, \xi = \frac{\xi'}{p},$$

which implies that ξ cannot become negative and a type can be classified as intermediate only if $q_i = p$.

Relative separability of prevalence from rarity

If no a *priori* criteria are available for the specification of the above levels of prevalence (p) and rarity (r), the shape of the profile must be directly explored with respect to discontinuities in order to detect tendencies for separation of frequent from rare types and thus for the existence of operating and latent genetic potentials. In such a situation, prevalence and rarity can only be defined relative to the most frequent type, which will then also serve as the defining criterion of preva-

lence. Further characteristics of a profile must then be viewed within this relative setting.

The most direct methods of detecting relative shape characteristics of a profile **q** can probably be based on its "step sizes" $s_i := q_i - q_{i+1}$. As was emphasized in the previous section, these step sizes determine the degree of separability of a profile. The absence of any variation in step sizes from the most frequent type to the last type with positive frequency apparently represents the absence of discontinuity in a profile in that it states the existence of all types "intermediate" between the most and least frequent type. This situation is realized only in profiles of the linearly declining form

$$q_i = \frac{2 \cdot (n + 1 - i)}{n \cdot (n + 1)} \text{ for } i = 1,...,n$$

where n is the number of types represented in the frequency profile and

$$q_1 = \frac{2}{n + 1}, s_i = \frac{2}{n \cdot (n + 1)} \text{ for } i = 1,...,n.$$

In the following, this kind of profile will be referred to as a *linearly declining profile* (for a demonstration, see the rightmost profile in Figure 2).

The other extreme is characterized by a single large step between the most and least frequent type. Since the smallest frequency is always zero, this is equivalent to a uniform distribution with all existing types of equal frequency, so that all of these types are to be classified as prevalent. Again, such profiles must necessarily be of the form

$$q_i = \frac{1}{n} \text{ for } i = 1,...,n,$$

which demonstrates that for both extremes the corresponding profiles are solely

determined by their numbers n of existing types. Particularly for large numbers of types in both the linearly declining and the uniform kind of profile, the relative (and thus limited) significance of considering the most frequent as the "prevalent" type becomes apparent.

Depending on the position a particular frequency profile takes in the continuum between the linearly declining and the uniform kind, one can distinguish various degrees of relative separability of rare from frequent types. The more a profile resembles the linearly declining kind, the less separable frequent types are from rare ones, and the separability increases as the profile becomes more uniform. To arrive at a meaningful measure of the degree of relative separability, it is thus necessary to specify for each frequency profile its "corresponding" linearly declining and uniform profile. At a minimum, this correspondence must reflect the fact that the maximum step size

$$\kappa=\kappa(\mathbf{q}):= \max_i (q_i - q_{i+1})$$

in the profile **q** must (*i*) neither exceed that of the uniform nor (*ii*) fall below that of the linearly declining profile.

Apparently, the first condition (*i*) is fulfilled if the number n' of types in the uniform profile obeys the inequality $1/n' > q_1$, since $q_1=\Sigma_i(q_i - q_{i+1})$, so that κ may approach q_1 arbitrarily closely. A *corresponding uniform profile* can therefore be found by setting its number n' of types equal to the largest integer $\leq 1/ q_1$. The maximum step size $\kappa_{max'}$ say, of this uniform profile then equals $\kappa_{max} = 1/n'$, and among all profiles obeying the restrictions of condition (*i*) it is the one that comes closest to the reference profile **q**.

The second condition (*ii*) can be made more precise by again considering the relation $q_1 = \Sigma_i(q_i - q_{i+1})$. It follows from this relation that for constant sum (q_1) of step sizes, the smallest κ is realized for least variation among the step sizes, and that this minimum value of κ decreases with decreasing q_1. Consequently, the actual value of κ can never fall short of the (invariant) step size in a linearly declining profile, the frequency of whose dominant type is less than or equal to q_1. The dominant type in a linearly declining profile with n'' types has frequency $2/(n'' + 1)$, so that condition (*ii*) is fulfilled if $q_1 \geq 2/(n'' + 1)$. Hence, a *corresponding linearly declining profile* can be defined by setting its number n'' of types equal to the smallest integer $\geq (2/ q_1)-1$, which again specifies among all profiles obeying the restrictions

of condition (*ii*) the linearly declining profile approaching most closely the reference profile. As explained above, its maximum step size κ_{min}, say, equals $\kappa_{min} = 2/(n''\cdot(n''+1))$.

It must be kept in mind, however, that monomorphic profiles cannot show a linear decline and that therefore the lower bounds for κ realized in linearly declining profiles are applicable to polymorphic profiles only. Hence, the largest lower bound κ_{min} is reached for all polymorphic profiles with $q_1 > 2/3$, since the corresponding value for n'' then equals 2. In other words, $\kappa_{min} = 1/3$ for all profiles with $q_1 \geq 2/3$.

Clearly, $\kappa_{min} \leq \kappa \leq \kappa_{max}$, where the fact that n' and n'' are integers implies that κ_{min} and κ_{max} are discontinuous functions of q_1. This is an undesirable feature in an intrinsically continuous concept of separability. Yet, for the upper bound the discontinuity can be removed by substitution of $1/q_1$ for n' in κ_{max}. This substitution makes sure that κ_{max} retains its property of an upper bound for κ and that $\kappa_{max} = \kappa$ solely for a uniform profile.

Finding a consistent continuous extension of the lower bound κ_{min} is more intricate since it requires specification of the minimum value of κ for all profiles with given value of q_1. The problem lies in the fact that only special values of q_1 (namely $q_1 = 1/m$ with m belonging to the set of positive integers) allow for linearly declining profiles. This problem is treated in the Appendix, and it is shown there that the substitution of $(2/q_1)-1$ for n'' in κ_{min}, i.e. $\kappa_{min} = q_1^2/(2-q_1)$, yields the desired lower bound. Recall, however, that this substitution applies only to profiles with $q_1 < 2/3$ For profiles with $q_1 \geq 2/3$, the lower bound κ_{min} remains fixed at 1/3, which continuously extends the value of $q_1^2/(2-q_1)$ for $q_1 = 2/3$.

Consequently, the relative position of the maximum step size κ of a profile **q** between the maximum step sizes κ_{max} and κ_{min} of its corresponding uniform and linearly declining profile, respectively, can be measured by

$$\eta = \eta(q) := \frac{\kappa - \kappa_{min}}{\kappa_{max} - \kappa_{min}}$$

where $\kappa_{max} := q_1$ and

$$\kappa_{max} := \begin{cases} \dfrac{q_1^2}{2-q_1} \text{ for } q_1 < \dfrac{2}{3} \\ \dfrac{1}{3} \text{ for } q_1 \geq \dfrac{2}{3} \end{cases}$$

so that

$$\eta = \begin{cases} \dfrac{\kappa \cdot (2 - q_1) - q_1^2}{2 \cdot q_1 \cdot (1 - q_1)} & \text{for } q_1 < \dfrac{2}{3} \\ \dfrac{\kappa - 1/3}{q_1 - 1/3} & \text{for } q_1 \geq \dfrac{2}{3} \end{cases}$$

Based on the relation between maximum step size κ and the frequency q_1 of the dominant type, the index η measures the degree to which a profile deviates from linear decline and thus from complete inseparability of "rare" from "frequent" types. The largest such deviation is reached in the case of a uniform profile. This is reflected by $\eta = 0$ only for linearly declining profiles and $\eta = 1$ only for uniform profiles. It is thus justified to call η a *measure of relative separation* of prevalent from rare types (see also the examples of η-values in Figure 2).

Though derived for a different purpose, the characteristics of the index η recommend it for the measurement of an additional profile characteristic commonly referred to as evenness. When viewed under this aspect, η is distinguished from all common measures of evenness by the fact that it explicitly includes a concept of complete unevenness as specified for each number of types by the intuitively appealing case of a strictly linearly declining profile (this basically differs from the diversity-oriented measures of evenness, where the situation of monomorphism serves as the lower bound; see e.g. Hurlbert, 1971, or DeBenedictis, 1973). Thus, $\eta = 1$ and $\eta = 0$ correspond to complete evenness and complete unevenness. In addition to these desirable features, η avoids all of the above mentioned conceptual and statistical problems encountered with most of the common measures of evenness.

Concentration of a frequency profile

It was noted in the last section that the specification of *relative* separability of prevalence from rarity may be of limited significance if the frequency q_1 of the dominant type becomes small. In such cases one would rather prefer to classify all types as rare, as was possible on the occasion of specified levels of prevalence and rarity treated in the second to the last section. If such levels are not specified, a measure reflecting both the degree of prevalence of the dominant types and their distinction from rare types is required. Since relative prevalence can be realized only for a limited number of types, distinct differences between prevalence and

rarity can be observed only in frequency profiles characterized by a few evenly distributed dominating types. In fact, this situation is commonly recognized as one of high "concentration" of the observed variation, and it is usually considered as the complement of diversity (cf. e.g. Pielou 1977, p. 309).

If separability between prevailing and rare types is of concern low diversity in the sense of small effective number is not a sufficient criterion for high concentration. It is rather required that both the number of prevailing types and their evenness in representation enter a measure of concentration such that, with increasing number of prevailing types and/or increasing unevenness in the profile, the concentration decreases. In fact, the maximum step size κ (in its non-normalized version) fulfills these requirements, since the upper bound $\kappa = 1$ is reached only for monomorphism, and the smallest value of κ for given number n of types is realized exclusively in a linearly declining profile. Therefore κ suggests itself as a suitable *measure of concentration* of a frequency profile.

When applied in combination, κ and η can be used for more qualified statements on the separability of frequent from rare types. While sufficiently large values of κ mark the existence of types referable to as prevalent (the number of which cannot exceed $1/\kappa$), η specifies the degree to which these types contrast with the rest. For example, when a profile has $\kappa = 1/3$, at most three types could be referred to as prevalent in this profile ($1/\kappa = 3$), and it would require a uniform profile (with $\eta = 1$) to realize this number; the contrast would then be complete, since rare types would not even exist. However, $\kappa = 1/3$ can also be realized in a linearly declining profile with two types. Both types are again to be classified as prevalent, but $\eta = 0$ reveals maximum unevenness in representation and thus no contrast even between the two. For arbitrary numbers n of types, the profile

$$q_1 = q_2 = \frac{n+1}{3n} \text{ and } q_i = \frac{1}{3n} \text{ for } i=3, \ldots, n \text{ has } \kappa=1/3 \text{ for all } n \text{ and two prevalent}$$

types. As n increases from 3 to infinity, η grows from 13/20 to 1, thus indicating growing contrast with the rare types (further examples are provided by Figure 2).

Numbers of prevalent types - While the estimation of numbers of prevalent or rare types is conceptually unambiguous when the pertaining levels are specified (p and r in the preceding section), various aspects may become relevant in the case of relative separability. The above statement that the number of prevalent types will never exceed $1/\kappa$ is of course not a sufficient specification even though it points out a basic relation of such specification to the concept of relative separability.

For example, if the maximum step size is realized only once in the profile and if

it sufficiently exceeds the other step sizes, then one might agree that the types located to the left of the maximum step size in the profile are the prevalent types. The less distinguished the maximum step size is from the rest, the more the ambiguity in the assignment of prevalence increases. As an intrinsic part of the present concept, complete ambiguity exists if all step sizes are equal and the profile is linearly declining. In fact, the measure η quantifies this ambiguity. Thus the large η values for the first three profiles in Figure 2 strongly suggest that all types to the left of the maximum step size (which is also large) be considered as prevalent, so that each of the first two profiles contains one prevalent type and the third profile contains two such types. However, this approach to the estimation of numbers of prevalent types will not be further expanded upon in the present paper.

ESTIMATION OF ADAPTIVE POTENTIALS FOR SPECIAL ENVIRONMENTS

We now return to the above problem of estimating in natural populations genetic potentials for adaptation to special environments which are recognizable by their effects on stress traits. For problems of feasibility, such estimates must resort to gene markers of at least partially unknown function, so that any method is limited to the degree to which such gene markers can detect adaptive potentials. To simplify the derivations, only two trait states, called “sensitive” and “tolerant” will be considered. The applied notation and assumptions are listed in Table 2. The assumption of stochastic independence between genotypes (D and G) and environments (U) is generally difficult to defend in naturally regenerating plant populations because of the possibility for the evolution of differential local adaptations. However the assumption is likely to be realized at least approximately in many cases, since gene flow within habitats may be considerable and the gene loci controlling the stress trait as well as those under observation may not be involved in micro-spatial adaptive differentiation. In addition, application of appropriate methods of structured sampling (Gregorius 1989) can aid fulfillment of the condition of independence.

The aim is now to distinguish the group of individuals with tolerant disposition from those with sensitive disposition on the basis of an observable genetic trait and observable stress symptoms. In the present context, usage of the term "disposition” presumes that the environment has no share in the modification of the concerned characteristics, which leaves genetic effects as the only cause for individual differences in disposition.

U:	specifies the environmental condition of an individual; $U=s$ indicates stress conditions.
D:	specifies the stress disposition of an individual; $D=t$ indicates the absence (tolerance) and $D=s$ the presence (sensitivity) of a disposition to react to stress.
R:	specifies presence ($R=s$) and absence ($R=t$) of stress symptoms for an individual (its phenotypic stress state).
G:	specifies an observable genetic trait (gene marker).
$P(...)$:	denotes the joint probability distribution of U, D, R, and G.
$\triangleright$	An individual is assumed to show stress symptoms ($R=s$) if and only if it possesses a sensitive disposition ($D=s$) and is subject to stress conditions ($U=s$), i.e. $[R=s] = [D=s\ U=s]$ (1)
$\triangleright$	D and G are stochastically independent of U

Table 2: Notations and assumptions for the estimation of adaptive potentials from stress traits.

The specifications in Table 2 imply that an individual with sensitive disposition ($D=s$) may display a tolerant phenotype ($R=t$), if it is not subjected to stress conditions ($U\neq s$). This can be made explicit in the equation

$$[R=t] = [U\neq s] \cup [U=s, D=t] = [U\neq s, D=s] \cup [D=t] \qquad (2)$$

Moreover, the chances of an individual to be subject to the stressing conditions neither depend on its disposition nor on its observable genotype.

As follows immediately from equation (1) in Table 2 and the assumption of stochastic independence.

$$P(G=g \mid R=s) \frac{P(G=g, D=s, U=s)}{P(D=s, U=s)} = \frac{P(G=g, D=s) \cdot P(U=s)}{P(D=s) \cdot P(U=s)} = P(G=g \mid D=s) \qquad (3)$$

i.e. the distribution of the observable genetic trait is the same among sensitively

reacting and sensitively disposed individuals. Consequently, by equations (2) and (3)

$$
\begin{aligned}
&P(D=t).[P(G=g \mid D=t)-P(G=g \mid D=s)] = \\
&\quad =P(G=g,R=t)-P(G=g,U\#s,D=s)-P(D=t).P(G=g \mid D=s) \\
&\quad =P(G=g,R=t)-P(G=g,D=s).P(D\#s)-P(D=t).P(G=g \mid D=s\ ) \\
&\quad = P(R=t).P(G=g \mid R=t) - P(G=g \mid D=s).[P(U \neq s).\ P(D=s)+ P(D=t)] \\
&\quad =P(R=t).P(G=g \mid R=t)-P(G=g \mid R=s).P(R=t\ ) \\
&\quad =P(R=t).[P(G=g \mid R=t)-P(G=g \mid R=s)\ ]
\end{aligned}
\qquad (4)
$$

This equation establishes the fundamental relation between the distribution of an observable genetic trait across phenotypic stress states and across (non-observable) stress dispositions. Since the term "disposition" addresses a purely genetically determined character, carriers of the same (multilocus) genotype coding for tolerant or sensitive disposition cannot appear in both sets *[D=t]* and [*D=s*]. Hence, *P(D=t)* equals the fraction of the population containing the genetic potential for adaptation to the stressing conditions, which, in agreement with the previously introduced terminology, will be called the **adaptively qualified fraction** and the estimation of which is the subject of this section.

The practical problem, however, stems from the fact that the observable genetic traits may only partially separate one class of stress disposition from the other in that carriers of a particular genotype may occur in either the class of sensitive and of tolerant disposition. It is therefore of central importance to determine the degree to which any particular genetic trait contributes to the distinction between the classes of stress disposition. The proportion of individuals with tolerant disposition that can be distinguished from those with sensitive disposition by the observable genetic trait is therefore all that we can identify from the target quantity *P(D=t).* This estimate constitutes a lower bound.

The principle of such a distinction involves for each attribute (observable genotype) the determination of the number of members of one set (tolerants) left after subtraction of those members from the other set (sensitives) showing the same attribute. The sum of these differences over all attributes specifies the extent to which the first set differs from the second. To exclude the possibility that characteristics other than those specified by the attributes of interest affect the measurement, the size of the second set must be the same as that of the first set.

Applying this principle to the present situation, where the first and second sets consists of the individuals with tolerant and sensitive disposition, respectively, and where the attribute variable is G, one has to assume that both sets have size proportional to $P(D=t)$. The distribution of G in the sensitive group is then characterized by the frequencies $P(G=g \mid D=s)$. $P(D=t)$. Hence, for each attribute $G=g$, the set with tolerant disposition differs from that with sensitive disposition by a number proportional to

$$\max \{P(D = t, G = g) - P(G = g \mid D = s) \cdot P(D = t), 0\}$$

the sum of which taken over all attributes (genotypes) yields

$$\pi_G := P(D = t) \cdot \sum_g \max\{P(G = g \mid D = t) - P(G = g \mid D = s), 0\}$$

$$= P(D = t) \cdot \frac{1}{2} \sum_g \left| P(G = g \mid D = t) - P(G = g \mid D = s) \right|$$

where the right side of this equation is a consequence of the identity $\max\{a,0\} = {}^1/_2(a + |a|)$. Hence, π_G equals the overall *proportion of individuals with tolerant disposition distinguishable by the genetic trait G from those with sensitive disposition.* So far π_G is a population parameter that does not depend on the assumption of stochastic independence. By application of equation (4) to the last equation (which now involves the assumption) one obtains the representation

$$\pi_G = P(R = t) \cdot \frac{1}{2} \sum_g \left| P(G = g \mid R = t) - P(G = g \mid R = s) \right| \qquad (5)$$

which shows that the adaptive potential detectable by the genetic trait G equals the proportion of phenotypically tolerant individuals reduced by the genetic distance between the phenotypically tolerant and the phenotypically sensitive group. This

is the required result.

Since $\frac{1}{2}\sum_{g} \left| P(G = g \mid D = t) - P(G = g \mid D = s) \right| \leq 1$, equation (4) implies

$$P(D = t) \geq P(R = t) \cdot \frac{1}{2} \sum_{g} \left| P(G = g \mid R = t) - P(G = g \mid R = s) \right| \qquad (6)$$

As suggested by the definition of π_G, quality is reached in this estimation only if the genetic trait G completely separates individuals with tolerant from those with sensitive disposition, i.e., where tolerant and sensitive individuals do not have any of the observable genotypes in common. This need not imply complete separation on the phenotypic level R of stress response, since phenotypically tolerant individuals may have sensitive disposition (as is the case for $P(R = t) > P(D = t)$). Hence, the adaptive potential as estimated by equation (5), i.e., the *adaptively qualified fraction detectable by the genetic trait G*, may reflect the total adaptive potential ($\pi_G = P(D = t)$), even though G does not completely separate the phenotypically tolerant from the phenotypically sensitive group. On the other hand, if G completely separates both groups on the phenotypic level, it also does so on the level of disposition, so that $\pi_G = P(D = t)$. This follows from inequality (6) together with the fact that $P(D = t) < P(R = t)$ always holds.

Since the genetic potential for adaptation to the stressing conditions is confined to the phenotypically tolerant part of the population, the quantity of primary interest is the adaptively relevant fraction detectable within this part by the genetic trait, i.e., the quantity $\pi_G / P(R = t)$. By equation (5) this is seen to equal the genetic distance

$$\rho_G := \frac{1}{2} \sum_{g} \left| P(G = g \mid R = t) - P(G = g \mid R = s) \right|$$

between the phenotypically sensitive and tolerant group of individuals.

An idea about the order of magnitude which estimates of ρ_G may attain for isoenzyme gene markers can be gained from the investigation of Konnert (1992),

who studied needle loss as a supposed reaction to air pollution in several German populations of *Abies alba*. Classes of phenotypically sensitive and tolerant individuals were formed according to the extreme percentages of needle loss, and three different sampling schemes were applied to account for possible effects of associations between genotypes and local environment. Table 3 provides an example for the computation of ρ_G for a set of Konnert's data showing one of the smallest genotypic differences between tolerant and sensitive collections at the diallelic enzyme locus IDH-B. In fact, taking the respective maximum value over the 9 analyzed enzyme gene loci, ρ_G ranged from 14.3% to 39.8% across eleven populations and averaged over the three sampling schemes for genotype frequencies, and it ranged from 8.0% to 20.7% for allele frequencies with a tendency towards the larger values.

		At enzyme locus IDH-B proportion (%) of genotype			
		$G=B_2B_2$	$G=B_2B_3$	$G=B_3B_3$	Σ
among the 30% trees} with least needle loss}	R = t	7.7	48.1	44.2	100
among the 30% trees} with most needle loss}	R=s	13.5	44.2	42.3	100
$\lvert P(G=g\lvert R=t) - P(G=g\lvert R=s)\rvert$	(%)	5.8	3.9	1.9	$\rho_G = 5.8$ (%)

Table 3: The computation of ρ_G for a set of data on needle loss in Abies alba taken from Konnert (1992, Table 4, Method 2).

Apparently, the ρ_G values vary considerably between populations, indicating that among their phenotypically tolerant members the populations harbour to different degrees genetic potential for adaptation to the environmental conditions causing needle loss. The ρ_G values for genotype frequencies refer to the fraction of individuals with tolerant disposition and therefore always exceed the corresponding values for allele frequencies. Considering that genes rather than genotypes are the units of inheritance, it might appear more realistic to estimate the genetic

potential for adaptation in the following generations (i.e. the evolutionary adaptive potential) by the ρ_G values for the allele frequencies. However, it is the system combining these genes into genotypes that determines the capacity to realize the inherent genetic adaptive potential.

Variability of the observable genetic trait - A problem of more general significance arises with the usage of highly variable genetic traits as can result from the inclusion of large numbers of polymorphic loci into a study. At the extreme, each member of the population is distinguished from each other by its observable multilocus genotype, which enforces a genetic distance of 1 between the groups of sensitive and tolerant individuals both at the level of disposition and phenotype. Thus $\pi_G = P(D=t) = P(R=t)$ irrespective of the joint distribution of D and U which is a contradiction. The reason for this is to be found in the complete association between G and L . which results from the fact that no genotype is repeated across the environments; the basic prerequisite of stochastic independence between G and U is thus invalidated.

Therefore, in contrast with many other applications such as tracing descent, highly variable genetic traits may not constitute the appropriate tool for the estimation of adaptive potentials. It may therefore be preferable, as was done in the above interpretation of the results of Konnert, to compute π_G or ρ_G for each of several genetic traits of intermediate variability and take the maximum of these values over traits as an estimation of the adaptively qualified fraction (or its part among the phenotypically tolerant individuals).

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APPENDIX

Lemma: For each $0 < q < 1$ there exists exactly one frequency profile **q** of the form

(a) $q_i = q - (i-1) \cdot s$ for i=1,....,m

(b) $0 < q_m = \leq s$

(c) $\sum_{i-1}^{m} q_i = 1.$

In this profile

s_i=s for i=1,....,m-1,

$\kappa(\mathbf{q})$=s,

$$s = \frac{2 \cdot (m.q - 1)}{m \cdot (m-1)},$$

m = the smallest integer $\geq(2/q)$-1

Proof: Applying condition (c) to (a), one obtains $1 = (q + s)m - sm(m + 1)/2$, and from this $s = 2(mq-1)/(m(m-1))$, which is the desired result up to the specification of m. The latter follows from condition (a) and (b), which imply $0 < q-(m-1)s \leq s$ and therefore $(m-1)s < q \leq sm$. Substituting in the last inequality for s one obtains $2(mq-1)/m < q \leq 2(mq-1)/(m-1)$, which can be rearranged into the form $(2/q)-1 \leq m < 2/$

q showing that m indeed equals the smallest integer $\geq (2/q) - 1$.

Proposition: Among all frequency profiles **q** with given first component $q_1 = q$ for some q, $\kappa(\mathbf{q})$ becomes minimal only for the profile specified in the above Lemma in which all steps, with the possible exception of the last (positive) step, equal the maximum step; i.e. for

$$\kappa_{min} := \min\{\kappa(\mathbf{q}) \mid \mathbf{q} \text{ is a frequency profile with } q_1 = q\}$$

$\kappa_{min} := \min\{\kappa(\mathbf{q}')$; where

$$q'_i = \begin{cases} q-(i-1)\cdot\kappa_{min} \text{ for all } i \text{ with } (i-1)\cdot\kappa_{min} \leq q \\ 0 \text{ for all } i \text{ with } (i-1)\kappa_{min} > q, \end{cases}$$

$$\kappa_{min} = \frac{2\cdot(m.q-1)}{m\cdot(m-1)} \quad \text{with } m := \text{the smallest integer} \geq (2/q)\text{-}1$$

$$\kappa_{min} \geq \frac{q^2}{2-q} \quad \text{with equality if and only if} \quad q = \frac{2}{m+1}$$

Proof: Let the last positive component of the profile **q** be the n-th. Suppose $s_i < s_{i+1} = \kappa$, and choose $0 < \varepsilon < \min\{q_n, \kappa - s_i\}$; then for a transformed profile $\mathbf{q}'$ with all components equal to those of **q** except for $q'_{i+1} = q_{1+1} - \in$ and $q'_{n+1} = \in$, it follows that $s'_i = q'_i - q'_{i+1} = s_i + \in < \kappa, s'_{i+1} = s_{i+1} - \in < \kappa, s'_n = s_n - \in < \kappa$, and $s'_j = s_j$ for all other indices j. This type of transformation can be repeated until there is no i left with $s_i < s_{i+1} = \kappa$. Consequently, all maximum profile steps would be lowered with the exception of the first step, if it were a maximum step. To analyze this case, consider $s_1 = \kappa > s_i$ for $i \geq 2$. If $n = 2$ the assumption $s_1 = \kappa > s_2$ implies that the profile already has the shape specified in the Lemma and that $q_1 > 2/3$ since $s_1 = 2q_1 - 1 > s_2 = 1 - q_1$. Hence, $m = 2$ and $\kappa = 2q_1 - 1 = \kappa_{min}$.

For $n \geq 3$ choose $0 < \varepsilon < \min\left\{\frac{n-2}{n-1}\cdot(\kappa - s_2), (n-2)\cdot q_n\right\}$. In the transformed profile

$q_1' = q_1$, $q_2' = q_2 + \varepsilon$, and $q_i' = q_i - \varepsilon / (n-2)$ for $i = 3,.....,n$, one now has the step sizes $s_1' = s_1 - \varepsilon < \kappa$, $s_2' = s_2 + \varepsilon \cdot (n-1) / (n-2) < \kappa$, $s_n' = s_n - \varepsilon / (n-2) < \kappa$, and $s_i' = s_i < \kappa$ for $3 \le i < n$ provided $n > 3$. Again, the maximum step size can be lowered without changing q_1.

In summary, without changing q_1, the maximum step size in a profile can be lowered as long as in the profile either a maximum step is preceded by a smaller step, or no step except the first is a maximum step. Hence, κ becomes minimal only in a profile in which all steps are maximum with the possible exception of the last. By the above Lemma such a profile exists and is uniquely specified. Finally to see that $\kappa_{min} \ge q^2/(2-q)$, consider that

$$\kappa_{min} - \frac{q^2}{2-q} = \frac{2(mq-1)(2-q) - q^2 m(m-1)}{m(m-1)(2-q)} = \frac{((m+1)q-2)(2-mq)}{m(m-1)(2-q)},$$

which follows after some rearrangement, and where the right side is non-negative as a consequence of $(2/q)-1 \le m < 2/q$. This proves the Proposition.

Remark: In profiles with $n = 2$ types and $2/3 < q_1 < 1$ one obtains $\kappa = \kappa_{min} = 2q_1 - 1$, so that the largest frequency step in the profile cannot become smaller in any other profile with the same q_1.

Chapter
11

MOLECULAR POPULATION GENETICS AND EVOLUTION: TWO MISSING ELEMENTS IN STUDIES OF BIODIVERSITY

Alfred E. Szmidt[1]

INTRODUCTION

Biodiversity has become the subject of intensive debate among politicians and scientists alike. Hardly a week goes by without a new report or conference about biodiversity. As a result, a massive amount of information has accumulated covering impressively diverse fields ranging from sociology to economics (e.g., Gershon 1992, Machlis 1992, Perrings *et al.* 1992). So pervasive is the use (and misuse) of this term in the mass media and scientific media that by now it can be viewed as a new buzzword, surpassing its recent predecessor: biotechnology (see Lovett (1994) for opposite view on this subject).

Biodiversity refers to the variety and variability among living organisms and the ecosystems in which they interact (Woodruff and Gall 1992). Therefore, it is intrinsically associated with the genetic system. Genetics and evolution sometimes enter the biodiversity debate but most of the current discussion is focused on taxonomic and ecological aspects of biodiversity (Faith 1994, Platnick 1991,

1 **Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå Sweden.**

Prendergast *et al.* 1993, Renner and Ricklefs 1994). When genetics is considered in biodiversity programmes, it is often concerned with collection, long term preservation and cataloguing of genetic variation detectable by an *ad hoc* chosen set of genetic markers rather than with assessing the processes that created its present pattern.

Rapid advances in molecular biology have furnished a wide array of new methods to study genetics and evolution of plants. Many of these methods provide excellent means for acquiring genetic information relevant for biodiversity conservation programmes. However, successful utilization of these methods requires a good understanding of the type of genetic information they can provide. In this contribution, I briefly describe currently available methods for the detection of genetic variation and suggest how they can be used in order to improve our knowledge about the genetic components of tree biodiversity.

CURRENT APPROACHES TO STUDY BIODIVERSITY

Species inventories are regarded as crucial to solving the 'biodiversity crisis' ; see Renner and Ricklefs, (1994) for discussion on this subject. Species richness and the presence of rare species are the most frequently cited criteria for site selection for conservationists (Prendergast *et al.* 1993). In the past, conservation decisions have been directed towards saving prominent species, representative ecosystems and threatened areas (Renner and Ricklefs 1994). However, species-rich areas frequently do not coincide for different taxa, and many rare species do not occur in the most species-rich areas (Prendergast *et al.* 1993). Thus, as noted by Platnick (1991) numbers of species alone are an inadequate guide to the relative importance of individual areas. Furthermore, predictions of species distributions due to the climate change have neglected the evolutionary potentials that exist within species (Eriksson *et al.* 1993). Thus, even taxonomists came to doubt whether detailed species inventories are needed to identify areas for conservation (Renner and Ricklefs 1994). First, full counts of all organisms are impossible on any scale. Second, saving species may not save all of their useful alleles and may not save the communities or their evolutionary dynamic (Namkoong 1992). Third, attempts to save communities may not even save the species they presently contain (Namkoong 1992).

GENETIC ISSUES IN BIODIVERSITY CONSERVATION

It is sometimes suggested that the extinctions of species due to modification of

environment are taking place so rapidly that the question of loss of genetic variability within species is moot because all individuals may have disappeared before drift has a chance to operate (Savolainen and Kärkkäinen 1992). The many ecological causes of extinction often operate before lack of genetic variation becomes an issue (Lande 1988). Although genetic research may not always be able to catch up with the pace of species extinction, the decline of many species is slow enough to warrant meaningful consideration of its genetic causes and effects. Moreover, the loss of genetic variation is not the only potential outcome of environment modification. Various genetic strategies and recommendations for biodiversity conservation have been formulated (Eriksson *et al.* 1993, Gregorius 1991, Hedrick and Miller 1992, Kresovich and McFerson 1992, Namkoong 1992). Most of these initiatives stress the importance of documenting patterns of genetic variation, as well as providing an understanding of the evolutionary determinants that influence these patterns.

Information on tree genetic variation, central to the design of appropriate conservation strategies is still scarce. Intraspecific variation has not been thoroughly studied in temperate regions, and there is only sparse information from tropical areas (Bawa and Ashton 1991, Ehrlich and Daily 1993). Likewise, research is lacking in the areas of taxonomy, phylogeny, reproductive biology and ecotypical differentiation, especially of tropical trees (Williams 1991). It is ironic that the start of interest in forest genetic resources was about the same time as that for crop genetic resources, but never attracted adequate funding (Williams 1991).

Genetic variation is a result of changing evolutionary histories and in itself is of value to the present and future individuals, populations, and species in which it occurs (Namkoong 1992). It is a prerequisite for future evolution and biodiversity conservation programmes should provide opportunities for it (Eriksson *et al.* 1993). Therefore, programs conserving genes in forest trees should be based on evolutionary concepts and the existing adaptations should be used when populations are appointed as gene resource populations (Eriksson *et al.* 1993). It is not clear however, how these adaptations can be assessed and evaluated. Obviously, we lack explicitly stated and realistic tactical means for implementation of the proposed strategies.

COMPONENTS AND DETERMINANTS OF GENETIC VARIATION

The biological function of plants relies on an intimate interplay between three distinct genomes: nuclear, chloroplast and mitochondrial. All these genomes harbour

genes which are vital to growth, photosynthesis, respiration and other biological processes. Therefore, studies of genetic variation should consider all these three components of the plant genetic system. Furthermore, each of these components harbours different structural, RNA and regulatory genes as well as non-coding sequences. The relative proportion of coding and non-coding sequences differs among chloroplast, mitochondrial and nuclear DNA. A substantial part of the nuclear genome contains non-coding sequences. In contrast, chloroplast genome is dominated by coding sequences. Ideally, studies of genetic variation should consider all these types of sequences.

Selection, mutation, drift, gene flow and mating system are among the most important evolutionary determinants of genetic variation. The relative significance of these determinants is likely to vary among genes, populations, species and habitats. Large populations may be immune to drift but may be exposed to highly variable selective pressures. Small populations may suffer loss of variation due to an increased inbreeding and drift but experience only weak environmental pressures.

The amount and distribution of genetic variation is also closely associated with the mode of its transmission and the rate of recombination among loci. In contrast to biparentally inherited nuclear genes, cytoplasmic genes show predominantly uniparental inheritance (Birky 1988, Clegg 1989). Chloroplast genes are generally maternally inherited in angiosperms, and paternally inherited in gymnosperms (Conde *et al.* 1979, Szmidt *et al.* 1987), while mitochondrial genes are maternally inherited in most plants (Palmer 1992). As a consequence of these different modes of inheritance, the extent of gene flow among populations may differ for biparentally, maternally and paternally inherited genes (Birky *et al.* 1989). Therefore, the extent of population differentiation is expected to vary among nuclear, maternally and paternally inherited genes for the same set of populations (Birky *et al.* 1989; Ennos 1994).

Because of the heterogeneous nature of evolutionary determinants of genetic variation we need specific, explicitly formulated approaches to study their effects. Most of our knowledge about the amount and distribution of genetic variation in forest trees comes from surveys of genetic marker variation. The validity of this knowledge depends on the type of genetic information provided by the markers used to generate it. One important question concerning the informativeness of genetic markers is: what *is their genomic origin, transmission and function ?* Another important question is: *which evolutionary determinant is most likely to affect the markers employed in our studies?* Depending on the nature of evolutionary determinants, individual markers may or may not respond to them. For instance, in the absence

of selection, genetic variation will be affected by mutation, gene flow and drift. These processes will affect all loci, regardless of their function. On the other hand, selective forces are more likely to affect variation of the structural, regulatory and RNA genes than that of non-coding portions of the genome. Thus, the patterns of variation at selected loci may differ from that of neutral loci (Hattemer 1991).

The wide array of currently available molecular techniques has greatly improved our ability to study genetic variation and to discern its evolutionary significance. However, there still appears to be much confusion among biodiversity students with regard to the genetic informativeness and feasibility of particular methods. In the next three sections, I briefly summarize these methods and describe the type of genetic information they provide.

MOLECULAR METHODS FOR DETECTING GENETIC VARIATION

Enzyme markers

Enzyme markers represent electrophoretically detectable forms of enzymatic proteins visualized by substrate-specific staining. The predominantly codominant character of enzyme variation, low cost and technical simplicity of the analysis (Weeden and Wendel 1989, Wendel and Weeden 1989) are among the main reasons for the widespread use of this category of markers in studies of genetic variation. In most cases, the genetic variation detectable by enzyme markers is associated with biparentally inherited nuclear genes. The nuclear origin of these markers also implies that their variation is influenced by recombination. Enzyme loci often show a considerable degree of polymorphism that makes them particularly useful for studies of gene flow, mating system and the effects of drift. A serious disadvantage of enzyme markers is their low number and a highly restricted group of structural genes they represent. Moreover, apparent technical simplicity of enzyme markers is not as great as sometimes suggested due to the lack of standard 'portable' protocols that are applicable to different species.

Restriction fragment length polymorphism (RFLP) markers

Restriction analysis and fragment hybridization are the most common methods for detecting genetic variation at the DNA level. When DNAs from two genetically distinct individuals are analyzed by these methods, polymorphism sometimes appears due to differences in the number of DNA sites that are cleaved by a restriction enzyme. The molecular basis of RFLPs is: loss or gain of a restriction site

due to a point or length mutation, or inversion. Such events result in a length difference in the DNA fragments detectable by restriction analysis or by fragment hybridization. Detailed descriptions of RFLP markers can be found in the published record *e.g.,* Gillet (1991), Szmidt and Wang (1992 and references therein).

Depending on the genomic origin of the probe, it is possible to obtain RFLP markers for both nuclear and cytoplasmic genomes, showing either biparental or uniparental inheritance respectively Similar to enzyme markers, nuclear RFLPs are typically codominant and display simple Mendelian inheritance. By using probes with at least partially known sequences it is possible to develop RFLP markers for both coding and non-coding sequences. A somewhat special category of RFLP markers can be obtained by using probes homologous to short multiple repeats (microsatellites). The genetic information yielded by this category of markers is difficult to determine at present.

In contrast to protocols for the analysis of enzyme variation RFLP protocols are easily standardized, and can be applied to various materials. Unfortunately, despite many advantages of RFLP markers their use in population analysis is constrained by several factors. First, RFLP analysis usually requires large amounts of DNA, making non-destructive sampling difficult. Second, well documented probes are still scarce, which seriously limits the number of available RFLP markers. The use of random probes retrieved from libraries constructed with total DNA digests often does not permit the unambiguous determination of whether the observed RFLPs are of nuclear or cytoplasmic origin. Moreover, it is not possible to determine the functional significance of genetic variation detected by such probes. RFLP variation is detected by restriction enzymes that have specific target sequence. As not all mutations alter restriction enzyme sites many potentially important mutations will go undetected. Therefore, a battery of restriction enzymes must be used which seriously increases the time and cost of analysis. Finally, the technique is complex and requires well equipped laboratories which further limits its use in many countries.

PCR-based markers

The advent of the polymerase chain reaction (PCR; Saiki *et al*. 1988) has profoundly improved both the speed and efficiency of detecting all types of sequence variation. The two most commonly used techniques employing PCR are DNA amplification by two-primer extension (Mullis *et al*. 1986, Mullis and Faloona 1987, Saiki *et al. 1988)* and random amplified polymorphic DNA (RAPD) that employs a single primer of arbitrary sequence (Gillet 1991, Williams *et al*. 1990). In both

techniques oligonucleotide primers hybridize with complementary sequences, located on template strands of single-stranded DNA. DNA polymerase begins extending the primers at their open 3′ ends by adding nucleotides complementary to the nucleotide sequence of the template. Primer extension continues in the 3′ 5′ direction until the end of the template is reached or until the termination of the cycle. The cycle is then repeated by heat denaturation of the double stranded DNA to separate it into single strands, followed by cooling to allow annealing and subsequent extension of the primers (Gillet 1991, Williams *et al.* 1990). In this way, any given DNA sequence can be amplified and studied. In the two-primer extension technique, the template nucleotide sequence to be amplified is known in advance, so that the two primers can be chosen to be short sequences complementary to the 3′ ends of the template and its complement (Gillet 1991). The RAPD method differs from the standard two-primer amplification in that sequence variation is detected using a single primer of arbitrary sequence instead of a pair of template-specific primers, uses more cycles and lower annealing temperature (Williams *et al. 1990).*

Variation of the amplification products can be analysed in several different ways. Amplification products can be separated by size on agarose gels. This approach is typically used to detect size variation of RAPD fragments, but is insensitive to sequence differences among them. Sequence differences can be detected either by digestion of individual fragments with restriction enzymes or by mismatch analysis (see Cotton 1989, for detailed descriptions of the latter method). The mismatch approaches to study DNA variation detect most mutations. This is particularly important in studies of conserved coding sequences. Restriction enzymes or mismatch detection are typically used to analyse sequence variation among products generated by two-primer extension. The fragments are then separated on acrylamide gels and visualized by silver staining (Bassam *et al.* 1992, Caetano-Anolles *et al.* 1991).

Depending on the primer, PCR-based markers can be either gene-specific or random. RAPDs usually detect variation in non-coding regions of nuclear DNA and show dominant Mendelian inheritance (e.g., Lu *et al. in* press, Roy *et al.* 1992). In contrast, two-primer extension with gene-specific primers provides detailed information about the genomic origin and coding function of the amplified sequence. Markers produced by two-primer extension show codominant variation and bi- or uniparental inheritance. Alignment of known gene sequences from various organisms enables construction of ‘consensus’ primers that can be applied to other species for which the sequence data is not available. For instance, in combination

with restriction fragment analysis, we used this approach for studies of chloroplast and mitochondrial gene variation in a wide range of plant species (Wang and Szmidt, in preparation). Fast accumulation of sequence data warrants that soon many additional nuclear and cytoplasmic genes can be studied in a similar way Relatively low cost, simple standard extraction and amplification protocols (McPherson *et al.* 1991) make PCR-based markers applicable to virtually any species. In contrast to the RFLP analysis, PCR markers can be studied in a minute amount of tissue allowing for non destructive sampling.

WHAT DO WE KNOW ABOUT GENETIC VARIATION AND HOW REPRESENTATIVE IS THAT KNOWLEDGE?

Most available data on genetic variation in trees come from surveys of enzyme variation (see Hamrick and Godt 1991, for recent compilation). This information is slowly being enriched with data on RFLP and RAPD variation (see Szmidt 1991, Szmidt and Wang 1992 for recent reviews). The question thus arises: *to what extent are these data sets representative of the genome as a whole?* At best, enzyme surveys are instructive as to the relative levels of variation in structural, biparentally inherited nuclear genes. Current surveys of nuclear DNA variation typically employ either random nuclear probes with unknown gene content or RAPD markers (*e.g.,* Devey *et al.* 1991, Roy *et al.* 1992, Lu *et al.* in press). Therefore, they are likely to be instructive as to the relative levels of variation in the non-coding portion of the nuclear genome. Our knowledge about other nuclear genes in trees is restricted to variation in the copy number of RNA genes (Strauss and Tsai 1988, Gorman *et al.* 1992, Govindaraju and Cullis 1992, Moran *et al.* 1992, Karvonen *et al.* 1994) and there is very little information about variation in mitochondrial, chloroplast and regulatory genes.

As mentioned earlier, most genetic markers employed in studies of genetic variation are of nuclear origin and do not provide information about variation of cytoplasmic genes. A common observation in most studies of allozyme and nuclear RFLP variation in trees is weak differentiation among populations (Hamrick and Godt 1991). This appears to be true even for extremely distant populations (Szmidt and Wang 1993). Available evidence for population differentiation with respect to cytoplasmic genes shows a very different picture. Analysis of mitochondrial DNA variation in *Pinus contorta* and *P. banksiana* revealed substantial differentiation within and between these taxa (Dong and Wagner 1993). Lower, but still substantial differentiation in the same set of species was found with respect to chloroplast

DNA (Dong and Wagner 1994). Similar discordance with respect to the apportionment of genetic variation between nuclear and chloroplast markers was found in populations of *P. densata* (Wang *et al.* 1990, Wang and Szmidt 1990, Wang and Szmidt 1994) and other Pinus species (Hong *et al.* 1993, Strauss *et al.* 1993). The extent of these differences is likely to be a function of the relative amounts of interpopulation pollen and seed flow (Ennos 1994). Research on gene flow has lagged because gene flow rates have been assumed to be insignificant (Ellstrand 1992). Now that gene flow rates have been recognized to occur frequently at levels that can influence the genetic fate of populations, we must re-evaluate the importance of gene flow in conservation biology (Ellstrand 1992). Simultaneous measurements of population differentiation for markers with different modes of inheritance can provide important information on this subject (Ennos 1994, Szmidt and Wang 1992). Geographic variation may also be generated by historical patterns of migration and inter-specific gene exchange. Examples of such variation have been demonstrated for several boreal and tropical tree species (Sigurgeirsson and Szmidt 1993a, Szmidt *et al.* 1993, Szmidt *et al.* 1988a, Szmidt and Wang 1993, Wang and Szmidt 1994).

There have been very few reports indicating useful correlation between levels and patterns of enzyme marker variation and adaptive morphological and physiological traits (Savolainen and Karkkainen 1992). Thus, these data are not informative with regard to adaptive patterns of genetic variation that are important for recommendations for genetic conservation (Woodruff and Gall 1992). This limits the usefulness of allozyme markers in monitoring the important genetic changes induced by natural selection. Random DNA markers are not likely to fare much better in this respect (Savolainen and Kärkkäinen 1992). Until recently, population analysis of sequence differences underlying allelic variation has been impractical because of the lack of sufficiently fast and efficient methods. This situation has changed substantially with the introduction of PCR-reaction and new methods for detecting nucleotide substitutions (see previous section). By devising primers for specific structural, RNA and regulatory genes it is now possible to select markers that are likely to show effects of selection upon allelic variation. We are currently using this approach to study such variation in some boreal and tropical trees (Szmidt and Wang, in preparation).

More genetic information is also necessary about the taxonomy and phylogenetic relationships among tree species. Such information is essential for the determination of the demographic units that should be conserved (Lacy 1988). Moreover, phylogenetic studies establish the basic data for identifying patterns of

historical biogeography, for testing hypotheses about the processes that produce these patterns and to identify how unique histories determine contemporary patterns; global patterns of biodiversity being a prime example (Renner and Ricklefs 1994). In the case of cytoplasmic DNAs, groups of associated restriction sites are not separated by recombination and the ancestry of individual haplotypes may remain recognizable even after many generations of sexual reproduction (Whittemore and Schaal 1991). These features of cytoplasmic DNAs have made them particularly useful for studies of phylogenetic relationships and gene flow among tree populations (Wagner *et al.* 1987, Szmidt *et al.* 1988b, Strauss and Doerksen 1990, Strauss *et al.* 1990, Wagner *et al.* 1991, Sigurgeirsson and Szmidt 1993b, Wang and Szmidt 1993). However, wide use of these markers is difficult because of the lack of probes, low sensitivity of restriction enzymes and complex RFLP technology Recent development of primers specific for various mitochondrial and chloroplast sequences (Paran and Michelmore 1993, Taberlet *et al.* 1991, Tripp *et al.* 1993), and mismatch detection of sequence variation offer much simpler and faster means for construction of non-recombinant cytoplasmic markers.

WHAT TO DO WHEN THERE IS TOO MUCH TO DO?

Even with new molecular technology, it is impossible to evaluate the genetic variation and population structure of all species. This is especially true for species-rich tropical forests. One way to circumvent this problem is to prioritize species for attention. Broad genetic management strategies could be formulated for biological groups by studying selected indicator species from a large group of species with similar attributes (Woodruff and Gall, 1992). A multidimensional matrix for classifying population genetic structure within life forms can be defined according to distribution, density, mating system, and pollen vectors (Woodruff and Gall, 1992). Representatives of each type can be studied to discover trends and generalisations (Woodruff and Gall, 1992). Unfortunately, selectivity may make inventory practical but introduces biases resulting from the need to judge the intrinsic values of species (Renner and Ricklefs, 1994). Such judgement requires that at least basic biological attributes of individual species are known which is often not the case in tropical regions. Detailed genetic studies of selected representatives should therefore be paralleled by 'quick and dirty' studies of additional taxa employing RAPDs and a limited assortment of gene-specific markers. Information gained from such heuristic assessments of genetic variation will help to interpolate genetic properties of additional species and to identify taxa deserving closer genetic scrutiny.

CONCLUDING REMARKS

Our present knowledge about genetic variation in forest trees is based on a highly restricted number of biparentally-transmitted enzymatic proteins and non-coding regions of the nuclear genome. It is doubtful that this data set gives even a remotely accurate picture of the amount and patterns of genetic variation and significance of individual evolutionary determinants affecting tree populations. The current arsenal of molecular methods offers excellent opportunities for precise studies of individual components of plant genetic systems. Unfortunately the choice of markers for particular studies still appears to depend more on personal preference and competence rather than on the capacity of individual markers to provide relevant information about particular determinants. There is a prevailing perception that genetic studies utilizing DNA markers are of limited use in population genetic analysis because of financial, competence and supply restrictions. This is certainly correct with respect to RFLP markers. For this reason, most studies of tree populations still employ enzyme markers that are deemed easier and cheaper. However, as demonstrated by our and other studies, PCR-based DNA markers are much faster and cheaper than RFLPs. At the same time, they provide far more precise information about the function and origin of the observed variation than enzyme markers. Such information is essential for predicting the evolutionary significance of this variation which should guide gene conservation decisions.

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Chapter
12

GENETIC DIVERSITY OF NORWAY SPRUCE *(PICEA ABIES* KARST.) POPULATION FROM BIALOVIEZA PRIMEVAL FOREST (POLAND) REVEALED BY ENZYME ELECTROPHORESIS

M. Krzakowa[1] and A.F. Korczyk[2]

INTRODUCTION

Forest trees are long-living organisms subject to short- and long-term fluctuations of the environment. Due to their typically outcrossing mating systems, they are generally found to retain amounts of genetic variation which are roughly twice as great as any other plant group (Bergmann 1991). Most of the genetic variation in tree species is located within populations, and only a minor proportion is distibuted among populations (El-Kassaby 1991). The threat of destruction of natural forest populations and attempts to conserve natural populations as well as a board genetic base, both for the current and future genetic selection, are now a major field of study (Krugman 1984).

The Norway spruce from Bialovieza Forest, the most undisturbed forest on the lowland of Central Europe, is known for its late growth initiation and fast growing characters. Late growth initiation is genetically determined, and consequently,

[1] Department of Genetics, Adam Mickiewicz University, ul. Miedzychodzka 5,60-371 Poznan, Poland.
[2] Forest Research Institute, 17-230 Bialovieza, Poland.

it results in the Norway spruce from Poland performing above average in many provenances tests and being well-adapted for growth in Northern regions of Sweden, Norway and North America.

Since the forest resources in Central Europe are highly threatened by air-pollution or other manmade environmental changes, there is a particular need to characterize the genetic variation within the natural populations in order to maintain genetic diversity.

MATERIAL AND METHODS

Genotypes of 131 trees aged between 35 - 250 years, and distributed over an area of 30 ha, were identified using seeds. Ten megametophytes per tree were examined using seven enzyme systems. The enzyme systems are as follows: formate dehydrogenase (FDH - EC 1.2.1.2), NADH - dependent dehydrogenase (NDH), malate dehydrogenase (MDH - EC 1.1.1.37), glutamate dehydrogenase (GDH - EC 1.4.1.2), shikimate dehydrogenase (SHDH - EC 1.1.1.25), leucine aminopeptidase (LAP - EC 3.4.1.1), and glutamicoxalacetic transaminase (GOT - EC 2.6.1.1.).

Electrophoresis was conducted in 12% starch gels in a lithium-boric buffer system pH 8.1 (Scandalios 1969) for GOT and LAP, and in a triscitrate (pH 7) buffer system (Muona *et al.* 1987) for other enzymes. The staining techniques were taken from Cheliak and Pitel (l984). Genetic variation was examined for polymorphic loci, using various measures of variation expected heterozygosity (He), observed heterozygosity (Ho), Wright's fixation index (F) and degree of polymorphism (Pg). Principal Component Analysis, which is usually used for illustrating the variability of quantitative characters, was adapted for discontinuous traits, and the results are depicted by scatter diagrams, showing groups of genotypes for each enzyme system. All trees were also compared according to all enzyme systems in a dendrogram, constructed on the basis of Euclidean distances.

RESULTS AND DISCUSSION

Formate dehydrogenase (FDH). This enzyme system has been utilized for population investigations of Norway spruce only quite recently (Bergmann and Reutz 1991). The enzyme is coded by one locus with two alleles in Norway spruce and four variants in Douglas-fir (Lewandowski and Mejnartowicz 1992). The genotype distribution (Figure 1) along two Principal Component axes (PC axes) shows the

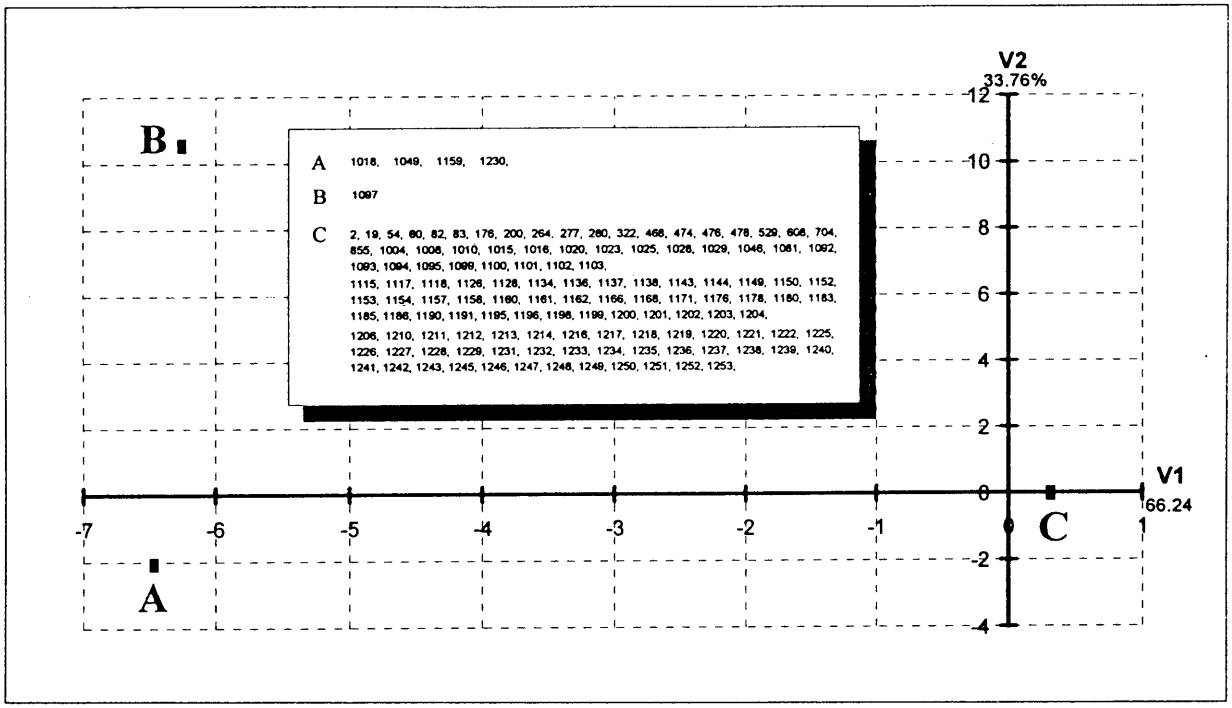

Figure 1: FDH. Distribution of genotypes on the plane of the two Principal Component axes.

most frequent group of faster migrating homozygotes (concentrated in group C). Well apparent is one alternate homozygote, i.e. tree no. 1097 and four heterozygotes (group A).

NADH - dependent dehydrogenase (NDH). In our work, this enzyme shows the highest polymorphism (Table 1) in comparison with all investigated enzyme systems. The occurrence of genotypes (Figure 2) on the plane of the PC axes shows that heterozygotes are the most frequent (see group A).

Malate dehydrogenase (MDH) is a polymorphic enzyme system which is frequently investigated for natural (Altuchow *et al.* 1986, Lundkwist 1979, Bergmann and Scholz 1989, Yeh and El-Kassaby 1980, Harry 1983, Geburek and Wuehlich 1989, Papageorgiou *et al.* 1993) and experimental populations (Paulsen *et al.* 1983, Muona *et al.* 1987, Lagercrantz *et al.* 1988, Ernst *et al.* 1987) of conifers. It is usually investigated in haploid endosperm tissue and very rarely in winter buds (Lagercranz *et al.* 1988).

The results obtained in our investigations correspond with those described earlier for Norway spruce (Lundkwist 1979, Muona *et al.* 1987). Four levels (loci) of

Locus	Population	He	Ho	F	Pg
LAP A	1	0.3093	0.3206	-0.0365	0.4933
LAP B	1	0.4446	0.4427	0.0042	0.6267
GOT A	1	0.0667	0.0687	-0.0305	0.1289
GOT B	1	0.4818	0.4275	0.1127	0.6351
GOT C	1	0.4803	0.4351	0.0941	0.6314
GDH	1	0.1664	0.1527	0.0826	0.2841
SHDH	1	0.0670	0.0687	-0.0251	0.1303
FDH	1	0.0520	0.0382	0.2656	0.0880
NDH	1	0.4997	0.4580	0.0835	0.6431
MDH B	1	0.1852	0.1679	0.0934	0.3112
MDH C	1	0.0301	0.0305	-0.0134	0.0591
Means for all loci :		0.2530	0.2373	0.0620	0.3665

Table 1

He - heterozygosity expected
Ho - heterozygosity observed
F - Wright's fixation index
Pg - polymorphism index

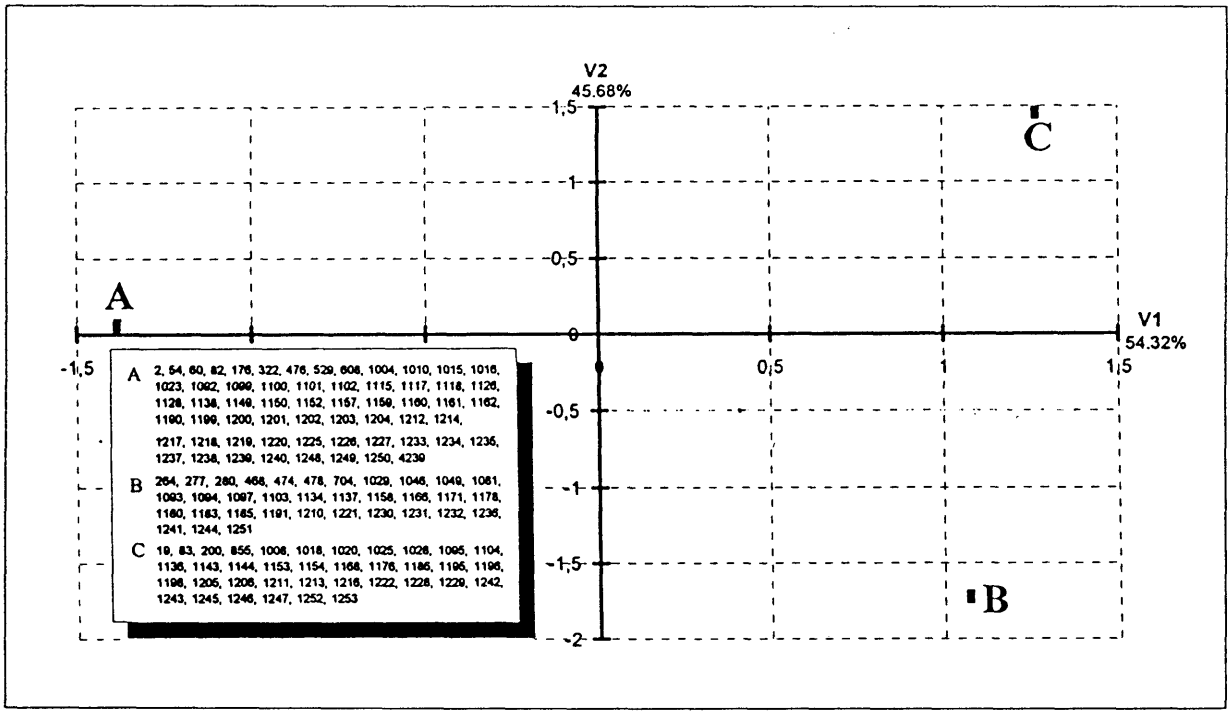

Figure 2: Distribution of NDH genotypes on the plane of the Principal Component axes.

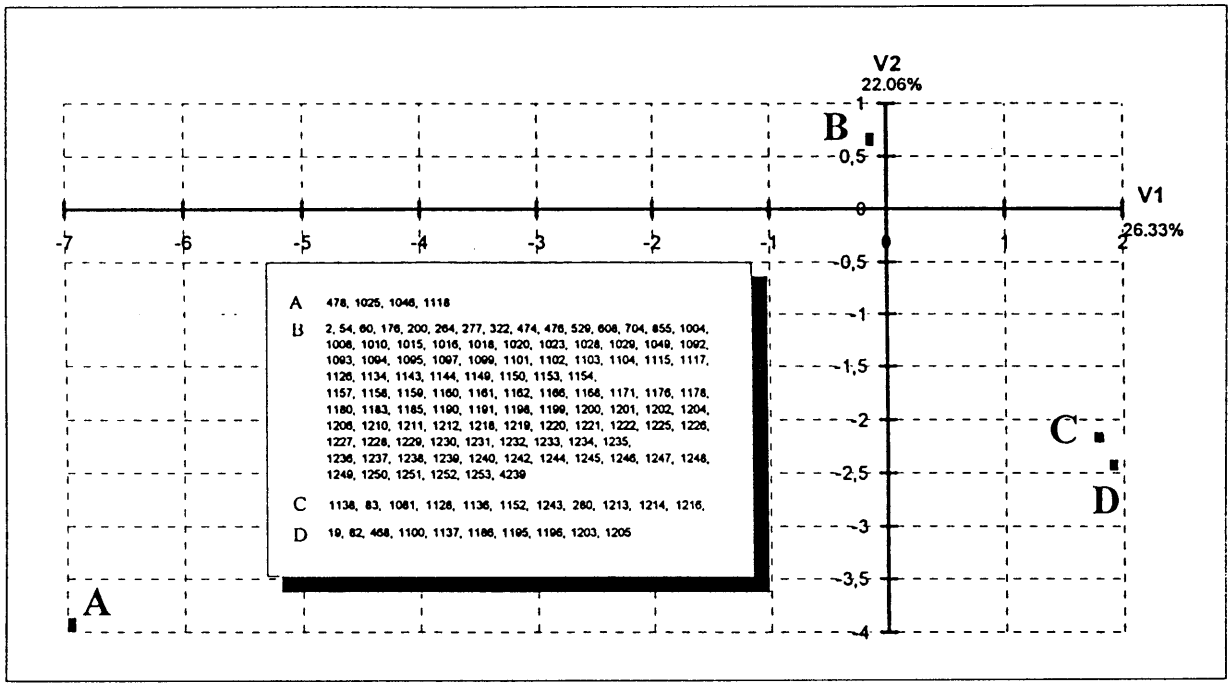

Figure 3: Principal Component analysis for all genotypes described for two loci MDH.

enzyme activity were found. In this paper the two polymorphic zones are called locus B and C. The most frequent genotypes were the homozygote B3B3 (at this locus we found three alleles), and the homozygote C2C2. The heterozygote C1C2 was found only with frequency 0.031. Trees characterised by all genotypes of these two loci are divided into four groups (Figure 3).

Glutamate dehydrogenase (GDH). According to some authors, in conifers GDH codes for one locus with three alleles (Muona *et al.* 1987). In our investigations, however , Norway spruce has only two alleles which corresponds to earlier investigations of Geburek and Wuehlich (1989). The most frequent genotype (Figure 4) is homozygotic, faster migrating genotype G1G1 (93.2%) visible on the PC diagram as group C, whereas the second homozygote was found with the frequency of 1.53%. The heterozygotes make up group A on PC axes plane.

Shikimate dehydrogenase (SHDH) shows a very interesting distribution of genotypes. The most frequent genotype is S2S2 (93.1%).The other two heterozygote genotypes, i.e. S1S2 (see Figure 5, group B) and S2S3 (group C), are less frequent. Two expected homozygotes, S1S1 and S3S3, were not discovered in the population in question.

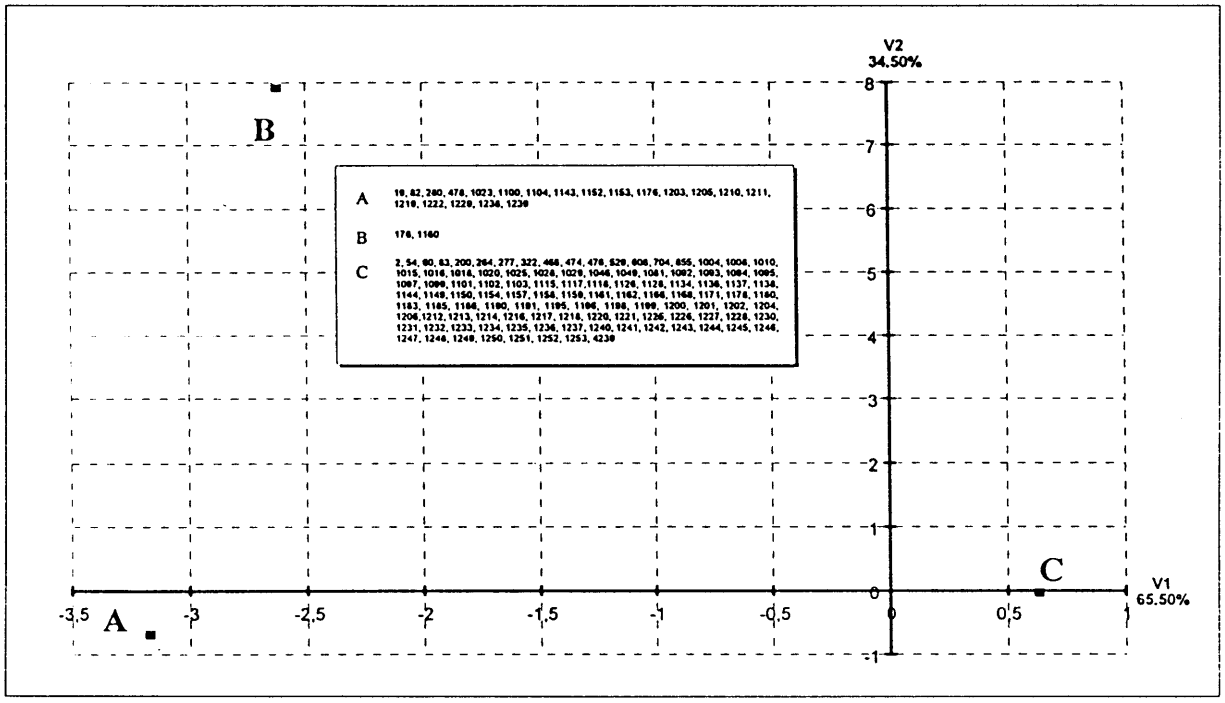

Figure 4: Distribution of all genotypes found in one locus GDH.

Leucine aminopeptidase (LAP) has been previously described for Norway spruce by Lundkwist (1979), Lundkwist and Rudin (1977), Muona *et al.* 1987, Geburek and Wuehlich (1989), and Bergmann and Reutz (1991). All authors agree that LAP has two loci. The faster migrating locus, A, has three alleles, and null alleles A0 also exist. The presence of null alleles in Swedish populations was also observed (Lundkwist and Rudin 1977). Locus B is more variable, has four alleles, and makes 8 different genotypes; only one genotype, B1B4, was not found. All discovered genotypes were compared on the plane of the two PC axes (Figure 6) and formed twelve groups composed of different genotypes.

Glutamate oxaloacetic transaminase (GOT) has three zones of activity. The fastest migrating locus A has two alleles. The most frequent is genotype A2A2. Only one tree, no. 1186 carrying the rare genotype A1A2, is well separated on the plane of PC axes (Figure 7). In the second locus, B, both types of heterozygotes (B1B2 and B2B3) were found, but the expected homozygotes B2B2 and B3B3 were not found. In the third locus, C, alleles were in Hardy-Weinberg proportions, i.e. heterozygote genotypes C1C2 were the most frequent.

The ratio between observed heterozygosity (Ho) and expected heterozygosity,

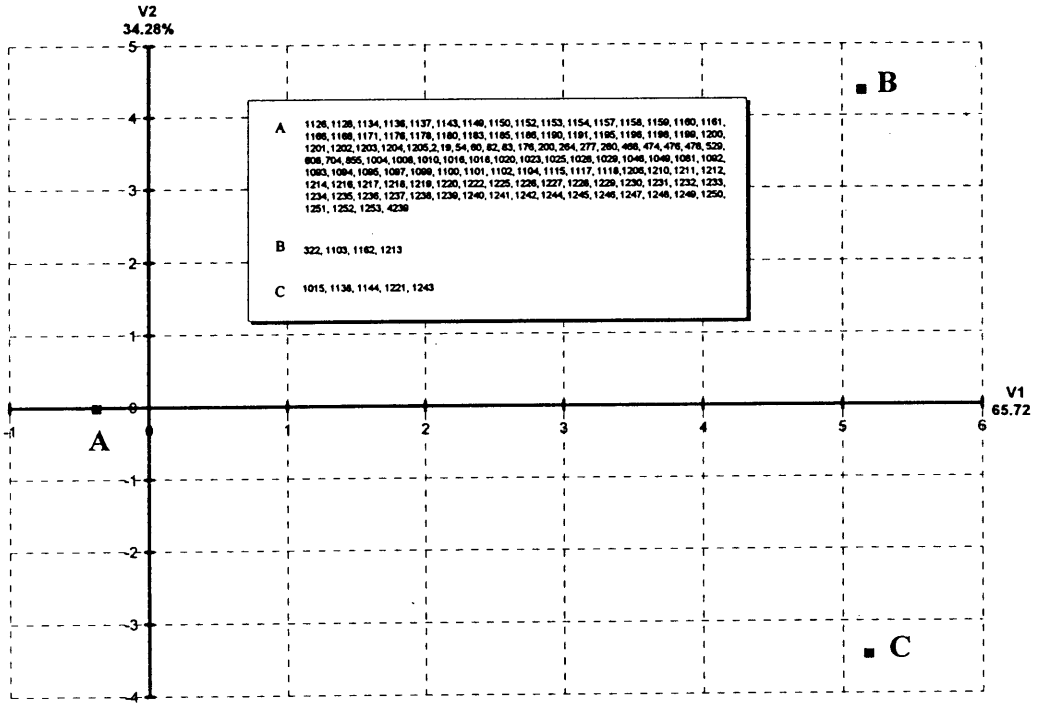

Figure 5: Distribution of SHDH genotypes, composed of two loci, in the space of the two PC axes.

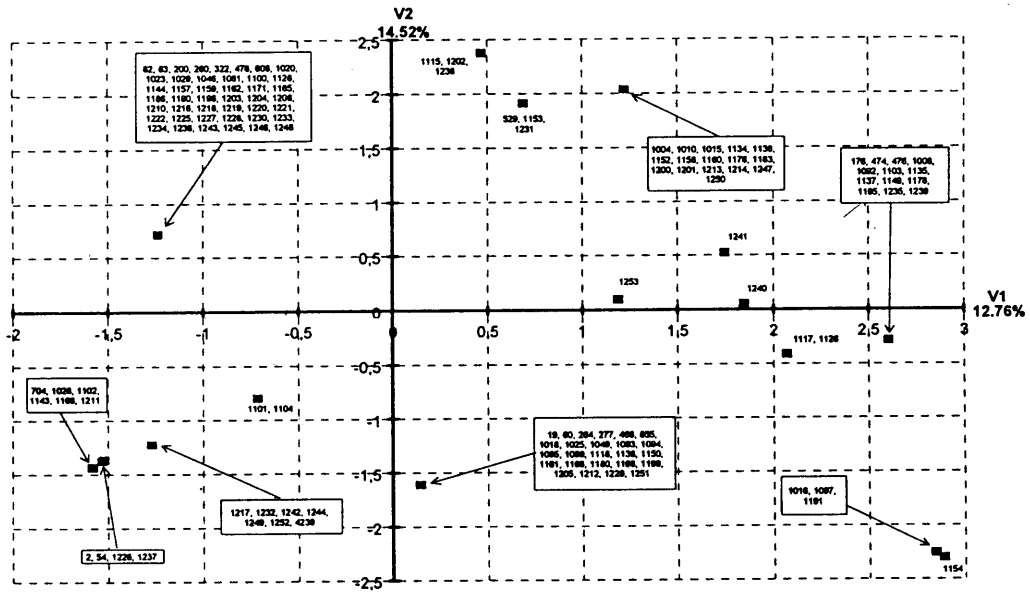

Figure 6: Scatter diagram of individual LAP genotypes, composed of three loci, dispersed on the plane of the two PC axes.

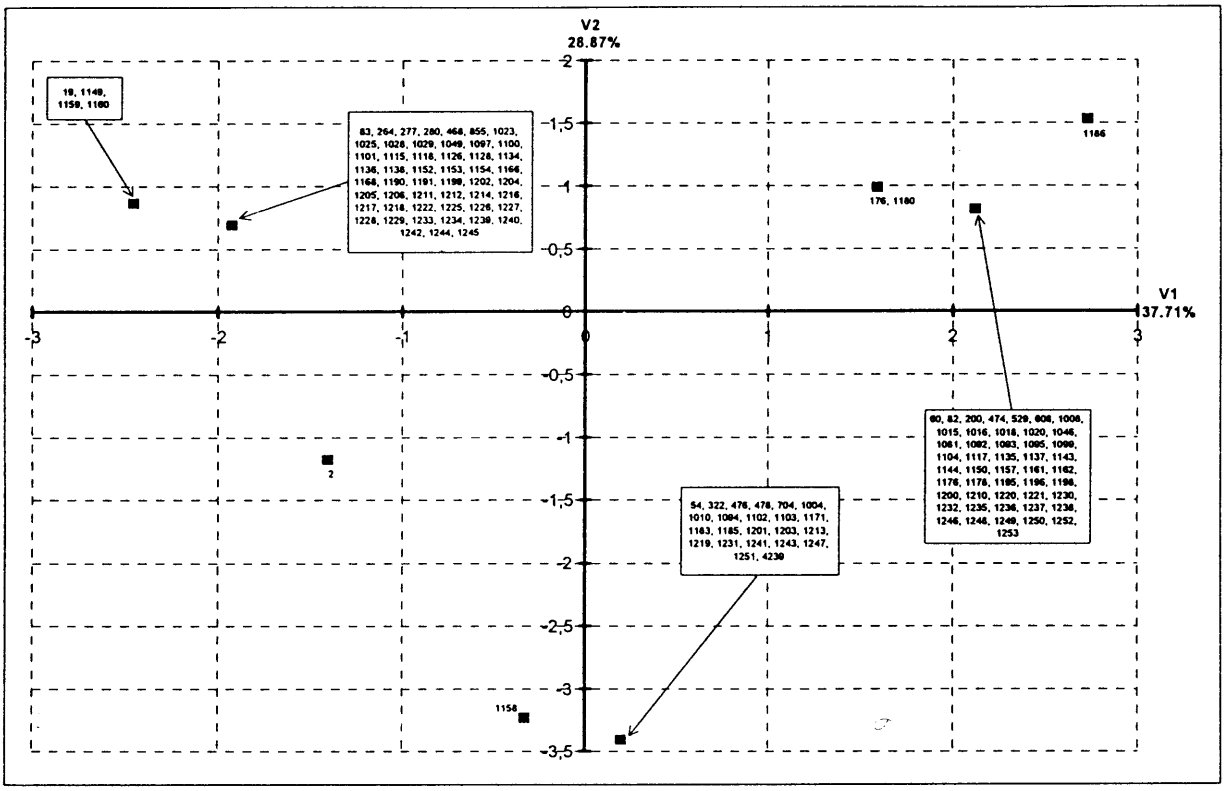

Figure 7: Intrapopulation variability revealed by GOT enzyme system.

which is in reality a measure of genetic diversity (Müller-Starck *et al.* 1992), characterises the population in question (Table 1). The Norway spruce from Bialovieza Forest is in Hardy Weinberg equilibrium as indicated by fixation indices (F) measured for the population and each enzyme system. The mean value of the fixation index (Wright's index F) suggests that the level of self-fertilisation is low, as expected from random mating. The most polymorphic systems were NDH, GOT and LAP (see Page 198, Table 1). NDH has shown differences in enzyme polymorphism resulting from air pollution (Bergmann and Scholz 1989). When sensitive and tolerant populations were exposed to SO_2 and HF fumigation, the lower frequency of heterozygotes suggests selection for different alleles in polluted areas (Bergmann and Scholz 1989) and changes in genetic structure via mortality and reduced fertility.

GOT is one of the most frequently used enzyme systems for description of interpopulation diversity. This is connected with the high polymorphism of the

enzyme and its sensitivity to environmental changes, especially in response to air pollution, which was subsequently tested by Bergmann and Scholz (1989). The results of their work suggest that a certain, yet unknown amount of Norway spruce genetic information runs a risk of being lost due to air pollution stress.

The relationships among the 131 individual trees were visualised by a dendrogram (Figure 8) constructed for all enzyme systems. Each tree is characterized by 11 loci. Some trees having the same genotypes make small groups, but most of them retain their individual specificity typical for a diversified population.

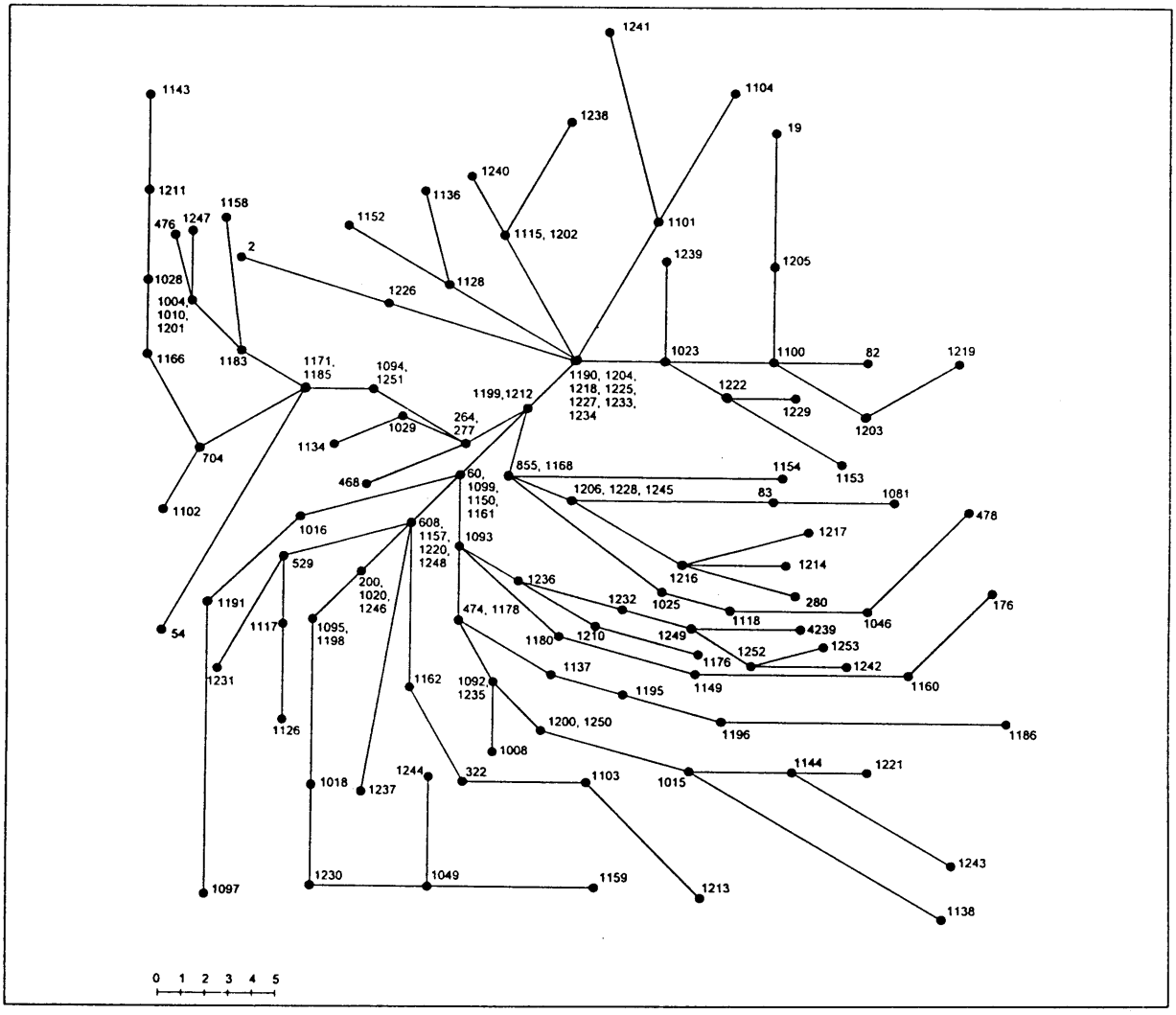

Figure 8: The dendrite (=minimum spanning tree) constructed on the basis of Euclidean distances.

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Chapter
13

A PRACTICAL APPROACH TO CONSERVATION OF GENETIC DIVERSITY IN MALAYSIA: GENETIC RESOURCE AREA

Lim Meng Tsai[1] and Chin Tuck Yuan[2]

INTRODUCTION

The Permanent Forest Estate (PFE) in Peninsular Malaysia is classified into Protection, Production, Amenity, Research and Education Forests. Protection forests are forests which are not exploited for timber, but are maintained in their natural state to protect the hilly areas and watersheds, and to conserve their genetic resources. Production forests are forests that are managed for timber production and they are logged under cutting cycles of between 30 years and 55 years. Amenity forests are those that are set aside and used for recreation, eco-tourism and public awareness in forestry while Research and Education forests are set aside for the conduct of research, education and the conservation of biodiversity and wildlife.

1 Faculty of Forestry, Universiti Pertanian Malaysia, 43400 UPM Serdang, Selangor, Malaysia.
2 Forestry Department HQ, Jalan Sultan Salahuddin, 50660 Kuala Lumpur, Malaysia.

Prior to 1979, almost all production forests (Lowland Dipterocarp Forests) were managed under the Malayan Uniform System (MUS) while currently, the system of management is either the MUS or the Selective Management System (SMS) which is more suitable for the Hill Forests. Under the MUS, the cutting limit was fixed. All trees with dbh over 45 cm were removed in 55 year cutting cycles. Under the SMS, the minimum cutting limit prescribed for dipterocarps is 50 cm dbh and that for the non-dipterocarps 45 cm dbh, the residual stocking should have at least 32 sound commercial trees in the diameter class 30cm-45cm or its equivalent per hectare, and the percentage of dipterocarp species in the residual stand, for trees with 30 cm dbh and above, should not be less than in the original stand.

Under the SMS, an area earmarked for harvesting is first surveyed by a pre-felling inventory (Pre-F) conducted at 10% sampling intensity. The results are then used to determine appropriate cutting limits based on stocking, as well as to ensure that the conditions mentioned above are fulfilled. The trees are then marked for felling based on the limits set by the department. The high cutting limit and the retention of a minimum number of stems is to ensure that residual trees can reach maturity (over 45 to 50 cm dbh) in 25 to 30 years.Where necessary, such as when the logged-over forests are in a poor condition, the areas are treated to enhance their regrowth.

As the SMS and the MUS are basically systems that selectively remove the biggest trees of selected species, there is a strong possibility of genetic erosion and degradation unless adequate adult trees and regeneration are assured. As such, there is an urgent need to conserve the genetic diversity through genetic management of representative populations of commercially exploited species. Also, the conservation of species and genetic variation is not specifically stated or addressed in SMS, although the conservation of genetic resources of the forest should be an inherent and dynamic component of any forest management and utilization plan (Boyle *et al.* 1993, Namkoong 1984, Salleh and Manokaran 1995, Yeatman 1987,1992).

Effective conservation of genetic resources implies that the selected representative populations can be maintained and regenerated from generation to generation (Yeatman 1987). Populations of indigenous tree species can be effectively maintained *in-situ* by natural regeneration or assisted by enrichment planting. Ex-*situ* gene resource plantations may be considered or required if *in-situ* management of a given species is not possible. The management of such genetic resources both *in-situ* and *ex-situ* is a new field and much research (such as on the actual genetic diversity and reproductive patterns) needs to be done in order to success-

fully maintain the selected populations.

A Genetic Resource Area (GRA) is one such strategy and is intended to conserve, manage, and utilize the gene pools of selected species that may be at genetic risk . It maintains, in perpetuity, the genetic diversity and integrity of sample populations of the selected species within the GRA (Yeatman 1992).

GRA

A GRA is a protocol for in-situ conservation of the genetic resources and diversity of selected species within the managed forests of Peninsular Malaysia and elsewhere. The objective of the management of the selected species is to maintain sufficient numbers of that species in order that it can maintain its genetic diversity within the population or subpopulations in the designated forest stands and ecosystems.

Specifically, the objectives are to maintain and perpetuate genetic diversity of economically important species in forests that are harvested; to utilize such selected genetic reservoirs for breeding and planting, research, education and possibly even plantation purposes; to reduce and halt genetic erosion and minimize the risk of genetic losses and maximize future options by maintaining a sound genetic base; to integrate sound genetic management into forest operations; to establish an operating scale of GRA and to demonstrate the feasibility, costs and benefits of systematic conservation of forest genetic resources.

The selected, or target, species are species that are considered to be critically important for the designated forest stands and ecosystems, and therefore worthy of being selected for special consideration, for a number of reasons. They may be commercially important species and in great demand, so that they are selectively chosen for harvesting; they may be species that are potentially important but found in such low numbers that their future may be threatened; they may be of high value and rare species or slow growing ones that may be threatened by any removal; or species that have low regeneration potential. Hence, there can be many species which fit into some or all of the above criteria and thus are considered to be worthy of being maintained in sufficient numbers to conserve their genetic diversity and retain their capacity for regeneration.

In addition to the conservation of genetic diversity of the target species, GRA's can also serve as a potential source of certified seeds and plants. These sources of known populations can be used for large-scale production and collection of seeds and/or seedlings for reforestation purposes and as potential genetic resources for further selection and improvement. By maintaining records of target species in

different areas, a reservoir of genetically diverse populations can be maintained for research and further investigations into the genetic make-up of the species as well as the breeding systems of the target species.

RESULTS

The GRA project reported here is the first such project in Malaysia. It is a joint project between the Forest Department Peninsular Malaysia (FDPM), Johor State Forestry Department (JSFD) and the ASEAN Forest Tree Seed Centre (AFTSC). The project was initiated in November 1992 with the AFTSC providing the technical expertise and training required to undertake the project. The JSFD allocated an area of 5517 ha within the Ulu Sedili Forest Reserve as a project site. It comprises 30 compartments, 19 of which have been logged while 11 are not logged but scheduled to be logged in the future. FDPM provided the expertise and overall management of the project, as well as data analyses with the assistance of two advisers/collaborators.

The Ulu Sedili Forest Reserve Genetic Resource Area is situated about 40 km north of Johor Bahru. The site is easily accessible by the Kota Tinggi-Mersing road and a forest road. The Ulu Sedili Forest Reserve was gazetted as a Reserve in Nov. 8, 1951, and lies around latitude 1°55'N and longitude 103°45'E. The GRA has an undulating topography with altitudes ranging between 50-750 m above sea level. The average elevation is about 300m above sea level. The mean annual rainfall recorded at the nearest rainfall station averages 2,480 mm.

The forest can be described as a Lowland Dipterocarp Forest. The upper or emergent storey is characterized by a dominance of the trees from the family Dipterocarpaceae, including species belonging to the genera *Dipterocarpus, Shorea, Dryobalanops, Neobalanocarpus, Hopea, and Anisoptera*. Other common large trees in the emergent and main canopy level include *Dyera costulata, Gluta* spp., *Intsia palembanica, Koompassia malaccensis, Melanorrhoea* spp., *Palaquium* spp., *Sindora* spp. and *Heritiera* spp. Other important (timber) species include trees from the families of Burseraceae, Guttiferae, Myristicaceae, Myrtaceae, Sapotaceae, Annonaceae, Euphorbiaceae, Flacourtiaceae and Rubiaceae.

The high diversity of the forest and the high commercial value of the various timber species in the proposed GRA made the selection of target species somewhat difficult. Log production data from the compartments that were logged previously, and recommendations of the JSFD officers in the field, were used. The eight target species were identified initially on the basis of priority rating (Table 1).

They are *Shorea singkawang* (Meranti sengkawang merah), *S. laevis* (Balau kumus), *S. curtisii* (Seraya), *Anisoptera laevis* (Mersawa durian), *Dryobalanops aromatica* (Kapur), *Neobalanocarpus heimii* (Cengal) belonging to the family Dipterocarpaceae, and *Dyera costulata* (Jelutong; family: Apocynaceae) and *Koompassia malaccensis* (Kempas; family: Fabaceae). Other important commercial species may subsequently be added to the list as required for genetic management and production of seeds and planting stock.

Species/ group	Size class 15	30	45	60	75	>90
S. singkawang (Meranti sengkawang Merah)	1.10	0.55	0.34	0.21	0.17	0.07
S. laevis (Balau kumus)	0.48	0.34	0.31	0.17	0.14	0.07
S. curtisii (Meranti Seraya)	1.03	0.89	0.82	0.65	0.41	0.21
A. laevis (Mersawa durian)	0.14	0.14	0.10	0.10	0.07	0.07
D. aromatica (Kapur)	5.15	3.44	2.54	1.58	1.07	0.65
N. heimii (Cengal)	0.38	0.38	0.38	0.34	0.24	0.17
D. costulata (Jelutong)	0.10	0.03	0.03	0.03	0.03	0.03
K. malaccensis (Kempas)	0.82	0.82	0.65	0.41	0.14	0.00
Total Dipterocarps	24.85	18.04	12.16	7.84	4.78	2.30
Total NonDipterocarps	83.09	39.86	16.12	6.77	1.89	0.24
Grand Total	107.94	57.90	28.28	14.60	6.67	2.54

Table 1: Relative density of target species, dipterocarps and nondipterocarps in the Ulu Sedili Forest Reserve (mean no per ha).

The first compartment in which the GRA guidelines were implemented was Compartment 115 with an area of 357 ha. The usual forest department Pre-F inventory (with a 10% sampling intensity) was conducted and the data from this inventory was summarized and used to make further decisions on the cutting limits of the target species.

In terms of absolute numbers, there are about 108 trees per ha over 15 cm dbh with Dipterocarps accounting for about 23 % of this number (equivalent to 24 trees). In contrast, there is an average of 2.5 trees per ha over 90 cm dbh, with dipterocarps accounting for over 90% of the number (equivalent to 2.3 trees). The mean numbers of trees of each target species on a per ha basis above 15 cm dbh ranged from 0.1 *(D. costulata)* to 5.15 *(D. aromatica)* (Table 2). Several of the target species have trees in the 90 cm and above dbh class they were *S. singkawang, S.curtisii, D. aromatica, N. heimii and D. costulata*. There were a number of non-target species with trees over 90 cm dbh. These include *S. leprosula, S. palembanica* and *S. acuminata* as well as *Scaphium* sp. (family: Sterculiaceae).

The numbers of the target species were tabulated according to dbh classes and the cumulative numbers above the respective size classes calculated (Table 2). The total number of the target species within the compartment varied considerably; *D. aromatica* occurred in high numbers, with over 1200 trees above 30 cm in dbh, while *D. costulata* was found in very low numbers, with less than 12 trees above 30 cm dbh in the whole compartment (of 357 ha) Assuming that 40-50 % of a (sub-)population should be preserved for genetic diversity (Namkoong 1984), it was decided that at least 50% of the trees over 30cm dbh should be left (uncut). Thus the size class with the cumulative number of trees equal to half (or a little lower than) the cumulative number at 30 cm was taken as the cutting limit for the species. The basis is that trees above 30 cm dbh are trees that can breed/ reproduce. In addition, absolute stocking was considered, such that no cutting was prescribed for the low incidence species, *A. Zaevis* and *D. costulata.* Based on these assumptions, the following were considered and recommended.

a) *No* cutting of *Anisoptera* sp. and *D. costulata.*

b) Cutting limit of >60 cm dbh for all other Dipterocarps except *Neobalanocarpus heimii,* whose cutting limit is >90 cm dbh.

c) Cutting limit of >55 cm dbh for all other non-dipterocarps except *K. malaccensis* whose cutting limit is >60cm dbh.

The trees in the compartment are in the process of being marked for felling and, following timber harvesting, another inventory (PostF) will be conducted to determine the status of the residual stand and to determine the types of silvicultural treatments needed.

Species	Total number of trees by dbh class (class midpoints indicated in cm)											
	>90	85	80	75	70	65	60	55	50	45	30	15
S. singkawang												
Prelogging	25	25	50	61	61	61	75	86	96	121	196	392
Logging removal	25	0	25	11	0	0	14	0	0	0	0	0
Postlogging	0	0	0	0	0	0	0	11	21	46	121	317
S. laevis												
Prelogging	25	25	50	50	61	61	61	75	86	111	121	171
Logging removal	25	0	25	0	11	0	0	0	0	0	0	0
Postlogging	0	0	0	0	0	0	0	14	25	50	60	110
S. curtisii												
Prelogging	75	96	111	146	161	171	232	246	282	293	318	368
Logging removal	75	21	15	35	15	10	61	0	0	0	0	0
Postlogging	0	0	0	0	0	0	0	14	50	61	86	136
A. laevis												
Prelogging	11	25	25	25	36	36	36	36	36	36	50	50
Logging removal	0	0	0	0	0	0	0	0	0	0	0	0
Postlogging	11	25	25	25	36	36	36	36	36	36	50	50
D. aromatica												
Prelogging	232	271	332	382	478	514	564	650	771	907	1228	1839
Logging removal	232	39	61	50	96	36	50	0	0	0	0	0
Postlogging	0	0	0	0	0	0	0	86	207	343	664	1275
N. heimii												
Prelogging	61	75	75	86	111	111	121	121	136	136	136	136
Logging removal	61	0	0	0	0	0	0	0	0	0	0	0
Postlogging	0	14	14	25	50	50	60	60	75	75	75	75
D. costulata												
Prelogging	11	11	11	11	11	11	11	11	11	11	11	36
Logging removal	0	0	0	0	0	0	0	0	0	0	0	0
Postlogging	11	11	11	11	11	11	11	11	11	11	11	36
K. malaccensis												
Prelogging	0	25	25	50	86	146	146	207	232	232	293	293
Logging removal	0	25	0	25	36	60	0	0	0	0	0	0
Postlogging	0	0	0	0	0	0	0	61	86	86	147	147

Table 2: Size class distribution of trees before and after logging removals.

DISCUSSION

The changes to the present system of management is relatively minor. The normal SMS procedures of conducting a Pre-F, tree marking and then tendering will be continued. GRA considerations are only applied at the stage between Pre-F and logging by altering some of the cutting limits of species in contrast to cutting limits based on commercial groups. Hence there is greater selection at the species level rather than at the commercial group level.

An obvious advantage of the GRA approach is that it blends in with the current management practices and it would result in minimum change to the harvesting operations. Only the cutting limits are modified to ensure the maintenance of genetic diversity following the harvesting operations. It was recognized that the harvesting would have to be economical (that is with an out turn of at least 28 cubic m per ha), otherwise there may be problems finding contractors to perform the harvesting operation. The volume of timber available for harvest with the above conditions was as estimated and projected to be still sufficiently economical for the area to be tendered out normally.

As with any new system that is being introduced, it is not perfect. We realize that there are limitations which should be remedied by further research and also by follow-up inventories of the areas after logging. The choice of the 8 target species selected in this report may seem limited. It is possible that additional, or even different species may be targeted in other compartments of the GRA. However, if the numbers are increased, the conditions imposed on the loggers would also increase and this may create problems in monitoring by the forestry field staff. The retention of 50% of trees of the target species over 30 cm dbh is also recognized as an important or critical assumption but we think we have to start at a point that is acceptable to the forest managers and the loggers. A corollary to the retention of 50% is the question of what should constitute a sufficient or appropriate minimum number of trees to be left behind. This is yet to be determined. The value of 50% of the total number of trees above 30 cm dbh could be valid for trees that are found in fairly large numbers but may not be meaningful when it comes to numbers less than 50 or even 100 in a compartment of over 300 ha. While this minimum number still needs to be investigated, the numbers of stems of target species that will be left in the first GRA compartment after logging at the abovementioned cutting conditions, will generally be over 100, except for S. *curtisii.*

Even with 100 trees per compartment, the average density is only about 0.3

trees per ha and may seem rather low. However, we must remember that this is a figure for trees above 30 cm in dbh and if the numbers of smaller trees and saplings are included the total number would increase quite substantially When the numbers of saplings and trees above 15 cm but below 30 cm dbh are included, the numbers do show a significant increase. When poles and saplings below 15 cm dbh are also considered the numbers will probably increase even more, thus giving a retention figure that is considerably greater than 50%.

During the logging process there are likely to be additional losses due to road construction, felling and skidding. These losses will be estimated through a Post-Felling inventory, but such losses are expected to be minimized through better supervision. The additional information from the post-F will also be used for further decisions on the silvicultural requirements of the compartment.

Since management of genetic diversity in Peninsular Malaysia is relatively new, studies on population genetics; flowering and seed phenology, regeneration ecology, seed storage and germination; ecosystem dynamics of (current and potential) target species and inventory survey methods applicable for GRA management need to be conducted.

Complementing the above in-situ study, a preliminary genetic screening of three target species, namely, S. *laevis, D. aromatica and N. heimii.* was conducted jointly with Forest Research Institute Malaysia (FRIM) to determine family estimates of genetic diversity and mating system parameters. Preliminary results indicate that the three species possess sufficient diversity and vigour (Wickneswari Ratnam, pers comm.) (Table 3). Genetic screening will continue for the rest of the target species. .

As a continuation of the study, Post-F inventories will be conducted in the logged over compartments in order to investigate the status of the forest stands so that comparison can be made with the Pre-F data and to determine if any treatment is required. As there are 30 compartments in the GRA, there is much information that needs to be gathered. The compartments that are to be logged will need to have their target species and cutting limits determined first. Subsequently, the overall success or failure of the GRA strategy needs to be evaluated. In addition to these, it is hoped that a network of Genetic Resource Areas in Peninsular Malaysia can be developed in conjunction with operational forest management and seed/seedling production; and subsequently a Register of Genetic Resources for Peninsular Malaysia for reference and use in planning reforestation.

Species	N	Ni	P	A	He	F	tm	Fs	Fe
S. laevis	70.5	11	45.5	1.5	0.182	0.327	1.498	0.999	0.199
D aroma tica	45.5	10	67.8	2.5	0.270	0.303	0.926	0.0	0.041
N. heimii	33.5	6	83.3	2.3	0.390	0.209	0.950	0.112	0.026

Table 3: Estimates of genetic diversity and mating system parameters of three target species.

N = mean number of seedlings per tree assayed
Ni = number of isoenzyme loci analysed
P = percentage of polymorphic loci
A = mean number of alleles per locus
He = mean expected heterozygosity
F = mean fixation index per locus
tm = multilocus outcrossing rate
Fs = mean fixation index among progenies
Fe = (1-t)/(1+t), the equilibrium coefficient

CONCLUSION

With the current world-wide concern for the depletion of the tropical rainforest, this pilot project aims to develop a better understanding of, and so ensure perpetuation of, the genetic diversity of target species. Knowledge gained from the GRA Pilot Project should enhance sustained yield management of the forest. Genetic diversity of the rainforest cannot be neglected and steps need to be taken to maintain and use these renewable resources.

As with any system of forest management, SMS has its fair share of shortcomings especially with regard to the response of the residual stands. Cutting limits are based on the stem sizes mentioned above. However, with the GRA approach, the cutting limits are also based on size but with due consideration for the numbers of the selected individual species. Although this has resulted in a generally higher cutting limit for most of the target species; the other non-target species were not affected at all. Further refinement of the basis of determining the cutting limit should be developed. Genetic screening is one way this can be achieved.

It is proposed that this GRA project will continue for at least 10 years, and it is also hoped the GRA guidelines will be incorporated into the SMS well before then. The stands will be monitored regularly, probably five (5) years after logging. The status and demographics of each target species will be reviewed and silvicultural measures prescribed to ensure their maintenance and enhancement. Broader

applications of these principles and methods will benefit Malaysian forestry by ensuring socio-economic returns from the forests, sustaining irreplaceable genetic diversity and forest ecosystems, and maintaining environmental protection associated with the forest.

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Chapter
14

GENETIC VARIABILITY OF TWO RATTAN SPECIES FROM ISOZYME MARKERS

M.C. Bon[1], B. Ali H. Basri[1] and, H.I. Joly[2]

INTRODUCTION

Rattans are spiny climbing plants belonging to the major group "Lepidocaryoid" of the Palm family. They are represented altogether by 600 species in 13 genera and distributed from West Africa to Fiji and from Southern China to Queensland. The greatest diversity of genera and species is in the western part of Malesia, as reported by Dransfield and Manokaran (1993).

Widely used in the village economies of Asia for centuries, rattans also enjoy an expanding and successful international market for furniture, basketry, binding, cordage and a wealth of other purposes. Due to the depletion of the forests and their natural resources, and as a result of the current rate of exploitation, some commercial species are endangered. The necessity for an international conservation programme and for strategies for resource development has been recognized by producing countries in South-East Asia. In Sabah (Malaysia), national agencies

1 CIRAD-Forêt/Yayasan Sabah, P.0. Box 60793,91017 Tawau, Malaysia.

2 CIRAD-Forêt, 45 Bis, avenue de la Belle Gabrielle, 94736 Nogent sur Mame, France.

like Innoprise Corporation Sdn Bhd are participating in this conservation effort by managing protected areas and setting up field gene banks of native and exotic rattan species. A total of almost 14ha of conservation stands has so far been established in Luasong, as has been presented by Garcia et *al.* (1993). Ex situ conservation efforts have started with two of the commercially most important large diameter cane species, *Calamus manan* and *CaZamus subinermis.*

Calamus manan occurs naturally in Peninsular Malaysia and Sumatra, and *Calamus subinermis* in Sabah (North Borneo) and the Palawan Islands (the Philippines) (Dransfield and Manokaran 1993). Both species are dioecious and produce a large diameter cane. As a solitary species which can only be harvested once, as it does not produce new shoots following cutting, *Calamus manan* is considered more endangered than the clustering species *Calamus subinermis,* for which commercial exploitation started more recently

To establish conservation programmes, involving both ex *situ* and *in situ* conservation, as well as to develop breeding strategies for rattan species, it is of primary importance to establish the variability of each species and the spatial distribution of its genetic diversity. Along with the establishment of field trials, CIIWD-For& and Innoprise Corporation are developing tools to evaluate the genetic diversity of rattan species. This paper presents the first results concerning the evaluation of the genetic diversity of *C. manan* and *C. subinermis,* using isozyme markers.

MATERIALS AND METHODS

Expeditions to collect rattan seeds from already severely depleted natural forests must compete with both legal and illegal cane harvesters. Added to this problem, only a small proportion of the dioecious rattan plants bear fruits in any year. Difficulties are exacerbated by a lack of precise information, within the region, on the period of fruit maturation and also by uncritical use of vernacular names. Harvested rattan seeds rapidly lose their germination ability and therefore have to be sown immediately on return from the collecting expedition. The seedlings raised in the nursery are finally transferred to the conservation stands in Luasong.

The material already established in the stands is described in Table 1. All populations were analyzed for the survey of genetic diversity; one plant was sampled per progeny. Leaf tissue was used for isozyme analysis in preference to seed because it is abundantly available from any individual irrespective of sex and flowering period. Young leaves from individual rattan plants aged 2 to 5 years were used.

Location		Latitude(N) (deg.min.)	Longitude(E) (deg.min.)	No.of progenies sampled	Origin
Calamus manan					
Kalimantan	*	nd	nd	15	Plantation
Brumas (Sabah)	*	4.35	117.40	18	Plantation
Jeroco (Sabah)	*	5.20	118.35	15	Plantation
Kepong (P.Malaysia)		3.11	101.42	9	Wild
Trenggun (" ")	*	4.15	102.00	11	Plantation
Sungai Pandan (" ")		nd	nd	4	Wild
Labis (" ")		2.19	103.03	4	Plantation
Tasek Kenyir (" ")		5.03	102.34	3	Wild
Calamus subinermis					
Brumas (Sabah)		4.35	117.40	17	Plantation
Putatan (")		5.50	116.00	7	Wild
Kuala Penyu (")		5.30	115.30	7	Wild
Penampang (")		5.50	116.10	7	Wild
Tamparuli (")		6.10	116.20	5	Wild
Kota Belud (")		6.30	116.30	6	Wild
Tuaran (")		6.10	116.20	4	Wild
Kinarut (")		5.50	116.10	6	Wild

Table 1: Details on the Seed Source.

Note: nd=no data

* Populations taken into consideration for the estimation of within and between population genetic diversity for *Calamus manan*. For *Calamus subinermis*, 3 populations have been considered: Brumas; Putatan, Penampang and Rinarut; TamDaruli and Tuaran.

Methods of enzyme extraction and of starch and acrylamide electrophoresis were adapted from Bon *et al.* (1992), Liengsiri *et al.* (1990) and Khasa (1993). We used 8 enzyme systems to assess genetic diversity: adenylate kinase (AR), alcohol dehydrogenase (ADH), colorimetric esterase (EST-c), glucose-6-phosphate dehydrogenase (G6PDH), hexokinase (HK), isocitrate dehydrogenase (IDH), phosphoglucoseisomerase (PGI), and shikimate dehydrogenase (SDH). For *C. manan* and *C. subinermis* 13 and 15 putative gene loci were identified, respectively.

Interpretation of allozymic banding patterns was carried out based on general information about enzyme structure (Pasteur et *al.* 1987; Wendel and Weeden 1989) and the study of phenotype segregation in progenies according to Gillet and Hattemer (1989), (Bon, in preparation).

Four parameters were used to assess genetic diversity: percentage of polymorphic loci, average number of alleles per locus, average observed, and average expected heterozygosity. A locus was considered to be polymorphic if the frequency of the most common allele did not exceed 0.95. Putative monomorphic loci were not included in the computation of genetic measures. The distribution of genetic diversity within and among populations was evaluated through Wright's F statistics (F_{IS} ,FI_{IT} , F_{SR})(Wright 1965). F-statistics were calculated for individual alleles in each locus according to Wright (1965). F, can be estimated by the formula:

$$l\text{-}F_{IT} = (1\text{-}F_{IS})(1\text{-}F_{SR})$$

These parameters were estimated using the BIOSYS-1 software package (Swofford and Selander 1981).

RESULTS

Genetic variation within populations

The value of genetic parameters are given for *Calamus manan* and *Calamus subinermis* in Table 2. The average number of alleles per locus (A) for all populations combined was 2.5 for the two species. The mean proportion of polymorphic loci (P) within the species was 85% and *77%,* for *Calamus manan* and *Calamus subinermis,* respectively. The mean observed heterozygosity (Ho) across loci was 0.37 and *0.42,* for *C. manan* and *C. subinermis,* respectively and the mean expected heterozygosity (He) was 0.47 for both species. At the species level, the fixation index, F, was 0.21 and 0.11, for *C. manan* and *C. subinernzis,* respectively. *C. manan* seems to exhibit a deficit in heterozygotes while C. *subinermis* seems to be in Hardy-Weinberg equilibrium.

Genetic differentiation among popda tions

In each species single populations seem to be in Hardy-Weinberg equilibrium (F_{IS}= 0.07 and F_{IS} = *0.05,* for *C. manan* and *C. subinermis,* respectively). The values of F_{ST} (Table 3) show that there is some genetic differentiation among populations of *C. manan* but that populations of *C. subinermis* from the west coast of Borneo do not show genetic differentiation.

Species	Mean no.of alleles per locus	Percentage of polymorphic loci	Mean heterozygosity Direct count	Hardy-Weinberg expected*	Fixation index
C. manan	2.5	85%	0.37	0.47	0.21
C. subinermis	2.5	77%	0.42	0.47	0.11

Table 2: Genetic variation for each species: *Calamus manan* and *Calamus subinermis.*

Note: All individuals are grouped in a single population for each species.
* Unbiased estimate (see Nei 1978).

Species	F_{IS}	F_{IT}	F_{ST}
C. manan	0.07	0.25	0.19
C. subinermis	0.05	0.11	0.06

Table 3: Summary of F-statistics for each species: *Calamus manan* and *Calamus subinermis.*

CONCLUSION AND RECOMMENDATION

These preliminary results show that both Calamus species exhibit a high level of genetic diversity (He= 0.47). It is surprising that the diversity of the narrowly distributed *C. subinermis* is of the same order as the diversity of *C. manan*, whose distribution is much larger. This may be due to the fact that only part of the range of *C. manan* has been surveyed in the present analysis as no material from Sumatra was available. Also, *C. manan* "populations" were mainly collected in plantations while *C. subinermis* were collected in natural forests. The diversity in the *C. manan* populations may therefore be artificially reduced by a two-step sampling procedure. For each species, populations seem to be in Hardy-Weinberg equilibrium, the higher value of F for *C. manan* at the global level being probably due to a Wahlund's effect (Wahlund 1928). The lack of differentiation among populations in *C. subinermis* should be confirmed for populations from the east coast.

Dioecy is an efficient way of reducing inbreeding; unlike many tropical trees, rattan populations do not exhibit an excess of homozygotes at the young stage as the production of inbred seedlings is reduced to crosses between relatives. How-

ever, more populations with larger sample sizes must be studied before a complete picture of the genetic diversity of C. *manan* and C. subinermis can be derived but, from a practical point of view, as the differentiation among populations is large for *Calamus manan,* one can recommend that a sufficiently large number of populations be sampled for conservation.

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Chapter
15

GENE DIVERSITY STUDY BASED ON ISOZYME ANALYSIS IN TEAK *(TECTONA GRANDIS* L.F.) PROVENANCES

A.W.S. Kertadikara[1,2] and D. Prat[1,3]

INTRODUCTION

Teak, *Tectona grandis* L.f., (Verbenaceae) is one of the most economically important tropical timber species. The tree is native to the tropical deciduous forests, of three disjunct regions: (1) Central and East India, (2) Myanmar, Laos and north west Thailand, and (3) Indonesia (Central and East Java). Altona (1922) supposed that its presence in Indonesia might be due to human introductions.

International provenance trials in the 1970s, supported by FAO, DANIDA and CIRAD-For& (formerly CTFT), have revealed large genetic differentiation among populations for quantitative traits (Kaosa-Ard, 1986). The present study was then focused on gene diversity within and among eight teak stands, both from

1 Laboratoire INRA-ENGREF de Sciences Forestières, Unité de Génétique des Populations d'Arbres Forestiers, ENGREF, 14 rue Girardet, F-54042 Nancy Cedex, France.

2 present address: Jurusan Manajemen Hutan, Fakultas Kehutanan, IPB, POB 168, Bogor 16001, Indonesia.

3 present address: Station d'Amélioration des Arbres Forestiers, INRA, F-45160 Ardon, France.

natural habitats (India, Thailand and Indonesia) and artificial stands outside its natural distribution area (west and east Africa).

MATERIALS AND METHODS

Plant material

Eight teak seedlots were investigated. These included three west Indian populations (I_1,I_2 and I_3); one Thai stand from a natural forest (T_1); two Indonesian stands from central (J_1) and east (J_2) Java, and two artificial stands from west Africa (A_1, Ivory Coast) and east Africa (A_2, Tanzania) (Table 1). Seedlots were bulked collections of seeds from an unknown number of trees (assessed to be greater than 50), except for I_3, which consisted of 10 open-pollinated families.

Teak fruits were exposed to 80±1 °C for 48 h, prior to germination. When the seedlings were 20 days old they were transferred into tropical greenhouse conditions.

Provenance	Province	Country	Longitude	Latitude	Elevation
I_1 Sakrebail Royal Forest Seed production area	Karnataka	India	75°29'E	13°48'N	600 m
I_2 Virnoli Seed production area	Karnataka	India	74°37'E	15°12'N	600 m
I_3 Thithimathy Royal Forest	Karnataka	India	76°00'E	12°15'N	850 m
J_1 Kandangan	Central Java	Indonesia	110°00'E	7°00'S	300 m
J_2 Saradan	East Java	Indonesia	111°00'E	7°30'S	320 m
T_1 Tam Bah Thai Mae Huat Natural Forest		Thailand	99°55'E	18°40'N	350 m
A_1 Kokondekro		Ivory Coast	5°02'W	7°38'N	280 m
A_2 Tanzania [a]		Tanzania	37°E	7°S	

Table 1: Geographic Origin of *Tectona Grandis* Provenances.

a: no more data available

Isozyme techniques

Enzymes were extracted from young leaf parenchyma of 2 month-old plants. Samples were ground in an extraction buffer (sodium tetraborate buffer 50 M, pH 8.3). Enzymes were separated by electrophoresis at 5 ±1 C, under an electric field of 12 $V.cm^{-1}$ for 4.5 to 5 h, in polyacrylamide vertical gel (stacking gel: 3%; running gel: 9%). The electrode and gel buffer was Tris (90 mM), borate (10 mM), EDTA disodium salt (0.05mM) at pH 8.38 (Kertadikara, 1992).

Out of 69 tested enzyme systems, the following 14 systems were recorded: Alanine aminopeptidase (AAP, E.C. 3.4.11.1), Aspartate amino transferase (AAT, E.C. 2.6.1.1), Acidic phosphatase (ACP, E.C. 3.1.3.2), Alcohol dehydrogenase (ADH, E.C. l.l.l.l), Diaphorase (DIA, E.C. l.6.4.3), Endopeptidase (ENDO, E.C. 3.4.-.-), Carboxyl esterase (EST, E.C. 3.1.1.-), Fluorescent ß-D-glucosidase (B-GLU, E.C. 3.2.1.21), Glycerate-2 dehydrogenase (G2DH, E.C. 1.1.1.29), Leucine aminopeptidase (LAP, E.C. 3.4.11.1), Lactate dehydrogenase (LDH, E.C. 1.1.1.27), Nicotinamine adenine dinucleotide dehydrogenase (NADHDH, E.C. 1.6.99.3), Peroxidase (PER, E.C 1.11.1.7) and Superoxide dismutase (SOD, E.C. 1.15.1.1).

Genetic interpretations of isozyme patterns were assessed from the observed segregations in ten half-sib progenies of Indian provenance I, (Kertadikara and Prat, in preparation). Genotypes of all others individuals were then deduced accordingly.

Within-population genetic variation was estimated by considering allele frequency, average number of alleles per locus, proportion of polymorphic loci (at criterion 95 %), observed and expected heterozygosity and fixation index. Mating system parameters (multilocus outcrossing rate) were assessed according to Ritland and Jain (1981) and Ritland (1983) for provenance I_3. Each open-pollinated family consisted of at least 20 seedlings.

The genetic structure among individual populations was estimated by using the level of differentiation among demes 6 (Gregorius 1985, Gregorius and Roberds 1986). Relationships among populations were analyzed according to Nei's (1978) and Gregorius' (1984) genetic distances, and represented by a dendrogram based on the unweighted pair-group method with arithmetic averaging (UPGMA) described by Sneath and Sokal (l973).

RESULTS

Eighteen polymorphic isozyme loci *(Aap, Aat-b, Aat-c, Acp-b, Adh, Dia-a, Da-b, Endo,*

Est, ß-Glu, G,dh-a, Lap, Ldh, Nadh-dh, Per, *Sod-a, Sod-b* and *Sod-c)* encoding fourteen enzyme systems were scored and considered for the analysis of genetic variation. Two monomorphic loci *(Aat-a* and *Sod-d)*were also noticed.

Genetic diversity within provenances

Over 20 loci were recorded (including two monomorphic loci), with 82 alleles being scored. On the average, over all unweighted populations, the number of alleles per locus was 3.0, the percentage of polymorphic loci was 88 %, the observed heterozygosity was 0.289, while the expected value after Hardy-Weinberg equilibrium (gene diversity) was 0.362 (Table 2). The values were, however, dependent on the sample size of population (9 to 263) which resulted from variations in germination rates.

The Indian provenance I_1 showed the highest values for both observed and expected heterozygosity. Average fixation indices were positive in each provenance, confirming a trend of heterozygote deficiency. The x^2 goodness of fit test indicated a significant deviation towards an excess of homozygosity in most provenances at *Aat-b, Acp-b, Dia-a, Dia-b,* and *Sod- b*loci. Negative values of fixation index (mostly not significant) were, however, found in some loci in all provenances.

Ten polymorphic loci were used in order to determine the outcrossing rate in the Indian population I_3. The multilocus outcrossing rate was 0.98.

Genetic diversity among provenances

Allelic frequencies were significantly different among provenances over all loci (x^2= 58.0***). Some major alleles, particularly DIA-b_2 and DIA-b_3, EST_3 and EST_5, AAT-b_2 and AAT-b_5, G2DH-a_1 and G2DH-a_3 and LDH_2 and LDH_4, allowed the differentiation of all Indian provenances in one hand and of African and Indonesian provenances in the other hand. The Thai population was quite similar to the African and Indonesian ones, except for Est and *G_2DH- a* loci, for which it exhibited intermediate allelic frequencies.

Using the methods of Gregorius and Roberds (1986) differentiation among provenances ( ) was high for loci *Aat-b, Ldh, Est* and *G_2DH-a;* and overall, the differentiation among provenances was about 19 %. The Indian provenances were the most distinct provenances, and African provenances the least distinct (Figure 1).

Provenance	Sample size	Average number of alleles	Polymorphic loci (%)	Average observed heterozygosity	Gene diversity	Mean fixation index
I_1 Sakrebail	9	2.3	85	0.371	0.406	0.038
I_2 Virnoli	55	3.4	90	0.320	0.372	0.079
I_3 Thithimathy	263	3.7	75	0.306	0.332	0.066
J_1 Kandangan	18	2.5	75	0.267	0.320	0.085
J_2 Saradan	10	2.4	80	0.210	0.340	0.271
T_1 Tam Bah Thai	16	2.6	80	0.225	0.338	0.252
A_1 Kokondekro	97	3.6	85	0.311	0.351	0.101
A_2 Tanzania	82	3.3	80	0.305	0.334	0.084

Table 2: Genetic Diversity within Tectona Grandis Provenances at 20 Loci (including two monomorphic loci).

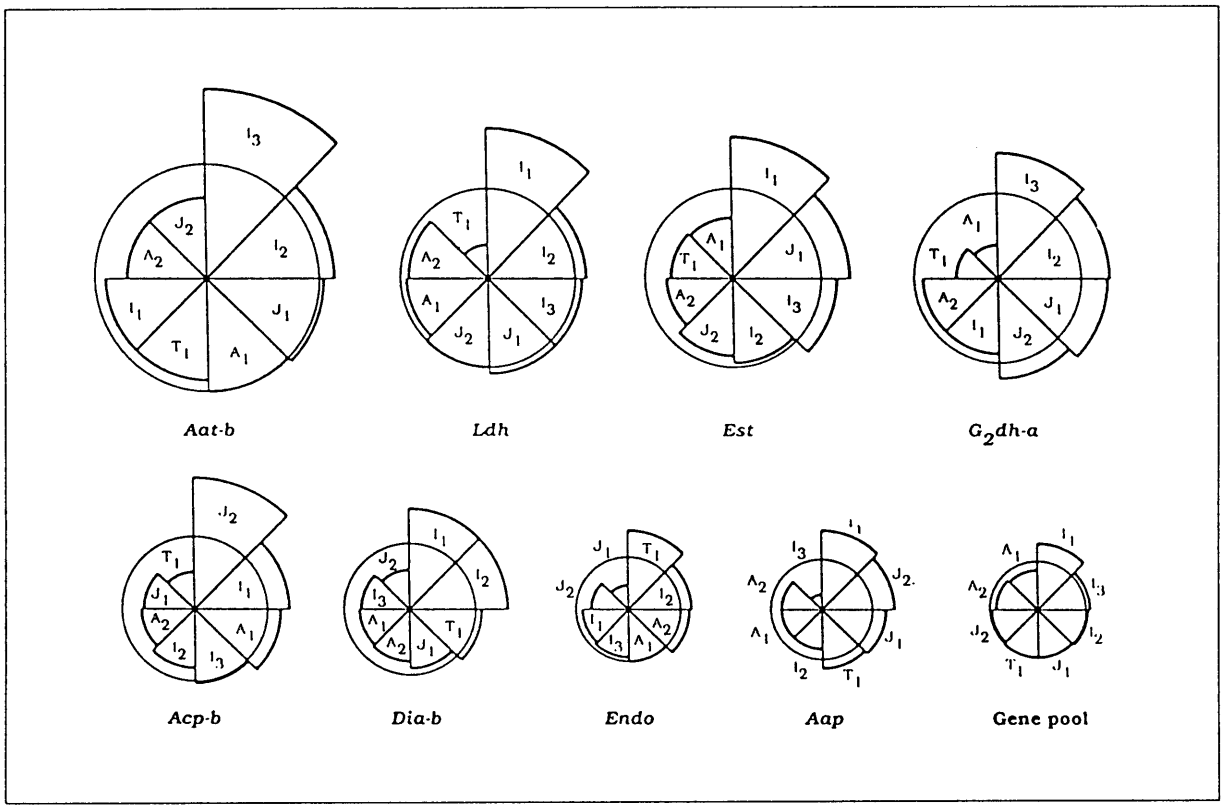

Figure 1: Genetic differentiation among provenances of *Tectona grandis* according to Gregorius (1985) at the 8 most differentiated loci and gene pool.

The Nei (1978) unbiased genetic distance and Gregorius (1984) genetic distance among individual populations provided similar interpretations. Provenances can be clustered into two groups according to their genetic distances (Figure 2). Indian populations can be considered as a group, and the other populations as another group. Distances among provenances ranged between 0.057 and 0.171 within groups and between 0.166 and 0.236 among groups.

DISCUSSION AND CONCLUSION

Genetic structure

The positive fixation index values (12 % on the average over all populations) indicated a general excess of homozygosity within populations. The excess of homozygosity detected at the seedling stage (2-month-old) cannot be due to self-

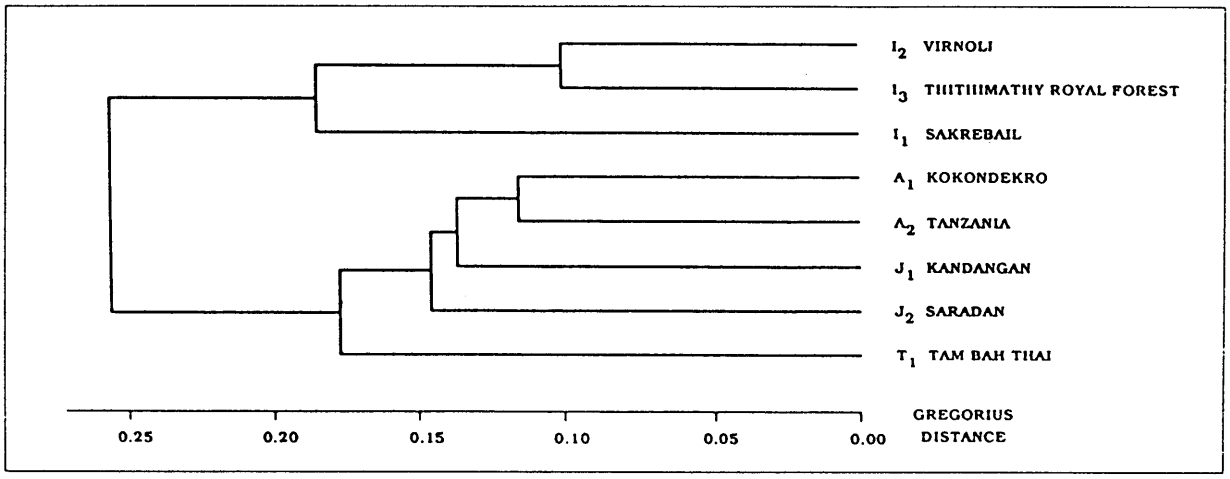

Figure 2: Relationships among *Tectona grandis* provenances according to the Gregorius genetic distance based on 20 loci (cophenetic correlation: 0.94).

ing, because of the high outcrossing rate (0.98) observed in provenance I_3. Indian provenances showed however, the lowest fixation index values. Outcrossing rates could not be assessed in other populations having higher fixation indices. Hedegart (1973) studied sexual reproduction of teak in Thailand, and did not get viable seeds from selfing. Selfing is very rare in teak and cannot lead to a significant positive fixation index. Fixation index values might come from consanguinity (crossing between related trees) or provenance subdivision (preferential crossing between close trees).

Genetic diversity and differentiation

Differentiation in *Tectona grandis* was mainly due to the disjunction of two different gene pools (one in India, one in south-east Asia). Differentiation among these two gene pools was observed at the provenance level as well as at the individual level on the basis of multilocus genotypes (Kertadikara and Prat 1995).

Introduction history of the African populations indicated that they came mostly from India, but several authors (Méniaud 1930, Madoffe and Maghembe 1988) have suggested that African populations consisted of mixtures of several seed origins (India, Myanmar, Java and Thailand). The Indian provenances were generally not adapted to African tropical conditions (usually high mortality: Delaunay 1977, Egenti 1978). It could be argued that African provenances became genetically similar to the Thai-Indonesia group due to directional selection of Indian material.

Dispersal of teak in south-east Asia

The hypothesis of teak introduction in to Java from India as a result of human activities about 1500 to 700 years ago, as suggested by Altona (1922) cannot be supported by our results. Such introduction could take place only from the Thai gene pool. Could introduction have occurred naturally ?

In mainland Asia teak is typically a monsoon forest species, as is also the case in the Indonesian archipelago, where teak is exclusively found in dry and seasonal climates. According to a hypothetical map of Pleistocene climatic conditions (Heaney, 1991) the seasonal forests covered a larger area than at present, including the centre of the Sunda shelf, extending in an arc from southern Thailand to eastern Java (Morley and Flenley, 1987). Glaciation caused a sea level decline, permitting a connection between the Asian continent and the Indonesian archipelago. It can be hypothesised that the pattern of teak dispersal was firstly continuous from its centre of origin, somewhere in Myanmar (Meniaud, 1930), to Java. The present ecological and geographical conditions led to the current disjunct area of teak. The palaeogeographic and palaeoclimatic data thus support the hypothetical natural migration of teak to eastern Java from Myanmar or Thailand during the Pleistocene. However, palynological data could not confirm this hypothesis since teak pollen has never been found in sediments. Human intervention was not absolutely required to explain the present distribution of teak in Indonesia.

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Chapter
16

SPECIES DIVERSITY OF SECOND GROWTH AT NGAO DEMONSTRATION FOREST, LAMPANG PROVINCE

Somboon Kiratiprayoonl, Jesada Luangjame[1],
Pralong Damrongthail and Metinee Tarumatsawasl

INTRODUCTION

The total area of Thai forest areas is decreasing at an alarming rate. Statistics complied over the past three decades (1961-1991) suggest that 0.46 million ha are deforested annually (RFD 1992). These rapid and profound changes endanger both the species diversity and genetic resources of Thailand's forested ecosystems. If the natural balance of the remaining forest ecosystems is to be maintained and shortages of wood avoided there must be a concerted and timely move towards conservation and protection of the Thai natural resources. However, before sustainable management strategies to protect forest biodiversity in Thailand can be developed the structure and function of the many diverse ecosystems must be better understood (Boontawee et *al.*, chapter 8, this volume).

As a point of departure we have chosen three questions relevant to the measuring and monitoring of forest biodiversity in Thailand: 1) Are there different patterns of diversity between different forest types occurring in Thailand? 2) Are

1 Royal Forest Department, 61 Phaholyothin Road, Bangkok 10900, Thailand.

there different patterns of diversity within the forest types? 3) What are the implications of variable levels of diversity between and within forest types on sustainable management practices?

The present study **is** an effort to provide a practical foundation for addressing these questions. To do this we have established permanent lha plots in each of three forest types common to northern Thailand: Dry Dipterocarp forest, Mixed Deciduous forest and Seasonal Dry Evergreen forest.

LOCATION

The study was conducted at the Ngao Demonstration Forest in Ngao District, Lampang Province. The site area is approximately 1,750 km^2 located at 18° 20′ - 19° 05′ N and 99° 45′ - 100° 05′E. For the past ten years the precipitation has averaged 1100 mm/year and the temperature 25.65°C. The Ngao Demonstration Forest contains three kinds of forest communities *i.e.* Dry Dipterocarp forest, Mixed Deciduous forest and Evergreen forest. All three forest types were studied. This paper presents the results from the Dry Dipterocarp and Mixed Deciduous forests.

METHODS AND MATERIALS

Site and plot preparation

Study sites were selected based upon three criteria 1) homogeneity of forest types, 2) reasonable access, and 3) protection from future human disturbance. In each forest type a 100 m x 100 m permanent plot was set up and divided into 100 10 m x 10 m subplots. Smaller temporary subplots of 4 m x 4 m and 1 m x 1 m were systematically established at a corner of each 10 m x 10 m subplot.

Data collection

From the permanent 100 m x 100 m plot, the following data was recorded:

1. In the 10 m x 10 m subplots all plants with DBH > 4.5 cm were tagged and the species, DBH, and height were recorded. All plants in this group are designated as being in the **tree group.**
2. In the temporary 4m x 4m subplots, all individuals taller than 1.3 m but with DBH < 4.5 cm were identified and measured for DBH and height. This is designated the **sapling group.**

3. In the 1 m x 1 m temporary subplots all individuals less than 1.3 m tall were identified and counted. This is designated the **seedling group.**

Data analysis

The data from the plots and subplots was analyzed for 3 measures of ecological importance: the importance value index (IVI), the Shannon-Wiener index for diversity, and the similarity index. The IV1 is a composite index based on measures of relative frequency, relative density, and relative dominance (Mueller-Dombois and Ellenberg 1974). The Shannon-Wiener index, borrowed from information theory, relates the proportional weight of the number of individuals per species to the total sample belonging to all species (Shannon and Weaver 1949). The similarity index is an arithmetic comparison of those values common to two groups with the total value of both groups (Bray and Curtis 1957)

RESULTS

Species composition

In the Dry Dipterocarp forest the dominant species were Shorea siamensis Miq. in the tree group, *Cratoxylum formosum* (Jack) Dyer in the sapling group and ferns in the seedling group. The IVI for each of the dominant plants was 95.99, 35.60 and 54.82, respectively (Table 1).

In the Mixed Deciduous forest, the dominant species in the tree, sapling, and seedling groups were *Tectona grandis* Linn, *Pterocarpus macrocarpus* Kurz. and *Kalanchoe verticillata* Eli., respectively. The IVI of these dominant plants was 53.74, 66.20 and 32.60, respectively (Table 2).

Species diversity

For the Dry Dipterocarp forest community, the species diversity indices of the tree, sapling and seedling groups were 3.51, 4.49, 3.63, respectively (Table 3). In the Mixed Deciduous forest community, the highest species diversity index occurred in the seedling group (3.87), followed by the sapling group (3.75), and the tree group (3.72) (Table 4). Both forest communities had the highest number of species in the seedling group, followed by the tree and the sapling groups. Some plant groups had lower species index values but a higher number of species due to higher densities of individuals from a single species unevenly distributed across the subplots.

Tree group		Sapling group		Seedling group	
Species	IVI	Species	IVI	Species	IVI
Shorea siamensis Miq.	95.99	*Cratoxylum formosum* (Jack) Dyer	35.60	Fern	54.82
Shorea obtusa Wall.	39.96	*Lannea coromandelica* Merr.	35.16	*Asdepias curassavica* Linn.	26.33
Canarium subulatum Guill.	23.37	*Millettia brandissiana* Kurz.	18.93	*Kalanchoe verticillata* Ell.	14.02
Millettia brandissiana Kurz.	17.52	Poojao	18.80	*Dalbergia dongnaiensis* Pierre	10.13
Terminalia alata Heyneex Roth.	12.58	*Shorea siamensis* Miq.	18.72	*Eupatorium odoratum* Linn.	9.85
Lagerstroemia cuspidata Wall.	11.47	*Dalbergia assamica* Benth.	15.14	*Cratoxylum formosum* (Jack) Dyer	9.71
Semecarpus reticulata Lec.	11.21	Seaokrue	15.14	Kruekeo	8.21
Vitex pinnata Linn.	10.16	*Vitex pinnata* Linn.	14.48	Mahaekkrue	6.55
Dalbergia paniculata Roxb.	7.55	*Boerhavia chinensis* (L.) Aschers. & Schwein f.	12.12	*Millettia brandissiana* Kurz.	5.27
Pterocarpus macrocarpus Kurz.	7.24	*Lagerstroemia cuspidata* Wall.	11.31	*Baphicacanthus cusia* Brem.	4.64

Table 1: Importance Value Index (IVI) of some dominant species of secondary Dry Dipterocarp Forest in Lampang Province.

Tree group		Sapling group		Seedling group	
Species	IVI	Species	IVI	Species	IVI
Tectona grandis Linn.	53.74	*Pterocarpus macrocarpus* Kurz.	66.20	*Kalanchoe verticillata* Ell.	32.60
Millettia brandisiana Kurz.	49.48	*Millettia brandisiana* Kurz.	39.25	Kruemun	31.25
Pterocarpus macrocarpus Kurz.	49.36	*Millettia auriculata* Bak.	37.03	*Dendrocalamus strictus* (Roxb.) Ness.	16.09
Xylia xylocarpa Taub.	25.63	*Hymenodictyon excelsum* Wall.	30.26	Saewdook	16.07
Cananga latifolia Finet & Gagnep	17.22	*Tectona grandis* Linn. f.	19.70	*Millettia brandisiana* Kurz.	12.02
Mitragyna brunonis Craib	13.19	*Schleichera oleosa* (Lour.) Oken	15.83	*Wrightia tomentosa* Roem & Gagnep.	9.22
Millettia auriculata Bax.	10.96	Klue jamung	12.19	*Dioscorea hispida* Dennst.	7.37
Dalbergia dongnaiensis Pierre	7.90	*Wrightia tomentosa* Roem & Schult	11.09	*Dalbergia floribunda* Roxb.	6.83
Bombax anceps Pierre	7.67	*Bombax anceps* Pierre	10.54	*Asdepias curassavica* Linn.	6.11
Lannea coromandelica Merr.	7.35	*Teminalia bellerica* Roxb.	8.99	*Asystasiella nessiana* Linbau.	6.00

Table 2: Importance Value Index (IVI) of some dominant species of secondary Mixed Deciduous Forest in Lampang Province.

Categories	Tree	Sapling	Seedling
Species no.	46	38	53
Species Index	3.51	4.49	3.63
Density (no./ha)	1,296	1,431	113,000

Table 3: Some characteristics of secondary Dry Dipterocarp forest.

Categories	Tree	Sapling	Seedling
Species no.	36	20	63
Species Index	3.72	3.75	3.87
Density (no./ha)	325	406	195,505

Table 4: Some characteristics of secondary Mixed Deciduous forest.

The existing species number

Species were further divided into woody and non-woody groups. Of the 66 species of woody plants in the Dry Dipterocarp forest 45 were found in the tree group, 31 in the sapling and 32 in the seedling group (Figure 1). The Mixed Deciduous forest, contained 59 woody species. Thirty-six of these species were in the tree group, 18 in the sapling group and 40 in the seedling group. In the Dry Dipterocarp forest 15 species were common to all groups; in the Mixed Deciduous forest 12 species were common to all groups (Figure 2).

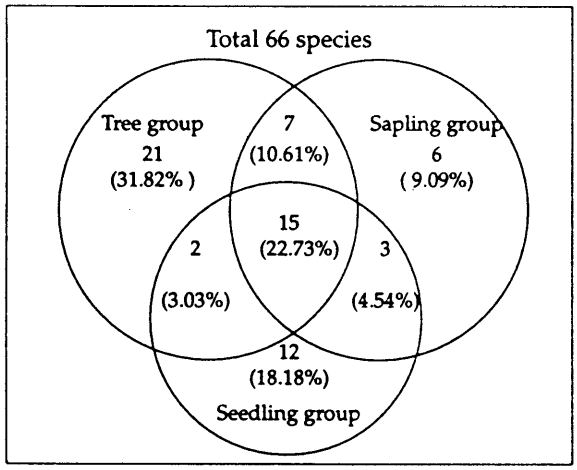

Figure 1: The existing woody species of secondary Dry Dipterocarp forest.

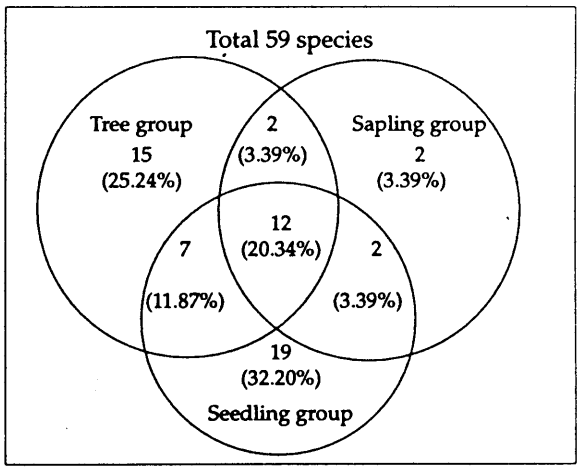

Figure 2: The existing woody species of secondary mixed deciduous forest.

For the non-woody species, most were the ground vegetation in the seedling group. Of the 23 non-woody species in the Dry Dipterocarp forest 19 were in the seedling group (Figure 3). In the Mixed Deciduous forest, the seedling group contained all 22 of the non-woody species (Figure 4).

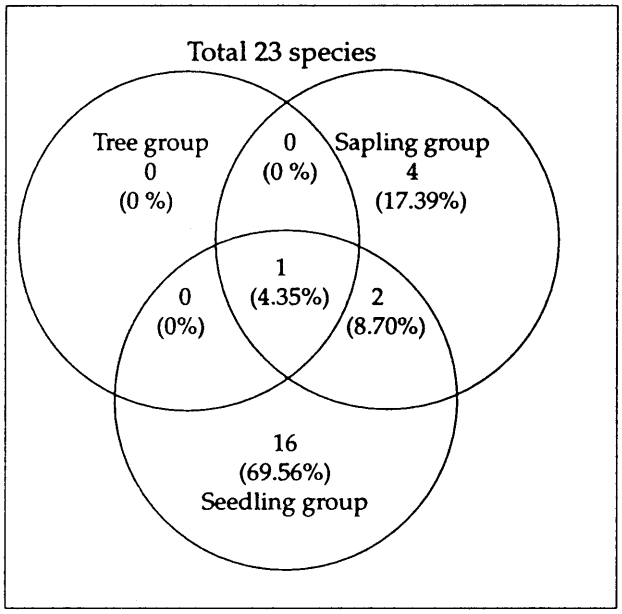

Figure 3: The existing non-woody species of secondary Dry Dipterocarp Forest.

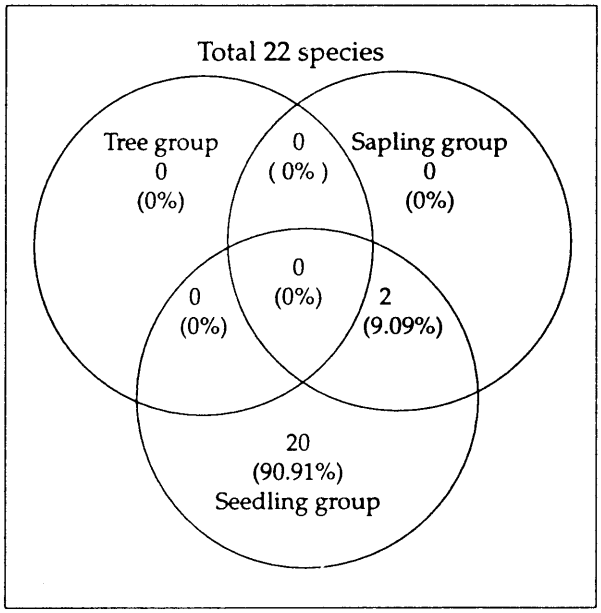

Figure 4: The existing non-woody species of secondary Mixed Deciduous Forest.

DISCUSSION

Patterns of diversity differ markedly both between and within the two forest types studied. In the Dry Dipterocarp forest *Shorea siamensis* dominates the tree group with an IVI (96.0) nearly 2.5 times greater than the second most dominant species, *Shorea obtusa* (IVI=40.0), In the tree group of the Mixed Deciduous forest three species, *Tectona grandis, Millettia brandisiana,* and *Pterocarpus macrocarpus,* all had comparable IVIs (53.7, 49.5, 49.4, respectively) although they were much lower than the IVI for *Shorea siamensis* in the Dry Dipterocarp forest. The seedling groups exhibited a similar, although less marked, trend. However, in the sapling group the Mixed Deciduous had one highly dominant species, *Pterocarpus macrocarpus* (IVI=66.2), whereas in the Dry Dipterocarp forest the IVIs of the dominant species were generally lower and more homogenous. Interestingly, it is

the sapling group of the Dry Dipterocarp forest with the highest Shannon-Wiener species index value (4.49). In the tree group of the Mixed Deciduous forest the distribution and magnitude of the IVIs of the dominant species was comparable to the IVIs of dominant tree species in tropical rainforest communities (Kiratiprayoon 1986).

In order to develop sound forest management practices based on sustainability, it does not suffice to know only the IVIs of each species, in each plant group, in each forest type, nor only values of species diversity for each plant group, in each forest type. The interrelationship of diversity and importance between different size groups must be appreciated. The tree group of the future will arise from the saplings of today; the future saplings will come from current seedlings and future seedlings, in turn, will be a result of the reproductive success of the mature tree group.

Measures of similarity between size groups within the Dry Dipterocarp forest and Mixed Deciduous forest studied provide two clear and contrasting examples. In the Mixed Deciduous forest the similarity index between the tree and sapling groups is 54.10 (Table 5). This suggests that a large proportion of the trees that are important or dominant in the tree group, based on measures of relative frequency, density, and dominance, also play an important role in the sapling group. If the Mixed Deciduous forest was deforested, thereby losing the large trees (typically the first to go), a similar group of species exhibiting similar patterns of interspecific dominance would be available to replace the removed overstorey.

By contrast, the Dry Dipterocarp forest has a much lower similarity index value between the tree and sapling groups (35.08) (Table 6). If the Dry Dipterocarp forest was deforested it is less clear which species would become dominant. The major structural component of the Dry Dipterocarp forest, *Shorea siamensis,* will be limited in the near future (IVI=18.7 in the sapling group vs. 96.0 in the tree group). The implications may be profound, not only for the 21 species that exist only in the tree group (and would presumably disappear upon removal of the tree group through deforestation) but also for those species existing only in the seedling and sapling groups that may depend upon the structural homogeneity of the *Shorea siamensis* dominated forest for their continued existence. The ecological uncertainty created by a deforested and, therefore, radically altered environment may make these species more susceptible to local-scale extinction.

Returning to the Mixed Deciduous forest example, we see that the high similarity between the tree and sapling groups provides this forest type a relative measure of flexibility or resilience in the face of encroaching deforestation If, however,

it suffered such severe deforestation that both the tree and sapling groups were wholly removed, equally serious problems of local- scale extinction would ensue. In order to return deforested lands to previous levels of diversity, aggressive reforestation plans would be required. Whether to promote natural regeneration through forest tending for seed germination and seedling survival or, in cases of poor natural regeneration, to initiate enrichment planting would depend on the circumstances particular to each case. We hope that this study will provide some practical guidelines necessary for assessing forest biodiversity and developing appropriate sustainable management strategies.

		SI		
		Tree	Sapling	Seedling
D I	Tree	100	54.10	15.23
	Sapling	45.90	100	17.60
	Seedling	84.77	82.40	100

Table 5: Index of similarity (SI) and dissimilarity (DI) between size group of Mixed Deciduous forest.

		SI		
		Tree	Sapling	Seedling
D I	Tree	100	35.08	12.96
	Sapling	64.92	100	22.83
	Seedling	87.04	77.17	100

Table 6: Index of similarity (SI) and dissimilarity (DI) between size group of Secondary Dry Dipterocarp forest.

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Chapter
17

BIODIVERSITY ASSESSMENT OF FOREST TREE SPECIES IN BIA NATIONAL PARK GHANA

A. A. Oteng-Yeboah[1]

INTRODUCTION

The Bia National Park (BNP) is located at the north-western tip of the Western Region of Ghana, between longitudes 3º 02'and 3º 08'W and latitudes 6º 32'and 6º 37 North. Since 1975, no exploitation of any kind has taken place there. In 1985, Bia National Park was designated a Biosphere Reserve and an UNESCO World Heritage site.

The position of the park is intermediate between the Moist Evergreen (ME) and the Moist semi-deciduous (MS) Ghanaian vegetation classification of Hall and Swaine (1976) corresponding to the vegetation classification schemes of Taylor (1952) and Mooney (1961). By its position, therefore, the Bia National Park is expected to show all the characteristics of the two rain forest types. An unpublished report by Hall, Swaine and Lock (1976) on the park indeed confirms this.

The situation of Bia National Park makes it ideal for base-line studies of forest

1 Dept. of Botany, University of Ghana, Legon, Ghana.

ecosystems in Ghana. One of these studies is the estimate of the relative abundance of tree species in order to provide an age distribution structure for predictive yield capacities purely for forest research purposes. A study of this kind is reported here.

MATERIALS AND METHODS

Ten permanent quadrats, each measuring 25m x 25m, were randomly demarcated along the north-south transect of the Park. The average distance among the plots was about half a kilometre, with the distance between the nearest and the farthest almost 3 kilometres. In each of the ten quadrats, woody plants with girth over 20cm at breast height **(1** metre from the ground level) were identified, counted and their girth measured. Species identification followed Hutchinson and Dalziel (195472), Irvine (1961), Hall and Swaine (1981), and Hawthorne (1990).

Calculations of means (X), diameter (2r), radius (r), and area of girth πr^2 were made from the tree girth measurements. The cover dominance measure was calculated from the total basal area of the trees. For convenience, the girth sizes were grouped into five arbitrary classes ranging as follows: a) 20 - 50cm b) 51 - 80cm c) 81- 110cm d) 111 - 140cm e) over 141 cm.

The Ghanaian timber classification, in which trees are classified into Classes I, II and III respectively for economically most desired, economically less desired, and lesser known species was used. Sub classes a, b and c for classes I and II refer to growth rate at above 50cm dbh with a the fastest and the slowest.

RESULTS

Species Occurrence and Diversity

A total of 364 trees were encountered in the 10 quadrats. These belonged to 63 species in 24 plant families (Table 1). On the average therefore, there were 36.4 trees in 19.2 species belonging to 12 families per quadrat. The list of species, their families, the total number of individual trees, their frequencies in the ten quadrats and girth size ranges have been given in Table 2. Species with 5 or more frequencies in the 10 quadrats were considered common. There were thirteen such species, which included *Anthonotha fragrans Baphia nitida, Bussea occiden talis, Cola gigan tea, Corynan the pachyceras, Dialium dinklagei, Diospyros canalicula ta, Guibourtia ehie, Nesogordonia papaverifera, Panda oleosa, Pycnanthus angolensis, S terculia oblong* and *Strombosia glaucescens.*

Tree Girth Size Classes

From the girth measurement of the 364 trees, a girth size range of 20cm to 350 cm (ie. 3.18 to 55.73 cm dbh) was observed. This was divided into five girth size classes at intervals of 30cm up to the first 140cm. The density, basal area and frequency of these girth size classes in each quadrat is shown in Table 2. Generally, the majority of trees (284 trees) representing 78% of all the trees were between 20cm and 80cm girth. Many fewer trees (29 trees), representing 7% of all trees had a girth over 141cm. The remaining 14% of the trees had girths between 81cm and 140cm. A total basal area of 56.42 m^2 was calculated as the total for all 364 trees. This figure gives an indication of the tree dominance per unit area.

Plot No.	Total No. of Trees	No. of Species Represented	No. of Families Represented	Total Basal Area Contributed (cm^2)	Girth Size 20-50cm	Classes			
						51-80cm	81-110cm	111-140cm	>141cm
1A	33	24	13	8389.85	12	4	10	0	7
2A	41	24	12	8418.5	21	7	2	5	6
3B	28	16	11	3722.9	16	7	3	0	2
4B	28	14	13	3113.4	7	15	3	1	2
5A	39	18	11	7457.89	23	5	5	2	4
6B	37	19	11	6595.45	23	9	1	1	3
7A	43	16	9	1862.95	30	9	4	0	0
8B	50	26	16	1975.38	40	7	3	0	0
9A	32	15	11	7743.95	14	7	5	3	3
10B	33	20	13	3148.05	20	8	2	1	2
Total	364	192	120	52,428.32	206	78	38	13	29

Table 1: Density, basal area and frequency distribution girth size classes of trees over 20cm girth.

	Tree Name	Family	Total Number	Frequency	Girth Range
1	Alstonia boonei	Apocynaceae	1	1	35
2	Amphimas pterocarpa	Caesalpiniaceae	2	2	53 - 57
3	Aningeria robusta	Sapotaceae	1	1	78
4	Anthonotha fragrans	Caesalpiniaceae	13	6	28 - 147
5	A. macrophylla	Caesalpiniaceae	5	4	53 - 216
6	Antiaris toxicaria	Moraceae	4	4	29 - 195
7	Antidesma laciniatum	Euphorbiaceae	1	1	43
8	Baphia nitida	Papilionaceae	54	10	20 - 70
9	B. pubescens	Papilionaceae	3	2	28 - 42
10	Bussea occidentalis	Caesalpiniaceae	22	7	20 - 105
11	Celtis mildbraedii	Ulmaceae	17	4	26 - 149
12	C. zenkeri	Ulmaceae	7	4	25 - 55
13	Chlorophora excelsa	Moraceae	1	1	22
14	Chrysophyllum albidum	Sapotaceae	2	2	37 - 42
15	Cleistopholis patens	Annonaceae	1	1	170
16	Cola chlanydanta	Sterculiaceae	1	1	21
17	C. gigantea	Serculiaceae	10	6	30 - 103
18	Corynanthe pachyceras	Rubiaceae	10	5	22 - 170
19	Dacryodes klaineana	Burseraceae	2	2	33 - 122
20	Daniellia ogea	Caesalpiniaceae	1	1	315
21	Desplatzia subericarpa	Tiliaceae	1	1	26
22	Dialium dinklagei	Caesalpiniceae	14	6	23 - 81
23	Diospyros canaliculata	Ebenaceae	8	5	20 - 40
24	Diospyros monbutteris	Ebenaceae	2	1	20 - 28
25	Discoglypremna caloneura	Euphorbiaceae	1	1	40
26	Distemonanathus benthamianus	Caesalpiniaceae	2	2	158 - 297
27	Enantia polycarpa	Annonaceae	2	1	27 - 40
28	Entandrophragma candollei	Meliaceae	1	1	189
29	E. cylindricum	Meliaceae	2	2	32 - 52
30	E. utile	Meliaceae	1	1	62
31	Ficus sp	Moraceae	1	1	89
32	Funtumia africana	Apocynaceae	1	1	55
33	F. elastica	Apocynaceae	8	3	31 - 42
34	Glyphaea brevis	Tiliaceae	3	3	27 - 37
35	Guibourtia ehie	Caesalpiniaceae	7	6	22 - 86

	Tree Name	Family	Total Number	Frequency	Girth Range
36	Holoptelea grandis	Ulnaceae	4	1	19 - 65
37	Isolona cooperi	Annonaceae	9	4	20 - 35
38	Lannea welwitschii	Anacardiaceae	3	3	72 - 153
39	Lophira alata	Onchaceae	1	1	445
40	Macaranga hurifolia	Euphorbiaceae	4	4	45 - 98
41	Massularia acuminata	Rubiaceae	1	1	32
42	Memecylon afzelii	Melastomataceae	7	2	25 - 50
43	Monodora tenuifolia	Annonaceae	5	4	21 - 53
44	Morus mesozygia	Moraceae	4	4	29 - 195
45	Myrianthus arboreus	Moraceae	7	3	32 - 139
46	M. libericus	Moraceae	3	1	44 - 53
47	Napoleonaea vogelii	Lycythidaceae	2	2	22 - 27
48	Nesogordonia papaverifera	Sterculiaceae	10	6	30 - 103
49	Panda oleosa	Pandaceae	9	6	55 - 180
50	Piptadeniastrum africanum	Mimosaceae	1	1	255
51	Pterygota macrocarpa	Sterculiaceae	2	2	52 - 91
52	Pycnanthus angolensis	Myristicaceae	11	5	31 - 280
53	Scottelia klaineana	Flacourtiaceae	3	2	40 - 65
54	Sterculia oblonga	Sterculiaceae	22	10	27 - 194
55	S. rhinopetala	Sterculiaceae	7	4	22 - 202
56	Strombosia glaucescens	Olacaceae	15	6	25 - 72
57	Tabernaemontana crassa	Apocynaceae	8	3	31 - 42
58	Terminalia superba	Combretaceae	4	4	47 - 270
59	Trichilia monadelpha	Meliaceae	1	1	138
60	T. prieuriana	Meliaceae	1	1	52
61	Triplochiton scleroxylon	Sterculiaceae	7	3	127 - 350
62	Xylia evansii	Mimosaceae	2	2	79
63	Xylopia quintasii	Annonaceae	1	1	170

Table 2: Trees with Girth Size over 20cm in the Plots.

Timber Class Representation

Tables 3 and 4 illustrate the classification of Ghanaian economic tree species observed in the ten quadrats. Table 3 relates to seedlings and saplings of economic species whose girth sizes were not estimated because they were below 20cm. Out

of an average of 70 species encountered in this category per plot, 8 to 14% of these were economic species. In Table 4, which relates to mature and marketable trees, with girth size above 20cm, 95 out of the total 364 trees found are extractable as timber. In all plots, the percentage of extractable timber was between 18 and 39%.

Thus between the two tables, there is evidence for potential increase in dominance of economic trees with time. In both tables, no representation of Class Ic was found. According to the Ghana Forestry Department listing, *Heritiera utilis* (family Sterculiaceae) is the only species that attains class 1c. This species was completely absent from the ten plots in Bia National Park.

Plot No.	Total No. of Species Present in Plot	Ghanaian Timber Classification Class (Used by Forestry Dept. of Ghana, 1977)						Total No. of conomic Species in Plot	% of Economic Species in Total Species Composition
		1a	1b	1c	2a	2b	3		
1A	83	2	1	-	-	4	5	12	14.45
2A	74	2	-	-	1	4	3	10	13.5
3B	73	1	-	-	1	2	4	8	10.95
4B	76	1	-	-	1	4	5	11	14.47
5A	67	1	-	-	1	4	3	9	13.43
6B	69	1	-	-	-	3	2	6	8.69
7A	56	1	-	-	-	3	2	6	10.71
8B	64	2	-	-	-	4	3	9	14.06
9A	65	1	-	-	-	3	3	7	10.76
10B	64	1	-	-	1	3	2	7	10.94
Total	701	13	1	-	5	34	32	85	

Table 3: Classification of Economic Species with Girth below 20cm.

Class 1a - *Entandrophragma cylindricum*
E. utile
Khaya ivorensis
Class 1b - *Triplochiton scleroxylon*
Class 2a - *Piptadeniastrum africanum*
Class 2b - *Antiaris toxicaria*
Guibourtia ehie
Mandonia altissima
Nesogordonia papaverifera
Class 3 - *Albizia adianthifolia*
Celtis mildbraedii
C. zenkeri
Pycnanthus angolensis
Stombosia glaucesens
Terminalia superba

Plot No.	Total No. of Species Present in Plot	Ghanaian Timber Classification Class (Used by Forestry Dept. of Ghana, 1977)						Total No. of conomic Species in Plot	% of Economic Species in Total Species Composition
		1a	1b	1c	2a	2b	3		
1A	33	1	-	-	2	2	8	13	39.39
2A	41	-	1	-	-	4	9	14	34.15
3B	28	1	-	-	-	-	6	7	25.0
4B	28	-	-	-	-	1	8	9	32.14
5A	39	-	3	-	-	1	10	14	35.9
6B	37	-	1	-	-	3	3	7	18.92
7A	43	1	-	-	-	5	2	8	18.6
8B	50	1	-	-	-	2	6	9	18.0
9A	32	-	-	-	-	1	6	7	21.88
10B	33	-	-	-	-	1	6	7	21.21
Total	364	4	5	-	2	20	64	95	

Table 4: Classification of Economic Species with Girth below 20cm.

Class 1a - *Entandrophragma cylindricum*
E. utile
Class 1b - *Triplochiton scleroxylon*
Class 2a - *Entandrophragma candollei*
Piptadeniastrum africanum
Class 2b - *Antiaris toxicaria*
Nesogordonia papaverifera
Class 3 - *Celtis mildbraedii*
C. zenkeri
Distemonanthus benthamianus
Holoptelea grandis
Morus mesozygia
Pycnanthus angolensis
Scottellia klaineana
Stombosia glaucesens
Terminalia superba

DISCUSSION AND CONCLUSION

In most forest enumerations in Ghana, trees with dbh over 30cm have been used purely for economic reasons of recruitment and marketability of exploitable trees (Forestry Department of Ghana 1988, Ghartey 1990, Hawthorne 1990). The data for the 364 trees in ten plots has served to give an insight into the density, basal area and frequency of the girth size ranges. It is obvious that there is abundance of

saplings and young trees at different stages of development, which need to be identified and nurtured for the future trade in timber.

It is interesting to note from the results above that four of the very common species in the ten plots are indeed classified as important timber species. These are *Guibourtia ehie, Nesogordonia papaverifera, Pycnan thus angolensis* and *Strombosia glaucescens.* It is also worth noting that none of the most desired timber species (in classes la, lb and 2a) particularly *Entandrophragma cylindricum, E. utile, E. candollei* and *Piptadeniastrum africanum* were common; occurring only once in the total observations. These species may be considered rare in the Bia National Park, and every effort must be made to ensure that their stock does not die out. If possible, enrichment planting of such species must be encouraged.

The abundance of species other than the currently desired ones of value for timber, demand further studies for their genetic diversity and their importance in terms of local uses by the people living near the park. There is a need, in future studies, to assess the variability among the individual plants in each of these species, in order to determine genetic variability for future silvicultural treatments and breeding. This is especially necessary if these plants assume positions of value in the future, or are over-exploited and therefore become rare.

The history of the timber industry in Ghana is quite chequered, previously involving the utilisation of only a few timber trees, through an expansion to involve additional species, now referred to as non-traditional timber trees is taking place. This history has seen changes in the emphasis of timber management and classification (Baidoe 1976) to now include several other species that were previously unclassified. A typical example is *Guibourtia ehie,* which was previously unclassified, but which has now been classified with a class 2b rating because of its promotion as export timber (Hall and Swaine 1981). Of the 364 trees examined for girth density and basal area, only 95 of these (25%) are currently known to be exploitable and therefore classified by the Forestry Department. The remaining 270 trees (74%) currently unknown for timber, may become classified in the future when the stock of the desired ones get exhausted, or when there is a diversification drive for all kinds of wood, as is currently happening in the country.

The Ghana Forestry Department refers to some 14 tree species as traditional timber species (Forestry Dept. 1988). All of these tree species are currently classified in Class I, namely: *Entandrophragma angolense, E. cylindricum, E. utile, Khaya an thotheca, K. gradifoliola, K. ivorensis, Militia (Chlorophora) excelsa, Nanclea diderrichii,* and *Tieghemella heckelii* in Class la; *Lovoa tridiilioides, Pericopsis elata, Terminalia ivorensis* and *Triplochiton scleroxylon* in Class lb; and *Heretiera utilis* in Class lc. The

observations at Bia National Park have shown the presence of five of these species, *En tandrophragma cylindricum, E. utile, Khaya ivorensis, Militia* (Chlorophora) *excelsa,* and *Triplochi ton scleroxylon.*

The status of the Bia National Park, both as a national park for the conservation of fauna and floral species, and a World Heritage site and a Biosphere reserve of UNESCO, will ensure the conservation of these tree species with potential to serve as sources of genetic resources. The park is situated within a predominantly rural farming community. As more lands around the park become converted into farms, particularly for cocoa plantations, several non-timber forest products which the people need for some of their other economic activities are also depleted. The park appears to be the only refuge where such products will remain available. Already pressure has begun to mount on the park to supply these products. A need for the understanding of the status of the park by the local people is necessary at this point in time. Several efforts, including education about sustainability and *in situ* and ex *situ* conservation methods/ techniques of non-timber forest products etc. should be undertaken and backed by appropriate incentives. These would ensure that the contributions of the Bia National Park in conservation and sustainable development of forest ecosystems are maintained for posterity.

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Chapter
18

MEASURING AND INVENTORYING ARTHROPOD DIVERSITY IN TEMPERATE AND TROPICAL FORESTS

N.E. Stork[1]

INTRODUCTION

The diversity of arthropods in forests is enormous. This is true of temperate as well as of tropical forests (Hammond and Owen 1995, Hammond 1990, Stork 1991, Stork and Brendell 1990). Hammond and Owen (1995), for example, recorded 959 species of beetle in the 1000 hectare Richmond Park during their intensive five year study of this woodland in southern Britain (Figure la). This represents a quarter of all British species of beetles. By comparison, more than 6,000 species of beetle were collected in a similar sized area of tropical forest in North Sulawesi in one year (Hammond 1990, 1994 and unpublished, Stork and Brendell 1990) (Figure lb). If we consider that beetles represent about 20% of the arthropod fauna in a forest (Stork 1988, 1993), then the total arthropod fauna in these examples of a temperate and a tropical forest may be at least 5,000 and 30,000 species respectively

Not surprisingly therefore, a full inventory of the arthropods in forests (let alone fungi and microorganisms) has never been completed for any site,

[1] Biodiversity Division, Entomology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

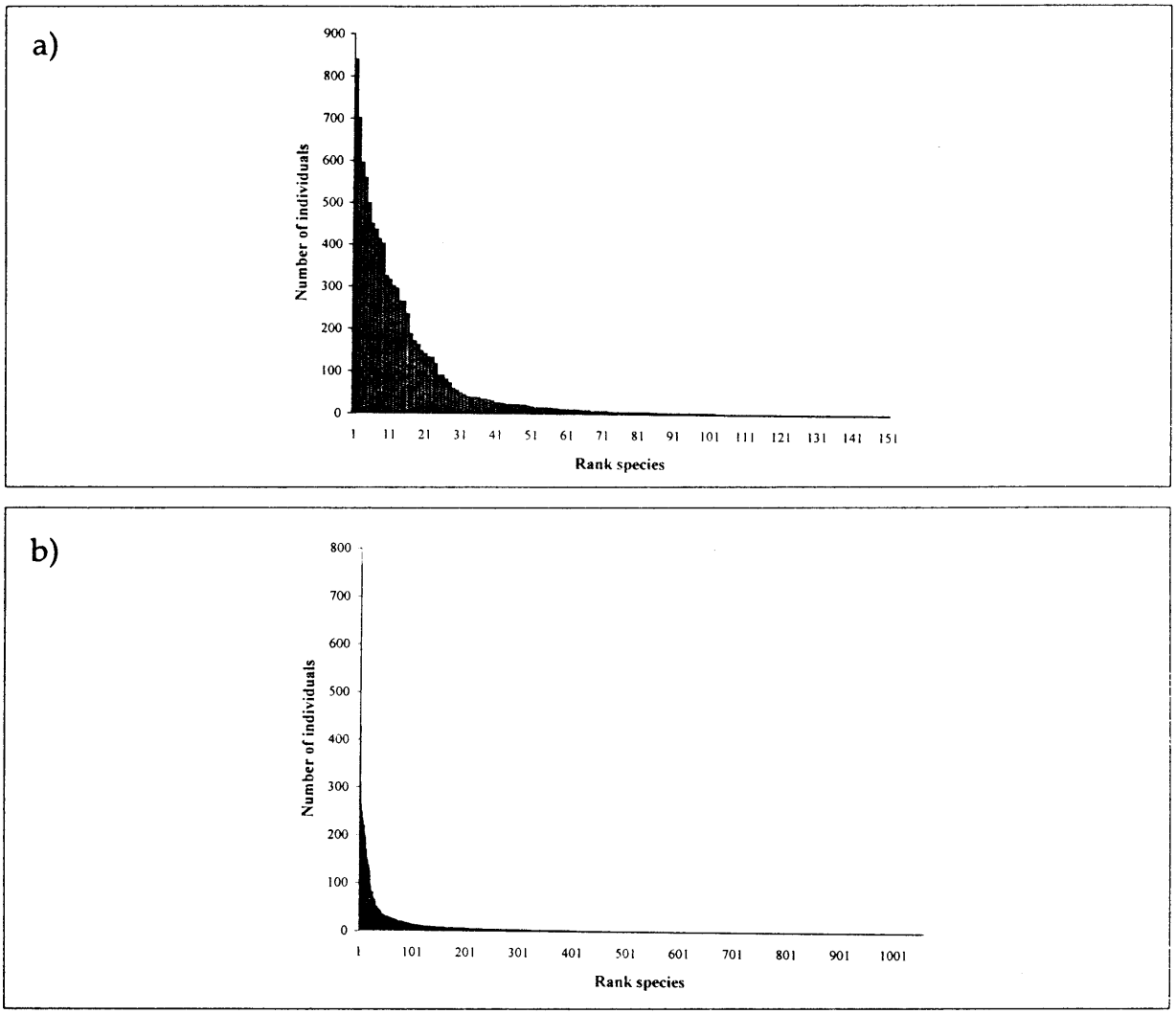

Figure 1: Rank species-abundance plots for samples of beetles collected by canopy fogging from a) oak trees in Richmond Park, UK and b) lowland rain forest in Dumoga-Bone National park, Sulawesi. The samples of beetles from Richmond park, representing 151 species and 5,018 adult individuals, were located from 36 trees which were samples three trees at a time at more or less regular intervals from May to October in 1984. The samples of beetles from Sulawesi, representing 1,056 species and 7,571 adult individuals, were collected from 10 forest plots each 144m^2 in area which were sampled six times (at approximately two-month intervals) in 1985. The total collecting area of trays used in Richmond park and Sulawesi was approximately 640m^2 and 672m^2 respectively. Note that the shapes of the curves are very similar but that the number of species involved and the length of the tail of species represented by single individuals is almost 10 times greater for the Sulawesi samples.

temperate or tropical, on Earth. For example, in spite of the efforts of researchers from Oxford University in the 1950's through to the 1980's, the full list of arthropod species from Wytham Wood - one of the best known temperate forest sites in the world - has never been completed. There are several reasons for this. First, arthropods are so taxonomically diverse and species rich that there are never enough taxonomists to cover all groups. Second, temporal and spatial variation in the abundance and distribution of species means that even intensive sampling of a forest over several years will inevitably fail to collect all species that use, or potentially use that forest. For this reason, accumulation curves for insects from forests never reach an asymptote but continue to creep upwards (see Figure 2 in Stork 1993) . At this near asymptote many of the new species being collected will be transients ('tourists' *sensu* Moran and Southwood 1982), having little to do with the area concerned. Over a 15 year period Owen (1991) collected 1782 species of animals and 422 species of plants in her 0.5 hectare garden and many of these species are tourists. The third and final reason is that no collecting method can collect all species present in an area and, however intensively an area may be sampled and whatever range of sampling methods are used, some species will be missed. The introduction of novel methods of collecting are testimony to this. For example, canopy fogging with knockdown insecticides has revealed an unimagined richness of insects in trees (Stork 1991). Noyes (1984) and Askew (1985) both described the immense diversity of Chalcidoidea collected by canopy fogging from trees in Brunei and Richmond Park, respectively (see Table 1). Probably more than 90% of the species in the Brunei samples were new species, collected for the first time. Sampling the fauna of leaf litter and soil using traditional Berlese-Tullgren funnel methods is extremely difficult in tropical forests and the readily portable Winkler bag has revolutionised the collecting of many arthropod groups for this habitat. The first five species of the very small chrysomelid, *Clavicornaltica,* were described from leaf litter samples in 1974 from Sri Lanka (Scherer, 1974). P.M. Hammond (unpublished) collected a further 70 species from the Mulu National Park in Sarawak in 1978 using the Winkler bag method. Subsequently, many other species - mostly waiting to be described - have been collected from leaf litter using this method, in pit fall traps, and even from trees by canopy fogging in other parts of South-east Asia.

These comments are not intended to deter researchers planning intensive sampling of forests for insects but rather to set the scale of the task involved. With such immense diversity, is it possible to carry out research programmes aimed at inventorying the arthropod fauna of forests or aimed at measuring the changes in

arthropod fauna resulting from changes in forest management? In the following section I discuss three aspects of sampling with particular reference to insects and arthropods: indicator groups, morphospecies, and rapid assessment. I first discuss why it is important to include inventories of insects and other invertebrates as part of any sites analysis.

	Brunei		Richmond Park	
	Indivs	Species	Indivs	Species
Agaonidae	16	14	0	0
Aphelinidae	250	146	431	8
Chalcididae	7	3	0	0
Elasmidae	10	6	0	0
Encyrtidae	296	170	1915	27
Eucharitidae	7	1	0	0
Eulophidae	512	229	433	50
Eupelmidae	105	41	53	2
Eurytomidae	23	13	28	2
Mymaridae	57	36	15	6
Ormyridae	4	2	7	1
Pteromalidae	61	32	761	41
Signiphoridae	2	1	0	0
Tanaostigmatidae	5	3	0	0
Torymidae	70	24	79	7
Trichogrammatidae	11	10	22	3
Total	1436	731	3744	147

Table 1: Numbers of species of Chalcidoidea collected by canopy fogging ten trees in Richmond Park, UK and Brunei (after Askew (1985), Noyes (1984) and Stork (1991)).

WHY INCLUDE INSECTS IN BIODIVERSITY ASSESSMENTS?

In the Introduction I highlighted the sheer magnitude of insect diversity and their abundance, but that on its own is not sufficient to warrant their intensive study in biodiversity assessments. It is widely recognised that insects and other invertebrates are essential for the 'ecosystem services' they provide in forests and other ecosystems. To be more direct, forests could not exist without these organisms.

Obvious examples are termites and earthworms which are essential for the production and maintenance of soil, whereas some species of thrips (Thysanoptera), beetles and bees are essential for the pollination of plants. Other species are less obviously important but are an integral part of the many complex foodwebs that are to be found in forests (e.g. Memmott et *al*. 1994). Measurement of biodiversity in forests, whether for studies of the diversity or health of the system, must include assessments of insects and other invertebrates.

As discussed below, for rapid or longer term assessments of biodiversity, inevitably choices have to be made as to which groups to use for inventorying. Usually, birds and mammals and large plants are first choices with few insects falling into this category. Butterflies, dragonflies and tiger beetles are perhaps, the most obvious exceptions. However, as several authors have shown (Prendergast *et al*. 1993, Yen 1987, Burbridge *et al*. 1992) the distributions of different insect groups or other taxa do not necessarily correlate with each other, and the conservation needs for different groups of insects may not be fairly represented by either these insect taxa or other groups of animals and plants. For example, Prendergast *et al.* (1993) showed that the richest areas of the UK for butterflies, dragonflies, liverworts, aquatic plants and breeding birds did not necessarily overlap, nor did their centres of endemism. In addition, measurement of the diversity of groups such as plants, birds and mammals may provide a poor indication of the conservation value of some temperate woodlands, particularly managed woodlands (Harding and Rose 1986). In these cases, the richness of saproxylic and other insects (particularly Coleoptera and Diptera) are more useful indicators of the age and health of these woodlands (e.g. Hammond and Harding 1991, Terrell-Nield 1990)

INDICATOR GROUPS

The term indicators has a variety of interpretations in different contexts. Some use the term in a general way to mean a variety of measures of the condition of a system. Reid *et al*. (1993), for example, provide a list of 22 biodiversity indicators (e.g. species richness, species threatened with extinction, species used by local residents) that can be used to measure the conservation status of an ecosystem. What they do not attempt to do is to determine for which taxa these data should be compiled. Clearly, we know so little about the Earth's fauna and flora that it would be impossible to measure these biodiversity indicators for all taxa and therefore certain taxonomic or morphological groups need to be selected as indicator groups. In the terms of Kitching (1993) we need a predictor set of organisms such that changes

in their biological status will reflect similar changes in a wider group of organisms. The term indicator group has been loosely used by many and has therefore come to represent a very broad term. Hawksworth (in press) compiled a list of alternatives for this term which are more specific in their application. For example, he suggests that biomonitors are concerned with the monitoring changes in individual populations over time. Here, I consider the term bioindicatorto be used for those taxa which through measurements of their presence/absence, abundance, distribution, species richness or other measure provide an indication of the health or state of a broader group of insects or other community. Many species of Chironimidae, for example, are extremely sensitive to changes in pH or pollution levels of freshwater and are therefore used as indicators of water health, or rather health of the freshwater animal community (Pinder and Morley in press). Similarly, carabid beetles and macrolepidoptera are commonly used as indicators in terrestrial ecosystems including temperate and tropical forests (e.g. Brown 1991, Luff and Woiwod in press). Others have made cases for their own specialist groups, such as Scarabaeidae (Halffter and Favila 1993) and Cicindelidae (Pearson and Cassola 1992), to be considered as candidate indicator groups. Brown (1991) analysed some of the qualities that might be required of an insect indicator group and devised a scoring system. This system indicated that amongst terrestrial insects, ants (Formicidae), some butterfly groups (Heliconiini, Ithomiinae), some beetle groups (Carabidae, Cicindelidae and others) and Isoptera, scored highest and therefore were important indicator groups. Brownś system is somewhat idiosyncratic and perhaps more appropriate for the neotropics than elsewhere. Clearly, which groups are selected as indicators will depend on what they are supposed to be indicating, the ecosystem concerned, geographical location and other circumstances. However, as Prendergast et *al.* (1993) have shown, we have to be sure that our indicator groups do truly provide a broad picture of the ħealth'of a wider range of groups. In this sense the term þredictor set'is particularly appropriate (Kitching 1993).

What is lacking is a truly objective analysis of which groups of insects to select as your indicators. This set would differ depending on the situation and the kind of assessment being made. Brownś (1991) set of values would not necessarily be suitable for a temperate or freshwater community. One approach to this problem is to select an appropriate śhopping basket'of taxa (Stork 1994). For example, rather than pick just one or two taxa which have their own peculiar biologies, it might be more appropriate to select a larger group of say 10-20 taxa with a much broader range of biologies and habitat preferences. This shopping basket of groups might thus be a better predictor set than just one or two groups. Stork (1994) identified a

number of characteristics that might be considered when selecting a shopping basket of groups including the following: taxonomic breadth, ecological diversity (e.g. ranges of body size, feeding guilds, reproductive biology). Where such information is available, it would be useful to consider the sensitivity of different taxa to natural and human influenced environmental factors such as pH, humidity/water availability, temperature, light, CO_2 and NO_X concentration, and heavy metals.

In addition to these biological factors there are important practical factors that need consideration when selecting a predictor set or shopping basket of groups. For example, these groups need to be ones that can be sampled cheaply. rapidly and reliably Groups selected should not be taxonomically intractable and also there must be expertise widely available or adequate literature sources such that taxa can be readily identified.

RAPID ASSESSMENTS

In recent years there has been an increasing demand for inventories of temperate and tropical forests. The UNCED meeting of heads of government in Rio de Janeiro in 1992 and the resulting agreements, such as Agenda 21, the Biodiversity Convention, and the Climate Change Convention, raised our awareness of the plight of biodiversity. As a result of these agreements, and because of the perceived urgency of the situation, many agencies such as the World Bank require rapid assessments of biodiversity both to assist conservation priorities and for the evaluation of the impact of large-scale development projects. Trueman and Cranston (1994) highlight the different perceptions of such rapid assessments. They suggest that the Biodiversity Rapid Resource Appraisal Study of the World Bank Environmental Facility (GEF) is concerned with the production of an assessment in a fixed and short time frame in order to provide practical conservation advice. Almost of necessity such assessments are desk-top studies using existing data from herbaria and museum collections with perhaps some computer simulations or computer mapping schemes to provide predictions. The United Nations Environment Programme Country studies and many national Biodiversity Action Plans are generally similar in their approach to rapid assessments of biodiversity. The UNEP Guidelines for Country Studies recommends a large range of measurements of biodiversity (see UNEP 1993) but only relatively few relate to species level data. Implicit in these guidelines is the use of existing data rather than the collection of new data from field surveys. Many of the measures they recommend

are socio-economic measures of biodiversity. This is not surprising as the sustainable utilisation of biodiversity is a high goal for many developing nations. Furthermore, documents such as Country Studies and National Biodiversity Action Plans, are highly political documents.

Another use of the term rapid assessment is more or less synonymous with fast field survey (e.g. Parker et *al*. 1993). As Trueman and Cranston (1994) point out, these field-based rapid assessments typically examine only trees, large mammals and birds (sometimes reptiles and amphibians) and therefore consider the diversity of a very small proportion of the total species in a forest or other habitat being examined. Perhaps more than 95% of the fauna and flora (arthropods, other invertebrates, fungi and other microorganisms) in the areas examined are not considered. Usually these assessments are single visits of a month or less and therefore, even if invertebrate groups or fungi were to be examined, the temporal nature of these organisms could not be addressed. Most insects are seasonal even in apparently aseasonal climates (see Paarmann 1976). However, it is usually possible to predict the most appropriate season for sampling the greatest diversity of insects at a particular site.

How then can rapid assessments be carried out for insects? First, it is important that some groups are recognised as front line indicator groups. As yet no coordinated effort has been made to select such indicators, predictors or sampling packages, although there is now much evidence from recent studies to make such a selection. Second, standardised methods of sampling need to be agreed. For groups such as amphibians and birds, such standards have been recognised (e.g. Heyer *et al. 1993).* Third, methods of statistical analysis need to be agreed. The latter is probably the area most lacking in agreement and understanding.

MORPHOSPECIES

For those biologists studying ecological patterns in species-rich communities, such as insects in temperate or tropical forests, sorting samples and dealing with the many species in them are major problems. For some studies, knowing the precise name of a species may not be essential as long as some aspects of the feeding biology or habitat can be determined. However, identifying species does provide some measure of confidence in the level of sorting and provides access to the biological literature associated with the named species. However, in most parts of the world there are neither sufficient taxonomists nor adequate collections of authentically named species to be able to identify all species found in samples. This problem is

further compounded by the fact that in many samples most of the species are new to science and are therefore unnamed. In such cases researchers sort their samples on morphological characters as near as possible to what they believe are species so called 'morphospecies' (also known as 'recognisable taxonomic units' (RTUs) or 'operational taxonomic units' (OTUs)). It is currently acceptable that once having defined the level of sorting (i.e. to morphospecies/RTUs/OTUs) in a paper, authors then use the term species throughout, as **if** their morphospecies are directly equivalent to real species. Thus as standards of sorting vary enormously, the term morphospecies has been somewhat abused in the literature and needs further definition. Editors of ecological journals often can be very demanding of authors when it comes to the statistical procedures used in a paper. This is because standard statistical tests and procedures are now widely recognised. Statistical standards have been raised by the widespread use of commercial computer statistical packages. However, similar taxonomic standards do not exist and therefore levels of taxonomic competence in sorting samples to species, varies greatly The current lack of sound training in taxonomy in many universities and personal experience of the level of species sorting of some postgraduates and more senior scientists completing community ecology studies indicates that this is an area which needs some serious attention.

Oliver and Beattie (1992) examine how well a technician compared to professional taxonomists in their sorting to morphospecies of samples of Australian mosses, polychaetes, ants and spiders after just a few hours of formal training. They found a very high level of agreement in the sorting (see Table 2) with 88% and 83% '1 to 1' level agreement at the species level for spiders and ant species, respectively However, a sample of one technician is not adequate to assess the taxonomic competence of technicians after limited training. Also it should be recognised that in spite of good correlations between the species sorting and the total number of species, the evenness of the sample, guild composition and so on may be quite different. In many insect samples there is often a long tail of singletons but it can be very difficult to assess whether these are really different species from each other or whether some of these may represent very variable species. Sexual differences between species in some groups (e.g. Pselaphidae) can make it very difficult to match males and females.

Here I propose a simple system of grading the level of accuracy of sorting to morphospecies and verifying this sorting (Figure 2). This system will not go as far as providing a 'certificate of taxonomic competence', equivalent to standard statistical procedures or well recognised standards of 'good laboratory practice',

but it may make those that use it more aware of the procedures necessary for accurate sorting and thereby raise standards. It is divided into two parts - sorting to species, and verification of the sorting - reflecting the two critical stages in identifying species. Those using these standards should refer to both parts of the system (e.g. samples of beetles from Malaise traps in Malaysian hill forest were sorted to morphospecies levels 1 and 5). Those sorting samples should try to aim for as high a level as possible (e.g. levels 3 and 7). Voucher collections are essential, except in some rare circumstances, such as when dealing with samples from a well-known fauna or flora (e.g. that of the British Isles), where it may not be necessary to take many voucher specimens. Authors should i) state what proportion of the samples have been prepared as a voucher collection and where that collection is housed, and ii) record the taxonomic support and verification as part of the Methods section of a paper.

	Number of morphospecies recognised by:	
	Technician	Taxonomists
Mosses	87	86
Polychaetes	29	21
Spiders	103	91
Ants	33	35

Table 2: Comparison of the number of morphospecies sorted from the same samples by a trained technician and by professional taxonomists (after Oliver and Beattie, 1984). See comments in text.

Initial sorting to species:

i) Morphospecies level 1 - specimens sorted to species without being removed from site (e.g. trees or large mammals) or without vouchers being removed and prepared from the sample and prepared in standard manner (e.g. mounted and labelled or pinned as for beetles).

ii) Morphospecies level 2 - Initial sorting to species in the sample being supplemented by preparation of a voucher collection of a representative set of specimens. Voucher collections of single or few specimens per species are usually inadequate for assessment of the distinctiveness of the species.

iii) Morphospecies level 3 - Preparation of all specimens and sorting of all to species. Thus all specimens form the voucher collection.

Verification of species sorting:

iv) Morphospecies level 4 - Sorting checked by a non-taxonomist.

v) Morphospecies level 5 - Sorting checked against a comprehensive and accurately named museum/herbarium collection.

vi) Morphospecies level 6 - Species sorting checked by an appropriate specialist taxonomist or taxonomists.

vii) Morphospecies level 7 - Species formally described or new records published for existing species from the samples by taxonomists.

Figure 2: A system of levels for morphospecies sorting.

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Chapter
19

MEASURING BIODIVERSITY DIVERSITY OF MICROFUNGI IN THE WET TROPICS OF NORTH QUEENSLAND

Kevin D. Hyde[1]

INTRODUCTION

This chapter will focus on the microfungi of rainforests in the wet tropics of north Queensland, Australia, choosing the fungi developing on palms and those in streams to illustrate how little is known. with respect to other rainforest substrates in north Queensland, the reality is we know very little about the microfungi present. There have been very few studies and it appears that no taxonomic mycologists have lived and worked in this region. The lack of information on the microfungi of north Queensland is typical for the tropics as a whole. Australia is regarded as a developed country and the situation is unsatisfactory. Most tropical rainforests occur in developing countries where even less is known.

Between May 1989 and October 1992, I was able to study some of the microfungi in the rainforests around Cairns. I focused my research on fungi developing on wood submerged in streams and on fungi developing on palms. The data that I am presenting is mostly the conclusion from my own research and I am aware of

1 Department of Ecology and Biodiversity, University of Hong Kong, Pokfulam Road, Hong Kong.

few other studies on th microfungi in north Queensland other than those in plant pathology.

Anon (1992) estimated that 85% of Australian plants (estimated 44,000 species) were either named or known, but that only 10% of fungi (estimated 200,000 species) were named. In another estimate, Pascoe (1990) indicated that there could be as many as 250,000 fungal species in Australia and that only 5% were known. There may be many more species than even these estimates suggest. Pascoe (1990) based his figures using a ratio of vascular plants (25,000) to fungal species (250,000) of 1:10. As will be illustrated with the studies of microfungi on palms, a ratio of 1:10 is very low.

A survey of the taxonomic mycologists in Australia in 1991 (Grgurinovic and Hyde 1993) concluded that there were only 32 mycologists whose research incorporated at least some taxonomic mycology - only one of these was working on rainforest fungi. Can this small number of mycologists deal adequately with the Australian mycoflora? Assuming a mycologist can describe 600 species during a working lifetime (40 years), then 19,200 species (32 x 600) should be described in the next 40 years. If we use Pascoe's (1990) conservative figure of 250,000 estimated fungal species, and assume optimistically that all Australian mycologists are active (and the habitats are preserved), then the last Flora of Australia will be written in the year 2515. This illustrates the dire plight of mycology in Australia.

WHY DO POLITICIANS NOT FUND MYCOLOGY?

Politicians and scientists alike are accountable for the decline of funding in mycology and some of the reasons and misapprehensions as to why fungi are overlooked and thus poorly funded are given:

1. Agriculturally and other economically important species of fungi are studied, while most others are disregarded.
2. Most people prefer to destroy rather than collect fungi.
3. There is a misapprehension that most fungi are poisonous.
4. The larger tropical fungi are seasonally present for short periods (usually when its raining!).
5. The public are unaware of the presence of fungi, most of which they can never see.
6. The public are uninformed of the important role of most fungi.

7. Fungi rot people's houses and grow on their bodies.
8. Most fungi are sessile.
9. Some fungi are offensive (stinkhorns).
10. Many fungi smell and some attract flies.
11. The ecological importance of fungi is often overlooked.
12. Mycologists do not promote mycology.

WHY SHOULD WE STUDY FUNGI?

With such a dreadful rating with the public, politicians and non-mycological scientists alike, what prospect is there for mycology? Perhaps the greatest promise is in biodiversity studies with some of the potential benefits in the form of novel compounds. Grgurinovic and Walker (1993) have given several reasons as to why mycological herbaria should be maintained. I have expanded this below, to give some reasons as to why we should study fungi:

1. Documentation of fungal biodiversity provides a basis for monitoring success of conservation and management practices.
2. Control of plant and animal diseases caused by fungi.
3. Biological control of weeds (e.g. *Mimosa pigra* in the.northem territory).
4. Biological control of arthropods (e.g. *Cordyceps, Mefarrhizum).*
5. Medicinal properties (e.g. *Cordyceps* tea, antibiotics, immuno-suppressants).
6. Quarantine.
7. Role of fungi in nutrient cycling and thus management of ecosystems (e.g. mycorrhizae, endophytes).
8. Attraction (e.g. *Phallus* sp.).
9. Biotechnology.
10. Mycotoxins (e.g. potent carcinogens - aflatoxins).
11. Pure science.

Numerous biotechnological products are produced industrially as a result of fermentation utilising fungi (Table 1). However, there are millions of undiscovered fungi world-wide that will have the genetic potential to produce a multitude of novel compounds. The examples below illustrate some of the recent achievements in this field of research.

Fungus	Production
Ashbya gossypii	Riboflavin (vitamin)
Aspergillus niger	Citric acid, Gluconic acid, a-amylase, protease
A. oryzae	a-Amylase
A. terreus	Itaconic acid
Mucor pusillus	Rennin
Penicillium ch ysogenum	Penicillin
Penicillium griseofulvin	Griseofulvin (antibiotic)
Rhizopus nigricans	Fumaric acid
Saccharomyces cerevisiae	Industrial alcohol
Trichoderma reesei	Industrial alcohol

Tabie 1: Some Biotechnological Uses of Fungi.

Cyclosporine

Cyclosporine, like penicillin one of the best known pharmaceutical successes, was discovered as a metabolite of *Tolypocladium inflatum* Gams. This fungus was isolated from soil in Hardanger, Norway in 1970 and was found to synthesise metabolites that were later called cyclosporins. It is this highly modified strain that is now used in the large scale production of cyclosporin A by fermentation (Bore1 and Kis 1991). Cyclosporin emerged as the prototype of a new generation of immunosuppressive drugs and is today important as the first-line treatment in organ transplantation.

Other novel *compounds from fungi*

Extensive screening of fungi for the production of novel compounds is currently under way and has resulted in the discovery of numerous potential pharmaceutical products (Nisbet and Fox 1991). Three examples are given here. Phomactin A, isolated from a marine *Phoma* sp.,is a novel platelet activating factor (PAF) antagonist. PAF may be implicated in many inflammatory, respiratory and cardiovascular diseases (Sugano *et al*.1991). Emeriamine, isolated from *Emericella quadrilineata* ¡s a new inhibitor of long chain fatty acid oxidation and may have potential utility as a therapeutic agent for treating diabetes (Kanamaru and Okazaki

1989). Two new depsidones, Auranticins A and B, were obtained from a mangrove isolate of the fungus *Preussia aurantica* and were found to exhibit antibiotic activity against *Bacillus subtili* and *Staphylococcus aureus* (Poch and Gloer 1991).

PALM MICROFUNGI

Fungi have been collected from eight of the sixteen native palm genera (38 species) represented in Queensland. Most palm fungi (48 species) have been recorded from *Archon tophoenix alexandrae* (F. Muell.) Wendl. and Drude. Many of these collections on *Archontophoenix* are the result of a short visit to north Queensland by Matsushima in May 1988 (Matsushima 1989), who lists 31 hyphomycetes, and of recent studies by Frohlich and Hyde (1994) and Hyde (1993c,d,e, 1994a,b) who record 6 ascomycetes. Fungi on other palms are virtually unknown. Only 4 fungal species have been recorded from *Cocos nucifera* L. (all plant pathogens) and 12 species from *Calamus* spp. (Hennings 1903, Hyde 1992d, 1993d, 1994b, Hyde and Fröhlich 1994, Hyde and Alcorn 1993, Matsushima 1989, Simmonds 1966). The low ratio of fungi recorded on palms (1.5:1) in north Queensland reflects what little is known of the mycoflora of all rainforest habitats.

Microfungi on palms include pathogens, endophytes and saprophytes. The symptoms of pathogenic fungi are varied, but many form leaf spots and these are often species or genus specific. Frohlich (1992), Fröhlich and Hyde (1994, 1995a, b, c) and Hyde and Frohlich (1994) identified 28 taxa, including 2 new genera and 11 new species associated with palm leaf spots in north Queensland. The implications of fungal pathogens to quarantine and the ornamental palm industry (estimated annual turnover of sixty five million dollars - Forsberg 1987) are enormous and this is a glaring example of important research that has not been carried out.

Endophytes develop within the tissue of plants and rarely produce external symptoms. Their nutrition is derived from the plant and in return they may provide some form of protection (e.g. from grazing by insects). There is very little available information on the endophytes of tropical plants (Rodrigues and Petrini 1995). Frohlich (personal communication) has recently isolated about 150 cultural morphotypes from three single *Licuala* sp. palms in north Queensland, while I have isolated similar numbers from *Calamus* sp.

Saprophytic fungi are able to develop on a wide range of dead palm material and are less likely to be host specific. However, one would expect some fungi to be selective to specific palm species or genera. This was found to be true of mangrove

trees (Hyde 1990). The number of palm saprophytes, appears to be extremely high. I have found several hundred taxa on palms in South East Asia (Hyde, unpubl.). In Australia *Archontophoenix alexandriae* is the host of 48 saprophytes, but this is the only palm examined in any detail.

It is possible to speculate on the numbers of palm fungi in Queensland. There are 38 native palm species and we can estimate that there are about 3 plant pathogens, 100 endophytes and 10 saprophytes that can develop on each palm species. If we are conservative and assume that 10% of microfungi are host specific, then in north Queensland we can anticipate finding 430 fungal species on palms. If we are less conservative and calculated that 25% are host specific, then 1073 microfungi should occur on palms in north Queensland. These figures have marked significance on the total numbers of fungi in Australia and world-wide. Pascoe (1990) estimated that there were likely to be 250,000 fungal species in Australia, using a host species to fungal species ratio of 1:10. Hawksworth (1991) calculated a world total of 1.5 million fungi using a host species to fungal species ratio of 1:6. With palms the host species to fungi ratio is (presumably) much higher.

FRESHWATER FUNGI

The microfungi (ascomycetes) occurring on wood in freshwater streams were reviewed by Shearer (1993) who listed about 300 species. Of these only seven were tropical, which reflects the lack of information on ascomycetes in tropical streams globally. Only three of these seven species were Australian collections, an inconceivably small number when compared to the number of habitats and the role of these fungi in nutrient cycling. This lack of knowledge also applied to other fungal types in freshwater habitats in the Australian tropics. With this realisation, studies of the fungi colonising wood submerged in freshwater in far north Queensland were initiated.

Forty fungi have now been collected on wood submerged in streams in north Queensland, and 25 are formally described or listed (Hyde 1992a,b,c, 1993a,b, 1995a,b,c, Hyde and Seifert 1992). They are a distinct ecological assemblage and belong to a diverse range of families. Taxonomic placement is not easy as few mycologists have such a wide expertise. Only 6 of the 40 species are also found in temperate streams, most species appearing to be restricted to the tropics. As little work of this nature has been carried out in the tropics many of the fungi collected are new to science; 7 new genera of ascomycetes, including 17 new species, one new genus of synnematous hyphomycetes and one new genus of Coelomycetes

have been described. These fungi are apparently unrelated to host substrate and are an extra group to add to biodiversity calculations.

WHY MEASURE FUNGAL DIVERSITY?

I have often heard the argument, why do we need to know what fungi are present in an ecosystem? Why not just measure their activity or why not use isozyme studies to indicate fungal presence? I hope that I have succeeded in convincing you as to why we should know what fungi are present in various habitats in the section "Why should we study fungi?". As arguments for maintaining insect biodiversity (Kim 1993) use impoverished biodiversity, loss of basic resources, and loss of potential food resources, similarly, these reasons are applicable to fungi. Because few fungal species are presently utilised in biotechnological processes, or in the production of novel compounds, there is a huge potential for their use. Remarkably little is known of microbial diversity, numerous species remain to be described, and the genetic diversity within those that are known is scarcely studied (Bull 1991). We need to collect, identify, name and maintain these fungi before they disappear. Furthermore, because of their integral role in ecosystems, e.g., nutrient cycling, plant growth, food source, sensitivity to air pollution and perturbation, fungi lend themselves to measuring and monitoring biodiversity (Rossman 1994).

THE NEED FOR HERBARIA AND CULTURE COLLECTIONS

An inventory of the microfungi present in any rainforest ecosystem is desirable, but it is also important to conserve the fungi as dried material in herbaria and living material in culture collections. There is a need for more national herbaria and culture collections, particularly within developing countries in the tropics from the following perspectives:

1. *Industrial* perspecfive. Fungi and bacteria are an important source of novel compounds used in medicine and food production. In South East Asia and China there is a pool of genetic material in the form of fungi and bacteria that could be important in developing any of these benefits and the material is presently not available to industry.
2. *Conservation and biodiversity perspective.* With the rapid destruction of the world's rainforests and natural environments thousands of species become extinct every year and this includes microorganisms. These microorganisms are pools of genetic material that can be extremely useful to mankind in medicine, industry

and numerous other avenues. We are therefore obliged to conserve as much of this material as possible for future generations.

These arguments apply to many countries in the tropics. However, culture collections can never hold more than a fraction of the fungal resource (17% of accepted fungal species are presently maintained in culture collections) and the only way to fully conserve diversity is by conservation of the ecosystems (Bull 1991, Olembo 1991).

MEASURING BIODIVERSITY OF MICROFUNGI

In its simplest form, species diversity is the number of different species of organisms found in a particular habitat or ecosystem (Dighton 1994). One of the problems in measuring the overall biodiversity of microfungi in rainforests is the large number of habitats one would need to sample and the diversity of organisms that would be encountered. In a rainforest situation there are numerous microhabitats (Figure 1) and each of these would need to be sampled. This would require input from numerous mycologists, since a soil fungi specialist is unlikely to be an authority on palm fungi. Furthermore, diverse groups of fungi will be encountered, which would again require the input of several mycologists, as no singie mycologist is likely to be an expert in all fungal groups. Several techniques would be employed, so that all groups of fungi present are isolated and catalogued. Finally, many of the fungi collected in any survey would be new to science and their identification may only be possible to genus or family level.

How then do we tackle the problem of measuring the immense biodiversity of microfungi in rainforests? Do we choose indicator organisms or target groups, in a similar way to those of entomologists. Could we train students or "biodiversity technicians" for short periods, to sort fungi into recognisable taxonomic units (Oliver and Beattie 1993), or do we approach the problem in a different way? A need for world initiatives in biodiversity databases has been stressed by Hawksworth and Mound (1991). Standard techniques for measuring diversity are required before meaningful comparisons can be made between geographically distinct regions and different habitats. Mycologists need to discuss and agree on these methods and a workshop to discuss approaches may be an appropriate forum (Rossman 1994). Such a workshop would consider techniques, from visual sampling using plots or transects, to laboratory isolation and culturing. In the remainder of this chapter I will briefly discuss some techniques propose one method for measuring biodiversity of microfungi in rainforest. It is my hope that it will promote the much needed discussion amongst mycologists.

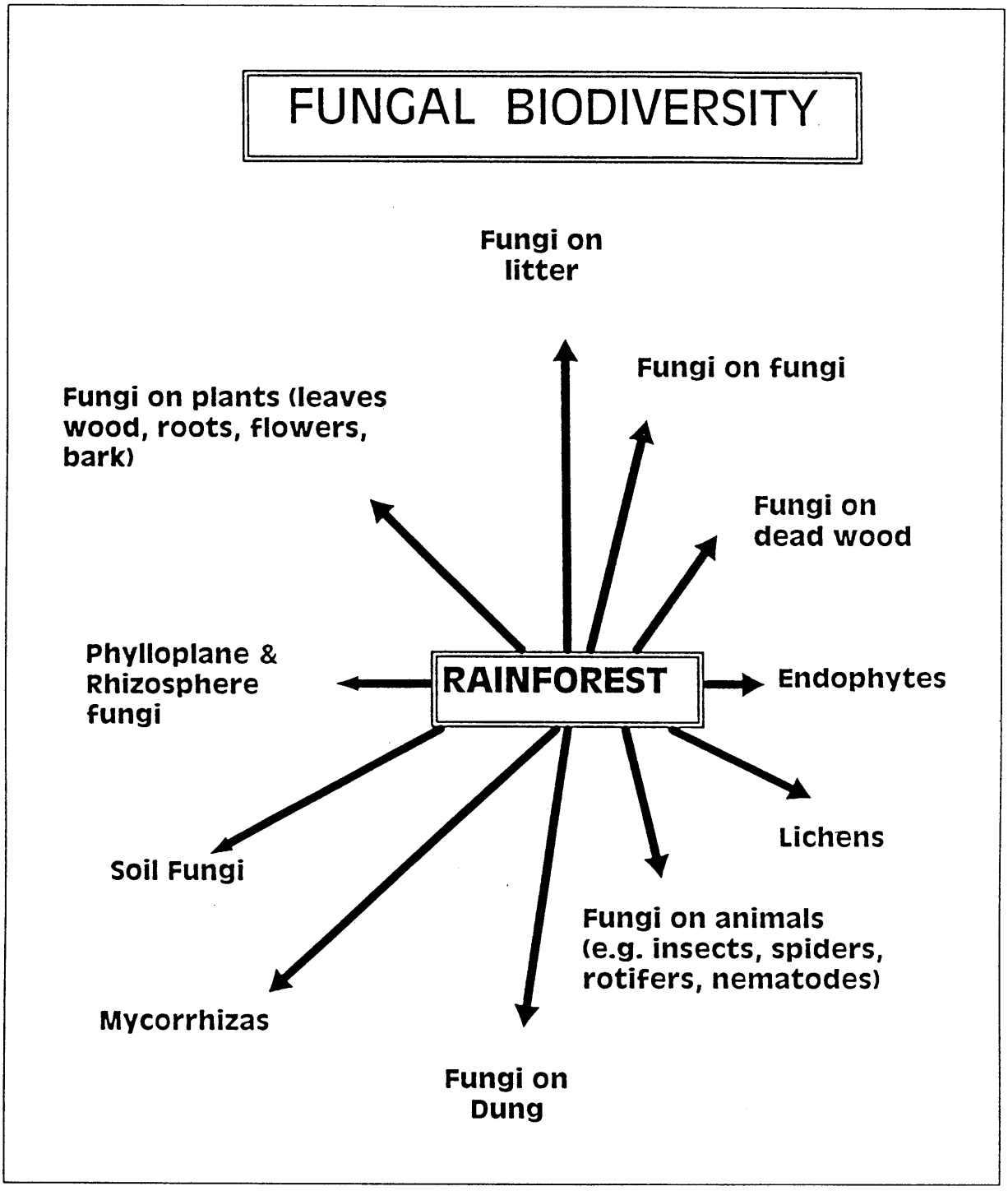

Figure 1: Possible Microhabitats for Fungi in a Rainforest Environment.

INVENTORY AND MONITORING

In Chapter 3, Burley and Gauld propose immediate assessment needs, new research required and the need for rapid monitoring methods for all organisms. Many of their recommendations also apply to microorganisms.

One way forward is to target genera or families of microorganisms or specific habitats, as a measure of biodiversity. However, there may be problems in this approach. If the ascomycete genus *Xylaria* was chosen to represent diversity in tropical rainforests, then the results might be misleading. In a rainforest near Lockerbie in north Queensland in March 1991, there was a large diversity of *Xylaria* species, while in Pasoh rainforest in Malaysia in November 1991, *Xylaria* species were scarce. If we extrapolated from these results we would conclude that the diversity of fungi in Lockerbie was much greater. Although this may be true, it may be equally true that the numerous *Xylaria* species at Lockerbie was the result of a recent destructive cyclone. Similarly, choosing habitats, e.g. bamboo, to measure biodiversity of microorganisms may also generate deceptive results. The number of native bamboo species in Australia is small when compared to Borneo and a measure of fungal diversity on bamboo would be very biased towards large numbers in the latter region. The timing of the survey would also be significant, as fungal diversity would differ between wet to dry seasons.

An integrated approach may provide a viable solution to measuring biodiversity in rainforests. Unfortunately it will be time consuming and require the expertise of several mycologists. A permanent protected plot of 100 m^2 (selected to incorporate high plant and habitat diversity) should be established under the auspices of a local scientist. The plant species within the plot should be identified and labelled where possible. A mycological inventory can then be carried out over a period of several years, with input from appropriate specialists. The larger basidiomycetes (e.g. polypores), ascomycetes *(e.g. Xylaria),* and some biological groups of fungi (e.g. entomophagous fungi, freshwater fungi) can be collected and identified (spatially and temporally) over the whole plot, as their numbers would be manageable.

Microfungi present the biggest challenge as they are the most abundant mycota (microfungi: larger fungi, about 30:1[2]) and an inventory would be unmanageable in large plots. For these fungi it may be necessary to select smaller plots (10 m^2) or individual host trees and sample within these elements. Methods for measuring fungal diversity in soils have been reviewed by Gray (1990) and by Frankland et *al.*

[22] Figures calculated from described basidiomycetes vs other fungi (Hawksworth *et al*. 1983).

(1990), with a critique of some of the methods by Dighton (1994). Bills and Polishook (1994) have measured abundance and diversity of microfungi in leaf litter of a lowland rain forest in Costa Rica. Four litter samples were collected from four arbitrarily selected sites, by standing at a single point and raking the surrounding litter into containers. They isolated between 78-134 fungal species from each litter sample, with few abundant species and a high proportion of rare species. Several methods for measuring ecological diversity have also been reviewed by Magurran (1988). It may be possible to adopt these, or similar techniques, as standards for measuring diversity of soil and leaf litter microfungi.

There are flaws in these methods. The microfungi present on leaf litter may be determined by the host component of the litter. If the litter contains palm remains, then the fungal community will differ as the genera of fungi developing on living and dead palm material is quite different from that associated with other hosts. Members of the Graminaceae (e.g. bamboo), Zinziberaceae (e.g. *Alpinia)* also have a somewhat unique mycota. Appropriate specialists may need to cover these substrates.

At present there are no standard techniques for measuring fungal diversity and measuring diversity of microfungi is one or our major challenges. Pilot studies to establish convenient techniques and protocols are essential, so that mycologists can eventually agree on international measuring and monitoring strategies.

CONCLUSION

In this paper I have presented information on the fungi known from two habitats in north Queensland. I must emphasize that for each taxon there is usually a single record and this is the only information that is available. We do not have distribution maps of the occurrence of the fungi as is published (or known) for most vascular plant species in north Queensland (Clarkson - personal communication). We know nothing of the mycobiota of most habitats, and most fungi remain unknown. With this lack of knowledge one would hope that enlightened government bodies such as Australian Biological Resources Study (ABRS) might give priority to funding mycological research in Australia. However, in 1993 and 1994 only 3 mycological projects ($213,071) were funded by ABRS as compared to numerous vascular plant projects ($ 17,702,467). The lack of knowledge of microfungi in Australian rainforests is reflected internationally, with most developing countries being in a worse state.

Difficulties in measuring biodiversity of microfungi in rainforests and the need

to develop standard techniques is discussed. A method for measuring biodiversity in rainforests is proposed, with the hope of promoting discussion amongst mycologists.

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Chapter

20

RESERVE SIZE AND IMPLICATIONS FOR THE CONSERVATION OF BIODIVERSITY IN THE ANDAMAN ISLANDS

Priya Davidar[1], Soubadra Devy[1], T. R. K. Yoganand[1] and T. Ganesh[1]

INTRODUCTION

The Andaman and Nicobar islands in the Bay of Bengal are one of the most biodiversity-rich regions of India, apart from the North-East and the Western Ghats. There has been a spate of interest in the conservation of the biodiversity of these islands. As this group, commonly known as the Bay Islands, consisting of more than 300 islands, stretches from the North Andamans in the North to the Great Nicobar Island in the south, spanning diverse latitudinal and climatic zones, conservation and maintenance of the biodiversity of this region requires information on species distribution patterns, the status of species, and the adequacy of the current protected area network (Burley 1988, Jenkins 1988). The task of conducting an inventory of all the species in an area is daunting, if not impossible, especially in areas of high diversity such as tropical rain forests. However, patterns of abundance and distribution of select taxa can provide insights for the protection and management of the biodiversity of an area.

[1] Salim Ali School of Ecology and Environmental Sciences, Pondicherry University, Kalapet, Pondicherry 605 014, India.

The Andaman and Nicobar islands have diverse forest types from giant evergreen forests to deciduous forests and mangroves (Champion and Seth 1968). These islands have come under pressure due to heavy commercial timber felling operations and increasing human impact (Saldanha 1989). To protect the fauna and flora, a total of 6 National Parks and 94 Sanctuaries have been created from 1977 to 1987. Ninety-three of these are whole islands, usually small in size. Recently, two more have been added but no information could he obtained on these.

We undertook a survey of butterflies and forest birds in the Andaman group of islands from 1992-1994, to study patterns of species distributions and status. Reliable records exist for birds and butterflies of the Andamans and Nicobars (Evans 1932, Khatri 1989, Ripley and Beehler 1989) but not for most of the other taxa. Birds and butterflies can be sighted easily, identified and surveyed rapidly over large areas.

STUDY SITE

The Andaman and Nicobar chain of islands lie off South-East Asia and extend from South-Western Myanmar to North-Western Sumatra lying between 6° 45′ N and 13° 41′ N latitude (Figure 1) (Srinivasan 1986). They are postulated to be part of the Arakan Yomas mountain range of Myanmar, which lies submerged. They are true oceanic islands as they were never connected to the continent during the Pleistocene glaciation and maximum over-water colonization possibly occurred before the Andaman sea expanded (Ripley and Beehler 1989). The Andaman group consists of 4 large islands, North, Middle, Baratang and South Andaman Islands forming a super island of over 5000 km^2 in area, surrounded by archipelagoes and isolated islands: The large islands have extensive human settlements and primary forest has been reduced by degradation and deforestation. The Nicobar island group is a chain of smaller scattered islands, the largest of which is Great Nicobar Island. The Little Andamans lie about 67 km south of the Andaman chain and are separated from the Nicobars by the 10 degree channel.

The climate is tropical and oceanic with rainfall from both the SW and NE monsoons. The average annual rainfall is 3000 mm (State Statistical Bureau 1989). The dry season extends from January to May with another short break in September-October.

About 38 islands in the Andamans and Nicobars are inhabited and the human population, which was 279,111 in the 1991 census (Census of India 1991), has more than doubled since 1971 (115,133). Most of the population growth is due to im-

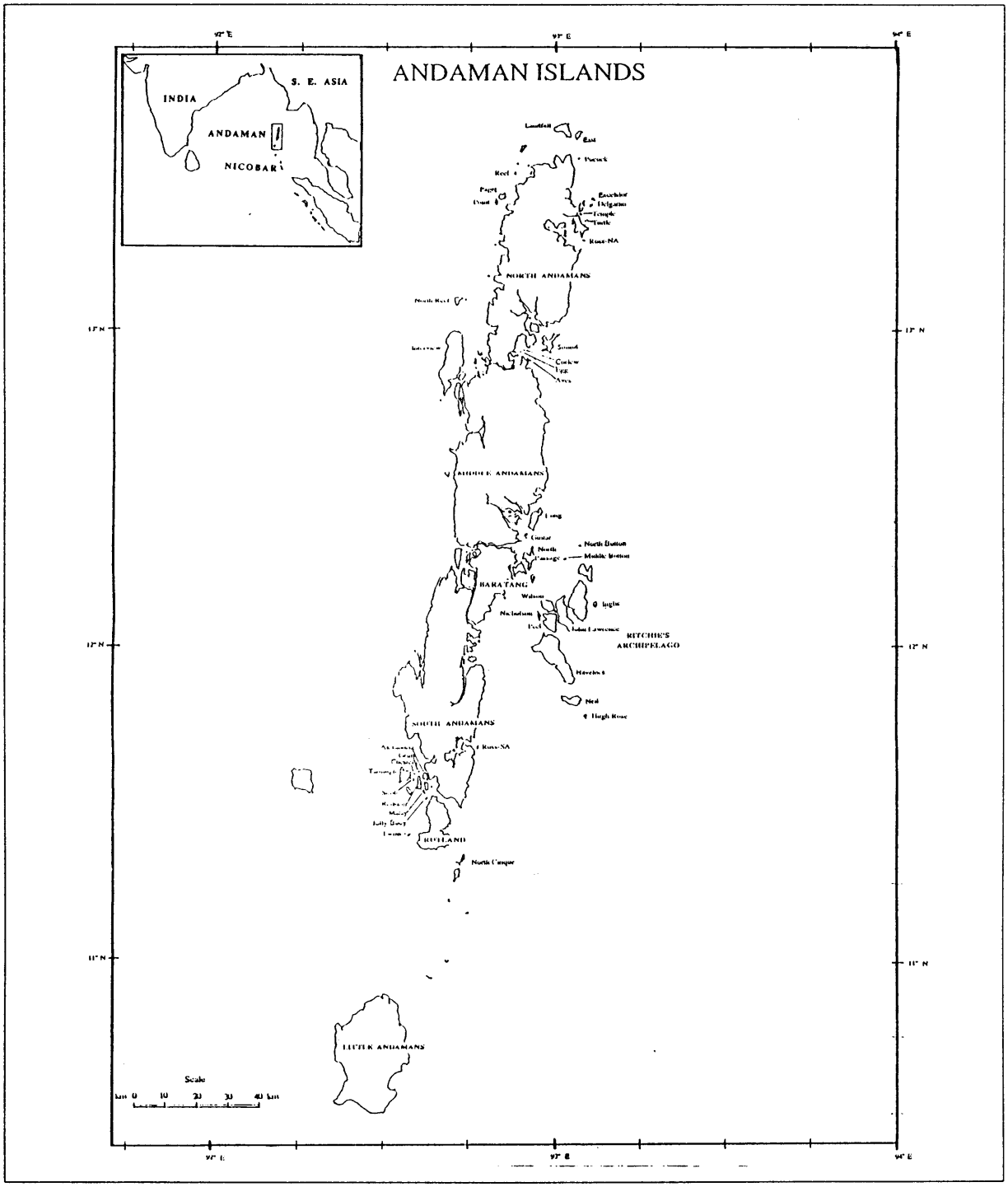

Figure 1: Map of the Andaman group of islands.

migration from mainland India, increasing the encroachments into forested land. The 6 tribal groups form 12% of the population. There are 5 tribal reserves which also serve as protected forest areas, and which cover a total area of 1069 km^2. There is a proposal to create two Biosphere Reserves, one in the North Andamans and another on Great Nicobar Island (Pande *et al.* 1991).

Commercial forestry operations in the islands started around 1853 (Saldanha 1989). Over time the volume of timber extracted has increased from 49,000 m^3 in 1949 to 145,000 m^3 in 1986 (Saldanha 1989). The number of species exploited has increased from 20 to 40 over this period. Almost 12 % of the land has been clearfelled (Whitaker 1985). Since 1989, clearfelling has been stopped and over time wood extraction for wood based industries will be phased out and expansion of current industries banned. The level of extraction has also been reduced from 150,000 m^3 to 100,000 m^3 per year (Sinha 1991).

These islands support a diverse forest vegetation (Champion and Seth 1968) and taxa such as birds, mammals and plants have been well documented (Ripley and Beehler 1989, Abdulali 1965, 1981, Rao 1986). However, little comprehensive information exists on other taxa. The flora and fauna show affinities with Myanmar, the Malay peninsula and the Indian subcontinent. Over 1416 species of flowering plants and 120 species of pteridophytes have been recorded (Rao 1986). About 187 species of flowering plants are endemic. There are almost twice as many flowering plant species in the Andamans group as compared with the Nicobars. Both groups share only about 28% of the angiosperm flora (Table 1). The Andaman flora shows general affinities with S. E. Asia and that of the Nicobars with Malesia (Rao 1986).

The Andaman butterflies were first recorded by Evans (1932). Ferrar (1951) listed 268 species from 9 families. Certain families were revised by Khatri (1989) who has listed 270 species from 6 families. Of these, 150 were recorded in the Andaman Islands, 84 in the Nicobars and 36 are common to both island groups (Table 1).

Ripley and Beehler (1989) did an analysis of the breeding birds of the Andaman and Nicobar islands. They identified 104 species of breeding birds of which 92 species are found in the Andaman group and 65 in the Nicobar group. There are 13 endemic species of birds and 86 endemic races. The Andamans and Nicobars share 53 species. The Nicobar avifauna appears to be a subset of the Andaman birds and both are most closely allied with that of south-western Myanmar and the Malay peninsula. Certain taxa are poorly represented whereas others are common. For instance hawks, herons pigeons and kingfishers are well represented whereas the

passerines are an impoverished group (Ripley and Beehler 1989). The data on other taxa are unreliable, however, a total of 10 species of amphibians and 83 species of reptiles have been documented (Table 1).

	NUMBER OF SPECIES				
	A	N	TOTAL	E	
PLANTS	1079	770	1416	187	Rao 1986
BUTTERFLIES	150	84	270	?	Khatri 1989
AMPHIBIANS			10*	2*	Rao 1989
REPTILES			83*	23*	Rao 1989
BIRDS	92	65	104	13	Ripley & Beehler 1989
MAMMALS#			55*	33*	Rao 1989

Table 1: Number of Species of some Taxa with Endemics in the Andaman and Nicobar Islands.

*** = includes subspecies** **# = includes marine mammals**
A = Andamans **N = Nicobars** **E = Endemics**

METHODS

In order to study the distributions of birds and butterflies, sites were selected in different habitats in the main large islands and on islands of different sizes lying off the main islands, to represent a north-south gradient. A total of 45 islands were surveyed (Table 2). These include the large islands such as North Andaman Island, Baratang, South Andaman Island, Rutland and the Little Andamans. Islands of different sizes in the Labyrinth archipelago, Ritchie's archipelago and other islands lying off the Andaman 'super-island' were included in the study. The sur-

veys were conducted in the dry seasons from February to May, 1992, February to May, 1993 and February, 1994 when birds and butterflies are more active and more visible. The South Andamans, Labyrinth archipelago and the Little Andamans were surveyed from February to May, 1992 for birds and butterflies. Baratang, the Ritchie's archipelago and seven islands off the North Andamans were surveyed for birds from February to May, 1993, and the North Andaman island and 11 associated islands were surveyed for birds and butterflies in February, 1994.

Birds were surveyed in all 45 islands, and butterflies in 12 islands in the North Andamans, 12 islands in the South Andamans and in Little Andaman Island (Table 2). The different habitats encountered in each island were identified with the help of Champion and Seth (1968) and classified as:

1. Evergreen forest; multistoreyed climax forest formations that occur mostly on low alluvial land or on moist loamy hillsides with representative trees such as *Dipterocarpus* spp.*, Canarium* manii, *Artocarpus* spp. and *Pometia pinnata.*
2. Semi-evergreen forest; containing both evergreen and deciduous trees. Some *tree* species are *Dipterocarpus alatus, Pterygota alata, Albizia chinensis, Bombax insigne, Artocarpus lakoocha* and *Pterocymbium tinctorium.*
3. Deciduous forest; forests of lower stature growing on lower hills and in drier areas. Common species are *Pterocarpus dalbergioides, Terminalia bialata, Dalbergia* spp., *Pterocymbium tinctorium, Albizia* spp., and *Tetrameles nudiflora.*
4. Littoral forest dominated by *Manilkara littoralis.*
5. Disturbed areas and edges composed of secondary moist deciduous forests resulting from selective felling with *trees* such *Canarium euphyllum, Pterocymbium tinctorium* and *Salmalia insignis,* and the transition zone between clearings and forest, invaded by weeds such as *Chromoleana odorata* and *Lantana camara.*

Forest birds in the Andaman group of islands were selected from the list of breeding birds compiled by Ripley and Beehler (1989). A total of 47 species of birds were selected out of the 104 listed. The herons, rails, ducks, brahminy kite and white-bellied sea eagle were not included. In addition, kingfishers, swifts and swallows, nocturnal species and birds of open fields were eliminated from the study. The Narcondam hornbill was not included because it was not possible to visit Narcondam Island.

Island	Area (km^2)	E	S-E	DC	L	DT	BR	BT
NORTH ANDAMANS								
NORTHANDAMAN @	1000	+	+	+	+	+	+	+
LANDFALL	13	-	-	+	+	-	+	+
SOUND	12.7	-	-	+	-	+	+	+
PAGET	4	-	-	+	+	-	+	-
NORTH REEF	3.4	-	-	-	+	-	+	-
EAST	3	-	-	+	+	+	+	+
POINT	0.8	-	-	+	+	-	+	-
REEF	0.6	-	-	-	+	-	+	-
DELGARNO	0.5	-	-	+	+	-	+	+
EXCELSIOR	0.4	-	-	+	+	-	+	-
ROSS	0.3	-	+	-	+	+	+	+
POCOCK	0.25	-	-	+	+	-	+	+
AVES	0.25	-	-	-	+	+	+	+
TURTLE	0.13	-	-	+	+	-	+	+
CURLEW	0.07	-	-	-	+	+	+	+
TEMPLE	0.06	-	-	+	+	+	+	+
EGG	0.06	-	-	+	+	+	+	+
MIDDLE ANDAMANS AND BARATANG								
BARATANG	230	+	+	+	+	+	+	-
HAVELOCK	92	+	+	+	+	+	+	-
JOHNLAWRENCE	35	+	+	+	+	+	+	-
PEEL	23	-	+	+	+	+	+	-
LONG	14	+	+	+	+	+	+	-
WILSON	14	+	+	+	+	-	+	-
NORTHPASSAGE	13	-	+	+	+	+	+	-
NEIL	12.6	-	+	+	+	+	+	-
NICHOLSON	1.8	-	+	-	+	-	+	-
INGLIS	1.4	-	-	+	+	-	+	-
GUITAR	1	-	-	+	+	-	+	-
HUGH ROSE	0.6	-	-	+	+	-	+	-
MIDDLE BUTTON	0.4	-	+	-	+	-	+	-
NORTH BUTTON	0.25	-	-	-	+	+	+	-

Island	Area (km^2)	E	S-E	DC	L	DT	BR	BT
SOUTH ANDAMANS								
SOUTHANDAMAN	1348	+	+	+	+	+	+	+
RUTLAND	116	+	+	+	+	+	+	+
TARMUGLI	11.5	+	+	+	+	-	+	+
ALEXANDRIA	3.6	+	+	-	+	-	+	+
REDSKLN	3.3	+	+	-	+	-	+	+
NORTH CINQUE	1.6	-	-	+	+	-	+	+
MALAY	0.7	+	-	-	+	+	+	+
TWINS	0.44	-	-	+	+	-	+	-
ROSS	0.28	-	-	-	-	+	+	+
SNOB	0.22	-	+	-	+	-	+	+
JOLLY BUOY	0.12	-	-	-	+	+	+	+
CHESTER	0.09	+	-	-	+	-	+	+
GRUB	0.03	-	-	+	-	-	+	+
LITTLE ANDAMAN								
LTTTLEANDAMAN	675	+	+	+	+	+	+	+

Table 2: Islands Surveyed and Habitat Characteristics.

E = Evergreen, S-E = Semi-Evergreen, DC = Deciduous, L = Littoral, DT = Disturbed, BR = Birds, BT = Butterflies.

The available habitat types in a site or island were classified into the above 5 categories. Transects of one km length were selected in different habitat types on large islands or across habitats on smaller islands. The number of such transects varied with the size of the habitat surveyed. The transects were walked in the mornings between 7 am to 10 am, and all birds seen and heard were recorded and identified using Ali and Ripley (1987) and King *et al.* (1975). Their distance along the transect line and approximate perpendicular distance to the transect line were noted. From this information species lists for each site and for each island were prepared, together with the relative abundances of all species. The bird species recorded on all the above mentioned sites and islands were ranked in ascending order according to the number of islands on which each was recorded. These ranks were transformed into an index of between l-5. Birds recorded from l-10 islands

were assigned a rank of l, ll-20 islands, a rank of 2 and up to 41-45, a rank of 5. The data on relative abundances were obtained from a total of 5028 birds on 70 km length of transects.

Individual butterflies were recorded 5 m on either side of variable length transects (Pollard 1977). The length of the transect depended on the size of each habitat. On smaller islands the transects cut across all habitats. Some butterflies were collected for later identification.

Sampling was repeated for several days depending on the size of the habitat or island and was discontinued when no new species were encountered.

Butterflies were identified to species, genus or family with the help of Wynter-Blyth (1957), Khatri (1989), and voucher specimens kept at the Zoological Survey of India office in Port Blair. Despite this, many specimens could not be identified.

RESULTS

There appears to be a north-south gradient in forest types from the North to the South Andamans (Table 2). The vegetation of the North Andamans is predominantly deciduous except for patches of evergreen forest on the main North Andaman island and a small patch of semi-evergreen forest on Ross. The other islands had deciduous vegetation. The proportion of evergreen and semi-evergreen forests increases on smaller islands off the Middle Andamans and Baratang and are found on even very small islands off the South Andamans. This probably reflects a north-south rainfall gradient, with drier conditions in the north (Ellis 1989). Very small, disturbed or very isolated islands had a secondary type of vegetation.

Of the 47 species of birds surveyed, all were recorded on South Andaman Island and 43 on North Andaman Island. On islands < 5 km^2 a total of 39 species were recorded on islands off South Andaman Island and 32 on islands off North Andaman Island (Table 3). The species missing from small islands off the North Andamans were *Terpsiphone paradisi, Dendrocitta bayleyi, Columba palumboides, Copsychus malabaricus, Cuculus micropteris, Euystomus orientalis* and *Dryocopus javensis.* These species have restricted distributions on large islands or occur at low densities on islands with evergreen forests (Davidar *et al.* unpublished).

Of the 65 species of butterflies recorded in the survey, 44 were found on South Andaman island and 40 on North Andaman Island. On small islands (< 5 km^2), there were 43 species in islands off the South Andamans and 22 on islands off the North Andamans. North Andaman Island recorded 4 species of evergreen specialists, whereas there were 8 on South Andaman island. The small islands off the

	NORTH ANDAMAN		SOUTH ANDAMAN	
	Main Island	Islands <5KM^2	Main Island	Islands <5KM^2
BIRDS	43	32	47	39
BUTTERFLIES	40	22	44	43
EVERGREEN SPECIALIST BUTTERFLIES	4	0	8	7

Table 3: Comparison of Bird and Butterfly Species Richness in the North and South Andamans.

North Andamans had no evergreen specialist butterflies whereas off the South Andamans there were 7 species of evergreen specialists (Table 3).

From the data on relative abundances, the status of endemic forest species were determined and rare species identified. Of the endemic forest species found in the Andamans group, *Dendrocitta bayleyi* and *Columba palumboides* were found only on the larger islands. *Macropygia rufipennis* occurred at low densities and the other 4 species were common (Table 4; Davidar *et al.* unpublished). Species that are very rare are *Coracina striata, Oriolus xanthornus, Chalcites xanthorhynchus* and *Terpsiphone paradisi.* These have restricted distributions on the large islands (Davidar *et al.* unpublished).

Of the existing National Parks and Sanctuaries, 58 reserves are less than 1 km^2, and 13 are less than 0.01 km^2. Only 4 reserves are greater than 30 km^2 in area (Figure 2). A mean of 9 species of birds was found on islands < 1 km^2, 24 on islands l- 5 km^2, 33 on islands 5-30 km^2 and almost all species were recorded on islands > 30 km^2. When butterflies are compared, islands < 1 km^2 have a mean of 6 species, l-5 km^2 a mean of 16 species and 35 species on islands > 30 km^2 (Figure 2). Many species of birds and butterflies were not recorded on smaller islands. For birds there is a gradual drop off in the total number of species recorded with island size, whereas for butterflies, the pattern is not clear except for islands < 0.01 km^2 in area. Many species of butterflies found on smaller islands were not recorded on the main North Andaman and South Andaman island, and certain species were restricted to particular islands (Table 5; Soubadra Devy *et al.* unpublished).

	SPECIES	STATUS REMARKS
ENDEMICS		
Dendrocitta bayleyi	Rare	Restricted to large islands
Columba palumboides	Uncommon	Restricted to large islands
Macropygia rufipennis	Uncommon	Occurs at low densities
Centropus andamanensis	Common	
Dicrurus andantanensis	Common	
Spilornis elgini	Common	
Sturnus eythropygius	Common	
RARE FOREST BIRDS		
Coracina striata		
Oriolus xanthornus		
Chalcites xanthorhynkhus		
Terpsiphone paradisi		

Table 4: Status of Endemic Forest Birds and Rare Species in the Andaman Islands.

	NUMBER OF SPECIES	
	BIRDS (n*=47)	BUTTERFLIES (n*=65)
NORTH ANDAMAN ISLAND	43	40
SOUTH ANDAMAN ISLAND	47	44
LITTLE ANDAMANS	41	21
ISLANDS > 30 km^2	47	57
ISLANDS > 5< 30km^2	44	31
ISLANDS > 1 < 5 km^2	43	40
ISLANDS < 1 km^2	36	39
ISLANDS < 0.1 km^2	20	21

Table 5: Total Number of Forest Birds and Butterfly Species Found in Islands of Particular Sizes.

n = total number of species recorded

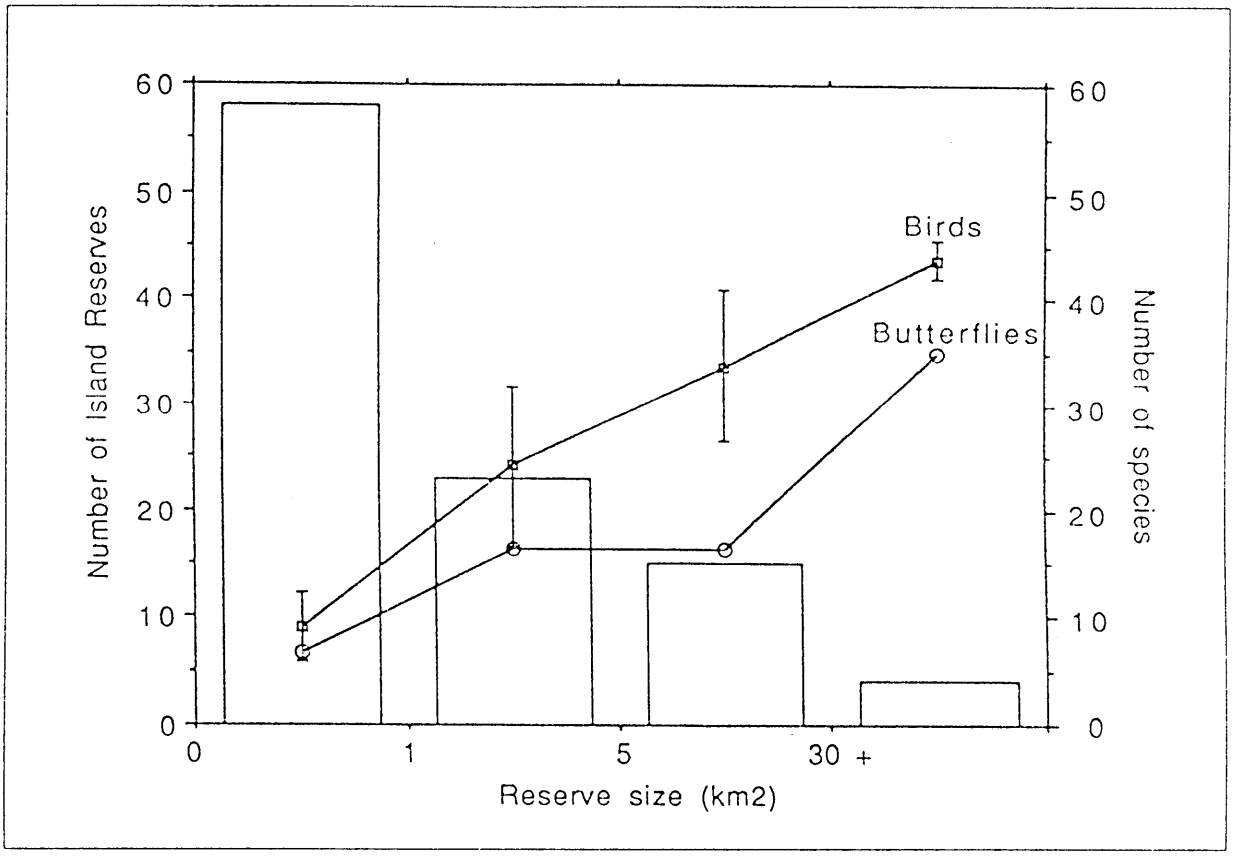

Figure 2: Distribution of sizes of national parks and sanctuaries in the Andaman and Nicobar islands with the mean number of birds (mean ± s.d.) and butterflies (mean) in each island size category.

DISCUSSION

The north-south vegetation gradient, with more deciduous forest in the northern islands and evergreen forest in the southern islands does not seem to have a marked influence on the bird distributions, except for a few species which may be restricted to evergreen forests (Yoganand and Davidar unpublished). However it has a large effect on butterfly distributions. Of the 65 species of butterflies recorded, 25 appear to be habitat specialists and 10 evergreen forest specialists, restricted to evergreen forest habitats (Soubadra Devy *et al.* unpublished).

The second factor which appears to influence bird and, to a lesser extent, butterfly distributions is island size. This is expected from the theoretical predictions of

MacArthur and Wilson (1967), where the number of species on an island is related to the size of the island and its degree of isolation from the mainland. The mean number of forest bird species drops with island size. However, the distributional pattern did not appear to be random as many species were not recorded at all on small islands and all forest bird species were recorded only on islands larger than 30 km^2.

The majority of reserves in the Andaman and Nicobar islands are whole islands less than 1 km^2 in area. The consequences of having many small reserves for forest species is that not all the vegetation formations are included. Small islands usually have drier forests which do not support habitat specialists. Large islands which have sizable extent of evergreen forests are under severe human pressure. This results in an inadequate protection of the biodiversity of this region.

The current rate of conversion of evergreen forests to a secondary deciduous type by selective felling and regeneration of commercially useful species will lead to the extinction of many habitat specialist butterflies, and will probably influence bird diversity as well, by reducing the quantity of fruits and other resources available. Large islands and forests on large islands should be notified as reserves and protected on a priority basis. There should also be adequate infrastructure to enforce protection. The legal status of many of these reserves is unclear as the legal procedures have not been completed in most cases. In many cases, there are no staff, funds and equipment to manage these sanctuaries and National Parks (Pande *et al*. 1991).

Islands are fragile ecosystems with high extinction rates because the species are confined to small areas and suffer disproportionately from habitat-destruction and other factors. Many of the species occurring in the Andaman and Nicobar islands, particularly those belonging to obscure taxa are yet to be documented. It is important that they are protected before it is too late.

ACKNOWLEDGMENTS

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Chapter
21

METHODS FOR MEASUREMENT OF SPECIES DIVERSITY

Jiragorn Gajaseni[1] and Kansri Boonpragob[2]

There are numerous definitions of biodiversity. Most treat diversity at genetic, species or ecosystem level. Current measures select different levels of the biosystem for emphasis; the species, population, ecosystem, or landscape levels.

Species diversity measures can be divided into 3 main categories (Magurran 1988):

1. species richness indices,
2. species abundance models, and
3. indices based on the proportional abundance of species.

SPECIES RICHNESS INDICES

These indices are essentially a measure of the number of species in a defined sampling unit. If the study areas can be successfully delimited in space and time,

[1] **Department of Biology, Faculty of Science, Chulalongkom University, Bangkok 10330, Thailand.**
[2] **Department of Biology, Faculty of Science, Ramkhamhaeng University, Bangkok 10240, Thailand.**

and the constituent species enumerated and identified, species richness provides an extremely useful measure of species diversity. If, however, a sample rather than a complete catalogue of species in the community is obtained, it becomes necessary to distinguish between numerical species richness, which is defined as the number of species per specified number of individuals or biomass, and species density, which is the number of species per specified collection area. It is not always possible to ensure that all sample sizes are equal and the number of species invariably increases with sample size and sampling effort. Hurlbert (1971) modified the technique called "rarefaction" for estimating the unbiased number of species expected in each sample if all samples were of a standard size.

Species richness measures have great intuitive appeal so long as care is taken with sample size. Species richness provides an instantly comprehensible expression of diversity. However the great range of diversity indices, and models which go beyond species richness, is evidence of the importance that many ecologists place on information about the relative abundance of species.

SPECIES ABUNDANCE MODELS

There is no community in which all species would be equally common. Instead, it is typically the situation that a few species are very abundant, some have medium abundance, while most are represented by only a few individuals. These common community patterns lead to the development of species abundance models. The species abundance models are usually classified into 4 models: log normal distribution, the geometric series, the logarithmic series, and MacArther's broken stick model (Magurran 1988). The diversity of a community may therefore be described by referring to the model which provides the closest fit to the observed pattern of species abundance.

These models describe the distribution of species abundance. Species abundance models range from those which represent situations where there is high evenness to those which characterize cases where the abundances of species are very unequal. While the species abundance models provide the fullest description of diversity data, they are dependent on some fairly tedious model fitting and for rapid calculation require the use of computers. In addition, problems may arise if all the communities studied do not fit one model and it is desired to compare them by means of a diversity index.

INDICES BASED ON THE PROPORTIONAL ABUNDANCES OF SPECIES

Indices based on the proportional abundances of species provide an alternative approach to the measurement of diversity. This type of diversity measure has enjoyed a great deal of popularity in recent years. The most widely used indices are Shannon's index of diversity and Simpson's index. Shannon's index of diversity is a useful method for comparing the diversity of different habitats, especially when a number of replicates have been taken (Gajaseni and Gajaseni, unpublished data). When the randomness of a sample cannot be guaranteed as, for instance, during light trapping where different species of insects are differentially attracted to light, or if the community is completely censused with every individual accounted for, Brillouin's index is the appropriate form of the diversity index (Pielou 1969, Pielou 1975).

DISCUSSION

The loss of biodiversity is one of the most profound global crises. Even though we may still disagree on the definition of biodiversity or how to measure biodiversity (Hurlbert 1971), there is unanimous agreement that biodiversity is being reduced at an accelerating rate (Wilson 1988). The vast majority of the past and current efforts to preserve biodiversity have focused upon species. Species inventory, mainly by listing names, has been the most common measure. This old paradigm on the methods for measurement of species diversity might satisfy one of the most fundamental questions in biology " How many kinds of living thing are there?" The answer to this question is still a matter of guess work. We have so far succeeded in naming and describing only a very fraction of the total number of species present. There are many satisfactory methods and statistical analyses to measure both richness and equitability (evenness) of species diversity. However, one of the most famous questions on species diversity still remains. The question was asked by a very famous ecologist, the late G. Evelyn Hutchinson, in 1959, who asked: "Why are there so many kinds of animals?" Disregarding political values and ethical issues, the quality of inventory data and their practicality will determine whether there is sufficient quantity of information to serve any useful purpose (Renner and Ricklefs 1994).

Any rationalized strategy for biodiversity conservation must be based on information. To set aside conservation areas that will protect the fullest range of species requires more complete knowledge of the distribution and abundance of

organisms than is currently available (Lubchenco *et al.* 1991). Uncertainties about the number of species that exist, the rate at which the number is being eroded, and the proportion of species threatened with extinction stress the need for alternative approaches to the maintenance of biodiversity. While we are fundamentally ignorant as to whether or not any conservation area is a self-sustaining ecosystem, we cannot even come close to attaining our goal of preserving biodiversity, if we continue to focus our efforts primarily on species. Conserving species is not the total solution. Efforts to preserve biodiversity must focus increasingly at the ecosystem level because of the immense number of species, the majority of which are currently unknown (Franklin 1993).

Conservation approaches at the levels of ecosystems and landscapes are the only way to preserve biodiversity (Franklin 1993). Ecosystems have long been described by traditional "biotic ecosystem models" by considering each species to operate in fixed trophic levels within constraints imposed by the physical environment (Caswell 1988). Therefore, populations of species at the various trophic levels become the focal point of most studies. The "collect, classify and store everything found in a given area" approach is the major method. This has limited utility because biodiversity has been shaped by millions of years of interactions between speciation and adaptation. Only recently, "functional ecosystem models" have emerged (Caswell 1988). Under these models, ecosystems are perceived as being composed of different functional elements through which energy and material move through. Organisms are placed into one of two general categories: energy capture and nutrient retention, and rate regulation. Instead of focusing on each species, we must conserve the processes that are defined by species' interactions within self-sustaining ecosystems (Georgiadis and Balmford 1992). Both approaches have been fruitful in the past, but the functional model of determining environmental factors that control the rate of energy flow and the movement of materials within ecosystems now appears to be a more promising approach for the future. Therefore, taking an ecosystem approach we have to monitor and study species diversity in order to adequately assess the roles of all types of interaction between species to maintain "healthy functional ecosystems".

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Chapter
22

TOOLS TO DIAGNOSE FOREST INTEGRITY; AN APPRAISAL METHOD SUBSTANTIATED BY SILVI-STAR ASSESSMENT OF DIVERSITY AND FOREST STRUCTURE

H. Koop[1], H.D. Rijksen[1] and J. Wind[2]

INTRODUCTION

In order to evaluate the consequences of the rapid decline of tropical rain forests, and assess the prospects for restoration of these forests, a functional monitoring system is required. For proper land allocation for conservation of biological diversity, it is imperative to know the structure of major classes of forest quality, from almost unimpaired forests to early stages of regeneration. Insight into the ecological conditions of different patches composing such classes is also important for harvesting and conservation management strategies.

Advanced remote sensing techniques can provide substantial information on the extent of serious forest damage. However, information concerning changes of forest integrity due to harvesting is hard to obtain. Timber exploitation does increase the scale and frequency of gap dynamics, but in the case of small scale selective cutting, only a temporary and limited effect on canopy closure may be caused.

1 Research for Forestry and Naturure Research, P.O. Box 23,6700 AA, Wageningen, The Netherlands.
2 DHV Consultants BV.

From the air, such a qualitative decline in forest integrity is hard to evaluate. It is nonetheless important to evaluate the impact of different timber extraction methods and the effects of forest management on the potential for restoration of biological diversity and functional integrity. Also, such an evaluation technique can be applied to assess the effectiveness of park protection and buffer zone programmes.

According to the Concise Oxford Dictionary, integrity is defined as wholeness, entirety and soundness. A forest is sound when it is able to maintain its structure at a landscape scale in the face of all regular and incidental natural disturbance factors, such as storms, flooding or drought. The main criterion for integrity is the occurrence of all species of organisms and age classes in a particular proportion of social organisation, as would occur in a natural situation, that is without human interference (Halle *et al.* 1978). The loss of particular species is the symptom of poor forest condition (Oldeman and Van der Meer 1988, Karr and Budley 1981).

With increased human induced forest dynamics, biodiversity in terms of numbers of species may decline, remain the same or even increase (e.g. Swaine and Hall 1983, Abdulhadi *et al.* 1987). New species may invade the forest and serious shifts in evenness occur. Pioneer species, that are rare in the almost undisturbed mosaic, spread in an highly dynamic landscape, while previously common species become rare or extinct. Species confined to the complex-structured mosaic of mature forest patches, with a limited percentage of young recently disturbed patches (e.g. primates and birds, or plant and animal species confined to high air humidity) are particularly susceptible to extinction.

It is almost impossible to make an inventory of species diversity and their relative population composition, in order to evaluate ecological integrity for planning and management (Hommel 1990). It would not only be too laborious, but also specialized taxonomic knowledge for species identification is inevitably deficient. Other approaches are needed to rapidly assess forest integrity without detailed inventories of all major groups of forest species. A diagnostic method for forest integrity may well be developed analogous to a physician's diagnosis of the loss of health in a patient, based on external symptoms indicating the quality of internal functioning.

Here we have raised the question, whether indicators of change in scale and frequency of gap dynamics, rather than direct measurements of biodiversity, can be used to diagnose forest integrity. We hypothesized that rapid simple measurement of the appropriate set of indicators could result in a feasible,

standardized appraisal technique.

The conditions for the development of a Rapid Ecological Assessment (REA) are:

1) The measurements shall provide relevant data. That is, the data must reflect the degree of decline of forest integrity or recovery in an objective and repeatable way.
2) The method must be reliable. That is, it must be constant in its diagnosis.
3) The indicators used shall not be rare: an indicator function implies that particular life-forms or species must occur commonly in particular patches of the specific classes of quality.
4) The method must be easily applicable even by people without detailed taxonomic knowledge. This implies that the indicators must be readily recognisable while the time and effort to gather data on their occurrence shall be optimised in terms of transect number and length.

The REA will be substantiated by SILVI-STAR assessment of diversity and forest structure in pristine and more and less disturbed sites.

METHODS AND MATERIALS

Procedure of method design

Within the borders of a regional climate, external stress factors, such as wind, flooding and drought, have determined frequency and extent of gap dynamics and thus provided the conditions for evolution and present biodiversity (Koop 1981). However, human activities in and around forests raise the levels of forest dynamics. Therefore, an absolute standard of virgin, unimpaired forest can hardly be found anywhere in the world. Nevertheless, examples of overuse and decline of forest structures are common and widespread.

During recent decades, the scale and frequency of human induced forest dynamics have increased drastically. Former non-mechanised small-scale selective cutting has changed into large scale mechanised harvesting, especially for industrial use. Due to high population pressure and economic needs, the frequency of human induced dynamics increased as well. Less time is left for regeneration to mature, late successional stages, characterized by big sized trees. Early successional stages become predominant.

The natural forest is subject to a particular dynamic range of life-processes

from germination to decay. Trees and other organisms may die due to senescence or calamities and predation. On a landscape scale, climatic factors may cause an almost regular pattern of local calamities that lead to a shifting mosaic patchwork of communities of young stages next to older ones. The older or so-called late successional patches may contain higher numbers of species and therefore contribute most to biodiversity (Budowski 1965, Jacobs 1988). Some species are strictly dependent on those mature patches while others depend on the complex structure of the mosaic as a whole.

Human disturbance commonly increases the proportion of younger stages of forest succession. Although affected by the extent of disturbance in space and time, the system usually reverts to pioneer stages. The decrease in area of old growth patches and the loss of connectivity between them causes a marked decline in biodiversity and hence in forest integrity, which can only be restored in the very long term.

Our method is based on measuring the proportional representation of different successional stages in the forest mosaic patchwork compared to the natural mature mosaic of sites on areas of similar geomorphologic conditions. To characterise the different successional stages, a literature survey and interviews with experts in the field of tropical rain forest biology resulted in a list of possible diagnostic features in addition to relevant parameters discovered during the study itself.

After the identification of three major classes of forest disturbance (undisturbed, selective cutting, abandoned shifting cultivation) in the field, a preliminary list of diagnostic features was selected. These features have been tested for their suitability to be included in the diagnosis method. Formulae have been developed to rate forest integrity in a range from 100 to 0, where 100 represents scores of indicators the same as in the reference plot of undisturbed forest.

For substantiation of the diagnostic method, the detailed forest structure and complete species composition of both disturbed and undisturbed forest plots are described according to the SILVI-STAR method (Koop 1989). In the same plots, different disturbance units were subjected to a rating of forest integrity according to the new diagnostic method. A disturbance unit is defined and delineated as a more or less homogeneous patch of forest represented by a transect section that has been prone to the same kind of disturbance. Disturbance units represented by a transect length of less than 50 m were ignored, because mean values of presence become too uncertain if only a restricted number of assessed plot& considered.

To prove the relation of indicators with forest structure, SILVI-STAR side views of representative parts of the disturbance units were plotted. The abundance of

indicators was plotted on the side views and percentages of indicator presence were calculated for each developmental phase.

For substantiation of the calculation of end scores of the diagnostic method, the mean indicator scores of the 400 m^2 transect intervals were subjected to detrended correspondence analyses (DCA) (Hill 1979). The results are compared with the diagnostic method scores. For one site, in addition to the indicator scores, the complete species composition of trees having a dbh greater than 5 cm, as well as recognizable samplings and seedlings in 10 x 10 m^2 intervals along the transects, was subjected to canonical correspondence analyses (CANOCO) (Ter Braak 1986). Species were recorded as present or absent. Environmental variables, basal area (mean value over 300 m^2), selective cutting, shifting cultivation, development phase (metric classification of forest patches according to tree height), the number of stumps and the crown area index (Koop 1989) were tested for significant contributions to the variance of species composition. Those variables that significantly attributed to the explanation of variance were subjected to a de-trended correspondence analyses.

Study area

The study area lies just below the confluence of the Alas and Ketambe rivers in Northern Sumatra (3º41' N,97º39' E) at an altitude of about 350 m above sea level. The Alas river flows through the Semangko Rift zone, a *graben* running the full length of Sumatra. Here the *graben* is only a few kilometres wide and contains a number of accumulation terraces (van Beek 1982). The lower slopes of the valley consist mainly of crystalline metamorphic schists, altering in places with hard limestones of late Palaeozoic origin (van Beek 1982). The area was selected because of the known management history of several disturbed sites, in the direct vicinity of a piece of undisturbed forest of a comparable site type.

From 1971 until 1990 an area from the confluence of the Alas and Ketambe rivers up to 5 km downstream, especially on the easily accessible accumulation terraces and lower slopes just inside the Gunung Leuser National Park, has been illegally cleared. Surrounding these cleared fields, the forest has been selectively cut for timber, mainly in 1985-1986. However, on several occasions, in 1974, 1984, and 1991, the settlers were forced to leave their illegally occupied land and since then these fields have been left unexploited. Forest on similar site types that supposedly has not been disturbed to any significant extent can be found directly below the confluence near the Ketambe research station in a piece of forest of about 200 ha (Rijksen 1978).

For an undisturbed reference plot of the terrace site type, a 10 ha topo-unit belonging to "terrace 4" (van Schaik and Mirmanto 1985), 200 m south of the junction of the Ketambe and Alas rivers, was selected - from here on referred to as "Ketambe 1". Different disturbance regimes were studied along a 750 m transect situated on the same terrace as the reference plot, 5 km downsteam from the confluence. For an undisturbed reference plot of the lower slope, a 10 ha topo-unit about 1200 m south-south east of the confluence was selected - from here on referred to as "Ketambe 2". For different disturbance regimes, three 70 to 130 m long transects were selected on the lower slopes of the valley, just opposite the reference plot and respectively, 2 and 3 km downstream from the confluence.

RESULTS

Description of the diagnostic method; indicator groups

Three groups of indicators have been developed, consisting of forest structure indicators, light indicators and moisture indicators. The indicators that have been used in the method are listed below:

(a) Forest structure indicators. Indicators that define reduced integrity include:

Lower basal area

Basal area can be estimated by a simple and quick distance independent method called the Bitterlich method (Bitterlich 1948, Kramer and Akca 1982). All trees which are viewed to be thicker than the thumb held at arm's length are counted. Depending on the thickness of the thumb and the distance between thumb and eye, a conversion factor can be determined. Multiplying the conversion factor with the number of trees thicker than the thumb gives an estimate of the basal area. In the case of relative comparisons, only the number of counted trees is used.

Presence of big trees (Smiet 1989).

Trees with a diameter greater than 50 and 100 cm are counted.

Maximum tree height (Budowski 1965).

Tree height is estimated in ten-meter classes.

A distinct layered structure (Budowski 1965, Jacobs 1988).

Young and old secondary forests have a single or double layer, while late successional stages have a more multilayered structure. Therefore three forest structure classes are recorded: one (1), two (2) or multilayered (3).

Characteristic diameter distributions (Koop 1989).
Diameter distribution patterns in secondary forest tend to have a characteristic distribution curve, which differs from the reverse J-shaped curve of undisturbed forest. Therefore a choice has to be made between a secondary (1) or a reverse J-curve (2).

(b) Light indicators. Indicators for reduced integrity in this group include easily recognizable empirically selected species groups or families of species that indicate high light intensities.

Indicative groups of pioneer tree species
The Euphorbiaceae: Cecropia, Ochroma and Trema in South America (Budowski 1965) and *Macaranga, Mallotus* and *Trema* spp. in South East Asia are typical pioneers. The number of stems of these tree species, that are well known by local inhabitants, must be counted.

Light demanding species or groups of species
Species such as grasses less than 1 m *(Graminaceae)* (Budowski 1965), big species of ginger, taller than 2 m *(Zingiber* spp.) (this study), big ferns taller than 1 m (in this study *Nephrolepis biserrata, Diplazium esculenturn, Pteridium aquilinum, Christella papilio, Dicranopteris curranii, Cyathea borneensis)* (Budowski 1965), and herbaceous lianas *e.g. Convulvulaceae* in secondary forest (Budowski 1965) were recorded as present or absent.

Light demanding exotic invader species
Species such as *Lantana camara, Piper aduncum, Chromolena odorata* are noted separately because they generally indicate severe disturbance over longer time periods. They tend to dominate the vegetation thus hindering natural regeneration of other tree species. Only the presence of these species has to be noted.

(c) Atmospheric moisture indicators. This indicator group consists of easily recognizable species groups or families of species that are common and widespread, that indicate high air humidity.

- Epiphytic ferns that grow lower than 5 m above ground level on small trees and lianas *(e.g. Antrophium* spp.)
- Epiphytic filmy ferns on small trees and lianas *(HymenophyllIaceae, e.g. Trichomanes* spp., *Hymenophyllum* spp.)
- Epiphytic mosses (Richards 1984 and Pots 1982) of the feather type - in this

study *e.g. Himanthocladium plumula (Nees), Homaliodendron flabellatum* (J.E. SMN.) Fleisch., *Pinnatella mucronata* (Bosch and Lat.) Fleisch.; the hanging *type e.g. Neckeropsis gracilenta* (Lat.) Fleisch.; and the ramicolous type, e.g. *Calyptothecium recurvulum* (C. Müll.), *Floribundaria pseudofloribunda* Fleisch. Floribundaria floribunda (Dozy and Molk.) Fleisch.
- Epiphyllous mosses on leaves -in this study *e.g. Hepaticae* (Richards 1984).
- The upper limit of the moss carpet on the boles of trees referred to as the moss line by Richards (1984).
- Presence of "bole climbers", being herbaceous species that stick with their leaves to the tree bole (Oldeman 1978, Budowski 1965).

Only the presence of these growth forms has to be noted.

Light and atmospheric moisture indicators were assessed in adjacent 10 m x 10 m blocks in a line transect according to their presence or absence. Only for coverage of the herbaceous layer was the decimal scale of Londo (1984) used, and for pioneer species stem numbers were counted. Forest structure indicators were assessed every 50 metres along the transect base line.

Besides the three groups of indicators mentioned above, direct indicators of disturbance by former land use were assessed. They are not used for the calculation of end scores but indicate the nature of the disturbance.

- number of stumps (Smiet 1989) (N)
- presence of charcoal, burnt stumps or logs (+ or -)
- number of timber tree species of a Dbh more than 25 cm (N); most of the time being primary forest tree species e.g. *Dipterocarpaceae*
- number of commercially valuable rattan species (N)
- number of planted exotic trees (N)
- presence of paths (Smiet 1989) (+ or -)
- presence of *sawah* dikes (+ or -)

Indicators that could not be used for the rapid appraisal method include indicators related to direct measurement of area of different phases of regeneration, such as innovation and aggrading gap phases (Oldeman and van der Meer 1988), because mapping proved to be too time consuming. Other indicators could not objectively be determined in the Sumatran rain forest, for example:

- crown shape -uniform, open and bright green in secondary forest, compared with dark green and highly varying crown shape in primary forest

(Budowski 1965)
- big leaves in secondary forest, compared with small leaves in primary forest (Budowski 1965)
- abundance of big fruits and seeds in primary forest (Jacobs 1988).

For the undisturbed reference plot and for each disturbance unit, the mean values of forest structure indicators and percentage presence of atmospheric moisture indicators and light indicators were calculated. Final rating per disturbance unit is achieved by scoring the indicators relative to the standard of the undisturbed reference as follows:

$$S = D/R \times 100$$

where:
S= indicator Score relative to reference standard
D= value of indicator in Disturbance unit
R= value of indicator in Reference

Thus the forest structure scores of estimated basal area, maximum tree height, numbers of trees greater than 50 and 100 cm dbh, and the score for canopy layering and diameter distribution were calculated in this way. Atmospheric moisture indicators were rated similarly, except that the direct indicator values were substituted by the percentage frequency of an atmospheric moisture indicator in the disturbance unit. Thus the scores of percentage presence of mosses on leaves, bole climbers, epiphytic filmy ferns and epiphytic ferns less than 5 m above ground level, and ramicolous, feather and hanging mosses were calculated.

Because light indicators increase with decreasing forest integrity, a reverse value has to be calculated to get similar scores from 100 to 0 with increasingly disturbed forest. Therefore, instead of the herbaceous cover (Cov) itself, assessed according the 1 to 9 scale of Londo (1984), the inverse (10 - Cov) was used. This inverse value decreases with decreasing forest integrity and thus behaves like indicators of moisture and forest structure.

For other light indicators assessed as frequency of presence, the score is calculated differently. Their frequency in the undisturbed reference plot (R%) is regarded as the standard. The difference between R% and the percentage in a disturbed forest (D%) is then rate against the range that is left between R% and the maximum of 100% presence of light indicators, i.e. 100 - R%. Because this ratio (S') still increases with decreasing forest integrity, the inverse (100 - S') is taken. Thus the new Score

calculated as follows:

$$S = 100 - \{(D\%-R\%)/(100-R\%) \times 100\}$$

where:
S= indicator Score relative to the reference standard
D%= presence of indicator in Disturbance unit
R%= presence of indicator in Reference

This implies that frequencies of light indicators close to the frequencies in the reference plot result in high scores close to 100. Higher frequencies of light indicators result in lower scores, indicating further opening of the canopy and thus decreased forest integrity.

Scores higher than 100 for individual indicators can occur if the value D is larger than R. This has been observed only twice. To prevent indicator scores greater than 100, those scores are set to a maximum of 100.

Finally, for each disturbance unit and for each group of indicators, an average score is calculated that ranges between 0 and 100. These three scores together result in the final indication of forest integrity presented in Tables 1 and 2.

1=Selective cutting 1974
2=Selective cutting 1974
3=Shifting cultivation abandoned 1974
4=Shifting cultivation abandoned 1984
5=Shifting cultivation abandoned 1991 (before 1974 a wet rice field)

	1	2	3	4	5
Light indicators	66	57	42	6	32
Atmospheric moisture indicators	56	40	6	5	1
Structure indicators	73	85	42	51	30
	65	61	30	21	21

Table 1: Final scores of indicator groups based on the percentage presence of indicators relative to their presence of 100 in the undisturbed reference plot for terrace sites.

1=Selective cutting 1984
2=Shifting cultivation abandoned 1986
3=Selective cutting 1984
4=Shifting cultivation abandoned 1988 after second cutting

	1	2	3	4
Light indicators	53	48	38	25
Atmospheric moisture indicators	73	32	29	0.3
Structure indicators	59	27	18	19
	61	36	28	15

Table 2: Final scores of indicator groups based on the percentage presence of indicators relative to their presence of 100 in the undisturbed reference plot for lower slope sites.

Substantiation of the diagnostic method

There is a relationship between the presence of indicators and the developmental phase for both undisturbed reference plots. However, there is a big difference in presence of the indicator groups between the two plots (Table 3) that is strongly related with the different character of the forest mosaic as mapped according to the SILVI-STAR method (Figure 1)

In the undisturbed reference plot Ketambe 1, the presence of the light indicators, pioneer trees and herbaceous lianas is restricted to areas in or near innovation and aggrading gaps. At the same time, the mossline drops to levels beneath 4 m and the number of woody liana declines to less than 6 in such gaps (Table 4). Ramicolous and feather mosses may be absent in the innovation gap phase. It is characteristic that the influence of a canopy gap (innovation or aggrading gap phase) extends further than the area classified as such on the phase map. For example only 10.3 % is mapped as innovation or aggrading gap phase in Ketambe 1 (Figure 1), whereas herbaceous lianas are found in 34 % of the transect plots. In the Ketambe 2 plot, the frequency of pioneer trees is much lower than in Ketambe 1 (25%, compared with 5 %) while herbaceous lianas did not occur in the 1 km transects (Table 5). Only 3.3 % was mapped as innovation or aggrading gap phase (Figure 1).

The light indicators, ginger species taller than 2 m and grasses, are rare in the

terrace undisturbed reference plot, Ketambe 1, and absent in lower slope plot, Ketambe 2. The frequency of tall ferns is low in both plots (6% and 3 %). In the Ketambe 2 reference plot, tall ferns are represented by the tree fern (*Cyathea borneensis*) only.

	Ketambe 1	Ketambe 2
HERB_COV	1.97	1.33
PIONEERT	25 %	5 %
LIGHTEXO	0 %	0 %
GRAMINEA	0 %	0 %
BGINGERS	1 %	0 %
BIGFERNS	6 %	3 %
HERBLIAN	34 %	0 %
WOODLIAN	98 % (6.9)	97 % (5.5)
MOSSLINE	5.2 m	2.2 m
EPIFFERN	86 %	27 %
FILMFERN	47 %	16 %
FEATHMOS	98 %	42 %
RAMICMOS	98 %	89 %
LEAF_MOS	76 %	7 %
BOLECLIM	7 %	11 %
TREE__50	1.30	3.00
TREE_100	0.61	1.83
DIAMDIST	1.87	2.00
LAYERING	2.70	3.00
MAXIM_HT	43.26	44.78
BA_THUMB	5.44	8.04

Table 3: Percentages of indicator presence and mean values of indicator values in the undisturbed reference plots Ketambe 1, on the terrace, and Ketambe 2, on the lower slopes.

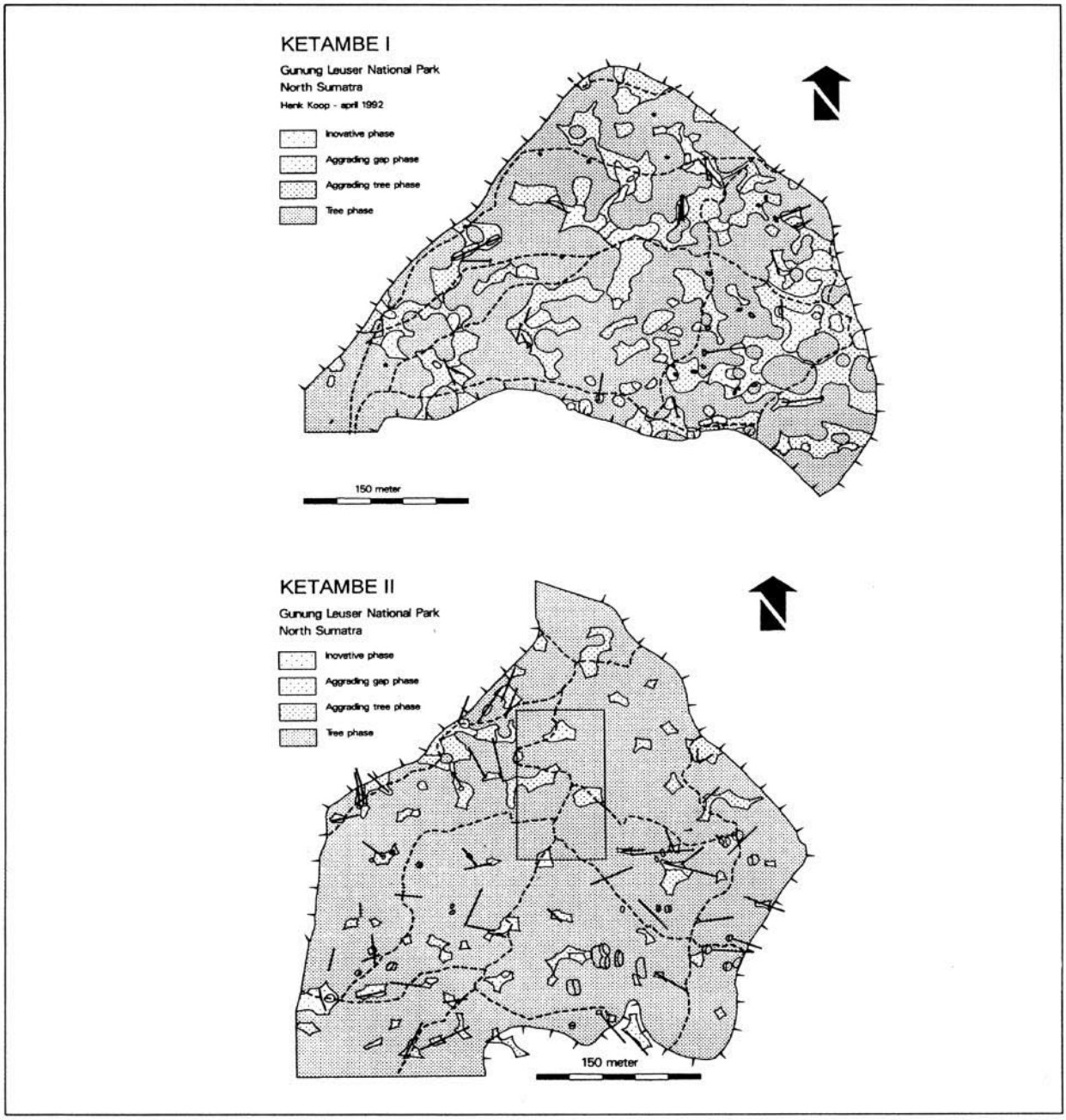

Figure 1: Phase mapping of the terrace and lower slope reference area Ketambe 1 and 2. Innovative phase height < 2m, Aggrading gap phase 2m< height< 10m, Aggrading tree phase 10m< height < 20m and Tree phase > 20m.

This group of light indicators is confined to the highest light intensities and is only rarely found in innovation gap phases. There it is represented by only a few individuals. In the 10 ha phase map of Ketambe 1, only 5, and in Ketambe 2, only 3 such spots were encountered, but these spots were not traversed by the 1 km diagnostic transects.

Atmospheric moisture indicators in the Ketambe 1 plot are absent in the innovation gap phase and are most frequent in the tree phase. Differences in scores between aggrading gap and aggrading tree are small, except for the light indicating pioneer trees and herbaceous lianas.

	Innovation Gap phase H<2m	Aggrading Gap phase 2m<H<l0m	Aggrading tree phase l0m<H<20m	Tree phase H>20m
HERB_ COV	6.5	1.9	1.8	1.9
PIONEERT	100 %	71 %	33 %	13 %
LIGHTEXO	0 %	0 %	0 %	0 %
GRAMINEA	0 %	0 %	0 %	0 %
BGINGERS	0 %	0 %	6 %	0 %
BIGFERNS	50 %	14 %	13 %	0 %
HERBLIAN	100 %	86 %	47 %	11 %
WOODLIAN	2.0	5.9	6.1	8.5
MOSSLINE	1.0 m	3.1 m	4.6 m	6.2 m
EPIFFERN	0 %	71 %	66 %	81 %
FILMFERN	0 %	36 %	47 %	49 %
RAMICMOS	0 %	100 %	100 %	100 %
LEAF_MOS	0 %	64 %	66 %	84 %
BOLECLIM	0 %	7 %	7 %	22 %

Table 4: Percentages of light and atmospheric moisture indicator presence and mean values of indicator values in the developmental phases in the 1000 m transect for the terrace reference plot, Ketambe 1.

Atmospheric moisture indicators have lower frequencies in reference plot Ketambe 2, while the average mossline height is much lower than in Ketambe l (2.2 against 5.2 m).

Figures 2 and 3 show the results of DCA ordination of samples and indicator scores along the first two axes for the terrace sites. The first axis explains 50 % of the variance (eigenvalue = 0.584), and shows clear correlation with the simple hand-calculated scores of the disturbance units presented in Table 1. The second axis only explains 4.5 % of the variance (eigenvalue=0.058) and is related to the developmental phase of the forest mosaic patch. Plots in the oldest closed tree phases show less atmospheric moisture indicators and woody lianas than the younger and lower mosaic patches.

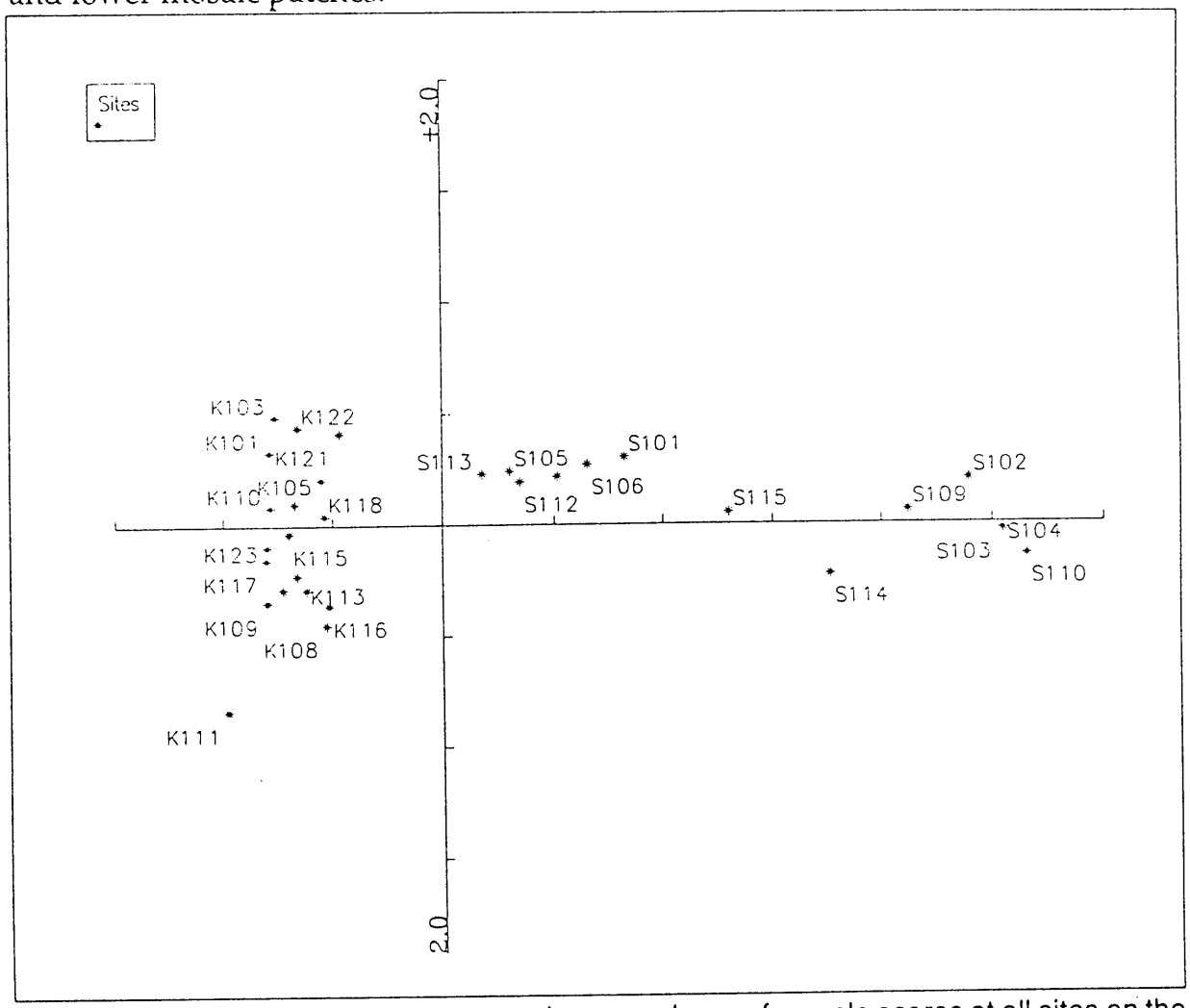

Figure 2: Biplot of detrended correspondence analyses of sample scores at all sites on the terrace. All K numbers represent the undisturbed reference plot, S102, S103, S104, S109 and S110 represent abandoned shifting cultivation since 1984, S114 and S115 represent abandoned shifting cultivation since 1974. Other S numbers represent selective cutting.

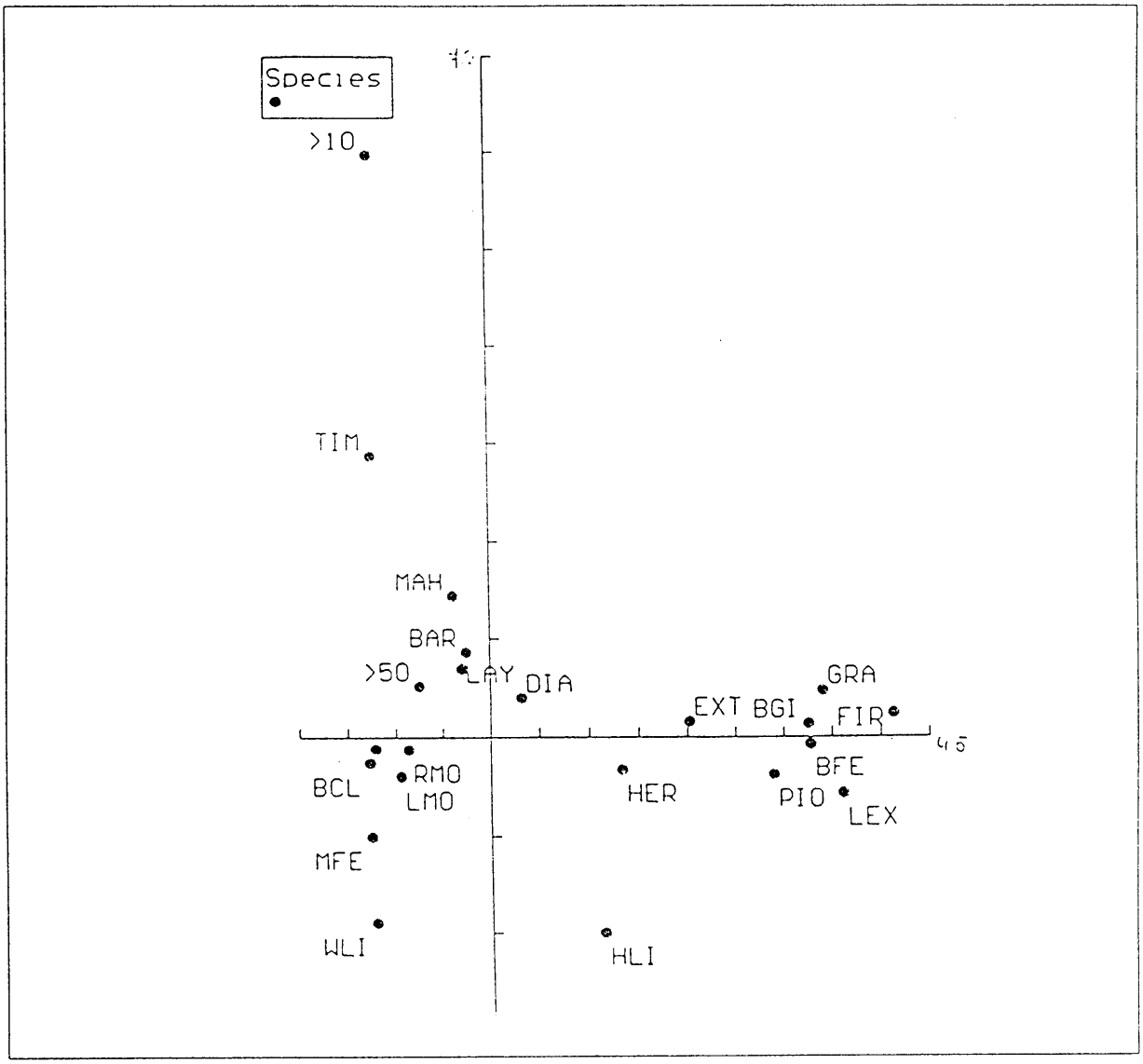

Figure 3: Biplot of detrended correspondence analyses of indicator scores at all sites on the terrace. Forest structure indicators: TIM=timber trees, MAH=maximum tree height, BAR=basal area, >50 and >10 trees more than 50 and 100 cm dbh, LAH=layering, DIA=diameter distribution, FIR=traces of fire, Atmospheric moisture indicators: BCL=bole climbers, RMO=ramicolous moss, LMO=moss on the leaves, MFE=filmy ferns, WLI=woody lianas, and the three points without indication are feather moss, moss line and epiphytic ferns. Light indicators: HER=herbaceous cover, EXT=exotic trees, BGI=big gingers, GRA=grasses, BFE=big ferns, PIO=pioneer trees, LEX=light exotics, HBL=herbaceous lianas.

The results of ordination of samples and indicators for sites on the lower slopes (Figures 4 and 5) show similar results to Table 2. The first axis explains 55 % of the variance (eigenvalue=0.538) and the second axis 7.5 % of the variance (eigenvalue=0.078) and is correlated with the elevation of the plots. Plots on the

	Innovation Gap phase H<2m	Aggrading Gap phase 2m<H<l0m	Aggrading tree phase l0m<H<20m	Tree phase H>20m
HERB-COV	1.0	0.5	1.6	**I.3**
PIONEERT	0 %	25 %	27 %	2 %
LIGHTEXO	0 %	0 %	0 %	0 %
GRAMINEA	0 %	0 %	0 %	0 %
BGKNGERS	0 %	0 %	0 %	0 %
BIGFERNS	0 %	25 %	0 %	2 %
HERBLIAN	0 %	0 %	0 %	0 %
WOODLIAN	2	3.5	4.5	5.8
MOSSLINE	2 m	2.25 m	2.5 m	2.1 m
EPIFFEJXN	100 %	25 %	75 %	26 %
FILMFERN	0 %	25 %	27 %	17 %
RAMICMOS	100 %	100 %	100 %	93 %
LEAF-MOS	0 %	0 %	0 %	8 %
BOLECLIM	0 %	25 %	9 %	11 %

Table 5: Percentages of light and atmospheric moisture indicator presence and mean values of indicator values in the developmental phases in the 1000 m transect in the lower slope reference plot, Ketambe 2. The number of plots for calculating the percentages of Innovation and Aggrading plots are 4 and 11, and therefore give inaccurate outcomes.

ridge have fewer atmospheric moisture indicators than plots in the valley.

The correspondence analyses of the environmental variables, basal area (mean value over 300 m^2), selective cutting, shifting cultivation and developmental phase (metric classification of forest patches according tree height), the number of stumps and the crown area index (Koop 1989) proved that only basal area, selective cutting, shifting cultivation and developmental phase contributed significantly to the variance of species composition of trees, saplings and seedlings, shrubs and high

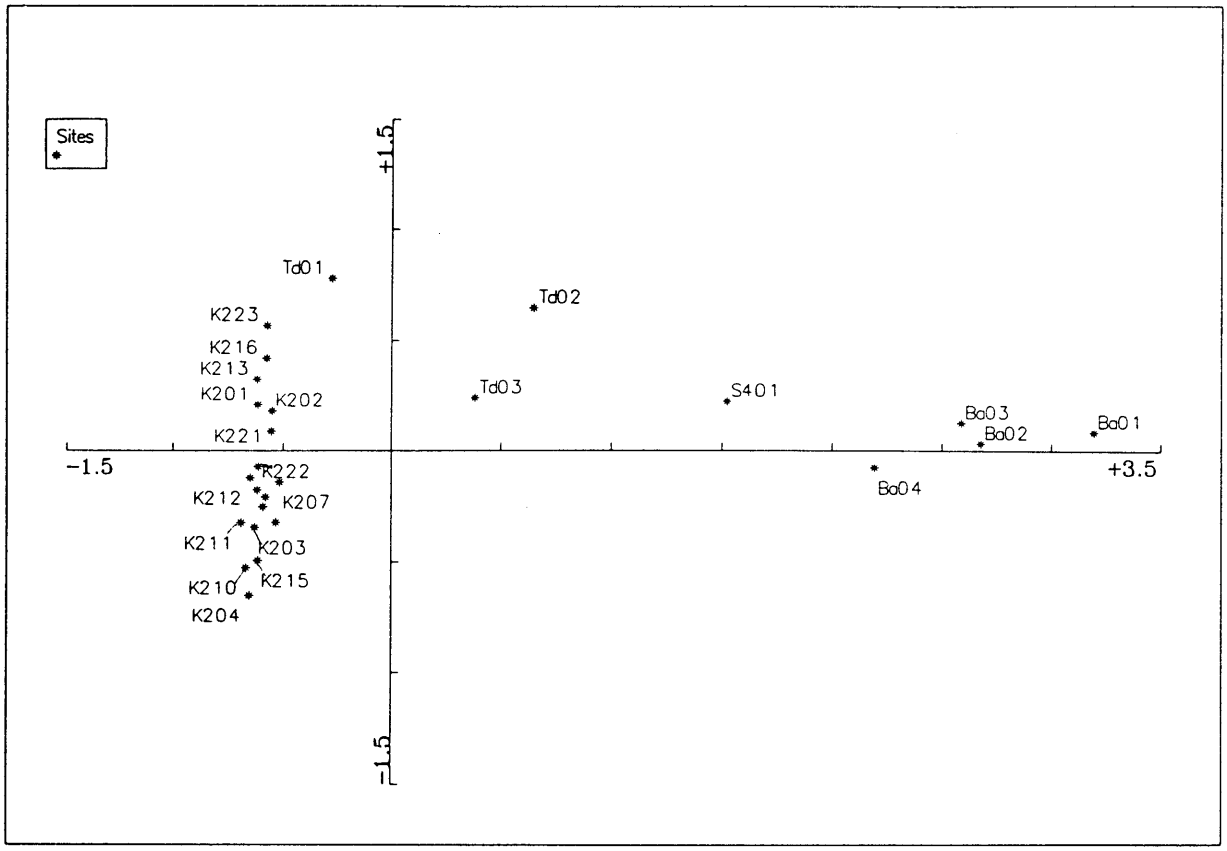

Figure 4: Biplot of detrended correspondence analyses of sample scores at all sites on the lower slopes. All K numbers represent the undisturbed reference plot, BA numbers represent abandoned shifting cultivation since 1984, TD01, TD02, TD03 and S401 represent selective cutting.

herbs. Those environmental variables subjected to a detrended canonical correspondence analyses explained, respectively, 23.7%, 23%, 18.4% and 14.5% of the variance in species composition. The first axis accounts for 42.5% of the variance (eigenvalue=0.496) and is correlated with the environmental variables selective cutting, shifting cultivation and developmental phase (Figure 6). The sequence of plots on the first axis is similar to the sequence of plots obtained by the DCA ordination of indicator scores solely (Figures 2 and 3) and the hand calculation of diagnostic scores (Table 1). The second axis explains 18.3% of the variance (eigenvalue=0.236) and is correlated with basal area, while the third axis explains 16.6% of the variance (eigenvalue=0.112) and distinguishes the plots with selective cutting from those with shifting cultivation.

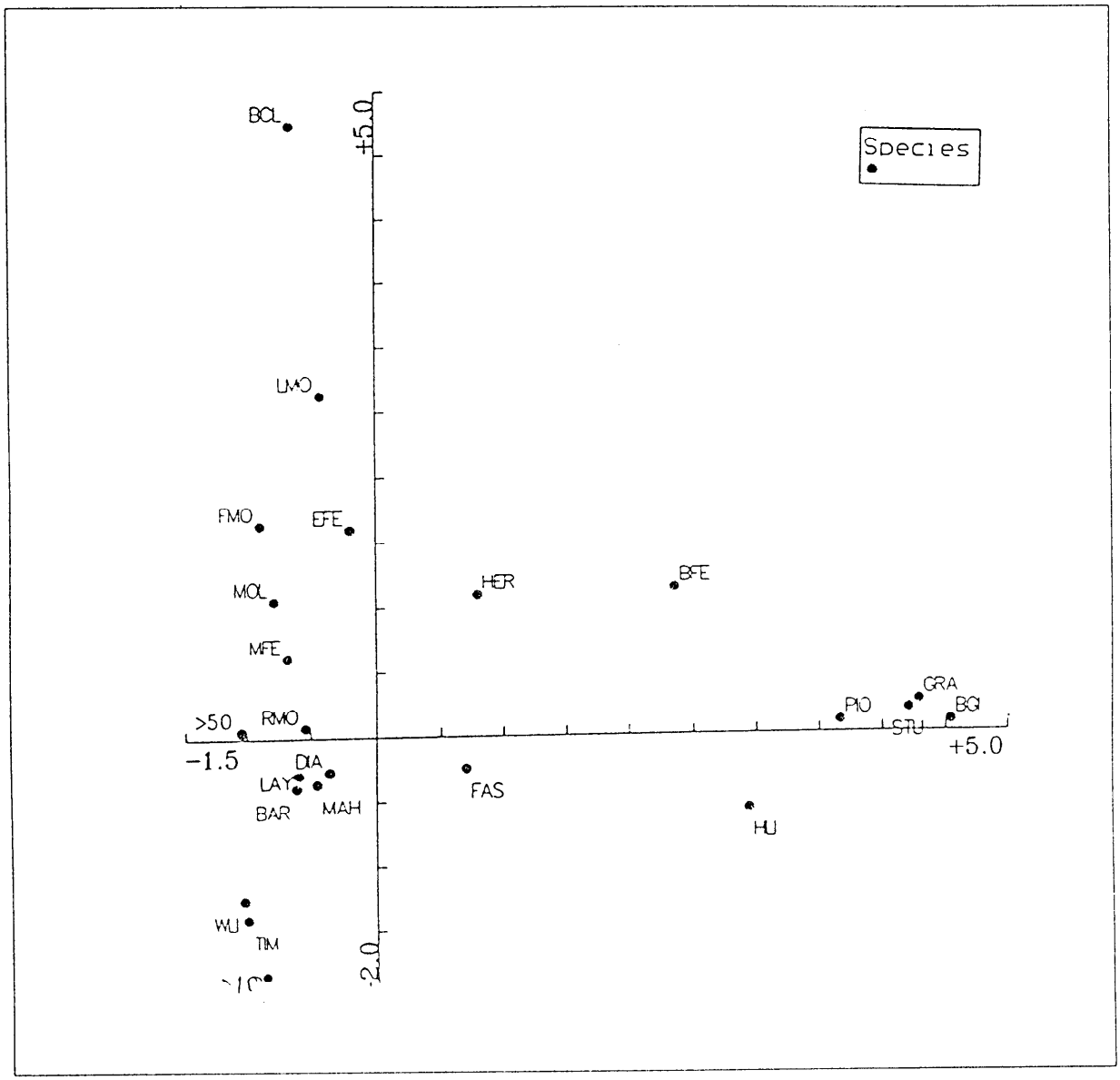

Figure 5: Biplot of detrended correspondence analyses of indicator scores at all sites on the lower slopes. Forest structure indicators: TIM=timber trees, MAH=maximum tree height, BAR=basal area, >50 and >10 trees more than 50 and 100 cm dbh, LAH=layering, DIA=diameter distribution, FIR=traces of fire, STU=stumps, FAS=developmental phase. Atmospheric moisture indicators: BCL=bole climbers, RMO=ramicolous moss, LMO=moss on the leaves, MFE=filmy ferns, WLI=woody lianas, FMO=feather moss, MOL=moss line and EFE=epiphytic ferns. Light indicators: HER=herbaceous cover, EXT=exotic trees, BGI=big gingers, GRA=grasses, BFE=big ferns, PIO=pioneer trees, HBL=herbaceous lianas.

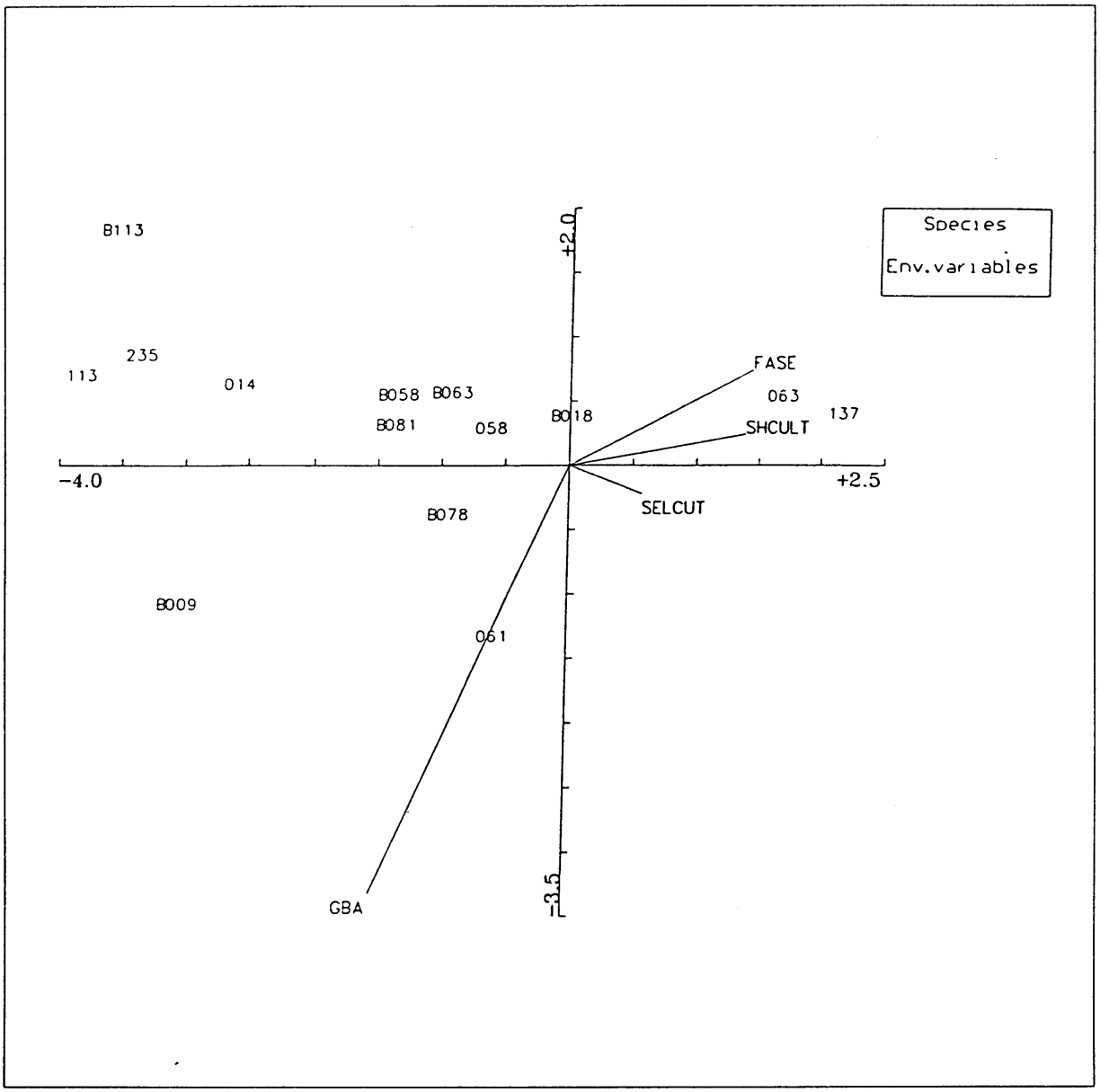

Figure 6: Biplot of canonical correspondence analyses CANOCO (Ter Braak 1986) of the complete species composition for terrace sites with the environmental variables basal area (GBA) (mean value over 300 m^2), selective cutting (SELCUT), shifting cultivation (SHCULT) and developmental phase (FASE) (metric classification of forest patches according to tree height) that contributed significantly in explaining the variance of species composition. Species (trees thicker than 5 cm Dbh as well as recognizable samplings and seedlings in all 10 x 10 m^2 intervals of the transects) were just scored as present or absent.

DISCUSSION

The final rating of forest integrity suffers from the fact that variables of a totally different nature are lumped together in a single figure. Nevertheless the method presented in this paper is substantiated by scientific processing of a more extensive data set on species composition and forest structure. The diagnostic method, applied in the Gunung Leuser area, gives reliable scores in plots from undisturbed forest to woodlands in which few trees are left. The sensitivity of the method in open areas, however, is limited. Recent cutting, mowing or burning reduces the presence of pioneer trees and big ginger species and therefore the absence of light indicators can give artificially higher scores.

Not all indicators react similarly in the whole range of forest disturbance. Atmospheric moisture indicators, including woody lianas, are sensitive to disturbance caused by selective cutting, whereas in young and old abandoned shifting cultivation they are absent. More severe disturbance is better covered by the indicators of herbaceous cover, light indicators and basal area.

Although the diagnostic method has now been tested along a 3500 m transect in Gunung Leuser National Park and in the Wanariset forest in East Kalimantan, experience with this method is still limited. Therefore it is necessary to test the diagnostic method on a larger scale.

In different areas of the world atmospheric moisture, forest structure and light indicators can be used to score forest integrity. The range of sensitivity of the three indicator groups also depends on the region in which the diagnostic method is used. The structure and light indicators are most generally applicable, even in regions without moist climates. Atmospheric moisture indicators, however, have a more restricted applicability. Even in plots on the lower slopes in the Ketambe forest the atmospheric moisture indicators are scarce. Two factors can be identified that may cause this scarcity. First, reference plot Ketambe 2 is situated on a ridge where the forest is more exposed to winds than in the flat and sheltered position of plots on the flat terrace. The most exposed portion of the ridge, with slopes of 25 to 35 degrees to the east, north, and west, shows total absence of atmospheric moisture indicators. The lower slopes in the north-south and the west-east transect have the highest mosslines and frequencies of atmospheric moisture indicators, even where the transect transverses an aggrading gap phase. The crest and upper slopes of the ridge again have lower average mosslines and lower presence of atmospheric moisture indicators. This implies that in areas of marked topographical differences, valleys as well as ridges have to be sampled and comparisons of disturbance units elsewhere should be based on similar conditions of relief.

A second explanation for fewer atmospheric moisture indicators is that the level of illumination may have become a limiting factor. Richards (1984) mentions air humidity as the critical factor for survival of feather, ramicolous and hanging mosses but stresses that light is often the most important limiting factor. Although low intensities of direct sun radiation favour high air humidity, it can be too dark despite sufficient air humidity. The lower presence of light indicators in the Ketambe 2 reference plot can be explained by the higher canopy closure (Table 2), with only 3.3% of the area in innovation and aggrading gap phases. This explanation is supported by a relatively higher score of atmospheric moisture indicators in the aggrading gap and aggrading tree phases (Table 5), where light intensities are probably higher because an emergent canopy of *Parashorea* is absent. For the same reason, the tree phase plots adjacent to an aggrading tree or an aggrading gap phase most often have common atmospheric moisture indicators. Oblique radiation can penetrate under tree crowns beyond the vertical projections of the tree crowns that delimit a canopy gap and the disturbance of falling trees often extends underneath crown projections of taller trees. With a limited opening of the canopy and an insignificant loss of air humidity, light is not the limiting factor anymore and atmospheric moisture indicators may increase. This explains why, in one selective cutting disturbance unit, an atmospheric moisture indicator (bole-climber) score was higher than in the undisturbed reference plot.

The indicator list of the diagnostic method so far is restricted to vegetation characteristics. Animal species that are highly indicative of primary forest can, however, be included in the list. Species that are easily recognized by their frequent and characteristic calls e.g. hombills *(Bucerotidae)* and barbets *(Capitonidae)* are most suitable. Other signs of the presence of big mammals can provide additional information. However, such data will be far from complete and the chance of finding the evidence of a species presence in the limited area of the transect is too low for these data to be used in the diagnostic method. The absence of evidence does not prove the absence of the species. However, forest characterized by forest structure, light and moisture conditions does not express diversity of animal life which may be affected by hunting pressure. Separate data are needed to assess the impact of hunting.

Increasing surface percentage of canopy gaps results in increasing homogeneity in forest structure in secondary forest (Budowski 1965, Jacobs 1988) and discontinuity of old growth patches, providing a more direct diagnosis of forest integrity (see Dale *et al.*, Chapter 4, this volume). Mapping areas of innovation and aggrading gap phases needs a different scale of assessment and is too time

consuming. The percentage of canopy gaps is, however, reflected by the frequency percentage of light indicators.

To apply the diagnostic method, a reference is necessary. This reference does not need to be a strictly virgin forest but a forest stand that has been unexploited for as long as possible will suffice. Comprehensive data from undisturbed plots can serve as a reference for the design of management methods for restoration management of heavily disturbed natural forest.

CONCLUSIONS

This method for rapid assessment of forest integrity is suitable for monitoring the effects of forest-people interaction. A set of simple and easy recognizable characteristics can assess the integrity of tropical rain forest. The method can be applied by local rangers and villagers such as para-taxonomists after practical training of 3-5 days, if supervised and monitored by a scientist who should also process the data.

Forest structure indicators and light indicators are not dependent on differences in macro and micro-climate. Atmospheric moisture indicators are restricted to rainforest. Because of micro-climatological differences of ridges and valleys in hilly areas that influence the presence of atmospheric moisture indicators, both should be sampled, and similar relief conditions should prevail in undisturbed reference plots and disturbance units. Light- and atmospheric moisture indicators have different ranges of sensitivity. Atmospheric moisture indicators proved to be sensitive to even slight human disturbance by selective cutting whereas light indicators differentiate more serious disturbance where atmospheric moisture indicators are already absent.

Forest integrity is related to biodiversity. However, forest characterized by structure, light, and moisture conditions does not reflect diversity of fauna1 species. Separate data are needed to assess the impact of disturbance on wildlife. For a wider application of the diagnostic method there is a need to conserve virgin forest reference plots for all site types within a particular region. In case no virgin forests are left, forest areas that have been least disturbed should be left to serve as future reference plots.

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Chapter
23

A GIS APPROACH TO MAPPING SPATIAL VARIATION IN TROPICAL RAIN FOREST BIODIVERSITY

Alan Grainger [1], Sam Rose [1], Yongyut Trisurat [2], Warren Y. Brockelman [3]

INTRODUCTION

The focus of conservation planning has switched over the past twenty years from protecting single threatened species to conserving biodiversity as a whole, but the techniques required to support this new goal are still lacking. Some aspects of biodiversity have been mapped, e.g. distributions of species density and centres of endemism, but biodiversity has not yet made the transition from wide-ranging concept to measurable quantity and this, together with poor data, is hampering conservation scientists and planners alike. New approaches are therefore needed that can enable biodiversity to be mapped comprehensively over large areas and provide the basis for improved conservation planning methods.

1 School of Geography, University of Leeds, Leeds LS2 9JT, UK.

2 School of Environment, Resources and Development, Asian Institute of Technology, Bangkok, Thailand.

3 Centre for Conservation Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand.

This paper suggests how geographic information system (GIS) techniques can be used to map the biodiversity of tropical rain forests. From a GIS perspective, biodiversity has vertical and horizontal structures, just like an ecosystem. Its vertical structure comprises the sum of the spatial distributions of many species of plants and animals, together with those of the ecosystems of which they are a part. Each of these distributions has a horizontal structure, corresponding to their spatial variation. By studying this variation conservation planners can identify areas of exceptional richness, or areas containing the minimum critical populations of species of high conservation priority. The first part of the paper looks at biodiversity as a multi-dimensional phenomenon, while the second explores the role of fragmentation in explaining the spatial heterogeneity of biodiversity.

BIODIVERSITY AS A MULTI-DIMENSIONAL PHENOMENON

Geographic Information Systerms

A geographic information system is a piece of computer software capable of the integrated handling and analysis of spatial data (Burrough 1986). It is a sophisticated database that stores data on the geographical location of spatial entities and one or more of their attributes, and can test for relationships between different entities and attributes. Information is stored either in vector format, where it refers to points, lines and polygons that correspond to actual features, or in raster format, where it refers to cells in a uniform grid into which a study area is divided. Most GIS programs now allow easy interchange between the two formats.

Human beings are limited in their ability to interpret complex geographical information, especially when, for the sake of economy, multiple features are combined on the same printed map, e.g. the distributions of towns, rivers and lakes. A GIS simplifies the picture by mapping the point distribution of towns, the line distribution of rivers and the polygon distribution of lakes in an area as separate digital data layers. So, while on a paper map these are overlaid in an inflexible way, on a GIS they can be overlaid selectively and flexibly for easier interpretation. They can also be quantitatively related.

The GIS approach is more than just an efficient method for presenting complex geographical information. It also offers a new way of looking at that information, by dividing it into major sets of individual features and allocating a separate digital map layer to each. A single feature can have multiple attribute layers associated with it, e.g. the attributes associated with an area of forest include its biomass density (mass of carbon per ha) and species density (number of species per ha)

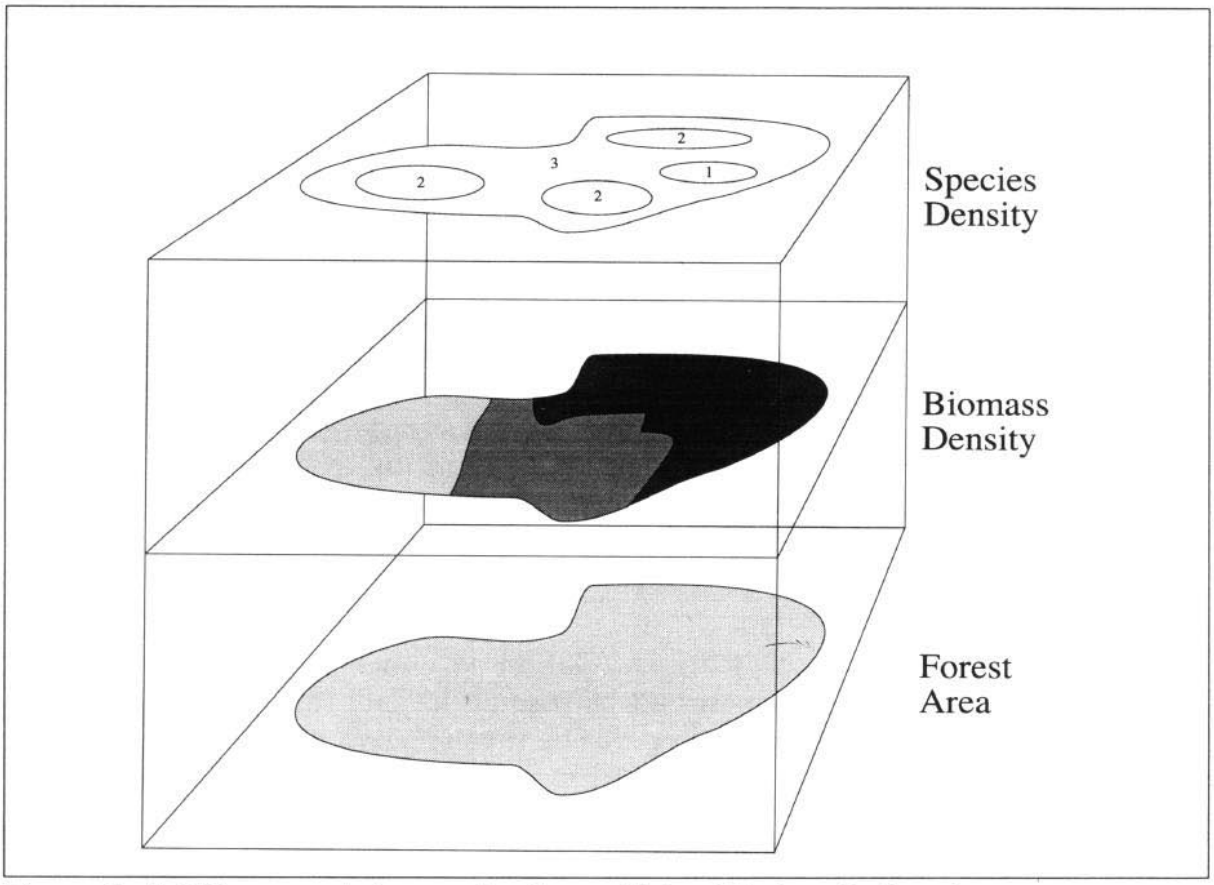

Figure 1: A GIS approach to mapping the multiple attributes of a forest area.

(Figure 1), and this multiple dimension approach forms the basis for the portrayal of biodiversity presented here.

The Multiple Dimensions of Biodiversity

The concept of biodiversity originated as simply "an umbrella term for the degree of nature's variety" (McNeely *et al.* 1990) but has subsequently been defined more specifically in terms of a number of different components. Three of these are commonly referred to: (a) ecosystem diversity, (b) species diversity and (c) genetic diversity. Other proposed components include endemic species concentrations and landscape diversity. Trophic and guild diversity have been considered as well (Solbrig 1992).

To quantify and map biodiversity as such, these components must be combined in a coherent and integrated way Little progress has been made in this endeavour so far. There have been attempts to create an aggregate national biodiversity index (WCMC 1992) and although this is valuable for some purposes, it omits a lot of detail and its spatial component is restricted to political boundaries that usually have little ecological meaning.

From a GIS perspective, however, the solution to this problem seems obvious: simply accept that biodiversity must be regarded as a multi-dimensional phenomenon comprising the sum of its spatially referenced components. The spatial distribution of biodiversity in an area can therefore be portrayed as a set of three related primary information layers, comprising ecosystem diversity, species diversity and genetic diversity, generated by combining a large number of raw data layers corresponding to the distributions of individual taxa (Figure 2). Maps of the aggregate distribution of biodiversity can then be produced using additional information layers derived from the primary layers (see below).

Ecosystem Diversity

The ecosystem diversity layer is the foundation on which the others are laid. In purely natural conditions undisturbed by human impact this shows the actual distribution of different ecosystem types. The detail shown in this layer depends upon the scale of the map. At global and regional levels it would show a small number of major ecosystems, or biome-types, such as tropical rain forest. At larger scales various ecosystem sub-types would be visible, e.g. in the humid tropics, evergreen lowland rain forest, semi-evergreen lowland rain forest, heath forest etc. However, production of detailed global maps is constrained by incompatibilities between different ecosystem classification systems.

Because human impacts on ecosystems have been widespread, such maps usually only show the potential distributions of the major climax ecosystem types. The real distribution of ecosystem diversity is very different, since many natural ecosystems have been cleared, and those which remain have been degraded in various ways, resulting in a complex mosaic of cleared, degraded and undisturbed areas. Maps of the actual distributions of tropical rain forests today are few and far between, and most of those which are available are out of date. IUCN recently combined the best available maps of tropical rain forest in Africa and Asia in its atlases (Collins *et al.* 1990, Sayer *et al.* 1992), but acknowledged the limitations of the original data in many cases. FAO's latest survey of tropical forests in 1990 did not include any maps at all (FAO 1993, Grainger 1995a).

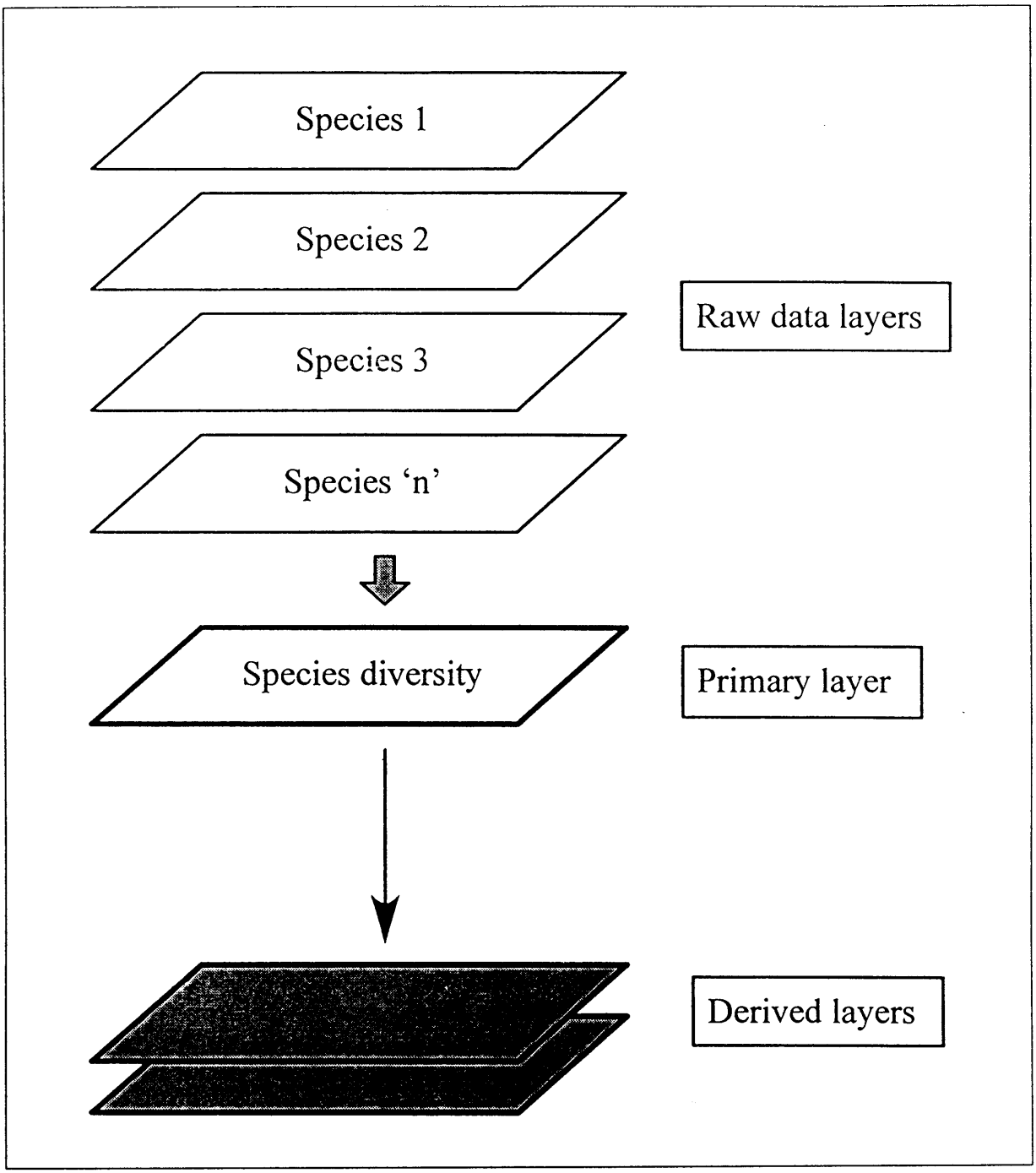

Figure 2: The primary species diversity layer is produced by combining a large number of raw data layers for individual species, and can then itself form the basis for various derived layers.

Species Diversity

The species diversity layer is ideally derived by combining thousands of individual data layers, each showing the distribution of a single species. At the moment, owing to lack of reliable data, this layer is usually restricted to measuring variation in aggregate species richness. But there is potential to devise more sophisticated measures and use GIS techniques to identify patterns that take account of the actual species present and their many qualities.

Moreover, because of lack of data, species distributions are frequently represented on maps either by points on a map (Figure 3a), continuous distributions over a large area (Figure 3b), or in terms of simple presence or absence of a species from a grid square, which may be as large as 1″ x 1″ (Figure 3c). Even if these maps were to reflect natural distributions they would be misleading, because many areas have not been properly surveyed and the apparent concentration of some species distributions may reflect collection bias (Nelson *et al.* 1990). But such maps only really portray potential natural distributions, since it is impossible to inventory everywhere and they rarely take account of human disturbance.

While recognizing existing constraints, it is important to show the possibilities that would be opened up were better spatial data to be collected, so as to strengthen the efforts of major herbaria which are just beginning to produce digital maps of the distribution of taxa. Hopefully, in future, many individual species distribution maps will be produced and stored on GIS databases, so making possible the kinds of analysis proposed here.

For simplicity, in this paper the second primary layer is restricted to species diversity only. But there are strong arguments for including other taxonomic levels, such as genera and families, so that the layer refers to the full range of taxonomic diversity.

Genetic Diversity

The third data layer shows genetic variation within the distributions of individual species, and hence builds on the second layer. Considerable genetic variation may occur in the populations of tropical tree species, and the provenance of trees is of prime importance when breeding improved varieties for different purposes (Burley and Wood 1976). Some species show high variability between populations in different areas, so distinct subpopulations are recognised, though variability within each sub-population is quite low. Other species have low variability between populations but high variability within populations. Such spatial genetic variabi-

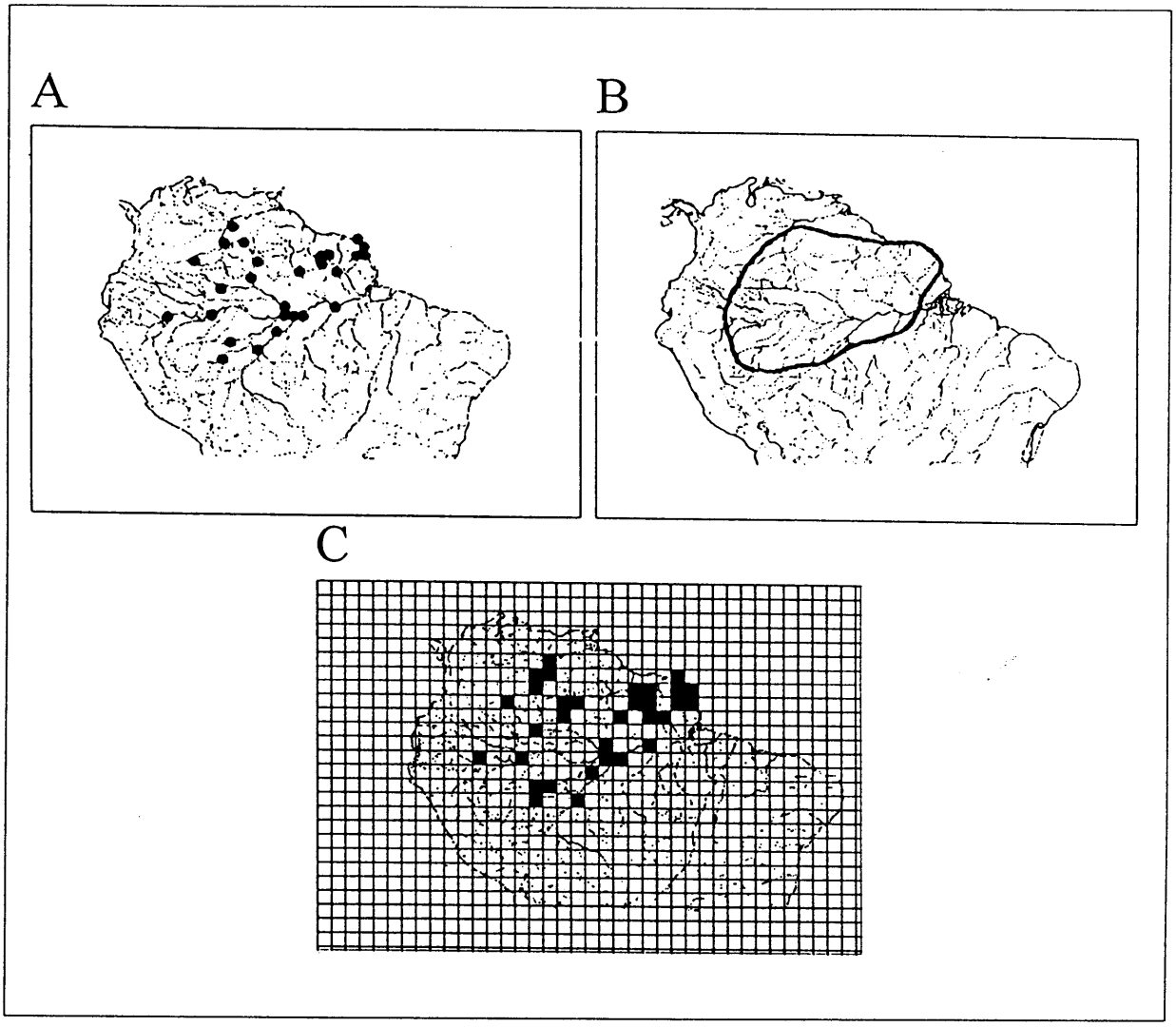

Figure 3: The distribution of Hirtella physophora shown in three common formats used to map species distributions: (a) Point map; (b) Continuous distribution; (c) Raster type map. Sources: Prance (1982, 1990).

lity will determine whether reserves established for the *in situ* conservation of a given species should comprise a single large reserve or a number of smaller reserves (NRC 1991). Although there have been intensive investigations of a few economically important species, for the majority of species the distribution of genetic diversity is as poorly known as their overall distribution, and so at the moment this layer is only useful for specialist purposes.

The Overall Appraisal of Biodiversity

As biodiversity is such a complex phenomenon there is no single way of portraying it. However, synthetic appraisals of biodiversity as a whole can be produced by using various mathematical operations to combine some or all of the primary layers to give a range of derived layers suited to particular purposes. One such layer, for example, might show the location of centres of endemism; another might separate an area covered by a single major ecosystem type into distinct 'biodiversity zones" ranked by their priority for conservation.

SPATIAL HETEROGENEITY IN BIODIVERSITY

To map variation in biodiversity as a whole requires searching for spatial patterns in the primary and derived layers. This section looks at how spatial heterogeneity can be characterised by fragmentation and clustering in the ecosystem diversity and species diversity layers.

Fragmentation of Ecosystem Distributions

Natural Fragmentation.

Ecosystem distributions are fragmented under natural conditions. The extent to which natural ecosystem diversity is shown on maps depends on the chosen map scale (and ecosystem classification system). As the scale increases, so does the natural fragmentation of areas with apparently homogeneous vegetation cover. Thus, tropical rain forest becomes fragmented into its major sub-types, e.g. evergreen lowland rain forest, semi-evergreen lowland rain forest etc., eventually fragmenting even further to match the distribution of landscape diversity.

Artificial Fragmentation

In practice, the natural distribution of ecosystems is heavily fragmented as a result of being replaced or degraded by human intervention. Fragmentation is most visible when forest is cleared. In areas where deforestation has just begun, a large contiguous block of forest will exhibit local fragmentation on its margins but its core will remain intact. As deforestation reaches a more advanced stage, for example in Peninsular Malaysia, preferential clearance in some areas leads to more widespread fragmentation (Figure 4).

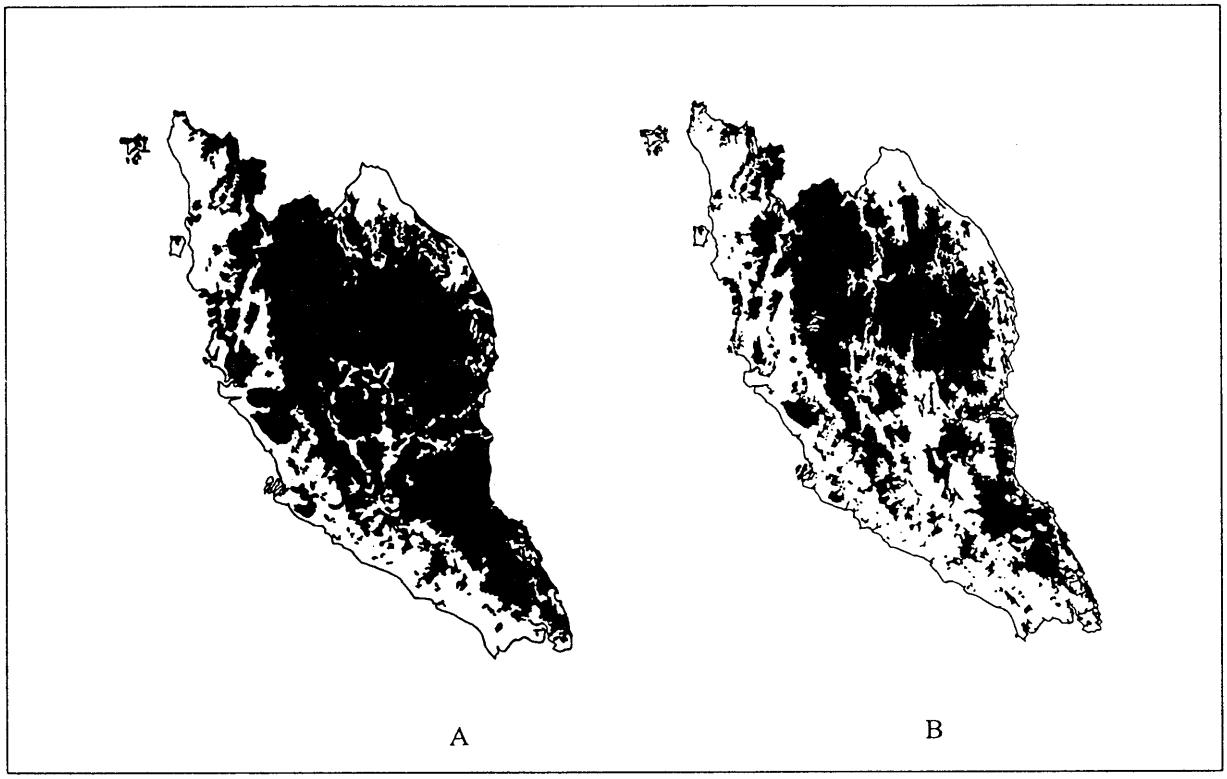

Figure 4: Increasing fragmentation of forest in Peninsular Malaysia with increasing deforestation from 1966 (A) to 1982 (B). Sources: A, based on Wong (1971); B, taken from Brown *et al.* (1994).

However, even where forest cover appears to be continuous, parts of the forest may be degraded, though this is difficult to spot except by detailed examination. In many areas, the original primary forest distribution is highly fragmented, with extensive patches of secondary forest regenerating after selective logging or clearance.

Artificial fragmentation has major impacts on species distributions. The distributions of primary forest plant species become more fragmented than under natural conditions, and since the species compositions of clearings and secondary forest differ from those of primary forest the biodiversity of the whole area is modified (Pickett and White 1985). Selective removal of some plant species, e.g. by logging, seriously affects animal feeding patterns.

Spatial patterns of ecosystem fragmentation have been studied in detail by the emerging discipline of landscape ecology (Forman and Godron 1986, Turner and

Gardner 1991). There has also been considerable work on the species compositions of ecosystem fragments from the perspective of island biogeography theory (MacArthur and Wilson 1967, Harris 1984). However, there is great potential to go further by combining the two approaches, in order to study how highly fragmented ecosystem diversity distributions affect the variation in species diversity over large areas.

A Taxonomy of Degraded Forest Types

A prerequisite for such work is a taxonomy that can introduce some degree of order into the artificial fragmentation of ecosystem distributions. Despite the large area of secondary forest in the tropics, forest degradation has received little attention from biogeographers. But this has begun to change, mainly because of the recognition of the importance of degraded forest in climate change, and the need to map spatial variation in biomass density.

Degradation has been defined as a "temporary or permanent reduction in the density, structure, species composition or productivity of vegetation cover". Using a set of indicators based on this definition an initial taxonomy has been proposed for Southeast Asia (Grainger 1995b). It includes six main types of degraded forest:

1. Extractive Forest, which has had trees or herbaceous plants removed from it. Examples include logged forest and forest modified by other extractive uses.
2. Damaged Forest, which has been degraded by drought, insect pests, pollution etc.
3. Regenerated Forest, which is regrowing after clearance. Examples include shifting cultivation forest fallow, and some forms of managed forest.
4. Planted Vegetation, which results from intentional tree planting, e.g. for silviculture, agroforestry, or tree crop plantations.
5. Interrupted Successional Vegetation, which has a low tree component and is usually dominated by grassland, *e.g. Imperata cylindrica* grasslands.
6. Dispersed Forest, which comprises whole landscapes that have been heavily modified by human impact and now contain mixtures of forest trees, tree crops and grasslands in a dispersed, heterogeneous mosaic. This is an advanced case of forest fragmentation.

This taxonomy can be used to map ecosystem diversity in a way that takes account of both natural and artificial fragmentation, so providing a better foundation for mapping the actual distribution of species diversity than has been possible hitherto.

Ecosystem Fragmentation and Conservation Planning

The study of fragmentation has major applications in conservation planning. The locations of national parks and other protected areas are generally chosen so as to include large continuous areas of different habitats where the viability of animal species populations is high, and avoid areas where deforestation and forest degradation have caused habitat fragmentation, although inevitably some parts of protected areas were disturbed prior to their establishment.

New techniques are needed to map biodiversity distributions rapidly over large areas, so that future protected areas can be sited to protect areas with the highest biodiversity, and existing protected areas can be managed more effectively. Lack of artificial fragmentation of habitats will be one criterion for choosing a potential protected area, but on the other hand both natural and artificial fragmentation need to be taken into account when undertaking management zonation. The long-term integrity and biodiversity of a protected area depends on choosing the most suitable management regime for each part of it, e.g. strict protection, public access for recreational purposes etc. Many protected areas were established without prior surveys of their biodiversity, and this deficiency may often have been remedied before they were divided into different management zones. Consequently, the choice of high public access areas may owe more to the proximity of roads than to the use of biological criteria.

GIS and remote sensing techniques are now increasingly used to study the distribution of animal species based on habitat distribution, because traditional ground survey methods, such as counting animals, trapping, collecting droppings, investigating feeding sites and mapping habitats on the ground, are very time consuming. Habitat maps for particular species are produced using satellite imagery supplemented by ground truth data (Wulf *et al.* 1988), and then inferences are drawn concerning the density of animals and the viability of species populations in that area.

This approach has been used to study the distribution of gibbons in the Khao Yai National Park in Thailand (Figure 5). Two species are involved, the pileated gibbon *(Hylobates pileatus)* and the white-handed gibbon (*H. lar).* Areas containing tropical evergreen forest below 1,000 m above sea level were designated as gibbon habitats, since areas above 1,000 m are usually occupied by hill evergreen forest which has fewer fruit trees, and mixed deciduous forest supports gibbons but at a lower density. Gibbons are also generally absent from the perimeters of protected areas because of poaching, habitat degradation etc.

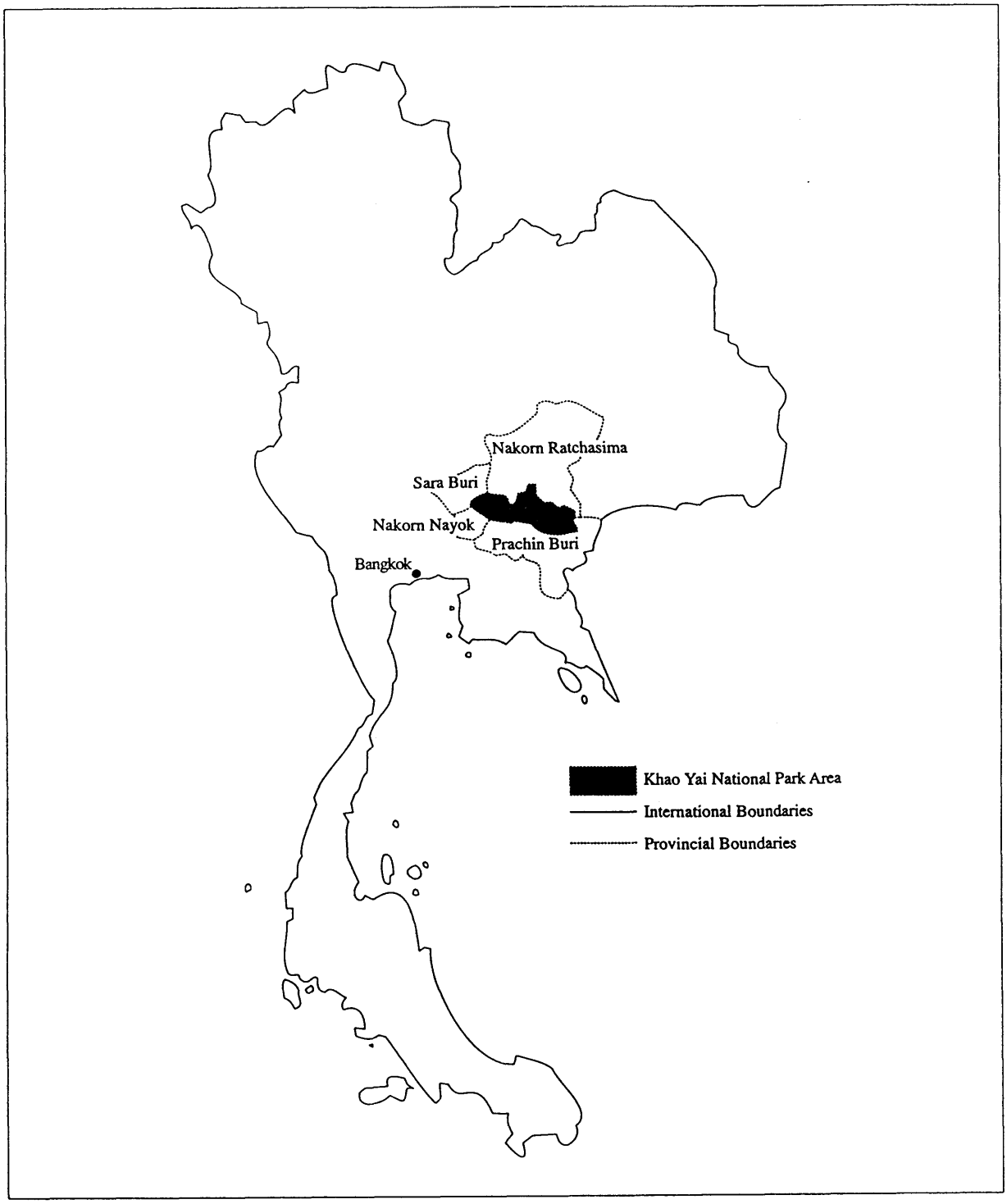

Figure 5: The location of Khao Yai National Park in Thailand.

A spatial database for the Khao Yai National Park was assembled using the ARC/INFO GIS program. The data layers comprised an elevation map, a 1985 forest map divided into the different forest types, and a 1993 forest map. By overlaying the three maps, gibbon habitats were identified by selecting areas containing moist evergreen and dry evergreen forest below 1,000 m. The overall habitat area was calculated and multiplied by the estimated minimum mean gibbon density (1 group per sq km, each with a mean size of 4) to estimate the gibbon population.

The resulting map (Figure 6) showed that 71% of the park area could possibly harbour gibbons. Of the remainder, 23% consisted of buffer areas within 1 km of the forest edge. The gibbon population was estimated as 5,000, which is much greater than the estimated viable population of 1,000 individuals (500 breeding adults). These initial results suggest that future conservation measures in the park should focus on protection rather than active intervention (Trisurat 1994).

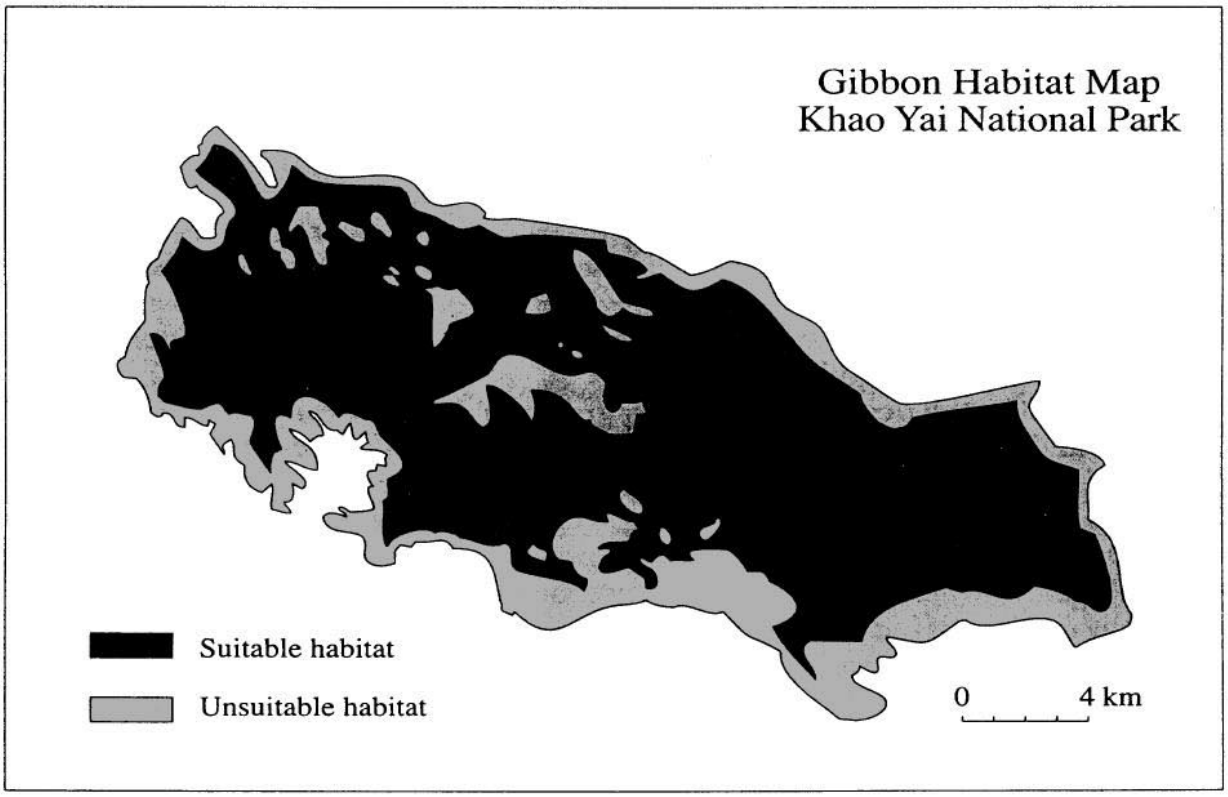

Figure 6: The distribution of areas designated as suitable gibbon habitats in Khao Yai National Park.

Fragmentation of Species Diversity

Spatial variation in species diversity reflects the sum of complex variations in the distributions of thousands of individual species. To measure this, in principle, would require superimposing all of these distributions and identifying the resulting spatial patterns. Given the large number of taxa in the humid tropics - there are approximately 1,800 genera and 30,000-50,000 species in Amazonia alone - this would be almost impossible to do manually. But it would be an ideal task for GIS techniques - assuming, of course, that reliable spatial datasets become available.

Measuring lndividual Species Heterogeneity

Under natural conditions, some species will actually have the kind of continuous distributions shown on maps, while others will be fragmented into a number of clusters, owing to historical reasons or natural ecosystem diversity. Furthermore, because of artificial ecosystem fragmentation, even naturally continuous species distributions will be fragmented to some extent.

The analysis of fragmentation in biodiversity often focuses on local endemics, i.e. those occurring in fragments or clusters of restricted size in an area. Indeed, the distribution of endemics is often used as a surrogate for the distribution of biodiversity. But it can be argued that endemism is merely a special case of fragmentation, and that in mapping the distribution of overall species diversity the distributions of endemics should be measured using the same method as that used for species whose distributions are fragmented over a larger area. In other words, endemics would be represented by single fragments (or patches) and fragmented species by multiple fragments.

Determining the degree of species fragmentation empirically will require a far more detailed knowledge of individual species characteristics than is generally available at the moment in the humid tropics. The apparent degree of fragmentation will also depend on the scale and mapping method used. For example, distributions mapped by denoting the presence or absence of a species in 10 km grid cells may appear to be continuous although such maps do not say anything about the density of individuals inside the grid cell - and maps with 1 km grid cells could show a very different pattern.

This can be illustrated by comparing three species from Amazonia. *Hirtella physophora* is fairly widespread throughout the region (Prance 1982) and even though it has not been found everywhere, the likelihood of its presence between confirmed observations is high, so its distribution can be assumed to be continuous (Figure 7a). On the other hand, *Eperua duckeana* is apparently a local endemic,

restricted to the area around Manaus, with no confirmed observations outside this area (Figure 7b) (Cowan 1975). The distribution of *Mouriri oligantha* is large, but fragmented into distinct populations in Guyana and West Amazonia (Figure 7c) (Prance 1982).

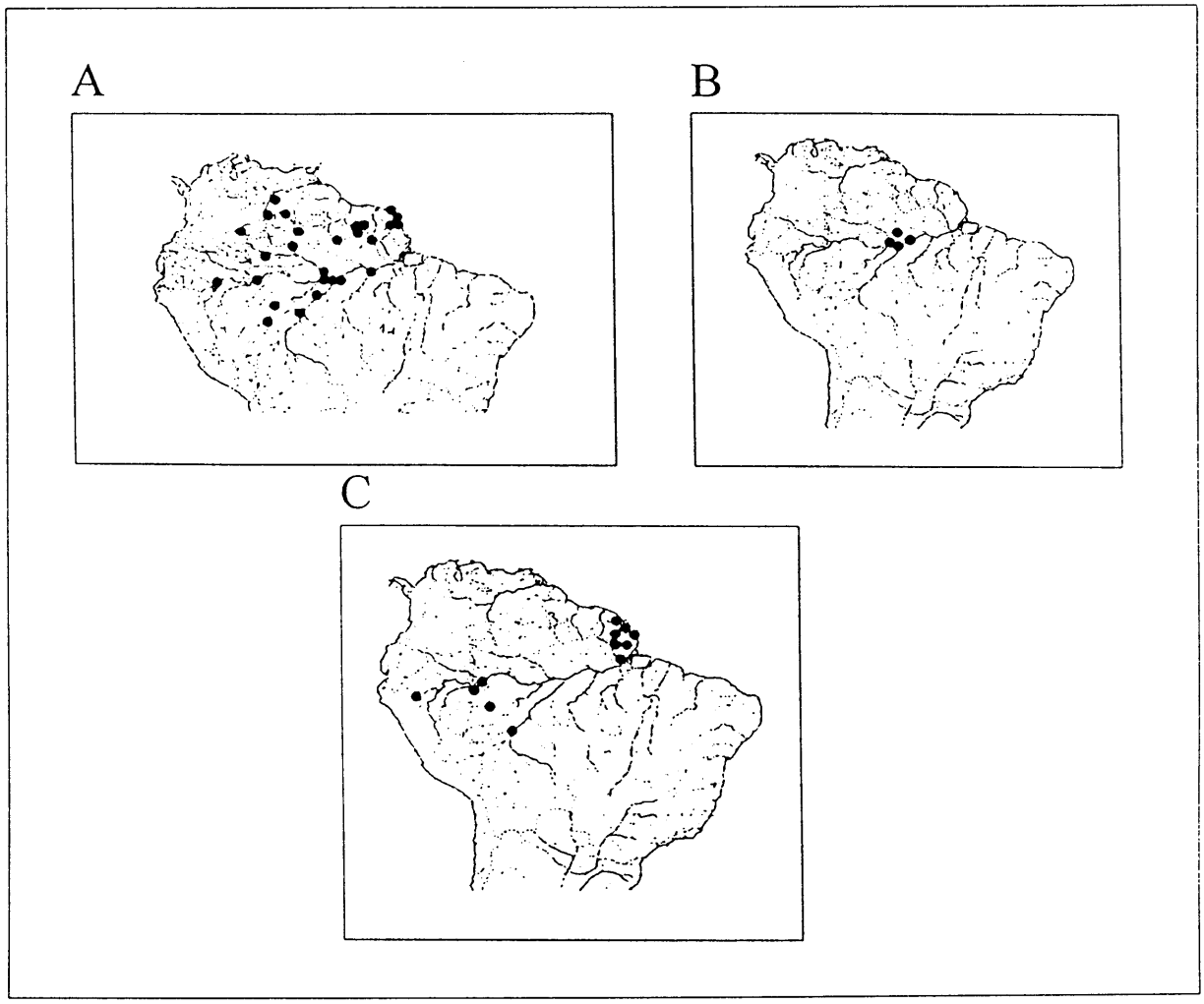

Figure 7: Three contrasting plant species distributions in Amazonia: (a) Continuous: Hirtella physophora (Prance 1982); (b) Local endemic: Eperua duckeana (Cowan 1975); Widespread but fragmented: Mouriri oligantha (Prance 1982).

The spatial heterogeneity of an individual species distribution can be measured by the degree of clustering and fragmentation and is a function of two components: the size of the distribution, and the number of discrete units within this. If the three

species distributions above were scanned using a GIS index that ranked distributions in proportion to the inverse of their size, then the local endemic *Eperua duckeana* would be ranked highest. The other two species might have the same rank because they have distributions of similar size, even though the distribution of *Mouriri oligantha* is fragmented into two parts while that of *Hirtella physophora* continuous. Clearly, a better index is required whose value is determined by distribution size and number of fragments, and is therefore able to characterise both local endemics and fragmented species on the same scale of measurement. A number of candidate indices are being tested at Leeds University.

Measuring the Spatial Heterogeneity of Overall Species Diversity

Mapping spatial heterogeneity in overall species diversity over a large area requires estimating the degree of fragmentation for all species present for which maps are available. This could be achieved by first generating a derived endemic species layer, and then integrating this with the species diversity layer employing a common fragmentation index (Fig. 8). Superimposition would be facilitated if a derived species diversity layer were used instead, which contained only the most heterogeneous species. This would entail removing species with relatively homogeneous distributions, as measured by some arbitrary critical value of the fragmentation index.

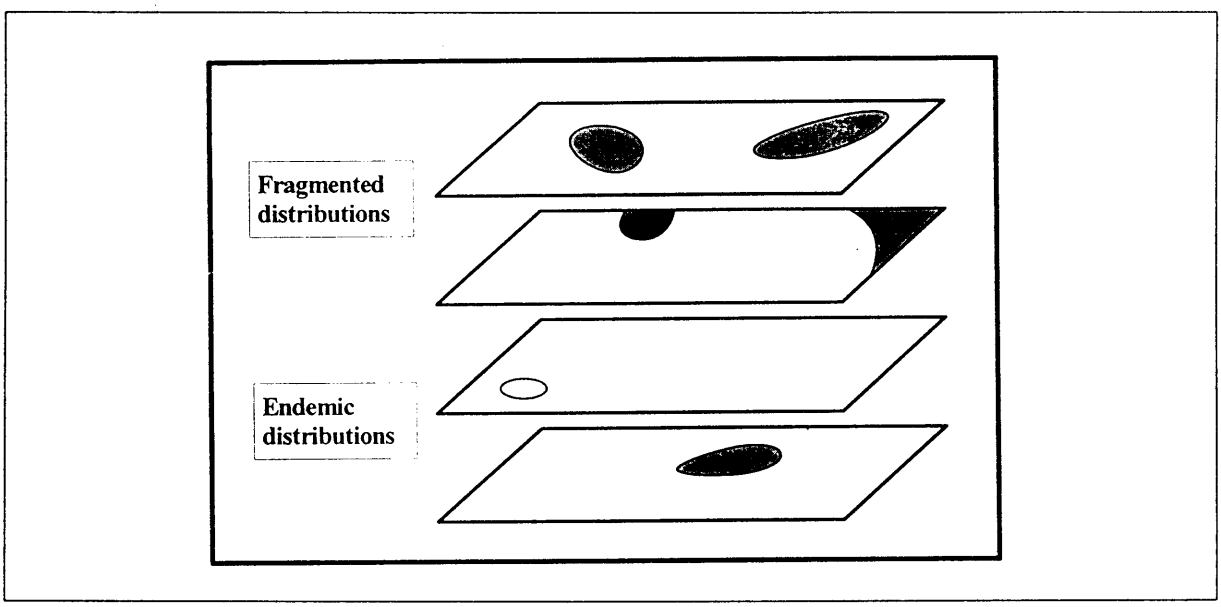

Figure 8: Characterising endemic species and species with fragmented distributions using the same scale of measurement.

This approach could provide a more comprehensive picture of the variation in biodiversity than has been available until now, encompassing many more groups of plants and viewing endemism as only part of a much greater heterogeneity in the distribution of biodiversity. A more elaborate approach would attempt to encompass species with fragmented distributions in areas affected by human impact. Their distributions will be related to patterns of natural and artificial ecosystem fragmentation; by means of relationships that will need to be modelled mathematically and incorporated into the mapping process.

Data Limitations

Implementing this approach in practice will encounter a number of obstacles. One of these is the severe lack of spatial data on individual species and genus distributions, largely due to the paucity of spatial information accompanying botanical collections and the huge number of species and genera in the tropics.

Another obstacle is collection bias. Some species may appear to be concentrated in certain areas, but only because these were visited by collecting expeditions and others were not, perhaps because the areas are close to cities or long-established research sites (Nelson *et al.* 1990). It is essential to compensate for this bias. For example, a good starting point would be to build spatial computer models of species distributions over their potential natural ranges, using maps of basic environmental data (Clinebell 1993, Phillips *et al.* 1994). Even better would be to supplement this by superimposing individual species distributions with the ecosystem diversity layer.

CONCLUSIONS

This paper has proposed that one way to overcome the many obstacles which impede the mapping of biodiversity as a whole is to simply accept that it is a multi-dimensional phenomenon comprising various primary information layers. If necessary, these can be combined to give various derived synthetic information layers as appropriate for particular purposes.

Until now, the only way to map biodiversity over large areas has been in terms of the variation in species density, or the density of endemic species. This paper has argued that this is a rather simplistic approach, and should be superseded by one which maps the spatial heterogeneity of all species, applying the same fragmentation index to both endemic species and species with wider but fragmented distributions.

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Chapter
24

ASSESSING PRIORITY AREAS FOR BIODIVERSITY AND PROTECTED AREAS NETWORKS

C.R. Margules[1] and I.J. Kitching[2]

INTRODUCTION

This paper is a brief review of a large body of scientific work by many colleagues, principally, and in alphabetical order, D.P. Faith, C.J. Humphries, C.R. Margules, A.O. Nicholls, R.L. Pressey, A.G. Rebelo, R.I. Vane-Wright and PH. Williams. A more thorough treatment of the entire field of priority areas analysis will be provided in a forthcoming book, edited by C. J. Humphries, C.R. Margules, R.L. Pressey and R.I. Vane-Wright, and to be published by Oxford University Press.

PRIORITY AREAS FOR BIODIVERSITY

Biodiversity priority areas are defined as a set of areas within a prescribed geographical region that together encompass all, or as much as possible, of the biodiversity of that region. They are so-called because they should receive priority

1 CSIRO Division of Wildlife and Ecology, P.0. Box 84, Lyneham, A.C.T. 2602, Australia.

2 Biogeography and Conservation Laboratory, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, Great Britain.

attention for protection and/or appropriate management. Such areas will not in themselves be sufficient to ensure the long term maintenance of biodiversity, but they should form the core of conservation plans for biodiversity protection.

To achieve the goal of identifying priority areas, there must be methods for measuring biodiversity, determining appropriate levels of representation and a cost-effective means of allocating available resources to secure it. The objective of this paper is to overview methods for deriving explicit statements about the relative contribution of different areas, both individually and in combination. These methods provide for maximum flexibility, for it is recognized that there are competing land uses and that these can and do impose severe limitations upon biodiversity protection. However, it is also accepted that there are areas that are indispensable if full representation is to be achieved, and such areas can also be recognized by application of these methods.

Attributes of organisms, the currency of biological diversity, are the characters that confer variety among taxa and hence govern their functional interactions. Protecting these attributes has been described as an exercise in maximising option value (e.g. IUCN/UNEP/WWF 1980, Faith 1994). However, the number of potential attributes of all taxa is phenomenal and to all intents and purposes unknowable. Yet the goal of biodiversity conservation is to preserve this variety. In theory, the pattern of phylogenetic relationships among taxa can be used as an estimate of the distribution of their attributes. In other words, attribute diversity can be predicted from taxonomic classifications. Thus an ideal goal for biodiversity priority areas might be that they should sample and maintain populations of all of the terminal taxa (usually species) of a classification. However, this goal must be revised in view of our imperfect knowledge of terminal taxa, their phylogenetic interrelationships and geographical ranges; and inadequate management prescriptions for ensuring their continued persistence in the long term.

BIODIVERSITY SURROGATES

The search for biodiversity priority areas ideally should be based upon a knowledge of the entirety of biodiversity. Although some moves have been made to acquire such knowledge (e.g. the all-taxon biodiversity inventories of Janzen 1993), the task of discovering, naming and determining the systematic relationships of all species is daunting. Complete inventories remain an impracticable option for most areas for the foreseeable future. However, changes in land use continue and so some type of biodiversity surrogate is required. Three kinds of surrogates are

realistically available: a subset of species or other taxa; ecological assemblages; and environmental variables.

Species are the usual units with which biodiversity is measured (Vane-Wright 1992). Higher taxa (genera, families) may also be used provided that a relationship can be established between the distributional patterns of the higher taxa and those of the species that they contain (Williams and Gaston 1994). Higher taxa are also cheaper and quicker to survey and identify. The search in the past has been for so-called "indicator taxa", small groups of species or other taxa that would act as general biodiversity predictors. Beccaloni and Gaston (in press) demonstrated that butterfly species richness at forest sites in the neotropics could be accurately predicted if the total number of species of the subfamily Ithomiinae was known. Nevertheless, it is clear that there is no such thing as a single indicator taxon that can accurately predict overall species richness for all groups at all sites. Kremen (1992) proposed "target taxon" for a group that could be demonstrated to be a better than average indicator of a wider range of biodiversity. We would also argue in favour of "focal taxa" (Ryti 1992), which are those about which we have good information and are taxonomically tractable in the short-term. Roger Kitching favours "predictor sets", a set of groups which, when summed, would approximate overall biodiversity. However, there is little evidence that any subset of taxa can fully or completely represent biodiversity as a whole (e.g. Prendergast *et al.* 1993, Williams and Gaston 1994).

An assemblage is a more generalized and heterogeneous entity than a taxon, and can be one of a number of ill-defined classifications, such as community, association, habitat type, ecosystem, etc. Assemblages can be derived subjectively by using a small number of dominant or prominent species or they can result from a numerical pattern analysis of field records of the locations of species. Assemblages represent various combinations of species and also include an element of their interactions. As such, they contain more ecological complexity than species. However, being more inclusive and less well-defined entities than species and other taxa, assemblages are yet further removed from the attributes of taxa. Furthermore, affording protection to an area as a means to representing an assemblage will probably miss some species (Pressey and Logan 1994), and some ecological complexity because it will be difficult to determine whether a given subset of an assemblage is representative of the whole.

Environments, a generic term covering land classifications based upon physical and climatic characteristics (with or without a biotic component), are even more remote from attributes. There is strong theoretical support for the use of

environments as biodiversity surrogates (Margules and Austin 1994). A network of priority areas designed to represent environments may encompass both unknown species and unknown distributional components of known species. Furthermore, environmental data are more widely available, with a greater consistency and detail across broad geographical areas, than unbiased biological data. However, environments suffer from similar drawbacks to assemblages regarding what is adequate representation, while the relationships between environmental variables and the distribution patterns of taxa are often vague and difficult to quantify. It is always possible that some species require an unrecognised combination of environmental variables (Pressey and Logan 1994).

Given the present limitations on knowledge and resources and the goal of adequate representation of each surrogate, it is likely that some combination of surrogates will be required. Whatever, the end result should be a data set of the chosen biodiversity surrogates in the form of maps, or stored electronically in a form suitable for mapping. It is these data, analysed using the methods summarized below, that can be used to identify biodiversity priority areas. Because species are surrogates frequently employed in biodiversity assessments, the following discussion will be simplified by using "species" instead of "attributes" (or "taxa", "assemblages", "ecosystems", etc.).

IDENTIFYING PRIORITY AREAS FOR BIODIVERSITY CONSERVATION

The methods for identifying biodiversity priority areas should be both explicit and efficient. Efficiency is necessary because the amount of land and water realistically available for the conservation of biodiversity is limited and there is a real possibility that this maximum limit (whatever it is) will be reached before biodiversity is adequately represented. The methods must be explicit in order that results are repeatable through independent verification, and hence networks of priority areas can be more readily justified and defended. The methods endorsed here are based upon four principles: complementarity, irreplaceability, vulnerability and viability.

The selection of biodiversity priority areas must proceed from the specifically stated goal of representing all species of the study set. It follows from this that each new area added to an existing network should contribute species not yet represented in that network (providing that complete representation has not yet been established). This common sense observation reflects the principle of complementarity. Priority areas should complement one another in the species they con-

tain, not just contribute repeats of species found in areas already acquired. It follows from this that the area thatcontributes most towards the goal of complete representation may not necessarily be one of the originally richest areas. This is why scoring and ranking procedures, and procedures that allocate high value to species richness regardless of the identities of those species are often so highly inefficient (Pressey and Nicholls 1989). They fail to take account of species turnover from area to area. Complementarity is vital because it results in efficient representation of species and consequently leads to the efficient allocation and use of often limited conservation resources.

Simply identifying a set of biodiversity priority areas, however, is not sufficient, as all sites within that set are not equal. Some sites are irreplaceable in that they contain species that are not represented in any other site within the set. If these sites were lost, they would compromise the goal of complete representation. There are two types of irreplaceable site. The first, termed globally irreplaceable, comprises those sites containing strictly endemic species. The loss of such sites would result in the extinction of those species in the wild. Goal irreplaceable sites are sites that could be replaced but only by substituting them with two or more additional sites. The loss of goal-irreplaceable sites would lead to a less efficient solution and would thus compromise the goal. The identification of irreplaceable sites is key to the design of efficient protected areas networks. Irreplaceable sites are not negotiable if the goal of representing all species is to be achieved. Their future is a matter of policy, not planning. They form the core around which such networks should be designed.

All other sites within the set of priority areas are termed flexible. A flexible site can be substituted by another without compromising the goal. Flexibility refers to the various spatial arrangements of priority areas that are available to achieve the goal. All flexible sites are negotiable. They provide opportunities for trade-offs with competing uses.

Once a set of biodiversity priority areas has been identified, the question then becomes one of establishing priorities for action within that set. Some species are more vulnerable than others to the effects of the various threats, natural and man-made, that impinge upon them. In some cases, the threats are quantifiable and this information can be used to set priorities for action. In addition, because the resources available for conservation planning are limited, not all areas of the world can be dealt with equally or at the same time. Assessments of vulnerability can aid in the initial selection of places where the identification of sets of priority areas is most pressing.

APPLICATION OF WORLDMAP TO OBTAIN SET OF PRIORITY AREAS

A number of heuristic algorithms that incorporate complementarity to identify irreplaceable and flexible sites have been developed (e.g. Kirkpatrick 1983, Margules *et al.* 1988, Margules 1989, Pressey and Nicholls 1989, Rebelo and Siegfried 1992, Nicholls and Margules 1993). WORLDMAP (Williams 1994) also uses heuristic algorithms to implement three of the most important elements for measuring and assessing biodiversity: taxon richness, character diversity and complementarity. Data files are created by entering the names of the taxa and a clade code (Vane-Wright *et al.* 1994) to identify their positions in the cladogram. Distributional records are then mapped onto individually designed map grids. Three measures of biodiversity are included: species richness, character richness and character combination, while a measure of range-size rarity ("endemism") is also available. Further details of these measures can be found in Williams (1994) and Williams (in press). Sets of priority areas can then be determined by using a heuristic 'near-minimum'set option. There is a further option included at this stage for selecting the minimum number of populations of each taxon to be represented, ranging from 1 to 10.

WORLDMAP proceeds by first selecting the globally irreplaceable areas, that is those that contain taxa with more restricted distributions than the representation goal. Other areas are then added in sequence so as to maximize the complementary endemism score at each step, selecting preferentially those areas with narrowly distributed taxa so as to find a near-minimum set of areas. Some of these areas will be goal-irreplaceable in that they contain unique elements of biodiversity with regard to the near-minimum set. The remaining areas are flexible. The term "near-minimum" is used because the procedure employed is heuristic. As such, it only examines a subset of all possible results and cannot guarantee to find a global minimum set or sets.

The near-minimum set is then checked for redundant areas before being prioritized using one of two procedures. The first method re-orders the areas by their overall taxon richness score, without regard for complementarity or tie-breaking. The second, used in single replicate analyses only, re-sequences the areas using one of the measures of biodiversity or by endemism, with complementarity. The results are then mapped onto the screen, with irreplaceable areas highlighted. Flexible and other types of area are distinguished using other colours.

ASSESSING THE EFFICIENCY OF AN EXISTING RESERVE NETWORK

The procedure described above identifies a set of priority areas that most efficient-

ly represents the chosen set of taxa. This set could be used as the basis for an idealized network of protected areas. But there are numerous constraints on the establishment of an ideal system. Among these are preexisting networks of protected areas, upon which future expansion and development must, in general, build. Such networks can be entered into WORLDMAP and used to "seed" an analysis. Such a constrained analysis can assess the efficiency of the network in achieving the stated goal and also identify the additional areas required to achieve a given level of representation of biodiversity.

When such analyses are performed, it is often found that existing protected areas networks are inefficient (Pressey 1994, Pressey and Tully 1994). In the past, parks and sanctuaries, areas currently interpreted as affording protection to biodiversity, have been set aside for numerous reasons, most of which have little or nothing to do with representing biodiversity. The very first national parks (e.g. Yellowstone National Park in the USA and Royal National Park near Sydney, Australia) were designated primarily as areas of outstanding natural beauty and intended as places of recreation and enjoyment for the general populace. A major function of national parks in Thailand continues to be tourism (Gray *et al.* 1991) and this can lead to conflicts of interest between development and biodiversity conservation. Reserves may also be designated to protect rare or spectacular species considered to be of particular importance. With such a limited aim, such protected areas may succeed very well. But the most common reason for a particular' area of land to be offered for wildlife conservation is that it is considered to be of little use for human habitation or commercial exploitation. Protected areas tend to be placed where they will cause least interference with extractive land uses (Runte 1979, Kirkpatrick 1987, Pressey and Tully 1994). In other words, they are chosen for what they are not, rather than what they are. Even when protected areas are designated because they are considered to include relatively untouched examples of particular assemblages or ecosystems, there is usually very little information available on just what and how much biodiversity is contained within them. Data are generally restricted to large vertebrates and selected plant groups. Furthermore, rarely is it considered to what extent, if any, a new protected area adds additional biodiversity to the existing reserve network - i.e. complementarity is not considered.

CONCLUSIONS

Overall, selection of protected areas has frequently been opportunistic and *ad hoc.* In some instances, site selection has been undertaken in response to a perceived,

although seldom quantified, external threat. Only rarely has a protected area been established specifically to represent biodiversity. This has had several consequences for the conservation of biodiversity as a whole. First, many elements of biodiversity (taxa, assemblages, ecosystems) that are most in need of conservation are not yet protected. As a result, the limited resources available for conservation are being used less efficiently than might otherwise be the case. Many newly gazetted protected areas simply add more examples of biodiversity that are already represented within protected areas. They may add little to the biodiversity complement already present in the existing reserve network (Harper and Hawksworth, 1994). There is a ceiling on the total area that will be available for biodiversity conservation. If future additions to networks do not take account of complimentarity, then this limit may well be reached before all, or even a significant proportion of biodiversity has been accounted for in the reserve network. Finally, there is now an unbalanced representation of biodiversity within existing reserves (Leader-Williams *et al.* 1990, Pressey *et al.* 1993).

Thus, if the goal is to represent all elements of biodiversity adequately, then the existing methods for selecting and designating protected areas must be reassessed. However, we must be careful not to judge past actions by our new standards. We should employ the gift of hindsight to ensure that future decisions are made on a more informed basis. The methods and procedures outlined above, which will be substantially elaborated upon by Humphries *et al.* (in prep.), are designed to remedy this situation.

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Chapter

25

SCANNED, ZAPPED, TIMED, AND DIGITIZED! ADVANCED TECHNOLOGIES FOR MEASURING AND MONITORING VEGETATION DIVERSITY

H. Gyde Lund[1], David L. Evans[2] and David S. Linden[3]

INTRODUCTION

The Convention on Biodiversity, opened for signature at the 1992 United Nations Conference on Environmental Development, marked a commitment by all the nations of the world to conserve biological diversity, to sustain biological resources, and to share the benefits arising from their use. Human subsistence depends on vegetation either directly or indirectly for food, shelter, fuel, and health. Hence, vegetation biodiversity surveys are becoming increasingly important at all levels of interest. Measuring, monitoring and maintaining vegetation diversity is necessary to the survival of humankind.

Of the many ways to describe vegetation diversity, the most common are extent, structure, composition, biomass/production, and condition. For this paper:

1 USDA Forest Service, Washington, D.C., USA.
2 USDA Forest Service, Starkville, MS, USA.
3 Colorado State University, Fort Collins, CO, USA.

Extent refers to vegetation area, spatial arrangement, and horizontal diversity. We often express measures of extent in terms of area, amount of edge (length), fragmentation, etc. Fragmentation is the deforested area plus an edge effect of 1 km; all isolated forest areas surrounded by deforestation with an area of 100 sq. km and all roads with an edge effect of 0.5 km (Tucker and Skole 1992).

Structure deals with vertical diversity - i.e. whether a forest stand is multi-layered or not. Units of measure usually include vegetation heights and profiles.

Composition refers to species richness. We usually describe composition by species number per unit area.

Biomass is vegetation weight, volume, or mass per unit area. When measured over time, it is a production gauge.

Condition is a measure of health and is an interpretation derived from a desired or preconceived ideal situation. Measurement of condition requires the use of monitoring and permanent plots.

CONCEPTS IN VEGETATION DATA COLLECTION

While we may want information on vegetation diversity nearly everywhere, we cannot measure it because of time and costs. Basically, we want to maximize the vegetal information we can extract from remote sensing and reduce the amount of time we have to spend in the field. To do this we use remote sensing coupled with sampling. Through sampling we measure or observe a small part of the population with the assumption that our observations represent the entire population.

There are two general approaches to sampling - one is to purposefully select where we will make our observations. This is subjective sampling. The other is to use a more random or unbiased method for selecting sample locations, or statistical sampling. Generally, researchers prefer statistical sampling to subjective sampling. With statistical sampling, we can calculate the reliability of the estimates generated, whereas we cannot do this with subjective sampling. On the other hand, subjective sampling is quicker and less costly than statistical sampling and is now gaining some acceptance in the scientific community. Many people feel it is better to have some information, subjective as it may be, rather than none.

No matter what kind of sampling one uses, some form of stratification is desirable in advance of sample selection. Stratification is the dividing of the population into relatively homogeneous classes. Through stratification, one can concentrate

samples in higher interest areas - such as forest lands versus agricultural lands. Thus, stratification is more efficient than not stratifying.

Common themes used for stratification include land cover, vegetation type, soils, topography (elevation and landform), and land use. Land cover and vegetation type are the most common themes used for assessing vegetation. Stratification by land cover and vegetation type requires a quick look at all the land areas of interest. We often use remote sensing from satellites and aircraft for this process.

Sample-based remote sensing from satellites, aircraft (including drones (McGeer and Holland 1993)), and the field can help in collecting data on vegetal composition, structure, biomass, and condition. Wall-to-wall remote sensing is then used to expand the sampled data to the inventory unit as a whole.

Remote sensing is available from various sources such as mineral and oil companies, military and intelligence departments, survey departments, census bureaux, utility and electric companies, highway departments, natural resource agencies, donor organizations, space agencies, and universities. Each may employ a variety of tools for collecting data.

TOOLS OF THE TRADE

For this paper, we separate remote sensing and associated geo-positioning instruments into scanners, zappers, and timers. Scanners are passive remote sensing systems that pick up energy that originates from a source away from the sensor. Examples are photography, videography, thermal imagery, etc.Zappers are active remote sensing systems that send out an energy pulse that reflects back from the target area. Examples are synthetic aperture radar and laser altimeters or profilers. Timers are instruments that receive time signals from a constellation of earth-orbiting satellites. These receivers are global positioning system (GPS) units that we use to determine our geographic location.

SCANNED!

To determine vegetal cover extent, we generally use remote sensing. The sensors may be mounted on a flying platform (helicopters, fixed-winged aircraft, satellites) or hand-held and used on the ground. With some sensors, especially those that operate in several parts of the spectrum, we can get an indication of composition and condition. Imagery acquired in different seasons aids in species identifica-

tion, especially in temperate areas. To determine structure and biomass, we often need high-resolution, stereo remote sensing coverage. Generally, the higher the resolution, the more costly is the imagery.

We include optical and electro-optical sensors in our discussion of scanners.

A. Optical systems are those that one thinks of as traditional cameras.
   1. Aerial photography at scales from 1:12,000 to 1:24,000 is the most widely-used form of optical remote sensing imagery for vegetation surveys in the United States. Modern camera systems and films can provide high-resolution imagery over a broad scale-range. Aerial photographic systems record reflected energy in the visible and near infrared portions of the spectrum. Factors that define aerial photography utility include: the coverage, mission date and time, the scale, film emulsion, the camera format, the lens focal length, and the atmospheric conditions during the mission.
   2. Hand-held photography Ground photos, taken at sample plot are useful for documenting conditions that are difficult to quantify on a field form. Vegetation attributes that can be interpreted from ground photography include species composition, structure, biomass, and health or condition. Takao (1992) has developed a camera system that can take stereo photographs in a 360-degree circle around the plot centre. From stereo photographs, one can make detailed measurements of the vegetation. As with other forms of remote sensing, periodic photographs taken at the same location provide a good means of monitoring changes in vegetation (Tappan *et al.* 1994).

B. Multi-spectral or electro-optical systems can be configured to get information from the ultraviolet through the visible, near, middle and thermal infrared to the microwave portion of the spectrum. The middle and thermal infrared portions of the spectrum are important in identifying and assessing the condition of vegetation. Sensing in several parts of the spectrum classes can help in vegetation life form and sometimes species identification (Lillesand and Keifer 1979).

There are two classes of electro-optical sensors: non-imaging and imaging. Non-imaging sensors acquire individual measurements rather than an array of measurements that form an image. Spectrometers mounted on aircraft or bucket trucks can acquire reflectance measurements from scene elements (vegetation, water bodies, etc.) to calibrate airborne and satellite imagery or develop reference data.

These electro-optical systems are not limited by the sensitivity of chemical reactions that occur when reflected light strikes the film in an aerial camera to create an image. Information from electro-optical systems may be recorded in analog or digital format. Video systems capture data in analog form, but most electro-optical systems convert the incoming energy directly to digital data. Although generally of lower spatial resolution than aerial photography, electro-optical sensor data have advantages for natural resource applications. Image analysts can directly manipulate the digital imagery using computer-based systems to rectify, classify, enhance, and display the imagery (Robinson and Dewitt 1983 and Norwood and Lansing 1983).

1. Satellite based systems.Digital imagery from remote sensors carried aboard earth-orbiting satellites provides extensive area coverage.

Meteorological or weather satellites provide information for specialized natural resource applications. Geo-synchronous satellites provide synoptic low resolution and hourly coverage. Imagery from the Advanced High Resolution Radiometer (AVHRR) carried aboard the United States National Oceanic and Atmospheric Administration (NOAA) series of satellites has been used in assessing forest fuel condition in Western United States and for developing national forest cover maps for both the U.S.A. and Mexico (Eggen-McIntosh and Zhu 1992, Evans *et al*. 1992, Zhu 1994, and Zhu and Evans 1994). AVHRR imagery has a nominal resolution of 1.1 kilometre at nadir, and daily coverage. A "scene" covers an approximate area of 1750 x 6000 km.

Multi-date AVHRR data are valuable for basic forest/non-forest mapping, landcover change detection, and trend documentation in vegetation conditions, especially in the temperate zones. We can get AVHRR data daily and therefore may be able to develop near-cloud-free composites based on several consecutive days of imagery. Furthermore, we can use these products, compiled over a one year interval, to identify phenological vegetation characteristics in development of spectral classifications for monitoring programs.

Development of an AVHRR-based vegetation cover map uses digital processing techniques such as those described by Loveland *et al*. (1991) and Zhu and Evans (1992 and 1994). Briefly, these procedures include: 1) development of cloud-free, multi-date composites of the AVHRR data, 2) estimation of percent land-cover components within AVHRR pixels, 3) classification of the AVHRR data into land-cover categories, and 4) verification of the products by use of high-resolution satellite (Landsat and SPOT) and other ancillary data (aerial photography, radar).

The United States Landsat and French SPOT (Systeme Probatoire d'Observation de la Terre) satellites provide easily accessible imagery with global coverage. Circling the earth in near-polar sunsynchronous orbits, the sensors aboard these satellites acquire imagery at a consistent solar time during each daylight pass. Repeat vertical coverage is available from a single Landsat satellite on an approximate 16 day cycle. When multiple satellites in the same series are operating, the repeat frequency of vertical coverage is proportionally increased.

The current Landsat satellites (4 and 5) carry the Multi-spectral Scanner (MSS) and the Thematic Mapper (TM). Both instruments are mechanical scanners that employ a rotating mirror to acquire data in the cross track direction. A full Landsat scene covers a land area of 185 by 185 kilometers. The Thematic Mapper has a resolution of 30 meters in six bands of reflected energy extending from the blue portion of the spectrum to the middle infrared and an emissive thermal infrared band with approximately 120 meters resolution. Thematic Mapper data have been available since 1982. There have been many successful examples of using Landsat TM for mapping vegetative cover, forest condition, and type. The mapping of old growth vegetation, forest type and structure in the Pacific Northwest Region of the United States is one example (Steffenson and Wilson 1993). Landsat TM has also been used to monitor subtle changes over time in vegetation such as that reported on the Mark Twain National Forest in the U.S. (Platt *et al.* 1993).

The Multi-spectral Scanner has an 80-meter resolution in four spectral bands in the green, red, and near-infrared portions of the spectrum. Multi-spectral scanner data have been available since 1972. The current Landsat 5 is the last satellite in the series to carry a multi-spectral scanner instrument. Although of significantly lower resolution than the Thematic Mapper, MSS data are available for a span of more than 20 years starting in 1972, making the data especially suitable for evaluating landscape change.

The French SPOT satellites carry two High Resolution Visible (HRV) instruments. Unlike the instruments carried aboard the Landsat satellites, the HRVs are solid state instruments that image the entire swath of the flight path simultaneously. Each of these sensors aboard SPOT 1, 2 (in orbit) and 3 can acquire imagery in the green, red, and near-infrared portions of the spectrum. SPOT 4, scheduled for launch in the middle of the decade, will add a mid-infrared band to the SPOT HRVs. A full SPOT scene covers a ground area of 60 by 60 kilometers. SPOT multi-spectral imagery has a resolution of 20 meters. The SPOT HRVs also can get panchromatic imagery with ten meter resolution. The capability to point these sensors off-nadir, parallel to the spacecraft ground track, permits the acquisition of additional ima-

gery of previous satellite overpasses and stereo imagery.

Table 1 provides broad guidelines to the various wavelengths and applications available using common earth-observing satellites. Thanks to the end of the Cold War, satellite based imagery with resolution of 3 meters or finer is becoming available (McLucas 1994). In addition, several special purpose satellite systems are being developed including one for forest applications in the tropics (Looyen *et al.* 1994).

Advanced Very High Resolution Radiometer (AVHRR) - resolution 1 & 4 kilometers. Bands or channels 1 and 2 used for vegetation vigour, mapping, and normalized difference vegetation index (NDVI).

Band	Wavelength	Application
1	0.55-0.68	Cloud mapping
2	0.725-1.0	Delineating land/ water and melting/ non melting snow, ice floes
3	3.55-3.93	Thermal mapping in cloudy areas
4	10.5-11.3	Sea surface temperature measurement
5	11.5--12.5	Removal of radiant energy contribution of water vapour.

Landsat Thematic Mapper (TM) - 30 meter resolution

Band	Wavelength	Application
1	0.45-0.52	Coastal water mapping, bathymetric mapping of shallow water, soil/vegetation differentiation, deciduous/conifer differentiation and cultural feature identification
2	0.52-0.60	Measuring green reflectance by healthy vegetation, vigour assessment and cultural feature identification, discriminating of vegetation types
3	0.63-0.69	Chlorophyll absorption for plant species differentiation
4	0.76-0.90	Biomass surveys, water delineation, vegetation type assessment, vigour, soil moisture
5	1.55-1.75	Vegetation moisture measurement, snow/cloud differentiation, soil moisture measurement. This band penetrates through thin clouds

6	10.4-12.5	Plant heat stress management, vegetation stress analysis, soil moisture discrimination and thermal mapping applications
7	2.08-2.35	Hydrothermal mapping, mineral and rock type mapping, assessing vegetation moisture content.

Satellite Probatoire d'Observation de la Terre (SPOT)

Multi-spectral - 20 meter resolution

Band	Wavelength	Application
1	0.50-0.59	Green band. Peak vegetation discrimination and vigour assessment
2	0.61-0.68	Red band. Chlorophyll absorption region aiding in species differentiation and culture identification
3	0.79-0.89	Near IR. Vegetation typing, estimating vigour and biomass content, delineating water bodies and soil moisture

Panchromatic 10 meter resolution

Band	Wavelength	Application
1	0.51-0.73	Updating existing maps and orthophoto maps, monitoring and change detection of features, updating land cover and forest inventory maps.

Table 1: Guide to and applications of various wavelengths available in common earth-observing satellites. All wavelength measurements are in microns.

2. Videography - Videography, especially airborne video, is a relatively recent addition to the remote sensing tools available for natural resource applications. Videography uses video cameras and cassettes that one might normally find for home use. The equipment and tapes are inexpensive and require no processing.

Aerial video is an inexpensive and effective way to image forest conditions for monitoring and measurement activities. Video systems are less sensitive to exposure problems of aerial imagery acquisition common to film camera systems. The resulting imagery is also captured in a form suitable for use on computers. We can use aerial video for visualization and possibly for measurements of the dominant canopy surface.

We also can use aerial video for detailed analysis of forest attributes (Evans and Beltz 1992). One scheme could employ video as a sampling tool to assess large areas for specific information associated with forest health. We can link this type of survey to information collected at field monitoring plots. Ground plots would be established at a uniform density across all forest lands. These field plots would be geo-referenced with global positioning system (GPS) units. We would then use the plot coordinates for video mission planning and execution to ensure accurate overflights of the field locations.

Video imagery would provide inexpensive and fairly detailed information about the canopy structure for field plots and all areas along transects between the plots. Stereo pairs from video can be used to generate 3-D anaglyphs for canopy characteristics visualization. One also can measure tree and stand attributes using digital video and photogrammetric techniques. Information derived from these analysis techniques can help researchers evaluate current conditions and changes in the forest canopy over time.

Video systems have lower resolutions than comparable photographic systems and currently lack calibration necessary for precision photogrammetric applications. They are well suited for many natural resource applications requiring sample or small area coverage. They are also cost effective for locating features such as isolated groups of insect-damaged trees within a larger survey area. System operators can evaluate video data during acquisition and change mission parameters as necessary. Improvements in camera design and the availability of higher definition recording formats such as Super VHS and HI8 video have increased the resolution and utility for natural resource application. Image analysts can manually interpret video imagery using a high resolution monitor and a playback unit with freeze-frame capability. For enhancement and geo-referencing, the analog data in individual video frames can be captured as digital data using a video "framegrabber." The low cost of video systems make them a good candidate for many monitoring applications (Myhre *et al.* 1991).

Airborne electrooptical remote sensing systems cover a broad range of capabilities. Airborne systems support working requirements and serve as test beds to test new sensor designs. Nixon *et al.* (1985) showed the utility of multiband videography to assess vegetal condition and species.

One must recognize that the data from many current airborne digital remote sensing systems are difficult and expensive to register to ground coordinates. In addition, specialized software and knowledge may be necessary to extract useful information from these data. Nevertheless, airborne systems have an extremely

wide range of capabilities and the potential for providing solutions to many unique requirements. Table 2 provides some comparative uses of satellite/airborne systems.

Data Source	AVHRR	Landsat		SPOT		Photography		Video
		MSS	TM	MS	PAN	1:24K	1:12K	
Basal Area	0	3bc	2-3bc	2-3bc	0	2-3b	1-2b	1-2b
Canopy Cover	3b	2-3bc	1-3bc	1-3bc	0	1-3b	1-2b	1-2b
DBH (Size Class)	0	2-3bc	1-3bc	1-3bc	0	1-3b	1-2b	1-2b
Species	0	3abc	2-3abc	2-3abc	0	1-3b	1-2b	1-2b
Existing Vegetation	3b	2-3abc	1-3abc	1-3abc	0	1-3b	1-2b	1-2b
Vegetation Height	0	0	0	0	0	1-3	1-2	1-2b
Vegetation Density	3b	2-3c	1-3c	1-3c	1-3c	1-3	1-2	1-2
Snag Condition	0	0	0	0	0	2-3	1-2	1-2
Forest/Non Forest	3b	1-3c	1-3	1-3c	1-3c	1-3	1-2	1-2
Hardwood/Conifer	3b	1-3bc	1-3c	1-3c	1-3c	1-3	1-2	1-2
Structure (Forest)	0	0	2-3bc	2-3bc	1-3bc	2-3	1-2	1-2
Insect/Disease Occ.	0	3b	2-3b	1-3b	2-3b	2-3b	1-2b	1-2b
Fire Occurrence	0	2-3b	1-3b	1-3b	1-3b	1-3	1-2	1-2
Forage Production	3ab	2-3bc	1-3bc	1-3b	2-3b	2-3b	1-2b	1-2b
Range Condition	3ab	2-3bc	1-3bc	1-3b	2-3b	2-3b	1-2b	1-2b
Range Cover Type	0	3bc	2-3bc	2-3b	0	2-3b	1-2b	1-2b

Table 2: Recommended uses for remotely sensed data sources for vegetation (Lachowski 1990).

Where recommended use is:

0. Not recommended for creation of data layer.
1. Recommended for small area project where great detail is required (e.g., riparian mapping).
2. Recommended for medium area projects where broader classifications are useful (e.g., district or forest).
3. Recommended for very large area mapping projects where little detail is needed (e.g., state or country).

a. Used with terrain data (slope, aspect, elevation).
b. Used with field collected data.
c. Used with photointerpretation.

3. Digital Cameras -The use of digital cameras is very new in forestry applications. The camera records images on a hard disk integrated with the camera. The image is transferred via a SCSI or parallel connection to the computer or transferred directly to the computer's hard disk by the same connections. Preliminary results by Bobbe *et al.* (1994) show that digital camera systems mounted in aerial platforms can provide good quality imagery under a variety of conditions. Digitized photographs from the ground can be used in fractal analysis to help evaluate the health and vegetation vigour (Mizoue and Masutani 1993).

ZAPPED!

Active remote sensing systems are those where the energy recorded initiates from the sensor. Zappers include radar and lasers. Radar can provide area coverage whereas lasers provide point data.

A. Radar. Radar is an active remote sensor using reflected radio signals. The all-weather capability of synthetic aperture radar (SAR) systems to collect information makes them ideal for use in tropical forest regions with frequent cloud coverage. Radar imagery can be collected from satellite and aircraft platforms. The European Space Agency's ERS-1 remote sensing satellite and the proposed Canadian RADARSAT have view areas of 50 x 50 to 500 x 500 km. RADARSAT will have a ground resolution of about 25 x 28 m and will be useful for monitoring severe changes in forest cover for areas > 100 ha.

Airborne SAR can be used to complement Landsat TM and SPOT for information on geomorphology and vegetation texture, particularly if stereo data are acquired. It is also useful for detecting changes in vegetation at larger scales (Ahem 1994). Short wavelength radar may penetrate upper vegetation layers and may provide information about forest understory diversity and the ground. Radar also may provide forest volume estimates (Wu 1990) and biomass assessments (Dobson *et al.* 1992 and Hussin *et al.* 1992). However, these predictive measurements may be dependent on terrain characteristics (van Zyl 1993). Other work has demonstrated the possibility that radar imagery could have utility in species group separation (Leckie 1990).

Used in combination with aerial videography and other sensor data and ground data, radar has the potential to provide information on forest biodiversity. Aerial video and high-resolution radar can supply information at the stand and plot level for detailed forest canopy characterizations. Ideally, radar sys-

terns should be capable of collecting data in short wavelengths with the anticipated detection of multi-storied characteristics within tropical forests. An aerial video system (colour or multi-spectral) could be flown with the radar. This detailed information will be invaluable for forest health or condition monitoring.

B. Lasers. Lasers operate by sending out a short burst of light timed to determine how long the light takes to travel to a target. This time is converted into distance (Carr 1993). We use hand-held lasers to measure distances to trees and their heights. Laser profilers, mounted in aircraft, can measure vegetation heights above the terrain (Ritchie and Weltz 1992). When coupled with airborne videography and global positioning systems, vegetation structure and biomass may be determined.

TIMED!

Although they were introduced less than ten years ago to the forestry community, almost everyone is now familiar with the use of GPS receivers and satellites to decide one's position. With a GPS receiver and time signals sent from a constellation of earth-orbiting satellites, we can determine our position to within 30 to 100 meters at any location on our planet. With two receivers and with one located on a known location (base station), we can determine our location to within centimetres using differential calculations (Hurn 1989).

There have been several articles in the past two years dealing with GPS and aerial videography integration. Evans (1992) demonstrated the usefulness of GPS with aerial videography and recommended the use of a gyro-stabilized camera mount to minimize the effect of aircraft attitude variations. Bobbe (1992) discusses the use of real-time differential GPS with airborne videography and discusses how the GPS data can be used to mosaic and geometrically correct digitized video data using manual methods. Bobbe *et al.* (1993) discuss similar procedures using a multi-spectral video camera. Graham (1993) discusses how Society of Motion Picture and Television Engineers (SMPTE) time coding is used to synchronize the GPS and video data. SMPTE time codes allow digital data to be stored on the second audio track of a video tape. One time code is stored for each frame. Each code holds 80 bits of data: 32 bits for GPS time, 32 bits of "user" data, and 16 bits of synchronized pattern.

DIGITIZED!

Digitization refers to the placement of geographic coordinates on observations for use in a Geographic Information System (GIS). Getting data into a GIS is essential for resource modeling. As indicated above, many forms of remote sensing automatically store data in digital form.

With the evolution of GPS, the determination of coordinates provides a quick way to digitize field information so it may be entered into a GIS. GPS units, coupled with field data recorders and portable computers, tag locational information to field observations.

Using GPS receivers, it is possible to quickly and accurately register remote sensing imagery for entry into a GIS. Linden *et al.* (1993) have developed a technique for using GPS to automate the digital mosaicing process of airborne videography.

We can use analytical stereo-plotters to make precise measurements (heights, lengths, widths) of individual plants. We also can use the same instrument to digitize information for entry into a GIS. In addition, there are many types of scanners and line followers available to convert photographs and maps to digital form for entering into a GIS (Gibso *et al.* 1983).

Once data are in a GIS, species occurrence and richness may be modelled from remote sensing, topographic and climatic data (Podolsk *et al.* 1992 and Steffenson and Wilson 1993). Through a GIS and appropriate models, sample data can be extrapolated using stratification criteria for information on vegetation extent, composition, structure, biomass, and condition portrayed for the entire inventory unit.

CONCLUSIONS AND RECOMMENDATIONS

Based upon our experience and observations we have four conclusions and recommendations:

1. New technology is available to measure and monitor key vegetation diversity attributes. Large area1 extent of vegetation can be determined from satellite imagery. Seasonal and multi-spectral imagery is useful for determining overstorey composition and condition. Modelling may have to be used for understorey composition. Structure and biomass usually require some height estimates that may be obtained through stereo imagery, radar or laser profilers. Rapid updates of conditions on small areas can be done using airborne

videography or digital cameras. Global positioning units are useful in linking remote sensing and field plots with a GIS. All remote sensing efforts, however, need ground verification either for accuracy assessment or to provide information that one cannot get directly from the imagery.

We need continued research to learn the extent to which these technologies can be used in multistage or multiphase sampling schemes. Training and technical assistance in implementing the technology can be provided by equipment vendors and by agencies such as the USDA Forest Service when linked to government requests and agreements.

2. To be most effective, collection of vegetation diversity information should be a part of a regular or multi-resource inventory program. Collecting data for biodiversity and then later visiting the same area for a timber or range resource survey is needlessly wasteful. Concepts for integrating inventories are presented in Lund (1986).
3. What to measure is not so much the question as where to measure. A common understanding of just what is forest land is in itself a problem - forest land may be defined administratively, by land use or by land cover. Land cover is the most easy and most consistent attribute to detect from remote sensing However, vegetation diversity, or lack of it, is of concern on all lands - urban, agricultural, rangelands, wetlands, as well as forest lands. We recommend that all lands be inventoried and monitored for the five vegetation components discussed in this paper.
4. Measurement of vegetation diversity is not a problem how to present the information to the analyst and decision maker is. Those that design and carry out inventories should strive to collect and present data in an unbiased manner. Interpretations should be left to those for whom the inventory system was designed.

We hope that through this paper we have introduced some emerging technologies that are available for measuring and monitoring vegetation diversity. Readers are encouraged to consult the references provided in this paper for more details about specific technology.

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Many estimates suggest that the world's forests are home to more than 50% of terrestrial biodiversity, yet temperate and tropical forests face numerous threats, including agricultural and industrial expansion, climate change, non-sustainable management, and pollution. If forests and their diversity of living organisms are to be conserved, there is a need to measure and monitor biodiversity, in order that the impact of human activities and the efficacy of conservation measures can be assessed. As the concept of biodiversity covers the range of life itself, from genes to ecosystems, measurement and monitoring is extremely complicated.

This book contains 24 papers selected from among those presented at a IUFRO Symposium on the subject of "Measuring and Monitoring Biodiversity in Tropical and Temperate Forests", hosted by the Royal Forest Department of Thailand, at Chiang Mai, August 27th - September 2nd, 1994. The papers were selected to give as broad a coverage as possible of key topics, including Principles of Measuring and Monitoring Biodiversity (8 papers), Genetic Diversity (6 papers), Species and Ecosystem Diversity (5 papers), and Methodology (5 papers). Forest trees are the subjects of many papers, but also included are papers dealing with diversity of arthropods, microfungi, birds and butterflies, and gibbons, and others dealing with the entire range of biodiversity.

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