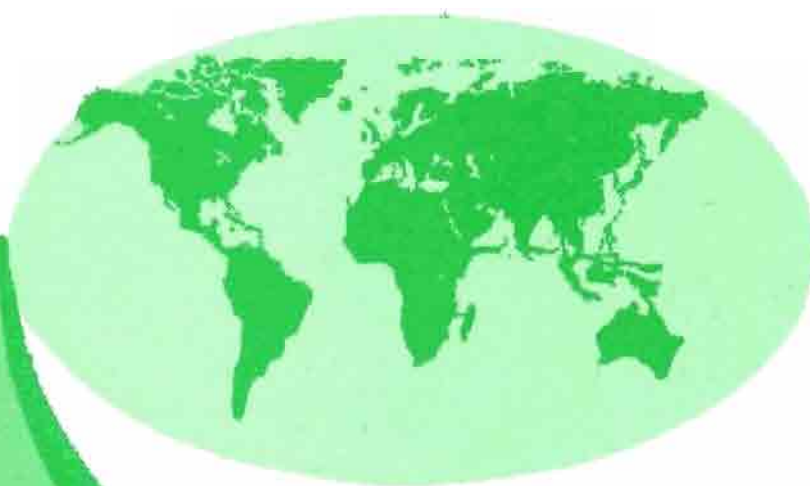


IUBS

SYMBIOSPHERE
Ecological Complexity for Promoting
Biodiversity

Edited by
H. Kawanabe, T. Ohgushi & M. Higashi



**Biology
International**

Special Issue N° 29

SYMBIOSPHERE

Ecological Complexity for Promoting Biodiversity

Report of an international workshop held
on 17-19 December 1992 in Kyoto, Japan

Edited by

Hiroya Kawanabe
Center for Ecological Research, Kyoto University,
Shimosakamoto, Otsu, 520-01 Japan

Takayuki Ohgushi
Institute of Low Temperature Science, Hokkaido University,
Sapporo, 060 Japan

Masahiko Higashi
Faculty of Science and Technology, Ryukoku University,
Seta, Otsu, 520-21 Japan

Special Issue-29
Biology International
(C) 1993 The International Union of Biological Sciences
News magazine

Table of Contents

Preface	3
SymBiosphere: Ecological Complexity for Promoting Biodiversity <i>Center for Ecological Research, Kyoto University</i>	5
Gross Difference in Community Structure between Forests and Grasslands Why are forests kept green? <i>T. Abe</i>	19
Habitat Structure and Biodiversity in the Coral Reef Areas: Ecological Process in Habitat Creation and Community Development on Microatolls of the Massive Coral <i>Porites</i> <i>M. Nishihira</i>	26
Forest Pattern along Hierarchical Habitat Gradients in East Asia <i>M. Ohsawa</i>	30
Biodiversity in The Tropics <i>D.E. Stone</i>	37
Biodiversity in Tropical Forest and Chemical Ecology <i>H. Ohgashi & K. Koshimizu</i>	48
Creation of Reserves in Tropical Forests and Researchers <i>S. Kuroda</i>	53
The Biodiversity Crisis: An Agenda for Global Research <i>N.E. Stork</i>	59
Biodiversity and Systematic Botany <i>K. Iwatsuki</i>	65
Environmental Changes and Biological Innovation in the Geologic Past <i>K. Minoura</i>	68
Evaluation of Biodiversity of Soil Microbial Community <i>K. Yokoyama</i>	74
Molecular Genetic Approach to Microbial Diversity (5S rRNA, replication origin, RNA polymerase, two component system) <i>H. Yoshikawa</i>	79
Providing a Scientific Backbone to Biodiversity <i>F. di Castri</i>	85

Preface

The "Earth Summit" held in Rio in June 1992 brought the global issue of biodiversity to world public attention. There is no doubt that the "biodiversity crisis " is real and one of the most serious impending environmental problems for the global community. On the other hand, expectations of the great potential in material and commercial use of the unexplored world's biodiversity are rising to the extent that it has already caused a new North-South problem. Although this theme emphasizes the social aspects of the problem, biodiversity is fundamentally a problem of biology.

We do not have a good answer for even the very basic biological question of how many species reside on earth at present. It is said that the unprecedented rate of extinction of species during recent several decades is mainly due to habitat destruction by one species, that is, *Homo sapiens*. Habitat destruction also tends to reduce the genetic diversity within a species. However, we do not know exactly how many species have been irreversibly lost during say, the last 50 years, simply because there are many species that have gone extinct without ever being recorded. Much less is known about the genetic diversity of species populations. Increasingly many instances have been discovered of the diverse and fascinating forms of life and their complex intricate interactions, including symbiotic relationships and plant-animal interactions. Many of these cause the species involved to "invent," through the coevolutionary process, a variety of amazing devices and chemical products. The instances are expected to be only the "tip of the iceberg."; so much more remains to be discovered. Another important question involves the role of biodiversity within the larger context of the ecosystem of which organisms and species are constituents. The diverse niches and functions in ecosystem processes can be realized and sustained only by diverse forms of life and the complex interactions they enable. These biodiversity characteristics revealed in the ecosystem context have just begun to be understood. We know too little about biodiversity, which means many fascinating discoveries await science.

For the conservation and recovery of biodiversity in nature, it is fundamentally important to understand how biodiversity is created and how it is sustained or declines. With the thesis that ecological complexity plays a key role in promoting biodiversity, an international cooperative research project, "SymBiosphere: Ecological Complexity for Promoting Biodiversity" was proposed to, and officially approved by, IUBS. With this approval, an international workshop was held from December 17 through 19 in 1992 at Kyoto, Japan, to promote the

oposed research project. The workshop was jointly organized by three organizations: the Center for Ecological Research, Kyoto University; Scientific Research on Priority Areas (#319), Project "Symbiotic Biosphere: An Ecological Interaction Network Promoting the Coexistence of Many Species," Japanese Ministry of Education, Science and Culture; and SCOPE (Scientific Committee on Problems of the Environment) Japan.

This special issue contains the proceedings of the workshop. We acknowledge that T. P. Burns helped us in editing. We sincerely hope this special issue will bring to a broader international community of scientists the essential ideas of our research project and our rising enthusiasm on the theme of biodiversity.

An International Cooperative Research Project

SymBiosphere: Ecological Complexity for Promoting Biodiversity

Center for Ecological Research of Kyoto University

Summary

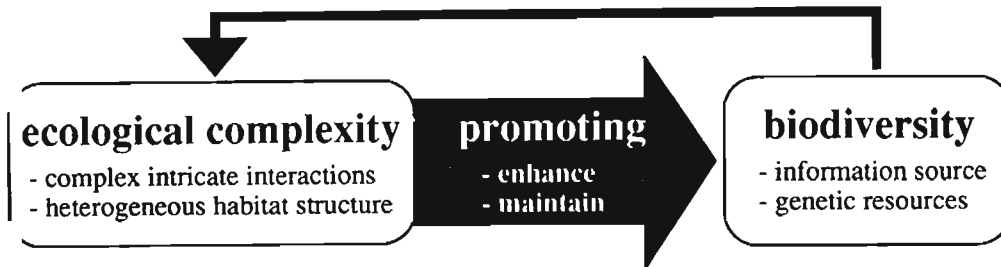
Accumulated evidence strongly suggests that ecological complexity, the complex intricate interactions among various forms of life, together with heterogeneous habitat structure, plays a key role in promoting the diversity of biological traits and functions in nature. Ecological complexity enhances biological diversity, or biodiversity, through evolutionary and biogeographic processes, whereas its degradation should quickly cause the diversity in phenotypic and genotypic traits to decline. Thus, for the conservation of biodiversity, it is not sufficient to preserve living organisms alone. In order to preserve in its vital state the biological diversity manifested in living organisms, they must be conserved in, and together with, their correct environments with sufficient ecological complexity.

The state of great biodiversity for the global biotic system (*i.e.*, Biosphere) supported by ecological complexity is here captured by the term, "symbiotic Biosphere" or "SymBiosphere" for short.

This note describes a cooperative research project aimed at intensifying, through close coordination, two distinctive but related activities: the science and the practice of conserving and restoring the ecological complexity that promotes biodiversity. The main objectives of the science are to clarify the precise relationships between ecological complexity and biodiversity, and to identify the processes and mechanisms through which ecological complexity promotes biodiversity. The practice of promoting biodiversity must be considered as an initial step of a much longer term program of conservation. Its immediate goals are to develop an operational methodology by which an objective evaluation can be made for a given system (area) in terms of the ecological complexity (*i.e.*, the degree of richness in interactions and habitat structure) pertaining to the conservation of biodiversity, and to carry out appropriate management measures that help restore and preserve the relevant ecological complexity.

Remark: The research project described here is a part of the first topic area "the ecosystem function of biodiversity" in the IUBS-SCOPE-UNESCO joint program on biodiversity called "Diversitas." Discussions on the research were initiated in a working group chaired by H. Kawanabe, the director of Center for Ecological Research, Kyoto University. This note was prepared by editing the contributions by M. Higashi, T. Kohyama, T. Ohgushi, M. Ohsawa and J. Takabayashi, who participated in the working group.

I. The rationale: what we should conserve



I-1. What is biodiversity

Biological diversity, or *biodiversity* for short, should be taken broadly as the diversity of biological traits and functions observed in nature. It is more than species diversity, it also involves a significant degree of phenotypic and genotypic diversity existing within a species. While these are both concerned with the range of traits and functions that individual organisms exhibit, there are another important sources of biological diversity: *i.e.*, sociality and symbiosis. These cooperative relations (interactions) between organisms of the same or different species generate novel biological traits and functions, contributing to biological diversity. This broader definition and characterization of biodiversity may open a new dimension in our understanding of the true richness embodied in the biological world.

The rich diversity of the biological world, which records the vast history of life within its environment (*i.e.*, biological evolution), is an unlimited source of information about the mystery of *life and nature*. Biodiversity is also a source of power or strength in *sustaining the global environment* because it provides "players" suitable for diverse functions or ecological niches in the global ecosystem. With both aspects, the fate of our future generations rests on the state of this important feature of the biological world, *i.e.*, biodiversity. Thus, no doubt our urgent task is to take immediate actions, and make intensive efforts, for conserving biodiversity on the earth.

I-2. Ecological complexity that promotes biodiversity

(a) Introduction

Accumulated evidence strongly suggests that *ecological complexity* plays a key role in *promoting* biodiversity in nature. Here, we use the term "ecological complexity" to mean the complex and intricate manners of *interactions* among various forms of life, and the heterogeneous structure of *habitat*. These two types of ecological

complexity are, however, not completely separable. As in the cases of trees and reef-building corals, biological organisms may produce an eminent physical structure, which provides habitat for other species of organisms. Indeed, much habitat for living organisms is biologically based. This biogenesis of habitat structure is a form of ecological interactions, making a close linkage between the two types of ecological complexity.

The state of great biodiversity for the global biotic system (*i.e.*, Biosphere) supported by this ecological complexity is here captured by the term, "symbiotic Biosphere" or "SymBiosphere" for short.

(b) Interactions promoting biodiversity

A clear example of external inputs promoting biodiversity can be found in the immunological responses of an organism against non-self material invading the body. The diversity of antibodies and restructured DNA sequences produced in immunological cells is based on the need to counter the diversity of potential antigens present in the environment.

Plant-animal interactions are another rich source of interactions promoting biodiversity. Plants develop defense systems against attacks by a variety of herbivores (plants consumers); the hard structure made of cellulose and other cell-wall substances serves as a basic physical defense, whereas the secondary substances plants produce and store in cytoplasm are effective chemical defenses. Those animals attacking plants also develop means for coping with these defenses. Thus, an evolutionary arms race takes place. This *coevolutionary* process may lead to the creation of amazing products by both sides. This is an example of how species interactions, through the evolutionary process, generate novel biological traits, enhancing biodiversity. Because the production of chemical defense substances demands a high cost, plants tend to reduce or may cease the production when they are kept free from their herbivores' attacks. Thus, interactions with animals are necessary for maintaining the function of plants to produce those special substances. This suggests that biological traits may not be maintained when an organism of concern is kept alone out of its natural environments, *i.e.*, the biotic community of which is a member.

Further, recent advances in chemical ecology and community ecology extend this pairwise scheme of species interactions into that of more complex interactions involving a third organism. These interactions are often indirect, asymmetrical and subtle.

The elucidation of the role of the plant in the tritrophic system shows plants are not passive interactants but may actively affect the other members of the system. Infochemicals (information + chemical) emitted from plants infested by herbivores mediate many different interactions among the members of the system. For instance, plants release a "cry substance" when they are attacked and need help from the enemies of their herbivores. Furthermore, a plant when attacked may "cause" uninfested neighboring plants to initiate defensive reactions. This may result in "hot spots" of relative immunity to the herbivore formed by undamaged plants in the neighborhood of the damaged plants, due to induced indirect defensive actions.

Species interactions among guild members sharing the same host plants are often asymmetrical. Asymmetric interactions occur among herbivorous insects that are very distinct taxonomically and utilize different parts of the shared host plant in very different manners, through changes in quality and quantity of host plants. Previous studies have mainly focused on interspecific competitions between closely related species.

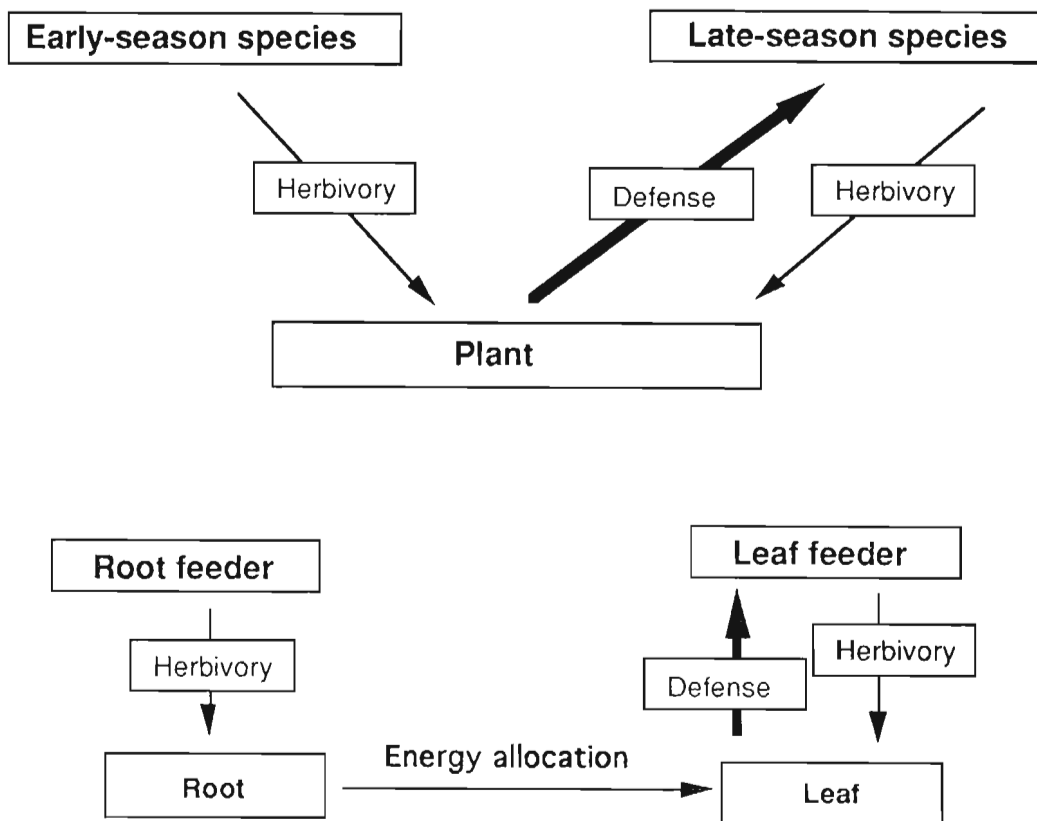


Figure 1. The interaction between temporally separated species (upper) and that between spatially separated species (lower).

Even insects feeding at different times or on different parts of a plant may have a substantial effect on the quality or quantity of resources available to one another (Figure 1). Thus, one species attacking the host plant early in the season can, for instance, change the performance or abundance of another species attacking late in the season, mediated by changes in host quality. Such indirect effects mediated by the host plant are more common than previously thought, and are especially common in insect-plant systems.

These complex interspecific interactions require that the involved species encounter and deal with a great range of variations in species interactions through time and space. This promotes diversity in their behaviors and functions.

In the natural world, there are many different degrees of mutualistic interrelationship, *i.e.*, symbiosis. As mentioned earlier, these mutualistic interactions also produce some biological traits that cannot be attained by either symbiont alone. These "synergetic traits" are new biological "innovations," and thus contribute to enhancing biological diversity. For example, neither termites nor their symbionts (bacteria, protozoa and fungi) can process the vast amount of litter (dead plants) in tropical forests and savannas to make good food for themselves, but in association with each other they become "super-decomposing machines" in the tropical terrestrial ecosystem.

Also notable is the fact that advancement in symbiosis may possibly lead to closer biological association, accompanied by gene transmissions which cause changes at the DNA level, and even ultimately to unification (fusion). This process is a source of gene-level biodiversity. Another source of gene-level biodiversity is interspecific hybridization, which may occur even in the natural environment and is known to be a significant mechanism for speciation especially among plants.

To summarize, the richer the set of interactions, the more diverse and surprising (biochemical, physiological, behavioral and other) biological traits are expected to result.

(c) Habitat structure promoting biodiversity

Another facet of ecological complexity is the heterogeneity of habitat structure. This provides diverse sets of environmental conditions, supporting diverse ways of living and, thus, promoting biodiversity.

- 2. Notably, heterogeneous habitat structure is in large part created and modified by living organisms themselves. Terrestrial plants, trees and

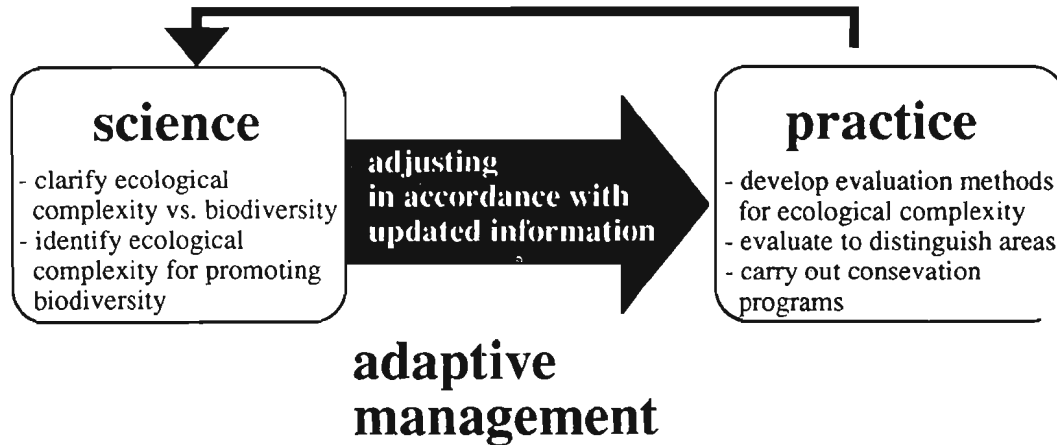
grasses, create three-dimensional structure, above and below ground, which produces habitats for diverse species of life. Corals also build huge complex structure and many benthic organisms inhabit and modify this structure over period of time, further diversifying the habitats.

For the case of vegetation, habitat complexity is manifested as gradational changes in environmental conditions or sequences of distinct habitats. The more different types of habitats that are connected with each other, the higher diversity in vegetation tends to occur. The humid east Asia is one such area, as the distinct types of habitat have had a high connectivity throughout geological time. Indeed, this region exhibits a much higher diversity than the other areas in the world at the same latitude. Also, the higher diversity of epibiotic elements such as primitive monotypic Gymnosperm and Angiosperm in this area supports the hypothesis that habitat complexity, when combined with high connectivity, should promote biodiversity. This should also hold for smaller scales of habitat structure; thus, it may offer a guiding principle for the practice of biodiversity conservation.

(d) *Conclusions*

To conclude, ecological complexity enhances *biodiversity* through evolutionary and biogeographic processes, whereas its degradation (*i.e.*, the simplification of ecological interactions and habitat structure) should quickly cause the diversity in phenotypic and genotypic traits to decline. For the conservation of biodiversity, it is not sufficient to preserve living organisms or their gametes alone, because keeping animals and plants in zoological and botanical gardens or their gametes in a freezer can not conserve the full range of biological diversity they exhibit in nature, due to the loss of the ecological complexity they enjoy in their original habitats. In order to preserve in its *vital* state the biodiversity embodied in living organisms, they must be conserved in, and together with, their *correct* environments with sufficient ecological complexity.

II. The research project



II-1. The scope and prospects

This cooperative research project aims to intensify and coordinate two distinctive but mutually relevant activities, the science and the practice of preserving and recovering the ecological complexity that promotes biodiversity. That is, the project combines science and practice. It intends to coordinate *scientific research activities* with *conservation programs* which are constantly "tuned" based on updated results from the basic research in progress. In other words, the conservation programs adopt an "adaptive management" scheme, in view of expected advances in relevant theories from the basic research phase.

One characteristic feature of the project is the interactions among scientists. First, a close collaboration is required between ecological scientists and biochemical and molecular biological scientists. Second, it is clear from the intention to coordinate scientific and practical efforts that close interactions are necessary between basic research oriented scientists and applied oriented researchers and management experts. These requirements should be crucial to the success of the project, and yet they may be very challenging. We have a good prospect, based on our recent experience, to meet, at least, the first requirement.

Recently, a research project with objectives closely related to the research project has been selected for intensive research funding by

the Japanese Government as a Priority Research Area. That research project, continuing until 1994, has brought together scientists with very diverse backgrounds and expertise, ranging from ecology and evolutionary biology to molecular biology and biochemistry. It focuses on complex interactions among diverse living organisms, in connection with major mechanisms for promoting the coexistence of many species and for shaping the community structure in different environments. The experience gained in this ongoing research project should prove useful for the research project, both in identifying focal research themes and in forming an effective research organization. In particular, productive collaboration between researchers with rather different backgrounds (*e.g.*, ecological scientists and molecular biologists) requires an effective "communication channel" or "translation system" between those scientists, which has been well developed through the current research project.

II-2. The common sites: to coordinate research and conservation activities

As a means to coordinate research activities in the project, in particular the two distinct types of activities, *i.e.*, science and practice, it is necessary to select a set of common research sites in which both basic research activities and conservation programs will be concentrated. To give the project a global extent and address relevant problems on a larger spatial scale, sites will be chosen in such a way that comparative and simultaneous research can be conducted along a latitudinal gradient.

The project can, and may eventually, be conducted worldwide. We, however, select only a single series of sites along a latitudinal gradient, for which we intend to initiate the research project. In light of past biogeographic continuity and geographical convenience for research, we have chosen a series of sites along a latitudinal gradient on the east side of the Eurasia Continent.

II-3. Basic scientific research

The basic scientific research is designed as intensive cooperative research. Two-way interactions are essential between ecological scientists and biochemical and molecular biological scientists.

The scientific research activities will be organized around the following two foci:

- i) to clarify the precise relationships between ecological complexity and biodiversity;

ii) to identify the kinds of ecological complexity that are most influential in promoting biodiversity.

A representative case for specific sets of "networking" (*i.e.*, comparative and simultaneous) field researches will be conducted with a network of forest systems (Figure 2) and aquatic (freshwater and marine) systems along a latitudinal gradient on the east side of Eurasia Continent.

Among biological communities, forest vegetation in the terrestrial part of the Biosphere is characterized by a unique feature; it forms a persistent complex architecture with maximum biomass accumulation. Huge and complex architecture offers a diversity of habitat for various living organisms.

There exists a unique trend for forest ecosystems; the latitudinal gradient from less-productive extratropical environment to the most productive tropical wet environment is coupled with the gradient of species diversity. The maintenance of persistent vertical architecture in forest systems provides a key to understanding the mechanisms that maintain species diversity. Persistent vertical architecture is represented by tree size distribution which classic production ecology did not deal with.

Dynamics of tree size distribution can be described by tree growth rate, mortality and recruitment rate through permanent plot censuses. A new hypothesis, developed from the one-sided competition (*i.e.*, light competition) model of size-structured tree populations (see Figure 3), posits the existence of stable equilibrium coexistence without considering any species-to-species-specific factors and stochastic fluctuation factors, both of which have been used to explain the coexistence of species at the same trophic level. One can calculate model parameters of each tree species from observed tree growth rate, mortality and recruitment rate as functions of tree size and the intensity of one-sided competition. It is valuable to compare parameters of such a realistic model between coexisting species in various forest ecosystems and to relate them with species-specific eco-physiological traits and forest-specific physical constraints. It will contribute to the construction of functional, predictive model of natural forest tree communities.

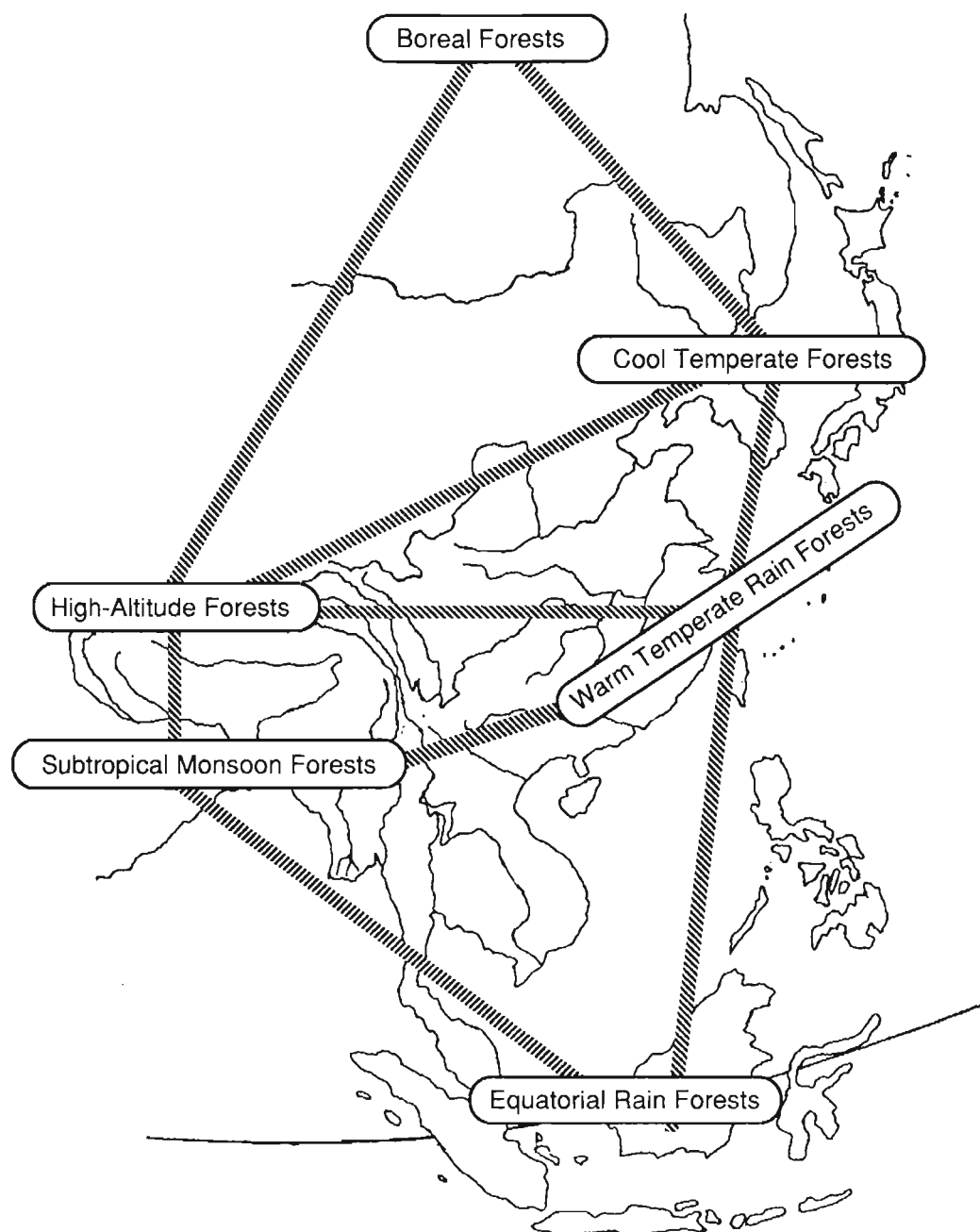


Figure 2. Simultaneous research network of forest ecosystems along east Asian habitat gradient.

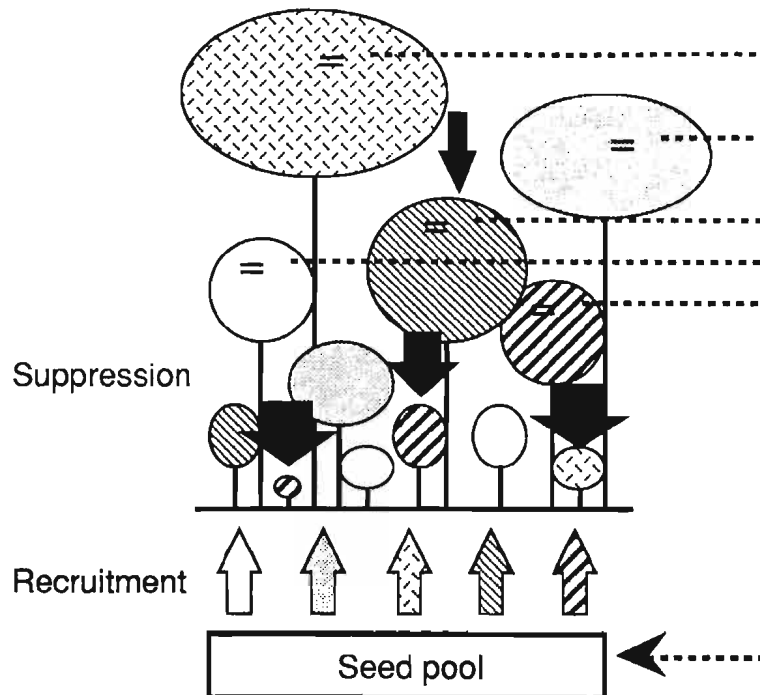


Figure 3. Multi-species system is maintained when population is size-structured. Potential recruitment depends on adult density of each species, while growth, survival and recruitment is suppressed by one-sided competition factor collective of species.

It is necessary to clarify the regeneration mechanism of self-organizing forest systems. Forest regeneration is the function of physiological attributes of tree species throughout life and biological inter-relationships between trees, pollinators, herbivores and soil mycorrhiza. Vegetative and reproductive success of trees is largely dependent on other living organisms of different trophic levels. For the understanding of these processes, long-term research projects involving both ecological and environmental censuses are primarily important. Particularly, seasonal censuses of physical environments and performance of living organisms at least for several years and including one El Nino cycle, which has been confirmed to relate to the mass reproduction cycle of dominant forest trees, are necessary for obtaining the minimum set of data by which possible theoretical hypotheses can be statistically tested.

Restoration of tropical lowland rain forests with extremely high species diversity and huge biomass stock is one of the most urgent issues in the present interest in the conservation of genetic diversity and environmental stability. Meanwhile, the existence of a latitudinal

gradient of species diversity provides a clue to solving the mechanisms of species coexistence. What is necessary is to construct networks of comparative and simultaneous research projects that span the latitudinal gradient. Even though many research efforts are made in various forest systems, in particular in tropical forests, they are still too fragmentary to create a mutually-comparable data set. We can predict the shift of forest ecosystems and species composition there in due to a global increase of atmospheric CO₂ concentration through results of simultaneous censuses from the research network across climatic regions.

For instance, the gradient of wet forests in the east of the Eurasia Continent ranging from East Siberian taigas to South-East Asian tropical rain forests via Himalayan monsoon forests and Chino-Japanese wet temperate forests provides an ideal research fields for the above purpose (Figure 2).

Parallel arguments can be made for aquatic systems, and we intend to take these two distinct types of systems for comparison.

II-3. Conservation Practice

The practical part of the project must be considered as an initial step of a much longer term conservation program, which needs to be organized based on the results of this project.

The immediate aim is to develop an operational methodology by which an objective *evaluation* can be made for a given system (habitat or area) in terms of ecological complexity (*i.e.*, the degree of richness in interactions and habitat structure) pertaining to the preservation of biodiversity.

The second stage is the application of this evaluation method to develop a systematic scheme for distinguishing regions and areas in terms of the potential for preserving and recovering ecological complexity for promoting biodiversity. Behind this goal of clear distinction among areas is a need to consider economic demands in the region. Unless a clear distinction among areas and regions in terms of land use is made based on an appropriate evaluation, we can not keep ecological complexity which is crucial to the conservation of biological diversity and the global environment.

The third stage is then to carry out management measures that may help preserve or recover ecological complexity.

At every stage, results from the progressing research should be utilized to constantly adjust conservation practices.

For the conservation programs developed through this project, *funds* specifically designated to each of the programs should be established in order to guarantee their full development following this project.

**Gross Difference in Community
Structure between Forests and Grasslands
-Why are forests kept green?-**

Takuya Abe

Center for Ecological Research, Kyoto University,
Shimosakamoto, Otsu, 520-01 Japan

Key words: *community structure, C/N balance,
cell-wall and cytoplasm consumers, detrital vs grazing chain.*

Introduction

There have been only a few studies in which all the community components were investigated. However, some generalizations are possible if we compare the gross features of contrasting systems such as forest, grassland and plankton communities (of ocean and of a large lake). The detrital chain has been thought to be responsible for the majority of secondary production in all of these three categories of communities. The grazing chain, on the other hand, has the greatest role in plankton communities, followed by grassland, and the smallest role in the forest. This pattern is well known, but has never been explained.

Abe & Higashi (1991) examined cellulose centered perspective on terrestrial community structure. This paper, based on the paper, intends to examine the gross differences in community structure between forests and grasslands in relation to the specialization of phytophagous insects into cell-wall specialists and cytoplasm specialists.

Cell walls and cytoplasm as food resources

One of the most significant differences between plant and animal cells is the presence of a cell wall. Although the cell wall and cytoplasm are both potential food resources for heterotrophs, they are quite different in their chemical compositions. The cell wall of higher plants, containing little protein and lipid, consists mainly of cellulose, hemicellulose and lignin, which are located almost exclusively in the cell wall. These three cell-wall substances constitute in weight about 47%, 22% and 22%, respectively, of deciduous wood, 16%, 13% and 21% of deciduous leaf, and 30-33%, 18-24% and 11-14% of grass. Therefore, cell wall is the primary component of the biomass of trees and grasses.

Because most plant materials (98%) on earth are terrestrial, and 75-90% of it is located in forests, cell-wall substances, especially cellulose, are the most abundant organic matter on earth. Cell wall thus provides the most abundant food resource, if only potentially, on this planet. Except for some types of molluscs, silverfish and a few earthworms, animals cannot directly utilize this super-abundant food resource because they cannot produce a complete set of cellulases; they must have direct or indirect associations with microorganisms to consume this food.

On the other hand, cytoplasm, which is abundant in pollens, seeds and new leaves of plants, is rich in proteins, lipids and starches. It is thus a potential food of high quality (*i.e.*, nutritionally well-balanced food) for animals. Higher plants produce, however, various kinds of toxic secondary substances, such as alkaloids, terpenoids and hydrogen cyanides, and keep them in cytoplasm. Therefore, animals that feed on plant cytoplasm must solve the problem of plants' chemical defenses.

Cell-wall consumers and cytoplasm consumers

The foregoing observations suggest a new categorization for heterotrophs or consumers: *cell-wall consumers* and *cytoplasm consumers*. The consumers of animals, *i.e.*, carnivorous animals, are all cytoplasm consumers, while those of plants may be cell-wall consumers or cytoplasm consumers.

Cell-wall consumers of plants, having acquired a means to cope with the hard construction materials of cell wall, utilize a food of low quality (*i.e.*, nutritionally less well balanced, having an extremely high C/N ratio) but available in high quantity. On the other hand, the cytoplasm consumers of plants, managing toxic secondary substances in cytoplasm, utilize a food of high quality but available in low quantity. It should be noted, however, that to utilize cell-wall substances successfully as their food, cell-wall consumers have to balance the C/N ratio of their food by either adding N or selectively eliminating C (*i.e.*, concentrating N in their food). Only microbes are capable of this, and animals cannot do it alone. That is another important reason cell-wall eating animals have to be associated with microorganisms.

What does this categorization of plant consumers generate when applied to insects, which constitute about a half of all living species excluding algae and microorganisms? Phytophagous insects make up approximately half of all insect species, but are included in only nine of the 29 insect orders. Hemiptera, Lepidoptera, Orthoptera and Phasmida are almost entirely phytophagous, but only about one-third of Coleoptera, one-fourth of Diptera and one-tenth of Hymenoptera feed

on the living tissues of higher plants. Although there is insufficient information on cellulose-digesting insects, comparison of phytophagous and cellulose-digesting insects at the family level shows that no cellulose-digesting insects are phytophagous, except for some Coleopterans (Coccinellidae, ladybirds; Scarabaeidae, scarab beetles; Cerambycidae, long-horned beetles) and probably Orthopterans (Table 1). The larvae of many species of Cerambycidae are cellulose-digesting and consume woody tissues of living plants. Because most woody tissues of trees consist mainly of cell-walls and contain only a little cytoplasm and thus can be considered "dead" cytologically, the larvae of these long-horned beetles are, in effect, cell-wall consumers. Therefore, we may conclude that most insects that consume plant materials have succeeded in solving either, but not both, of two problems: 1) the detoxification of secondary substances in cytoplasm, and 2) the degradation of cell-wall components with the aid of microorganisms.

Table 1. The classification of vegetarian insects into phytophagous ones (cytoplasm consumers) and cellulose-digesting ones (cell-wall consumers) [based on Strong *et al.* (1984) and Martin (1987)]. Boldface type denotes families with representatives in both classes.

Orders	Families that contain phytophagous insects	Families that contain cellulose-digesting insects
Hemiptera	Delphacidae and 16 families	-
Lepidoptera	Micropterigidae and 28 families	-
Orthoptera	Tettigoniidae, Acrididae	Gryllidae
Phasmida	Eumastacidae	-
Coleoptera	All species Scarabaeidae, Cerambycidae Coccinellidae, Tenebrionidae Mordellidae, Chrysomelidae Languridae, Apionidae Curculionidae	Scarabaeidae, Cerambycidae Coccinellidae, Anobiidae Buprestidae
Diptera	Cecidomyiidae, Dolichopodidae Drosophilidae, Ephyrididae Anthomyiidae, Agromyzidae Chloropidae, Tephritidae	Tipulidae
Hymenoptera	Xyelidae, Cephidae Blasticotomidae, Diprionidae Tenthredinidae, Ichneumonidae Braconidae, Cynipidae Agoonidae, Eurytomidae	Siricidae
Collembola	Sminthuridae	-
Thysanoptera	Thripidae	-
Thysanura	-	Lepismatidae
Isoptera	-	Mastotermitidae, Kalotermitidae Hodotermitidae, Rhinotermitidae Termitidae
Plecoptera	-	Pteronarcyidae
Trichoptera	-	Limnephilidae
Blattaria	-	Cryptocercidae, Blattidae

-: not recorded

Cell-wall consumers include dead plant feeders of great variety besides termites, while cytoplasm consumers include human beings, ants, bees and many other animals. In addition to herbivorous ruminant mammals, those organisms that utilize both cell wall and

cytoplasm may be called *generalists*. We note that in this categorization, microbes that break down the living plant tissue are classified as generalists.

An alternative view on community structure

The new categorization of heterotrophs that we have developed also leads to an alternative view on community structure. Division of the plant cell, representing the primary producer world (or the resource world), into cell wall and cytoplasm, is projected into the classification of plant consumers into two corresponding categories: cell-wall consumers and cytoplasm consumers. The overlap of cell-wall consumers and cytoplasm consumers corresponds to generalist consumers, such as herbivorous mammals with rumens, which cope with both defense systems of plants.

Cell-wall specialists, i.e., cell-wall consumers that are not cytoplasm consumers, having acquired a means to cope with the hard construction materials of the cell wall but not the toxic secondary substances in the cytoplasm of plant cells, should utilize mostly dead fallen plants. As a result, they transmit the cell-wall components in dead plants to "detrital food chains". On the other hand, *cytoplasm specialists, i.e.*, cytoplasm consumers that are not cell-wall consumers, which possess a means to cope with the toxic secondary substances in the cytoplasm of plant cells but are not able to utilize cell-wall components, tend to utilize only the soft parts of living plants, and transmit the cytoplasm components in these parts to "grazing food chains". Generalist consumers, having acquired means both to cope with the toxic secondary substances and to utilize cell-wall components effectively, naturally tend to feed on living plants, which are more nutritious than dead plants. They utilize both the cell-wall and cytoplasm components of plants, expanding cytoplasm flows to grazing food chains, and also redirecting into grazing food chains some portion of the cell-wall components of living plants that would lead to detrital chains without generalists' grazing.

From the overall picture developed here, it is easy to see the correspondence between the new categorization of heterotrophs and the conventional one that classifies heterotrophs into "consumers" and "decomposers" according to the state of their food resources, alive or dead. Cytoplasm consumers, including cytoplasm specialists and generalist consumers of plants, as well as consumers of animals, correspond to the former, whereas cell-wall specialists correspond to the latter. The only exceptions are those cell-wall specialists that feed on woody tissues of living plants, like the larvae of certain long-horned beetles.

Detrital versus grazing food chains in forests and grasslands

The community structures of forests and grasslands differ in the relative significance of detrital and grazing chains: the quantitative significance of detrital chains relative to grazing chains tends to be greater in forests than in grasslands. The new view on community structure that has just been presented can be applied to this issue, and an answer is offered to the question why this tendency exists.

Trees contain more cell-wall components and less nitrogen than grass. Nitrogen contents of grass and wood (in parenthesis, tree and shrub foliage) are 1.2-4.5% and 0.04-0.3% (0.6-6.6%) respectively. Thus, in the context of the basic structure, the abundance of cell-wall relative to cytoplasm components is higher in forests than in grasslands. If no generalist consumer existed, this would imply the quantitative significance of resource available to detrital food chains relative to grazing food chains is greater in forests than in grasslands.

In forests, insects that can decompose cellulose with the aid of microorganisms usually do not attack living plant tissues (*i.e.*, they are cell-wall specialists). On the other hand, most phytophagous insects, having no association with microorganisms for cellulase, consume only nutritious portions of plants, such as fruits, seeds, pollens and young leaves, and do not destroy major parts of trees, such as mature leaves, branches and stems (*i.e.*, they are cytoplasm specialists). Although certain phytophagous insects may feed on mature leaves in some natural or managed forests, phytophagous insects that feed on mature leaves in natural forests are uncommon.

Herbivorous mammals, which harbor microorganisms in their guts and decompose cell-wall substances, and other generalist consumers are scarce in forests though herbivorous primates are important exceptions in some forests. On the contrary, in grasslands, herbivorous mammals, especially ungulates, are abundant, and sometimes consume much of the living grass. The following two points, though, must be noted: 1) herbivorous mammals with rumens cannot digest cellulose completely, but only 43-73%, mainly due to the presence of lignin and silica, and 2) the inclusion of cellulose, lignin and silica in grass place an upper limit to the grazing of herbivores below the availability of this food, because their feeding ecology can be explained largely by the behavioral adaptations to maximize protein consumption and minimize consumption of tough lignified or silicated fiber. The scarcity in forests and, by contrast, the abundance in grasslands of generalist consumers increases the difference between forests and grasslands in the relative

significance of detrital and grazing food chains, because generalists expand cytoplasm flows to grazing food chains and redirect into grazing food chains some portion of the cell-wall components in living plants.

Coexistence of many species of insects in the forest

The specialization of insects into either cell-wall or cytoplasm consumers leads to an interesting consequence. Old leaves, branches and trunks of living trees are not consumed by both of cell-wall specialists and cytoplasm specialists, because the amount of their secondary substances may be too high for cell-wall specialists while the amount of cell-wall substances may be too high for cytoplasm specialist. Therefore the main parts of living trees are more or less free from the attack by both types of insects. This may be one of the most important reasons why forest is kept green in spite of abundant species of plant-consuming insects.

Tall trees in the forest provide various scales of relatively stable heterogenous habitats. In the tropical rain forests the heterogeneity of habitats is accelerated by high species diversity of trees, which produce various kinds of secondary substances. Edible food resources such as young leaves tend to be scattered, ephemeral, asynchronized and furthermore separated by "barriers" of old leaves and branches which are not edible to most animals. It is highly probable that old larvae of insects are able to eat old leaves but young larvae are able to eat only young leaves. This may make it very difficult for adult phytophagous insects to lay eggs on adequate stage of leaf development. This may decrease intra- and inter-specific competition on leaves, and promote the coexistence of many species.

In conclusion, phytophagous animals represented by insects do not play an important role in the energy flow in the forest ecosystems, because of chemical defense by plants and specialization of phytophagous insects into cytoplasm consumers. This inability of phytophagous insects, in turn, make it possible for many species of insects as well as other animals to coexist in the forests. Insects in the forests are rich in the species diversity, because they are important as accessory except for pollinators. Motorcars are rich in the variety of their appearance, but poor in the variety of engine structure.

References

- Abe, T. & Higashi, M. (1991). Cellulose centered perspective on terrestrial community structure. *Oikos* 60: 127-133.

Martin, M. M. (1987). *Invertebrate-Microbial Interactions*. Cornell University Press, Ithaca, New York.

Strong, D., Lawton, J. H. & Southwood, R. (1984). *Insects on Plants*. Blackwell, Oxford.

**Habitat Structure and Biodiversity in the Coral Reef Areas:
Ecological Process in Habitat Creation and Community
Development on Microatolls of the Massive Coral *Porites***

Moritaka Nishihira

Laboratory of Animal Ecology, Biological Institute,
Tohoku University, Sendai 980 Japan

Key words: *coral reefs, habitat structure, biodiversity, habitat
creation, microatoll.*

Introduction

High complexity of habitat structure has been suggested to support a high biodiversity. In coral reefs, physical structure of habitats is created or modified principally by macrobenthic organisms (Morton & Challis, 1969; see also Sebens, 1991).

Based on an extensive survey of major habitats in coral reef areas, the following three different processes involved in the structuring of microhabitats were recognized (Nishihira, 1992):

1: *Provision* refers to the process whereby the body of an inhabitant provides secondary space for colonization by other species. For example, sessile colonial corals, macroalgae and seagrasses provide diversified microhabitats (Mukai, 1990).

2: *Creation* refers to the modification of substrata by the activity of living organisms (Mukai, 1992), leading to the creation of new microhabitats. Borers and grazers are major animal groups which are engaged in this process.

3: *Conditioning* refers to the maintenance of the new environmental conditions of a microhabitat by the presence or activities of living organisms. Burrowing animals such as spatangoid urchins and ghost shrimps as well as territorial animals condition particular ecological circumstances in their zones of activity.

Colonial sessile corals and assemblages thereof build enormously intricate structures on substrata which have themselves been built up by carbonate-producing organisms. Many kinds of organisms inhabit and modify this structure and add more diversified microhabitats to it.

This chain or iteration of creation-inhabitation is a major process in promoting the coexistence of many species in a given area.

Aims and methods

The development of communities on microatolls of massive corals offers good examples for testing the hypothesis that the three principal processes listed above are involved in the ecological genesis of communities and biodiversity. The microhabitat structuring process involves 1) growth of corals, 2) physical stresses caused by emergence at low tide, 3) generation of microhabitats principally by benthic organisms, and 4) chains of colonization of newly structured microhabitats. Observations were conducted to evaluate all aspects of these ecological processes.

In the shallow (<1.5m depth at low tide) moat of Kudaka Island, Okinawa, microatolls of massive *Porites* of various sizes were selected for study. The tops of the microatolls were carefully scanned, and algae, corals and other macrobenthic animals were recorded. Surface irregularity was measured. Benthic foraminifers were censused using a 5cm x 5cm quadrat.

Results and discussion

Surface irregularities on the tops of microatolls seem to be created and increased through the activities of benthic organisms. With growth, the top begins to emerge at low tide, which causes the formation of a microatoll. Exposed dead skeleton is first colonized by blue-green algae and an early macroalgal colonizer such as *Padina minor* Yamada. With further growth of the coral, the top of the microatoll increases its area, and the surface irregularities also increase. During this time, boring activities of the giant clam *Tridacna crocea* Lamarck and grazing by the sea urchin *Echinometra mathaei* (Blainville) play major roles. Colonization of *Tridacna* occurs from the early phase of microatoll formation, and *Echinometra* establishes its population by occupying empty burrows left by dead clams and continues to enlarge and deepen the burrows as a result of its grazing activities over a long period of time.

Two representative tubicolous animals embedded in the coral skeleton of *Porites* are *Spirobranchus giganteus* (Pallas) and *Dendropoma maxima* (Sowerby). After death, their empty tubes become available for use by the obligatory tube-dwelling hermit crab *Paguritta harmsi* (Gordon) and by certain facultatively tube-using fishes, thus adding unique animals to the associated fauna.

Larger microatolls support more abundant and more diverse benthic macroalgae. The more irregular surface of larger microatolls seems to facilitate the colonization by many species. The irregular surface with deep, excavated places retains water even at low tide, thereby supporting luxuriant growths of more kinds of algae.

Benthic foraminifers were represented by more than 100 species. Algal growth enhances the trapping of sediment, and thus conditions favourable circumstances for colonization by certain foraminifers. In addition, the increase in abundance and species of macroalgae with microatoll size provides more diverse microhabitats for epiphytic species and seems to explain the higher species richness of foraminifers on larger microatolls.

Corals are one of the late colonizers of microatolls. Many more corals grow on microatolls with more irregularly excavated tops. Presence of a variety of corals, no doubt, induces colonization by coral-associated organisms.

All of the processes mentioned above occur in the context of a sophisticated network of interactions among various species. Therefore, treating all the organisms and interactions in a community must help to bring about deeper insights into the mechanisms whereby many species live together in a limited area. By treating only a portion of the community members and interactions, our understanding of the mechanisms involved in the promotion and maintenance of biodiversity may be limited.

It is indispensable to include habitat structuring and subsequent colonization relationship in discussions of biodiversity. However, it should be noticed that sometimes these processes inhibit the existence of certain species. With regard to the provision and creation, it should be noticed that the microhabitats sometimes become available for later colonizers only after the deaths of organisms which provide or create microhabitats.

Rich coral assemblages provide diversified microhabitats and thus guarantee more kinds of animals places to live. This suggests that the conservation of entire coral assemblages, together with that of a set of macrohabitats or biotopes, is essential for biodiversity conservations in coral reef ecosystems.

References

- Morton, J.E. & Challis, D.A. (1969). The biomorphology of Solomon Islands shores with a discussion of zoning patterns and ecological terminology. *Phil. Trans. Roy. Soc. B* 225: 459-516.
- Mukai, H. (1990). Macrophyte-phytal organisms interactions. In: *Introduction to Applied Phycology*. I. Akatsuka (Ed.) pp. 347-365. SPB Academic Publishing, The Hague, The Netherlands.
- Mukai, H. (1992). The importance of primary inhabitants in soft bottom community organization. *Benthos Res.* 42: 13-27.
- Nishihira, M. (1992). Biotic creation of habitat structure and multi-species coexistence. In: *What is Symbiosphere?* M. Higashi & T. Abe (Eds.) pp. 86-100. Heibon-sha, Tokyo. (In Japanese)
- Sebens, K.P. (1991). Habitat structure and community dynamics in marine benthic systems. In: *Habitat Structure*. S.S. Bell, E.D. McCoy & H.R. Mushinsky (Eds.) pp. 211-234. Chapman and Hall, London.

Forest Pattern along Hierarchical Habitat Gradients in East Asia

Masahiko Ohsawa

Laboratory of Ecology, Faculty of Science, Chiba University,
1-33, Yayoicho, Chiba 263 Japan

Key words: *leaf size, topography, life zone, temperature factor, tropical mountain.*

Introduction

The forest ecosystem in humid east Asia exhibits various patterns of distribution and differentiation along hierarchical habitat gradients which are controlled by climatic, topographical, and small scale disturbance factors. The rich diversity of forest types in east Asia is due mainly to the geo-historical continuity of the humid forest climate since at least the Tertiary without any marked interruptions during the Ice Age. Moreover the region comprises mountainous terrain including volcanic belts and high mountain ranges, and this mountainous topography modifies the macro-climatic conditions into a micro-scale habitat mosaic of forests.

To understand the pattern and process of differentiation of these rich forest ecosystems, I first studied the geographical pattern of forest formations in the east Asiatic region and tried to explain it in relation to temperature conditions. Then the distribution of leaf forms in relation to humidity factors in the subtropical/warm-temperate zone in south to east Asia was studied, because all the major leaf forms, such as evergreen, deciduous, broad-leaved, and needle-leaved, coexist in this region. Furthermore the ecological interrelationships among different leaf forms were investigated along meso-scale habitat gradients as, for instance, topography.

I adopted the comparative approach for generating a hypothesis regarding forest patterns, habitat preferences and leaf traits such as leaf forms and leaf size. The leaf traits are a useful link among different scales such as ecophysiological mechanisms, community processes, and geographical distribution (Box, 1981; Schulze, 1982; Chabot & Hicks, 1982; Givnish, 1987; Woodward, 1987; Reich *et al.*, 1992).

Geographical pattern of forest ecosystems and their controlling factors in East Asia

Two temperature factors, *i.e.*, temperature sum and low temperature in winter, have a decisive effect on the diversification and distribution of tropical vegetation along altitudes in tropical high mountains and latitudes in the mid-latitudes of the Northern Hemisphere respectively (Figure 1). On the one hand, the decrease of temperature sum without any marked seasonality leads to the zonation on equatorial mountains, and on the other, the drop of the minimum temperature in winter without any marked decrease of temperature sum in summer leads to latitudinal zonation in the middle latitudes of the Northern Hemisphere (Ohsawa, 1990). The former causes replacement of the evergreen noto/mesophyllous forest of the lower montane zone by the evergreen nano/microphyllous forest in the upper montane zone on tropical high mountains (Ohsawa, 1991). The latter causes gradational floristic depauperation of evergreen trees depending on the critical low temperature-limit which differs by species. Further north the evergreen leaf form is replaced by deciduous and/or needle-leaved trees at middle latitudes where the coldest month temperature is below 0° to -1° C (Ohsawa, 1990, 1991). This replacement takes place without any appreciable difference in forest height, which indicates that it is not due to a shortage of productive potential but to winter coldness that determines the tolerant leaf forms.

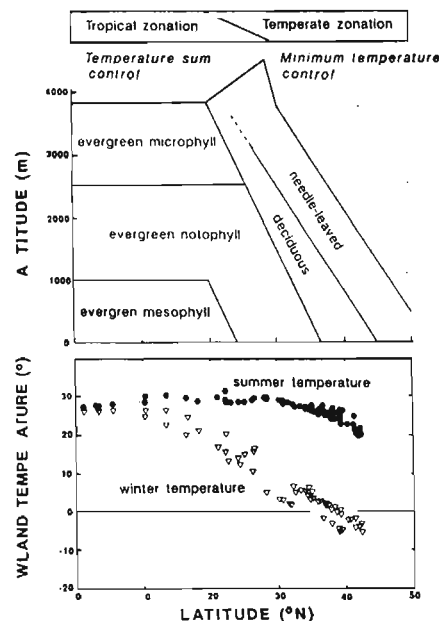


Figure 1: Geographical pattern of forest ecosystems in east Asia and its controlling factors.

Thermo-hygic pattern of subtropical/warm-temperate forest

The subtropical/warm-temperate forest of east Asia varies in leaf forms depending on various habitat factors. In humid climate, most trees have evergreen leaves which must endure occasional or seasonal environmental extremes during their growing periods. Thus trees may respond physiologically, or their leaves may undergo morphological changes, *e.g.*, with regard to leaf size, texture, pubescence, *etc.* If the conditions are too extreme to maintain evergreenness, *e.g.*, low temperature, excessively dry or humid edaphic conditions, evergreen leaf forms may be replaced by other types of leaves, such as deciduous or needle.

The replacement of evergreen broad-leaved forests by other forests such as needle-leaved and/or deciduous forest, was analyzed in detail according to Holdridge's life zone (Holdridge, 1967). The results showed that each leaf form was specialized to specific habitat conditions; namely, evergreen noto/mesophyllous forest is found in the favorable moist core habitat and needle-leaved or deciduous forest in marginal habitats characterized by extremely dry, wet or cold conditions (Ohsawa & Ozaki, 1993). The needle-leaved tree genera were characteristic to each of the following environmental extremes; *Pinus* forests at subhumid or dry forest sites, *Cryptomeria* forests at superhumid or rain forest sites, and *Abies* forests at cold sites. The general trend of this pattern may be ascribable to differences in stress tolerance among these leaf forms or genera (Bond, 1989).

Thus the variety of leaf forms of subtropical/warm-temperate forests can be generalized as follows: the most favorable sites are occupied by evergreen noto/mesophyllous trees, while the stressful habitats are occupied by other leaf forms, *i.e.*, sclerophyllous, needle-leaved, or deciduous trees, which are supposed to be tolerant to adverse factors such as shortage of water and/or nutrients, excess of water, and mechanical stress.

Ecological mechanisms implying forest differentiation

The adaptive significance of leaf traits has been widely discussed by many researchers (*e.g.*, Chabots & Hicks, 1982; Givnish, 1987; Sprugel, 1989; Gower & Richards, 1990). To formulate a general rule on the regular arrangement of forest types having a specific leaf size, the leaf size spectra for evergreen broad-leaved forests were studied along environmental gradients, such as altitude in tropical mountains (decrease of temperature sum), degree of windward exposure between mountain top and foothills, and complex factors of water/nutrient

availability on ridge and slope habitats on a small hill slope (Ohsawa & Ozaki, 1993). The leaf size spectra exhibited a similar pattern through the different environmental gradients; that is, the more favorable sites always were dominated by noto/mesophyllous trees, while stressful habitats were dominated by nano/microphyllous trees.

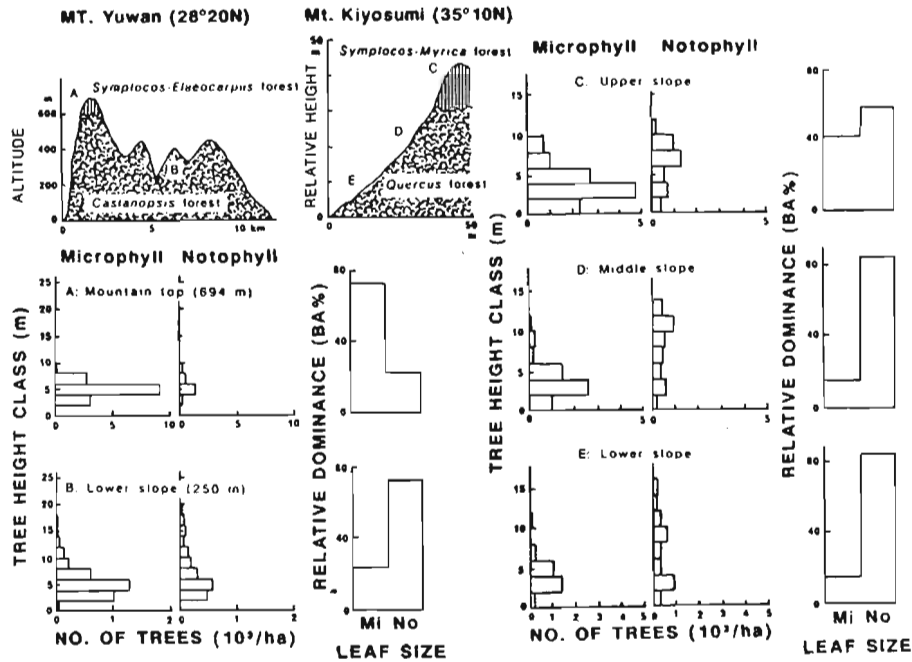


Figure 2: Height class frequency distribution of microphyllous trees and notophyllous trees in five forest stands (A to E) along two environmental gradients in Mt. Yuwan, Amami-Oshima Island (calculated from data by Tagawa *et al.*, 1989) and Mt. Kiyosumi, Chiba (calculated from data by Ohsawa *et al.*, 1982), subtropical/warm-temperate Japan. Topographical location of each community and leaf size spectra are also indicated.

The reason why noto/mesophyllous forest is always replaced by nano/microphyllous forest towards the stressful habitat may need to be investigated ecophysiologically for each leaf form as well as for niches within a community. Here, however, I would like to seek further evidence to elucidate the underlying ecological mechanisms that create the general pattern. The height class frequency distributions of the two contrasting leaf size trees, microphyllous vs. notophyllous, were studied along two gradients, *i.e.*, windward exposure gradient and ridge-slope gradient in southern Japan (Figure 2). The overall pattern of changes observed in the community structure from favorable habitat to stressful habitat includes: 1) noto/mesophyllous trees overcast nano/microphyllous trees in the community at favorable sites, 2) the tree height decreased toward adverse habitats in windward exposed habitat and in ridge habitat, 3) the height class distribution of noto/mesophyllous trees was more

compressed than that of nano/microphyllous trees in adverse sites so that the two trees constitute the same canopy, 4) nano/microphyllous trees became dominant in stressful habitats.

These findings indicate that stressful habitat conditions suppress the noto/mesophyllous trees more strongly than the nano/microphyllous trees, and that the reduced vigor of the noto/mesophyllous trees (shorter tree height, less abundant or even absent in a community) makes possible an alternative dominance of the nano/microphyllous trees in stressful habitats. The microphyllous trees generally occur as an understory component if they coexist with the other leaf forms such as notophyllous trees. Nevertheless they can form scrub communities in adverse/stressful habitats such as high altitudes on equatorial mountains, ridge tops, windward exposed forests, and early successional communities in subtropical mountains. Most of the microphyllous trees, Theaceae, Myrsinaceae, Symplocaceae, and Aquifoliaceae, which constitute the understory of notophyllous forests at favorable sites, become the dominant canopy trees of the microphyllous forest. Thus the nano/microphyllous trees occupy the stressful marginal habitat of the noto/mesophyllous trees.

HABITAT COMPLEXITY PROMOTE FOREST DIVERSITY

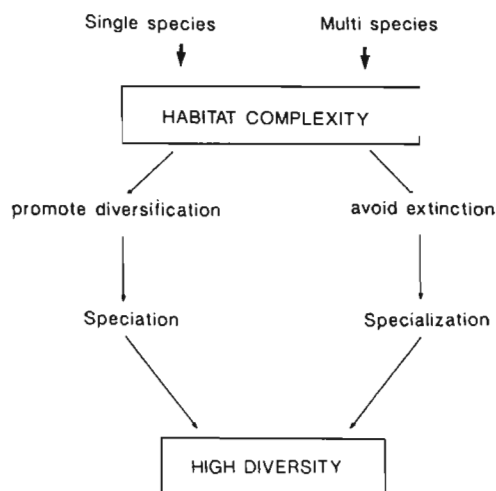


Figure 3: Schematic diagram indicate habitat complexity promote forest diversity.

Concluding remarks

The primary factor controlling macro-scale diversification of forest formations in humid east Asia is temperature conditions. In addition to

this, humidity factors manifested by topography promote differentiation of forest types within a thermal realm or a climatic zone. A detailed analysis of community patterns along meso- and micro-scale habitat gradients can yield clear information on behavior among different ecological groups defined by various characteristics such as leaf traits. Macro-scale climatic changes inevitably alter habitat conditions along an environmental gradient and cause shifting of interspecific relationships. Thus a multi-species assemblage can respond to habitat gradients, or in more general terms, habitat complexity, by diverging their habitat preferences so that they can coexist by spatially segregating their habitat, thus avoiding local-extinction (Figure 3). This is a specialization of species distribution into a respective specific partial habitat along the gradient. On the other hand, a single species may respond to habitat complexity by diverging into different ecotypes or incipient species. Both of these processes promote high diversity or complexity of the forest ecosystem along habitat gradients. Accordingly, the conservation of habitat complexity is the key to promoting forest biodiversity.

References

- Bond, W. J. (1989). The tortoise and the hare: Ecology of angiosperm dominance and gymnosperm persistence. *Biol. J. Linn. Soc.* 36: 227-249.
- Box, E. O. (1981). *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Dr. W. Junk, The Hague, The Netherlands.
- Chabot, B. F. & Hicks, D. J. (1982). The ecology of leaf life span. *Annu. Rev. Ecol. Syst.* 13: 229-259.
- Givnish, T. J. (1987). Comparative studies of leaf form: Assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* 106 (Suppl.): 131-160.
- Gower, S. T. & Richards, J. H. (1990). Larches: Deciduous conifers in an evergreen world. *BioScience* 40: 818-826.
- Holdridge, L. R. (1967). *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica.
- Ohsawa, M. (1990). An interpretation of latitudinal patterns of forest limits in south and east Asian mountains. *J. Ecol.* 78: 326-339.

- Ohsawa, M. (1991). Structural comparison of tropical montane rain forests along latitudinal and altitudinal gradients in south and east Asia. *Vegetatio* 97: 1-10.
- Ohsawa, M., Nozaki, R. & Sakura, T. (1982). Assessment of tree population state using tree architecture. In: *Assessment of Terrestrial Environment using Higher Plants*. K. Okutomi (Ed.) pp. 1-24. *Report on Environmental Science* B149-R12-3.
- Ohsawa, M. & Ozaki, K. (1993). Hierarchical analysis of vegetation /environment pattern for east Asian extra-tropical evergreen broad-leaved forests. *Jpn. J. Biometeor.* 30.
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1992). Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62: 365-392.
- Schulze, E.-D. (1982). Plant life forms and their carbon, water and nutrient relations. In: *Encyclopedia of Plant Physiology. New Ser. 12B. Physiological Plant Ecology II*. O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler (Eds.) pp. 615-676. Springer-Verlag, Berlin.
- Sprugel, D. G. (1989). The relationship of evergreenness, crown architecture, and leaf size. *Am. Nat.* 133: 465-479.
- Tagawa, H., Kawakubo, N., Suzuki, E. & Kohyama, T. (1989). Vegetation of Amami-Oshima Island, Nansei Islands, Japan. In: *Study of Essential Factors for Preservation of Wildlife in Nansei Islands*. Environmental Agency (Ed.) pp. 75-105. Environmental Agency, Japan.
- Woodward, F. I. (1987). *Climate and Plant Distribution*. Cambridge University Press, New York.

Biodiversity in The Tropics

Donald E. Stone

Organization for Tropical Studies, Duke University
Box 90630, Durham, NC 27708-0630

Key words: *arthropods, biodiversity, birds, ecological regulation, flowering plants, tropics.*

Introduction

The biodiversity of plants, animals and microorganisms reaches its zenith in tropical regions where 7% of the Earth's land surface contains in excess of 50% of the world's biota. While some 1.4 to 1.8 million species have been described to date, a variety of estimates places the total inventory somewhere between 3 and 30 million (Wilson, 1988). Most of these are undescribed species of arthropods which, according to Erwin (1988), will be found principally in tropical forest canopies. Extrapolations based on a very, very limited sample of the total pool of biodiversity have been used to arrive at these numbers, so there is by no means a consensus amongst scientists as to the validity of the higher estimates (Stork, this volume). Nevertheless, extrapolations have been used by May and others to provide a more realistic estimate of biodiversity for a whole range of groups (May, 1992). In the fungi, for example, approximately 69,000 species have been described to date, and many of these are specialists on vascular plants (Hawksworth, 1991). By some estimates there are six fungal specialists for each of the 250,000 species of vascular plants. If this is so the biodiversity of fungi may approach 1.5 million species, some 20 times the confirmed number.

What this totality of species diversity means to the structure and function of ecosystems is not addressed by these particular studies, of course, and no values have been assigned to the importance of a particular species in an ecosystem (*e.g.*, keystone species) nor recognition of the fact that biodiversity is not uniformly distributed, either in an ecological or taxonomic context. One only need recall, for example, that marine diversity is far greater at the phylum level than in any other realm, including freshwater, terrestrial and symbiotic (Grassle *et al.*, 1991; Ray & Grassle, 1991). While it is clear that our knowledge about biodiversity is rudimentary at best, in some sense these academic aspects of understanding biodiversity are just that, "academic." The international community of concerned citizens is now

very aware of species loss due to the deterioration of our environment and the massive destruction of tropical rainforests, in particular, and there is, rightfully, an impatience with the methodical, scientific approach which can easily be misunderstood as standing by while "watching Rome burn."

Notwithstanding the urgency of doing something now about stemming the loss of biodiversity, a point that I will return to in closing, the fact remains that intelligent decisions about the global commons depend on having good information. Without solid scientific evidence and understanding of the real and potential role of biodiversity, good recommendations will be wanting and credibility will rapidly be lost when hard decisions have to be made because of finite resources. The purpose of this presentation, then, is four fold: to identify the principal centers of biodiversity; to examine some of the explanations that have been proposed to account for the development and maintenance of biodiversity; to outline examples of biodiversity research in Costa Rica that have relevance to studies elsewhere; and to reflect on the importance to society of understanding the role of biodiversity.

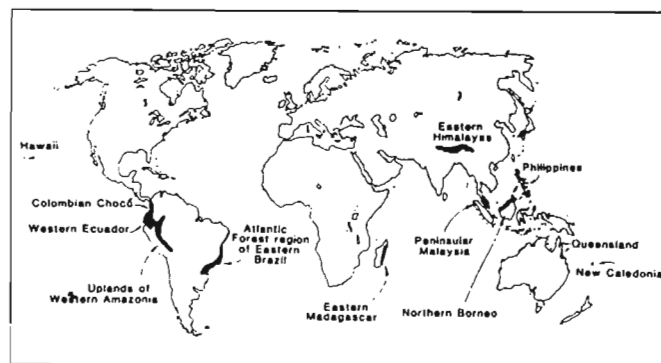


Figure 1: Hotspots in tropical forests (from McNeely *et al.*, 1990; after Myers, 1988).

Biodiversity hotspots and scientific considerations

Precisely which areas in the tropics are richest in species and of most interest to the conservationist and scientist alike is a question that led Norman Myers (1988) to identify so-called "hotspots" of biodiversity (Figure 1). The idea of hotspots is based on the observation that some regions are inherently richer in endemic species. Madagascar, for example, has a flora of 6,000 species, and 82% of these are endemics. Likewise New Caledonia shows 89% endemism in its 1,580 species of vascular plants (McNeely *et al.*, 1990). In all, Myers recognized 12 areas, including 10 in developing countries, namely: New Caledonia, Madagascar, Atlantic Forest of Brazil, Western Ecuador, Chocó of

Colombia, Western Amazonian Uplands, Eastern Himalayas, Peninsular Malaysia, Northern Borneo and the Philippines. In addition, Hawaii and Queensland, Australia were singled out as critically sensitive areas in the developed world. In spite of the recognition of these 12 hotspots, I need emphasize that the biogeography of biodiversity is not well known for plants. The regions that have the highest species diversity are the least explored, and they are most often in countries that are the most exploited and have the least interest and capability of undertaking floristic inventories (Campbell & Hammonds, 1988). Of the 240,000 or so species of flowering plants, 65% are thought to be tropical; and of these 19% are African, 22% Asian and 58% are from Central and South America (Table 1). Species richness in ferns is somewhat different, with Asia and the Americas having approximately equal numbers. The striking and sad state of affairs is that we, the systematists, have done a poor job in assembling the knowledge at hand.

Table 1: Continental distribution of tropical plant species (adapted from Prance, 1977).

Taxa	Worldwide		%	Asia	Tropical	
		#			Africa	America
Flowering plants	240,000	155,000	65	35,000	30,000	90,000
Ferns	12,000	11,000	92	5,000	1,000	5,000
Mosses	10,000	5,000	50	+	++	++
Hepatics	11,000	?	?	?	?	?
Total	273,000					

Not surprisingly we have a far better understanding of endemism in birds. Of the 9,600 species of birds in the world, 27% of the landbirds have a breeding range of 50,000 sq. km or less. This size area was proposed by Terborgh and Winter (1983) as a manageable and biologically meaningful sample size that is useful in defining areas of concentrated endemism, referred to as endemic bird areas, or EBAs. By dividing the world into 6 regions, South America shows up as the continent with the highest percentage (26%) of EBAs, with South East Asia (19%) and the combined continents of Africa/Europe (18%) vying for a distant second (ICBP, 1992). The concentration of bird diversity, like that of many groups, has a latitudinal distribution, and in the case of EBAs, 76% are found in the tropics. In fact, 63% of the EBAs occur in just 10 countries, in descending order: Indonesia, Peru, Brazil, Mexico, Colombia, China, Papua New Guinea, Ecuador, Argentina and the Philippines (Figure 2).

Without doubt all of these hotspots are important to conservation, but from an objective point of view it is also clear that there are considerable differences between sites based on the "quality" of species that are present. Systematists from the British Museum of Natural History have asked "if all species are equal," what should we be protecting (Vane-Wright *et al.*, 1991)? If we had to make hard choices between saving two species, for example, would we choose *Welwitschia* or *Taraxacum*, or is the panda equivalent to a species of rat? The answer is obviously no on both counts, so these researchers are trying to develop a weighted system that is sensitive to both taxonomic rank and the number of species. And by extension, they have also asked the question if "all places are equal?"

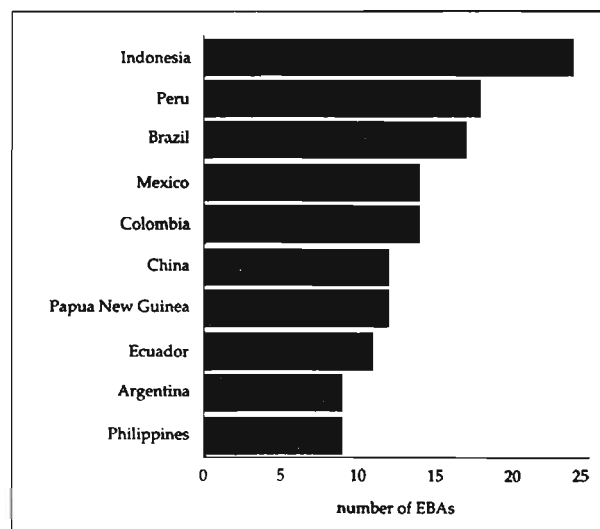


Figure 2: Countries with the highest numbers of endemic bird areas (from ICBP, 1992).

Still another consideration in dealing with biodiversity is the desirability of having knowledge about the historical record and the changes that have occurred over time in regard to both the species and its habitat. Quite obviously what was seen in forest cover and biodiversity in Costa Rica in 1940 is not what the same habitat or community looked like in 1970, and certainly there will be little resemblance to pre-World War II vegetation by the year 2000. The composition of communities has changed over time, either through abiotic or biotic disturbances and interactions. The most dramatic effects in our lifetime have been the unrelenting devastation by man and society on tropical rainforests. Less obvious are the historical effects, as can be readily demonstrated by looking at the modern-day distribution of the walnut family, Juglandaceae (Stone, 1989). This is a family of flowering plants that consists of wind-pollinated trees with

highly diversified fruit types and both wind- and animal-dispersed seeds. The 8 genera are found today in temperate forests of Asia (3), Asia/Europe (1), Asia/Americas (2) and the Americas (2). Since 6 of the 8 genera are known from Asia today, one might conclude that this region is the epicenter of speciation for the family. In fact, however, this conclusion is erroneous. If one looks at the modern and fossil records together, a very different picture emerges. All of the extant genera, plus some fossil taxa not found in Asia, are known from either extant or fossil collections from North America. A true understanding of the biodiversity of this family of flowering plants would certainly be incomplete without knowledge of the exceptional fossil record.

Table 2: Diversity along a latitudinal gradient (adapted from Ricklefs, 1983).

Latitude	Ants	Birds
70°		56 (Greenland)
60°	10	
40°	50-100	105 (New York)
20°	100-200	
15°		469 (Guatemala)
10°		830 (Costa Rica)
5°		1,395 (Colombia)

Explanations for high biodiversity in the tropics

It is important to note that high species diversity in the tropics is, in fact, part of a gradient that extends from the poles to the equator. The majority of the animal and plant groups shows a latitudinal gradient, with low biodiversity in the high latitudes and increasingly higher diversity as one approaches the equator (Stevens, 1992). At 20° N latitude, for example, there are 10 to 20 times as many species of ants than there are at 60° N (Table 2). And with birds it is much the same story. Colombia at 5° N has 20 times more species than Greenland at 20° N. The biodiversity gradients from pole to equator are positively correlated with the increase in both precipitation and temperature. It is not surprising therefore that the 12 or so hypotheses advanced to explain the richness of the tropical regions integrate these two major climatic factors. The six principal hypotheses proposed to explain the biodiversity gradient were summarized by Pianka (1966) and Lugo (1988), and they include: *time* (areas least disturbed for the longest time will diversify and accumulate the most species); *spatial heterogeneity* (a greater number of habitats provide more niches for more species); *competition* (greater competition narrows and thereby

increases the number of species niches and species diversity); *predation* (greater predation holds down prey populations and reduces competition, thereby allowing more species to coexist); *climatic stability* (stable regions allow evolution of finer specializations and smaller niches); and *productivity* (greater productivity results in more energy to be partitioned among more species).

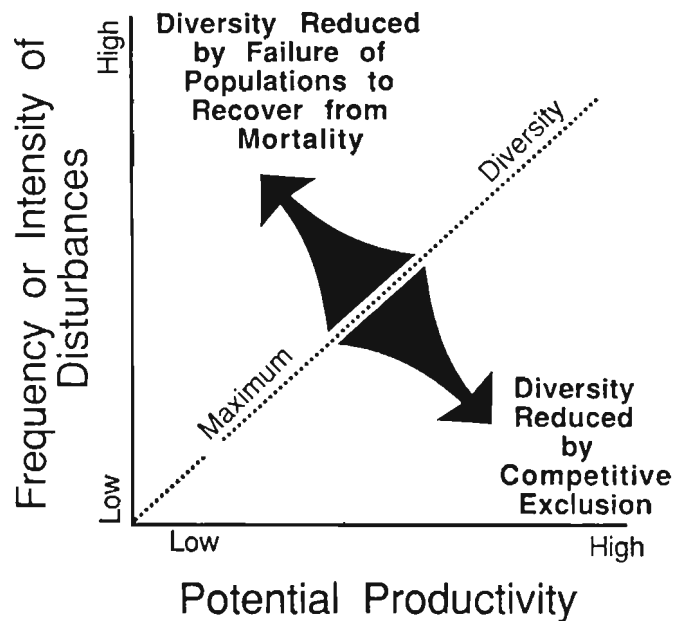


Figure 3: Predicted effects of disturbance and productivity on the number of coexisting analogous species within a particular functional type in a community (in Solbrig, 1991; after Huston, in press).

These hypotheses have all been subject to criticism, and most particularly to the complaint that there are too many dependent variables which do not lend themselves to testing. In still another effort Michael Huston has outlined a promising new conceptual framework that is based on ecological regulation (Huston, in press). According to Huston the major factors affecting biodiversity include: 1) spatial and temporal heterogeneity of resources and physical conditions; 2) the number of different species available in the regional pool, because species themselves are often resources for yet other species and diversity tends to be self-amplifying; and 3) the ability of populations to recover from low population densities that result from mortality by disturbances and stress, or from random fluctuations in population size. The general diagram expressing these factors plots *potential productivity* along the horizontal axis and the *frequency or intensity of disturbance* on the vertical axis (Figure 3). Productivity is defined here as the maximum growth rate of populations, in terms of

individuals or biomass, under specific conditions of resource availability. Disturbance, on the other hand, is defined as the mortality of individuals caused by abiotic processes such as fire, floods or extreme climatic conditions, or by biotic processes such as predation, parasitism, disease or herbivory. The implication here which fits predictions and observations is that "in general, the more constant or predictable a resource, the more likely [it is that] such a resource is [able] to support other species" (Solbrig, 1991). This model also interprets species richness as a balance or dynamic equilibrium between the opposing forces of competitive displacement and forces that prevent or delay competitive exclusion. And finally if one looks at life-history strategies, high intensity of disturbance and productivity result in high biodiversity of *r*-selected weedy species. Conversely low disturbance and productivity result in the co-existence of many life-history strategies. And perhaps most importantly in terms of a tropical rainforest, low disturbance coupled with high productivity results in the classical *K*-selected characteristics, namely species with: 1) long life spans; 2) long periods of reproduction; 3) large size individuals; and 4) high resource-use efficiency. Note too that temporal asynchrony in patch dynamics across the landscape would favor nearly all life-history strategies and maximize diversity in a region.

Biodiversity research in Costa Rica

Costa Rica is a country that has long been a friendly haven to scientists throughout the world who were interested in pursuing research in tropical biology. Because of this attitude, the small size of the country and the high diversity of ecosystems, habitats and species, studies have focused on biodiversity for quite some time. There are two ongoing programs in particular that have captured the attention of those interested in inventorying biodiversity and putting it to use in a meaningful and sustainable way. The two programs have approached the general problem of cataloguing the immense diversity of species in different ways. In the first case, represented by the highly successful National Institute of Biodiversity (INBio, 1992), the philosophy might best be described as a "get-them-all" approach (Longino, in press). This is where the effort is made to collect everything in sight, catalogue the collections, assemble information on the morphology, behavior, natural history and distribution, publish taxonomic keys and descriptions, name the new species, and ultimately determine phylogenetic relationships and construct classification systems. The second camp, represented by the *Arthropods of La Selva* project (ALAS), is designed to "sample a few and estimate the rest" (Longino, in press).

The "get-them-all approach" has reached its zenith in INBio where they are engaged in a country-wide inventory of all plants, animals

and microorganisms estimated to comprise some 500,000 species. This mission is made all the more incredible with the self-imposed deadline of 10 years. To reach these objectives INBio "relies on a network of trained field collectors called parataxonomists." They are individuals from rural communities who "exhibit a penchant for natural history and a willingness to try a non-traditional profession. They attend a 6-month crash course in entomology and botany, and then return to their communities where they establish a biodiversity office" (Longino, in press). The goal of this vast undertaking is to put biodiversity to use for the good of the Costa Rican people, both through educating them about the many values of biodiversity, as well as taking advantage of the direct benefits anticipated through chemical prospecting (Holden, 1991).

The ALAS project really combines the "get-them-all approach" with a rather sophisticated sampling scheme that is designed to answer a very basic question, namely: *How many species of arthropods are there in a lowland tropical rainforest?* The project is simple in principle but complicated in design. The project is concentrating its attention on two sets of arthropods: 1) there are the so-called *Focal Taxa* which comprise one or a few families, such as the ant family Formicidae; and 2) there are the *Survey Taxa* such as the Vespoidea which include the Formicidae plus 11 additional families (e.g., velvet ants, vespid wasps, etc.). All told there are 15 *Focal Taxa*, 9 of which are insect families (e.g., ants, parasitic wasps, pomace flies, moths, scarab beetles, weevils and termites); 2 families are spiders; and 4 families are mites.

The collecting procedures involve two basic approaches: 1) the "get-them-all approach" uses all means to obtain the full complement of species diversity. This involves field work, looking at museum collections and searching the literature. The species diversity of the *Focal Taxa* become the known universe against which the efficiency of sampling techniques is compared; and 2) the sampling or quantitative approach to collecting which is much more selective and regularized. There are strict protocols and schedules, and the samples are stratified according to primary vs. secondary forest, species of tree, type of soil, and time of year. Collecting quantitative samples involves the complete range of techniques that are appropriate for the taxa and habitat, including blacklights, malaise traps, Berlese funnels, pitfall traps and canopy fogging. The quantitative sampling method is applied to both the *Focal Taxa* and the *Survey Taxa*, so in effect 3 data sets are obtained (Longino, in press): 1) total species number on the *Focal Taxa*, referred to as $T(focal)$; 2) a quantitative estimate of the number of species in the *Focal Taxa*, $\hat{Q}(focal)$; and 3) a quantitative estimate of the number of species in the *Survey Taxa*, $\hat{Q}(survey)$:

$$\frac{Q \text{ (focal)}}{T \text{ (focal)}} = \frac{Q \text{ (survey)}}{T \text{ (survey)}}$$

Since the samples provide both a total species number and a species estimate of the number for the *Focal Taxa*, these two numbers do in fact provide a measure of efficiency in calibrating the quantitative sampling method. With this information, *T (survey)*, which is a sizable portion of the arthropod fauna of La Selva, can be calculated. This is one methodology that is expected to give a better estimate of the "grail number" of species and advance our understanding of global diversity patterns.

Societal implications

As noted in the introduction, biodiversity research is in some sense too academic and out of sync with the biodiversity crisis. If we extrapolate the 1990 rate of deforestation, for example, the current forests will be extinct by the year 2050 (Terborgh, 1992). The clock has nearly run out, and there simply is not time to research the issues at our own academic pace. So what are our choices? I see three. We in the developed world need to: 1) finance the establishment and protection of parks while working with the local people to get them compensated, involved and committed; 2) foster population control and projects leading to environmentally sound and sustainable development and economic well-being; and 3) work with policymakers to ensure that they have a sound ecological basis for making decisions. So where does this leave the issue of research on biodiversity? I think that we cannot afford to neglect it. After all, from where is the sound ecological advice going to come if not from scientists? If scientists do not provide a solid understanding of the structure and function of biodiversity, we will rapidly lose credibility in the government circles and with the public at large, and political decisions will reign unchecked by the potential biological consequences.



References

- Campbell, D. G. & Hammond, H. D. (Eds.) (1988). *Floristic Inventory of Tropical Countries: The Status of Plant Systematics, Collections, and Vegetation, plus Recommendations for the Future*. The New York Botanical Garden.

- Erwin, T. L. (1988). The tropical forest canopy. The heart of biotic diversity. In: *Biodiversity*. E. O. Wilson (Ed.) pp. 123-129. National Academy Press, Washington, D.C.
- Grassle, J. F., Lasserre, P., McIntyre, A. D. & Ray, G. C. (1991). Marine biodiversity and ecosystem function. *Biology International*, Special Issue No. 23: 1-19.
- Hawksworth, D. L. (1991). The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological Res.* 95: 641-655.
- Holden, C. (1991). Briefings: The hunt for drugs from nature. *Science* 254: 28.
- Huston, M. A. (In press). *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- ICBP. (1992). *Putting Biodiversity on the Map: Priority Areas for Global Conservation*. Cambridge, U.K.: International Council for Bird Preservation.
- INBio. (1992). *Informe Anual de Labores 1991*. Santo Domingo, Costa Rica: Instituto Nacional de Biodiversidad.
- Longino, J. T. (In Press). *How to Measure Arthropod Diversity in a Tropical Rainforest*. *Biology International*.
- Lugo, A. E. (1988). Diversity of tropical species: Questions that elude answers. *Biology International*, Special Issue 19: 1-37.
- May, R. M. (1992). Past efforts and future prospects towards understanding how many species there are. In: *Biodiversity and Global Change*. O. T. Solbrig, H. M. van Emden & P. G. W. J. van Oordt (Eds.) pp. 71-81. IUBS Monograph Series No. 8, IUBS, Paris.
- Mcneely, J. A., Miller, K. R., Reid, W. V., Mittermeier, R. A. & Werner, T. B. (1990). *Conserving the World's Biological Diversity*. IUCN, Gland, Switzerland; WRI, CI, WWF-US, and the World Bank, Washington, D.C.
- Myers, N. (1988). Threatened biotas: "Hotspots" in tropical forests. *The Environmentalist* 8: 243-256.
- Pianka, E. R. (1966). Latitudinal gradients in species diversity: A review of concepts. *Am. Nat.* 100: 33-46.

- Prance, G. T. (1977). Floristic inventory of the tropics: Where do we stand? *Ann. Missouri Bot. Gard.* 64: 659-684.
- Ray, G. C. & Grassle, J. F. (1991). Marine biological diversity. *BioScience* 41: 490-498.
- Ricklefs, R. E. (1983). *The Economy of Nature*. 2nd ed. Chiron Press, New York.
- Solbrig, O. T. (Ed.) (1991). *From Genes to Ecosystems: A Research Agenda for Biodiversity*. Cambridge, Massachusetts: IUBS.
- Stevens, G. C. (1992). The elevational gradient in altitudinal range: An extension of rapoport's latitudinal rule to altitude. *Am. Nat.* 140: 893-911.
- Stone, D. E. (1989). Biology and evolution of temperate and tropical Juglandaceae. In: *Evolution, Systematics, and Fossil History of the Hamamelidae*, Vol.2, *Higher Hamamelidae*. P. R. Crane & S. Blackmore (Eds.) pp. 117-145. Systematics Association Special Volume 40B. Clarendon Press, Oxford.
- Terborgh, J. (1992). *Diversity and the Tropical Rain Forest*. Scientific American Library and W. H. Freeman, New York.
- Terborgh, J. & Winter, B. (1983). A method for siting parks and reserves with special reference to Colombia and Ecuador. *Biol. Conservation* 27: 45-58.
- Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. (1991). What to protect?--Systematics and the agony of choice. *Biol. Conservation* 55: 235-254.
- Wilson, E. O. (Ed.) (1988). *Biodiversity*. National Academy Press, Washington, D.C.

Biodiversity in Tropical Forest and Chemical Ecology

Hajime Ohigashi and Koichi Koshimizu

Department of Food Science and Technology, Faculty of Agriculture,
Kyoto University, Kyoto 606 Japan

Key words: *allelopathy*, *medicinal plant*, *chimpanzee*,
Baillonella toxisperma, *Vernonia amygdalina*.

Introduction

Tropical forests are perhaps the richest biospecies habitat on earth, in which diverse interactions between organisms exist. In such interactions, some chemicals occurring in each organism are known to play important interactive roles. We have investigated such chemicals (bioactive compounds) from plants in the tropical forests of Africa. Here we describe how these compounds are involved in biological interactions, by citing two examples found to occur between plant and plant, and plant and animal.

Interaction between plant and plant: Allelopathic factor of *Baillonella toxisperma* Pierre

In field surveys of the rain forest of Cameroon, an outstanding phenomenon was observed in *Baillonella toxisperma* Pierre (Sapotaceae) (Ohigashi, *et al.*, 1989). This tree is found only in a limited area of the forest, and in the vicinity of the mature tree, only the saplings are able to grow. The area of growth for the saplings is restricted to that under the crown of the mature tree. Furthermore, the methanolic extracts of both the aerial part and root of the tree exhibit strong plant growth inhibitory activity. Thus, this is thought to be allelopathy, a phenomenon first described by Molisch (1937), which is caused by specific secondary product(s) of the tree.

By monitoring the growth inhibitory activities against cucumber and rice seedlings, a new compound, 3-hydroxyuridine (Figure 1), was isolated as the inhibitory agent (Ohigashi *et al.*, 1989). 3-Hydroxyuridine shows strong plant growth activities in laboratory bioassays, particularly against dicotyledons.

3-Hydroxyuridine occurs most abundantly in the leaves (0.60 mg/g dried leaf), followed by the stem (0.16 mg/dried stem) and root (0.09 mg/dried root). This compound was expected to exude from the root

and to be accumulated in the surrounding soil. However, significant amounts of 3-hydroxyuridine were not detected in the soil extract. The water solubility of 3-hydroxyuridine may be unsuitable for its accumulation in the soil. On the other hand, such solubility should be favorable for the leaching ability from the leaves and stems. Although further study is necessary, the allelopathy of *B. toxisperma* may be most simply understood by the following explanation: 3-hydroxyuridine is leached from the leaves or stems with water flow to the ground. This may in turn be converted chemically or biologically into less water soluble derivative(s) such as 3-hydroxyuracil, whose plant growth inhibitory activity was also confirmed. In this form the accumulated compounds may exhibit allelopathy.

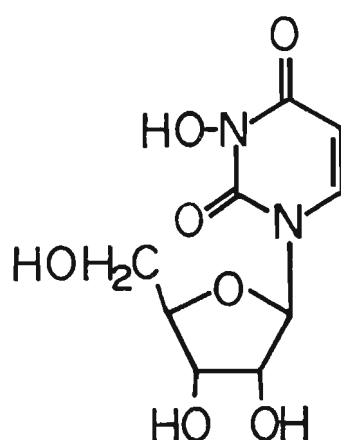


Figure 1: 3-Hydroxyuridine.

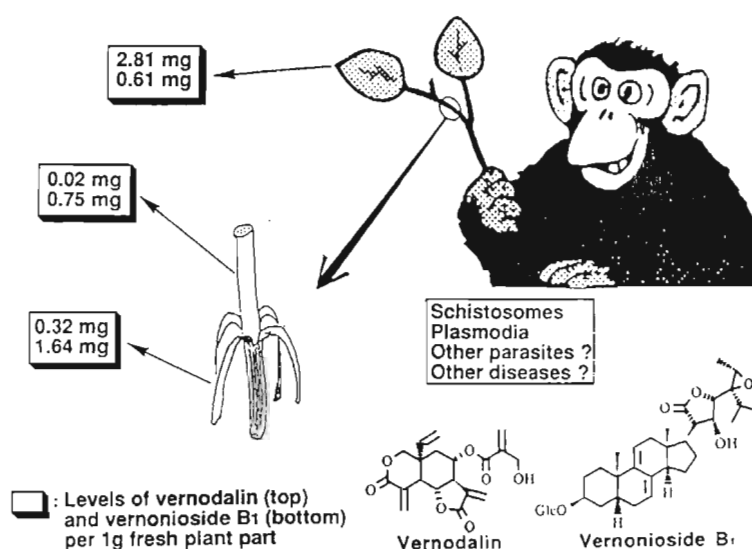
Kaji (1985) further indicated by a clear analysis of the distribution pattern of trees that some habitat segregation occurs among plants even in the mixed forest of Cameroon. It may in particular by allelopathic factors.

Interaction between plant and animal: Medicinal use of *Vernonia amygdalina* Del. by wild chimpanzees

Plants possibly used for medicinal purposes by wild primates have recently been reported (Phillips-Conroy, 1986; Takasaki & Hunt, 1987; Wrangham & Nishida, 1983). The uses indicated in these reports seem to have been preventive because of the consumption by apparently healthy individuals. Huffman and Seifu (1989) first reported that a wild chimpanzee might consume plants for their curative purposes. An apparently sick adult female chimpanzee chewed the pith of a plant, *Vernonia amygdalina* Del. (Compositae), to extract its bitter juice. This plant is not a common part of the chimpanzees' diet. Moreover, she

seemed to have returned to regular health, within 20 hours after ingestion.

Based on this, we began an extensive study of the physiologically active substances of *V. amygdalina* first by monitoring bitterness. Bitter compounds are known to carry several important biological and physiological activities. Two classes of bitter constituents have been isolated (Jisaka *et al.*, 1992a). One was a group of known sesquiterpene lactones including vernodalin and three other related compounds. Another class was a series of new steroid glucosides, named vernonioside A₁-A₃ with bitterness and B₁ without bitterness.



leaves and 0.32 mg/g fresh bark, respectively). On the other hand, the levels of vernonioside B₁ in the pith, bark and leaf were constantly high (Figure 2) (Jisaka *et al.*, 1992b). Recently, antiplasmodial and antiamoebic activities of the steroid glucosides and their derivatives have also been clarified (C. W. Wright, G. C. Kirby, D. Allen, D. C. Warhurst and J. D. Phillipson, unpub.). Thus, the use of the pith of *V. amygdalina* by wild chimpanzee may partly be understood by the antiparasitic properties of the steroid glucosides such as vernonioside B₁ as illustrated in Figure 2.

Conclusion

Biological interactions in the tropical forest are much more diverse and complex than that in other environments. However, only a little knowledge has thus far been accumulated about such diverse interactions. Chemicals involved in each interaction may be valuable tools for the analysis of biological interactions, contributing to a better understanding of the factors responsible for biodiversity.

References

- Huffman, M. A. (1991). The use of naturally occurring medicinal plants for the possible treatment of parasite related disease by wild chimpanzees. In: *Window on Wildlife: Research in Tanzania*. E. Niemi & A. Outwater (Eds.) pp. 39-41. Tanzania Printers, Dar es Salaam, Tanzania.
- Huffman, M. A. & Seifu, M. (1989). Observation on the illness and consumption of a possibly medicinal plant *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park, Tanzania. *Primates* 30: 51-63.
- Jisaka, M., Ohigashi, H., Takagaki, T., Nozaki, H., Tada, T., Hirota, M., Irie, R., Huffman, M. A., Nishida, T., Kaji, M. & Koshimizu, K. (1992a). Bitter steroid glucosides, vernonioside A₁, A₂, and A₃, and related B₁ from a possible medicinal plant, *Vernonia amygdalina*, used by wild chimpanzees. *Tetrahedron* 48: 625-632.
- Jisaka, M., Kawanaka, M., Sugiyama, H., Takegawa, K., Huffman, M. A., Ohigashi, H. & Koshimizu, K. (1992b). Antischistosomal activities of sesquiterpene lactones and steroid glucosides from *Vernonia amygdalina*, possibly used by wild chimpanzees against parasite-related diseases. *Biosci. Biotech. Biochem.* 56: 845-846.

- Kaji, K. (1985). Study on the floristic composition and the structure of tropical rain forest in south western Cameroon. In: *Search for Useful Plants in Tropical Rain Forest in Cameroon, and Chemical Studies on Biologically Active Substances of the Plants*. K. Koshimizu (Ed.) pp. 12-42. Department of Food Science and Technology, Kyoto University, Kyoto.
- Molisch, H. (1937). *Der Einfluss einer Pflanze auf die Andere-Allelopathie*. Fischer, Jena.
- Ohigashi, H., Kaji, M., Sakaki, M. & Koshimizu, K. (1989). 3-Hydroxyuridine, an allelopathic factor of an African tree, *Baillonella toxisperma*. *Phytochemistry* 28: 1365-1368.
- Phillips-Conroy, J. E. (1986). Baboons, diet, and disease: food selection and schistosomiasis. In: *Current Perspectives in Primate Social Dynamics*. D. M. Taub & F. A. King (Eds.) pp. 287-304. Van Nostrand Reinhold, New York.
- Takasaki, H & Hunt, K. (1987). Further medicinal plant consumption in wild chimpanzees? *Afr. Stud. Monogr.* 8: 125-128.
- Wrangham, R. W. & Nishida, T. (1983). *Aspilia* spp. leaves: A puzzle in the feeding behaviour of wild chimpanzees. *Primates* 24: 276-282.

Creation of Reserves in Tropical Forests and Researchers

Suehisa Kuroda

Laboratory of Physical Anthropology, Faculty of Science,
Kyoto University, Sakyo-ku, Kyoto 606-01 Japan

Key words: *tropical forest, conservation, animal-plant relations, primates, Zaire, Congo.*

Introduction

The African tropical forests have decreased by 17% during the last decade due to timber exploitation and slash-and-burn cultivation (Marcier, 1991). It is an urgent problem to increase protected areas as well as to promote sustainable use of the forest resources. Researchers working in the tropical forest are also responsible for contributing to resolve these problems.

Because conservation projects are often concerned with multiple aspects such as the livelihood and culture of local people, national policy and economy, implementing of such projects often exceeds the capabilities of the researchers. Nevertheless, their contribution is essential. Only they can provide the implementors with ecological data for the establishment of new reserves. They can look after the people's benefits so that long-term conservation may be realized.

Studying African great apes, we, members of the Kyoto University primatologist group, have been contributing to the establishment of two new reserves in Zaire and Congo, in collaboration with researchers of these countries. These reserves have contrasting features. One reserve in Zaire covers a small area neighboring to a village; whereas the other in Congo covers a large area of virgin forest, being established by a large international project. Many problems we face in these projects, are similar to those faced by those involved in other projects in tropical Africa.

In this report, I describe the process and problems of establishing these reserves in hope that this may be useful for other planning similar conservation projects. Also I will describe the important role of larger mammals, especially great apes, in the maintenance of plant diversity in the forest.

Great apes as seed dispersers

It is becoming well known that animals contribute to the regeneration of the forest by seed dispersal (Tutin *et al.*, 1991; Yumoto, 1992). Many fruit species cannot well germinate or grow without first eaten and carried of by animals (zoochory). From this view, apes and elephants have a special important role for plant species with large-size seeds and hard skin that many other animals cannot process of swallow.

Pygmy chimpanzees (bonobos, *Pan paniscus*) in central Zaire feed on fruits of more than 60 species (Kano & Mulvwa, 1984) and they contribute to seed dispersal of more than 55 species. Combining gorillas and chimpanzees in the Ndoki Forest of northern Congo, they disperse fruits of more than 53 species (Kuroda, unpub.). Many species of *Cola*, *Sterculia* and *Landolphia* bear hard skinned fruits up in the canopies and they do not open the skin even after ripen. Although monkeys sometimes eat such fruits slowly, these species are considered to be exclusively dispersed by apes. In the Lope National Park of Gabon, gorillas also disperse many fruit species (probably about 70 species) including an endemic plant species *Cola lizae*, which is dispersed by gorillas exclusively (Tutin *et al.*, 1991).

Animals' contribution to forest regeneration can be clearly demonstrated by Table 1, which compares the frequencies of fruit species seedlings in the virgin forest and in forest in which primates are no longer found by over-hunting. Most seedlings of the virgin forest could be considered to originate from great apes' feces because in many cases they were densely bundled within an area for 20-30 cm in diameter, and contained species those elephants did not eat.

It is a common occurrence in the central Africa for many hunters to enter the deep forest, following roads constructed by logging companies. This results in the rapid depletion of larger mammals. Workers of the companies in the forest, are also often join responsible for the loss of wildlife. This must be cautiously controlled because such acts will damage not only the animal populations but also regenerating mechanism of plant diversity.

The Luo Special Scientific Reserve

The pygmy chimpanzee is an endangered species, but they inhabit the upper Luo River region in high densities because people observe a taboo that forbidden them to kill this ape (Kano, 1992). The Kyoto University team started a study of the ape in 1974, and from 1976 Dr. T. Kano, the team leader, repeatedly proposed to the local and central

Zaire Governments that a reserve for pygmy chimpanzees should be established in this area.

Table 1: Distribution frequencies of seedling sites containing fruit species eaten by primates and elephants in the virgin forest and the forest neighboring to villages.

	Virgin Forest (Ndoki)					Bomassa Forest
Census rout	1	2	3	4	5	6
Vegetation type*	M.S.	M.S.	M.S.	R.G.	R.G.	R.G.
Distance (m)	335	110	1157	112	202	1500
No. of seedling site	31	18	115	21	54	13**
Rate (No. of s.s./m)	0.093	0.16	0.10	0.19	0.27	0.011
No. of species	14	4	16	7	9	5!
Rate (No. of spp./m)	0.042	0.036	0.014	0.063	0.045	0.003

Note: seedlings of 28 species were checked. Fruits of these are apes' common food and seedlings are relatively easy to identify. Young trees less than 1 m high are counted, if a mature tree of the same species cannot be found around. An assemblage of seedlings of similar height within 40 cm is counted as 1 site. The Ndoki Forest has been free from any human activity during the last 50 years (Kuroda 1992). Bomassa forest is located around Bomassa village, the closest village (25 km) to the Ndoki Forest. *: M. S. is mixed species forest or tropical semi-deciduous forest, R. G. is riverine *Gilbertiodendron* forest. **: only 18 seedlings were found in all 16 sites, whereas many seedling sites in the Ndoki Forest contain plural seedlings. In the virgin forest, we found 5 species of *Landolphia*, but they were counted as 1 species in this study. In Bomassa forest, at least two of 5 species are lacked. !: 3 species are eaten and possibly dispersed by human.

In 1986, Centre de Recherche en Science Naturelle (CRSN) planned to establish a reserve as its primatological field, and the following year CRSN, local governments, and villagers signed a treaty to setting aside the area around Wamba and Ilongo villages as a reserve. In 1990, it was official with a regional government's approval (Idani, 1990).

Because it was impossible to create a national park to protect pygmy chimpanzees without removing more than 1,000 people from their native lands, both Zairean and Japanese researchers set about to plan the reserve such that it would harmonize with the people's benefits while not compromising the protective status of the pygmy chimpanzee population. This is a small reserve covering only 180 km², but it is very rich in fauna. Fifty nine mammal species are recorded (Idani, 1990) and 500-600 pygmy chimpanzees are estimated to inhabit the area. Gun-hunting, all hunting of primates, wire snares, and clearing of primary forest are forbidden but otherwise people can gather plant materials for daily life and hunt games not protected by Zairean law by traditional means.

The key factors which encourage the local people to agree on the establishment of the reserve were: mutual understanding between

villagers and researchers brought about by a long research history, respect for the people's traditional rights to the forest, people's awareness of a rapid decreasing of game animals due to uncontrolled gun-hunting, economic contribution through research activities, accordance between tradition and the aim of the reserve, and the active involvement of Zairean researchers, especially Dr. N. Zana, the General Director of CRSN and Mr. E. Wina, the Director of the CRSN Mabali Station. However, the reserve is too small to completely preserve pygmy chimpanzee population, and no guard system has been established. Besides, bushmeat shortage will surely occur in the future, threatening integrity of the reserve. We plan for the New Luo Project to expand the protected area for pygmy chimpanzees to the whole upper Luo region area (6,000 km²), to establish a conservation system, and to promote a study of alternative meat supply systems.

Proposing this project to GEF through the International Bonobo Protection Fund, we have partially started the project (The Bonobo Protection Funds, Bonobo News), however, it has been at deadlock because of the chaotic political situation of Zaire since September 1991. This has also made researchers impossible to stay in the reserve, threatening its integrity.

The Ndoki-Nouabale National Reserve

In 1987 and 1988, a joint primatological research team involving Kyoto University and the Ministry of Science of Congo, surveyed northern part of the Sangha Region, and proposed to the Congolese Government to establish a reserve in the area. A huge area remains as almost virgin forest, very rich in fauna. In 1989, this team and the Bomassa villagers, who traditionally have the right to use the southern area on the proposed reserve, agreed to protect the richest areas of fauna. In the same year, the Ministry of Forestry Economy accepted the plan proposed by Dr. R.A. Oko, a member of the team, to establish a new reserve.

The Wildlife Conservation International (WCI) team also surveyed the same area successively, and arranged for GEF and UASID to support the Congolese Government in establishing a national reserve covering 4,600 km². Consequently, a USAID project started in 1991, and a GEF project in 1993. This reserve will be the most important one in the African tropical forest zone, because many endangered species, such as great apes, elephants, and bongos inhabit this area in high population densities.

The projects will continue until 1997 with a total budget exceeds 3.6 million US\$. WCI is playing the main role in implementation of the

projects, making a conservation system, constructing infrastructure, and organizing concerned Congolese officials and scientists. GTZ also will join this by helping to construct infrastructure. Primatologists and anthropologists of Kyoto University are contributing to this project with the Congolese voluntarily, by conducting such research project of the forest ecology, indigenous people's traditional knowledge of the forest, sustainable use of forest resources.

However, there remains several problems. First, these projects are too big and thus carry a considerable high possibility to render damage to the local societies. Also it is possible that this will attract too many people. Nothing is guaranteed after the 5 years project end. Furthermore, the budget for the training of young Congolese scientists is currently insufficient. Study programs for long-term conservation such as the exploitation of non-timber resources, and alternative animal protein supply systems are not much considered. It is needed to strengthen a check and feed back system monitoring these project from the view point of long-term conservation.

Acknowledgement

This is the revision of the paper presented at the International Workshop on Symbiosphere: Ecological Complexity for Promoting Biodiversity. The Ministry of Science and Technology and the Ministry of Forestry Economy of the Congo permitted our study in the Ndoki Forest. Dr. M. Fay and Mr. Matthew Hatchwell of WCI Brazaville kindly helped us and gave useful information on the Nouabale-Ndoki Project. I make acknowledgement to these people and Ministries. Data used here are the results of the Ndoki Project of Kyoto University, supported by the Research Fund of the Ministry of Science and Education (#02041046 to S. Kuroda).

References

- Kano, T. (1992). *The Last Ape: Behavior and Ecology of the Pygmy Chimpanzee*. Stanford University Press, Stanford.
- Kano, T. & Mulvwa, B. (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In: *The Pygmy Chimpanzee*, R. L. Susman (ed.), pp. 233-274. Plenum, New York.
- Kuroda, S. (1992). Ecological interspecies relations between gorillas and chimpanzees in the Ndoki-Nouabale Reserve. In: *Topics in Primatology*. N. Itoigawa, Y. Sugiyama, G. P. Sackett, & R. K. R. Thompson (Eds.), vol. 2: pp. 385-394. Tokyo University Press, Tokyo.

- Idani, G. (1990). The Luo Reserve of pygmy chimpanzees in Wamba, Zaire. *J. African Studies* 37: 65-74.
- Mercier, J. R. (1991). *La deforestation en Afrique: Situation et Perspectives*. Edisud, Chaudoreille.
- Tutin, C. E. G., Wiliamson, E. A., Rogers, M. E. & Fernandez, M. (1991). A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lope Reserve, Gabon. *J. Tropical Ecol.* 7: 181-199.
- Yumoto, T. (1992). Studies on seed dispersal by animals: Purpose and method. *Biological Science* 44(2): 98-107. (in Japanese)

The Biodiversity Crisis: An Agenda for Global Research

N. E. Stork

Biodiversity Division, department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Key words: *ecosystem function, species inventory, global changes, sampling.*

Introduction

The term "biodiversity" coined by Wilson (1988) is now commonplace and has a wide range of meanings for groups as different as economists, ecologists or even school children. To all, however, it is automatically linked with our concern that man is endangering life on earth in an unprecedented manner. This concern was shown by more than 150 countries who signed the biodiversity convention agreed at the UNCED meeting in Rio this year.

Biodiversity typically has been described as the diversity of life expressed at three levels: genetic, species, and ecosystem. In reality, there is a continuum with diversity being also expressed at population, community, habitat, niche, landscape, continent and historical levels (Holloway & Stork, 1991). To most biologists though, the most easily recognised level is the species.

But what do we know of biodiversity at the species level? Estimates of described species of 1.4-1.8 million and the number of undescribed species for insects alone, of 2-30 million, demonstrate the uncertainty of both what we know and what we do not know. A working estimate of 12 million for all species of organisms on earth suggests that most are undescribed (Hammond, 1992; Stork, in press).

How is biodiversity distributed? On a geographical scale this question is hard to answer as it does not automatically follow that the patterns of distribution found for groups such as birds and large mammals are the same for insects, nematodes or other smaller organisms. On an ecological scale we similarly have difficulty in answering this question. Most communities are very species rich and taxonomic problems alone can hinder major ecological studies (see Stork, 1988).

Scientists need to consider carefully how their research efforts can be channelled most profitably to understand patterns of biodiversity and

the consequences of environmental change on local, regional and global biodiversity. Taxonomists and ecologists are particularly important in determining patterns of biodiversity. Information and hypotheses resulting from their studies, can be used to predict both the likely results of environmental change and the best courses of action to conserve the earth's living resources at local, national and international level. I present below a personal view of what I believe to be key elements of an agenda for global research on biodiversity:

Improve ecological and taxonomic performance

In general, scientific standards in the disciplines of ecology and taxonomy have improved considerably over the last thirty years. However, there are many ecologists and taxonomists who fail to apply appropriate scientific methodology in their studies. A taxonomist examining a set of specimens determines whether some of them are sufficiently similar to each other and sufficiently distinct from other individuals to merit recognition as a separate species. In effect, the taxonomist's new species is a hypothesis to be tested. Given that individuals from different localities, and even a population at a single locality, can vary considerably, it is noteworthy that almost half of all species are described from singletons or from single localities (Stork, in press). The high levels of synonymy in most groups of organisms (Gaston & Mound, 1993) demonstrate just how poor taxonomists have been at proposing such "species hypotheses".

Ecosystem function

Although there have been many classic studies of biomass, trophic and energy components of organic systems in terrestrial and aquatic environments, the precise contribution of the different biological components is poorly known. We do not know the importance of most individual species to such systems. Are many species unessential to the continued maintenance of a system or are they effectively "functionally redundant"? If the answer is yes then identification and protection of key species or groups of species may help in the conservation or restoration of ecosystems. If the answer is no, then these processes are made much more complex.

Intensive study of single sites

There is not a single biome or even a hectare of a biome on earth where we can provide the answer to the question of ecosystem function posed above. The reason is that we do not know for any such hectare all the biological components. Species accumulation curves for even relatively well-sampled sites rarely asymptote indicating that

continued sampling will produce many more species. Even in temperate countries all species are not described and their distributions known. Early indications from one intensive study of ichneumonid wasps in Costa Rica are that 40% or more of all Costa Rican species of this group may be found at a single site (I. Gauld pers. comm.). If we are to understand how ecosystems function then it is essential that a few sites in the world are intensively studied with all organisms being examined. Perhaps the nearest approach to this ideal has been that of Schaefer & Schauer mann (1990) and others who in their examination of the trophic and energy budget of soils in beech woodland had to study a wide range of different groups of organisms. The intensive study of single sites, particularly in the tropics, is a massive task requiring major input of funding and man-power but should tell us how important individual species and groups of species are to ecosystem function.

Species range and species turnover

We have little idea of the distribution of most species, even for the best known groups such as birds and large mammals. Although there are some indications that tropical species are distributed over a narrower latitudinal range than temperate ones, the evidence is poor. We therefore need to use available data to determine more accurately patterns of distribution and determine the biogeographical and ecological causes of these patterns. Such studies are essential if we are to make predictions about the effects of global change on patterns of biodiversity. In the absence of empirical data on species distributions we may be able to make predictions through modelling of species turnover with variables such as distance, latitude, and altitude as well as a variety of climatic variables.

Extensive study of many sites

The intensive study sites will provide indications of the relative importance/abundance of different organisms. Examination of a smaller number of "indicator" groups or species at a more extensive range of sites will show if or how these patterns change. Selection of indicators must take into account a wide range of factors such as body size, relative species richness of group, taxonomic distinctiveness or representativeness of a group, trophic group and so on. Studies of the same indicator groups at this extensive range of sites will also provide information of patterns of species distribution.

If real comparisons are to be made of the results of sampling at both the intensive and extensive study sites then standardisation of methodologies is essential. Sampling protocols need to be produced and

adhered to. At present there is a paucity of sampling manuals or examples of sampling packages. These need to be produced as soon as possible.

Gradients of diversity

The general increase in diversity for most groups of terrestrial organisms with decreasing latitude is well known but how general this is and what causes this is not precisely known. We also know that man-induced changes in land use perhaps mirror natural changes. Studies of natural gradients and of gradients of man-induced changes are urgently needed.

Effects of global climate change

Models of climate change show increases in temperature and rise in sea level through global increases in carbon dioxide levels. These and other effects will vary across the globe and have different effects on the composition and distribution of biodiversity. A better understanding of present biodiversity patterns and of the causes and maintenance of such patterns may help better predict the biodiversity consequences of climate change. Such predictions will be greatly enhanced through information, tested hypotheses and subsequent models derived from studies of ecosystem function, intensive single site studies, species turnover, species distributions and ranges, and gradients of diversity, as discussed above.

Determine conservation priorities

Those concerned with decision-making concerning what areas to protect or not to protect often have very limited information on which to base their decisions. The science supporting such decision making is developing rapidly (see Margules & Austin, 1991; Forey *et al.*, in press). Particularly important issues that are being examined are complementarity, representativeness, and endemism (Vane-Wright, in press).

Global species inventory

In the last 200 years inventory of the earth's fauna has been slow, haphazard, and often repetitive. Working estimates of 1.8 million described species and a further 10 million undescribed species are evidence of the lack of real progress. Sharper focus on what exactly is most urgently required of taxonomists would help. I believe that the products most urgently required are regional inventories, major taxonomic revisions rather than numerous single species descriptions,

and regional keys and field guides for taxa (e.g., Bolton, in press). A global register of all species, surprisingly absent so far, and increasing use of technological advances, such as computerisation and networking will help the inventory process. The most important question that taxonomists face, however, is whether the costly process of publication on paper should be replaced with electronic publication.

References

- Bolton, B. (In press). *Identification Guide to Ant Genera of the World*. Harvard University Press, Massachusetts.
- Forey, P. L., Humphries, C. J. & Vane-Wright, R. I. (Eds.) (In press). *Systematics and Conservation Evaluation*. Oxford University Press, Oxford.
- Gaston, K. J. & Mound, L. A. (1993). Taxonomy, hypothesis testing and the biodiversity crisis. *Proc. Roy. Soc. B.* 251: 139-142.
- Hammond, P. M. (1992). Species Inventory. In: *Global Diversity. Status of the Earth's Living Resources*. B. Groombridge (Ed.) pp. 17-39. World Conservation Monitoring Centre, Chapman & Hall, London.
- Holloway, J. D. and Stork, N. E. (1991). The dimensions of biodiversity: The use of invertebrates as indicators of human impact. In: *The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture*. D. L. Hawksworth (Ed.) pp. 37-62. CAB International, Wallingford, UK.
- Margules, C. R. & Austin, M. P. (Eds.) (1991). *Nature Conservation: Cost-effective Biological Surveys and Data Analysis*. CSIRO, Canberra.
- Schaefer, M. & Schauermann, J. (1990). The soil fauna of beech forests: Comparison between a mull and a moder soil. *Pedobiologia* 34: 299-314.
- Stork, N. E. (1988). Insect diversity: Fact, fiction and speculation. *Biol. J. Linn. Soc.* 35: 321-37.
- Stork, N. E. (In press). Inventories of biodiversity: More than a question of numbers. In: *Systematics and Conservation Evaluation*. P. L. Forey, C. J. Humphries & R. I. Vane-Wright (Eds.) Oxford University Press, Oxford.

Stork, N. E. (In press). How many species are there? *Biodiversity and Conservation*.

Vane-Wright, R. I. (In press). Systematics and the conservation of biodiversity: Global, national and local perspectives. In: *Perspectives on Insect Conservation*. K. J. Gaston, T. R. New & M. Samways (Eds.) Intercept, Andover.

Wilson, E. O. (1988). The current state of biological diversity. In: *Biodiversity*. E. O. Wilson & M. P. Peters (Eds.) pp. 3-18. National Academy Press, Washington, D.C.

Biodiversity and Systematic Botany

Kunio Iwatsuki

Botanical Gardens, University of Tokyo, Tokyo, Japan

Key words: *conservation biology, endangered species, phylogeny, species diversity, systematics.*

Species diversity

Systematic biology has contributed in elucidating biodiversity in various ways. Description of biodiversity has been made through great efforts exploring throughout the globe, both on lands and in ocean. Some 1.5 million species are now recognized, although it is generally suggested that the ever recognized species are less than 10 percent of the species living on the globe. It is evident, therefore, that one of the most important subjects of biology to be elucidated at the moment is basic research of biodiversity, or exploration of what kinds of species actually living in which part of the earth.

Database of ever described species of plants is now under preparation by an international collaboration project, or the International Organization of Plant Information. This Organization was established in 1991, and now a check list of all the flowering plants recognized on the earth is under construction. We generally summarize that some 250,000 species of the flowering plants have been recognized, but no one can say exactly about the number. We only suggest that there are some half a million species living on the earth. Based on this compilation of an enumeration of the flowering plants on the earth, more exact information on species diversity of them will be available.

Fundamental research on species diversity in algae and fungi is less performed, and it is urgently expected to promote this type of basic research.

Phylogeny and biodiversity

Although we can expect at the moment to know actual phase of species diversity only less than one-tenth of all on the globe, our knowledge on phylogenetic relationships among recognized taxa is elucidated day by day. Applying the techniques in molecular levels, genetic distances among taxa are measured more precisely and phylogenetic relationship among the taxa treated is known much better. A field of

so-called molecular systematics contributes a lot of valuable informations in elucidating biodiversity, and a great advance in research on phylogeny has been made in a few past decades.

Based on such an advancement in systematic biology, it is now expected to have evaluation of taxonomic characters on the basis of evidence available in genetic research in molecular levels. Until recently, evaluation of characteristics to trace phylogenetic relationships was made only by comparing phenetic features. As the phenetic features are complicated results of development, it is quite difficult to trace phylogenetic resemblance, or difference, only through the phenetic features, even though variously valuable biological efforts have variously been given in elucidating the problems. Even at the moment, it is still not very easy to analyse genetic relationships among taxa in comparing the phenetic features as we know hardly on their genetic basis.

The organisms are living on the earth through various biological activities, and most of them are represented by their phenetic features. The lives of organisms are maintained through their phenetic characters, and evolution of organisms is performed through the phenetic features. Thus, it is inevitable to elucidate biological relationship between phenetic features of every species and their genetic basis. In analysing this relationship, it is possible to understand biological dynamics of evolution of species.

Biodiversity crisis

A crisis on biodiversity threatening us at the moment is found in a problem on endangered species and is a crisis for biology as well as under strong social impact.

Ginkgo biloba is an only extant species of Division Ginkgophyta. This species is recognized to be endemic to Zhejiang, although it is suggested to be extinct in its original locality. As this interesting species is cultivated everywhere on the earth, we have a lot of trees alive. We have one memorial tree in our Botanical Gardens: the first observation of spermatozoids on seed plants was made on that plant. As the Division Ginkgophyta, dominant during Permian and the middle Mesozoic, has a variety of interesting biological features, it is quite convenient for biology to have living materials of one species, even though the species itself is extinct from its native habitat. Through the living materials of this extinct species, we have had and will have much information comprehensive to elucidation of biological subjects.

In this case, a protection of extinct species in cultivation has been much contributive to biology. Crisis in biodiversity is, however, more evident in environmental problems as well as loss of potential genetic resources; these problems are dangerous either as biological or social crisis. The details of biological and social impacts will be discussed in this workshop, and I am now introducing here some information on the crisis found in Japanese flora.

Japanese Archipelago is under good natural condition especially for its flora. Under humid and warm climate best for the lives of various species, diverse habitats are available for various species to live in, and ample genetic resources are occupied from the richest warm temperate flora of Sino-Himalayan areas. Thus, Japanese Archipelago has more than 5500 vascular plant species, in addition to green coverage of most part of the Archipelago. Some people even say that the green coverage of Japanese Archipelago is in ideal condition, and environmental crisis is found in Japan only in city areas. However, this is erroneous, and we have to say that the green coverage of our Archipelago is just superficial.

We surveyed the dynamics of flora of Japan and found that about 900 species are now threatened, or according to the IUCN categories ranked in extinct, endangered, vulnerable, and indeterminate. One to every six species, or some 16 percent of all the flora, is an awful figure. In spite of apparent green coverage of the Archipelago, the green itself has strongly been damaged. In an enumeration of threatened species, we see such species as: *Eupatorium japonicum* one of the seven popular autumn flowers; *Lithospermum officinale* var. *erythrorhizon*, a famous flower in Japanese classics published one thousand years ago; and many popular horticultural species as *Primula sieboldii*, *Adonis ramosa*, *Magnolia tomentosa* and so on. We suspected the factors to bring them threatened, and rather roughly compiled them to count: one-third of total species are under serious influence of land development; the other one-third are threatened by over collection, especially by collectors hired by traders; and the rest are rare species and becoming rarer by poorer environmental conditions as higher density of CO₂ as well as NO_x, warmer temperature, less cover of the green, and so on.

In protecting the threatened species, we should have promotion of research in so-called conservation biology. There are only a few examples of such studies on plants in Japan. An example of trials of reintroduction of endangered species is effectively performed by *Melastoma tetramerum*, an endemic species seriously endangered on Chichijima Island of the Ogasawara Islands.

Environmental Changes and Biological Innovation in the Geologic Past

Koji Minoura

Institute of Geology and Paleontology, Faculty of Science, Tohoku
University, Sendai, Miyagi 980 Japan

Key words: *phanerozoic, extinction, atmosphere, ocean, plate tectonics, climate.*

Evolution and extinction

Living organisms have made essential contributions to the surroundings; plants and animals have, by reaction with the environments, established the composition of the atmosphere and oceans as it is today. With the passage of time, individuals of organic species have been reproduced from generation to generation, leading to changes in an average set of physical characteristics of the population. This change is termed organic evolution. It follows, therefore, that the origin and organization of our environment are closely linked to the evolution of life.

The greater part of genera ever lived have been extinct to date, and the fossil record documents that 20 thousand out of approximately 25 thousand known genera have been extinct. Worldwide extinctions of considerable magnitude occurred repeatedly in the geologic past, allowing large numbers of species of faunas and floras newly evolved. During the period of disappearance of dominant species, the new ones expanded in a manner of abrupt advancement. It has generally been assumed that these revolutions in the structure of life communities can be attributed to remarkable changes in climate and oceanic conditions. There is increasing evidence, however, that some extinctions were short-lived events due to unfavorable conditions. Which is the cause of biological crises, a purely biological phenomenon or a fatal change of living circumstances, or both?

Phanerozoic history of life

Based on statistical analyses of the post-Paleozoic fossil record, Raup & Sepkoski (1984) concluded that the extinction events had taken place at intervals of 26 million years. This periodicity of tens of millions of years shows that recurrent extinctions may have been related to such extraterrestrial influences as cyclic changes of solar radiation, solar or

galactic systems. The single great extinction which happened at the end of the Cretaceous is generally ascribed to the catastrophic impact of a giant meteorite with a diameter reaching up to 10 km (Alvarez *et al.*, 1980). Some 120 impact basins are currently known on the Earth (Grieve *et al.*, 1987) and 20-30 km-sized cratering is suggested to have occurred approximately every ten million years. Astronomical cycles of this order seem to be plausible.

Through the eras of abundant life, environmental stress has affected the struggle for existence, causing major turnover in taxonomic composition. Many paleontologists studying fossil marine invertebrates understand that the stress has resulted from terrestrial processes (continental and oceanic plate motion, sea-level fluctuation, glaciation, *etc.*). The most critical event in the Phanerozoic life history took place at the end of the Paleozoic Era (250 million years ago). At that time, a reduction in familial diversity was brought about by nearly 50%, and four marine groups (*Blastoidea*, *Rostroconchia*, *Hyolitha* and *Trilobita*) completely disappeared from Early Mesozoic seas (Sepkoski, 1981). A marked contraction of classes also occurred among groups that survived the critical event. The food habit of marine benthic communities greatly changed from immobile suspension feeding to mobile deposit feeding (Thayer, 1979). Such a change is suggestive of pervasion of undesirable environments for suspension feeders. Such momentous difficulties for the survival extended over a period of several million years, which supports the interpretation that the extinction was a biological or earth-bound physical event. The concept of sea floor spreading elucidates a number of important geological features: the lithosphere moves horizontally on Earth's surface, and the distribution of continents and oceans has changed drastically.

Plate tectonics and climate

Sufficient data are now available for the reconstruction of paleoceanographic situations through the Phanerozoic Era (*e.g.*, Smith *et al.*, 1981). The increasing rate of ocean floor spreading caused active plate convergence, obduction and subduction of sediments, and large ridge volumes. Active convergence of the lithosphere gives rise to deliverance of metamorphic and diagenetic carbon dioxide to the atmosphere at subduction zones. A ridge volume increase brings about a rise of the global sea level. Spreading rates of ocean floors in Late Paleozoic and Early Mesozoic time were much lower than those in both the earlier and later eras (Gaffin, 1987). A decreased rate of production of oceanic ridges provoked low sea level stands at the end of the Paleozoic. A large drop of sea level is interpreted to have involved oxidation of exposed marine sediments and consequent lowering of atmospheric oxygen levels (Minoura, 1991). During the

global sea level minimum, CO₂ production through geochemical processes at subduction zones declined, resulting in a net consumption of CO₂ by erosion of carbonates and metal-silicates, and a large decrease in atmospheric CO₂ levels (Figure 1). Dry and cool global climates led by the reduced green house effect are likely to have inflicted great damage on terrestrial organisms. Probable low oxygen contents of the atmosphere seem to have deteriorated the vital function of breathing animals.

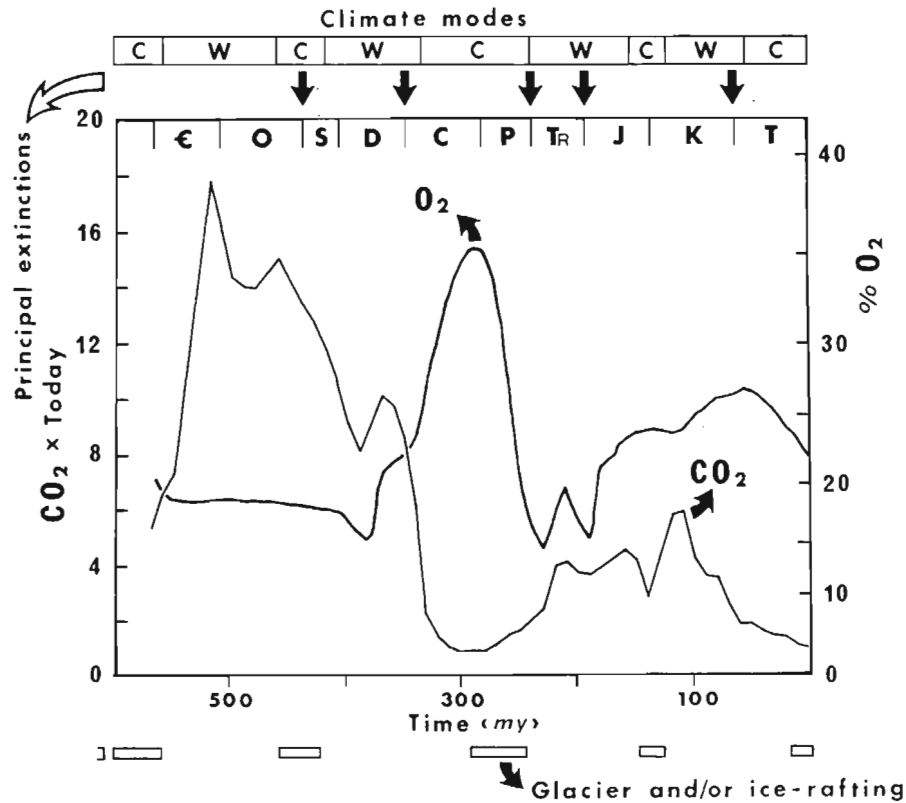


Figure 1: Secular changes in atmospheric oxygen (Berner & Canfield, 1989) and carbon dioxide (Berner, 1991) during the Phanerozoic. Top and bottom rows show warm (W) and cool (C) climate modes (Frakes *et al.*, 1992) and glacial episodes (Chumakov, 1985), respectively.

The supercontinent of Pangaea extending from pole to pole was formed by this time, involving exposure of a vast, continuous area of land. As its interior was isolated from ameliorating influences of the surrounding ocean, the continent became especially warm or cold, which resulted in the development of a low or a high pressure pattern of atmospheric circulation over the landmass. The low pressure cell,

formed in the northern summer, over northern Pangaea must have contrasted with a continental high in the south, and vice versa in the northern winter. The establishment of such an atmospheric pattern on a global scale seems to have resulted in the development of the "monsoon" in the Early Mesozoic world. This extreme form of atmospheric circulation must have kept the interior of that supercontinent very dry and maximized seasonality in coastal regions (Parrish & Curtiz, 1982). Such a change of climatic conditions is supposed to have influenced largely on-land vegetation: Paleozoic floras with constant growth rates all the year round were displaced by seasonally growing Mesozoic floras. Flowering plants rose on land at this time. Plants' consumers in shallow marine basins may have struggled against a restricted food supply in winter. Such a plant-animal interaction must have caused selection within marine benthic communities: newly evolved deposit feeders displaced immobile suspension feeders from Early Mesozoic seas.

Biological diversity: a consequence of global catastrophes

It is suggested that terrestrial processes have been interrelated so as to sustain life on the Earth. Biological actions seem to have been an essential factor of this interrelation. A close connection between extinctions and global catastrophes is documented by investigations of fossil and stratigraphic records. In addition, these catastrophes seem to stand in causal relations to astronomical phenomena (Grieve *et al.*, 1987). I suggest that extraterrestrial forces triggered those changes which were then amplified by feedback mechanisms of circulation in the oceans and atmosphere. Secular changes in the rate of ocean floor spreading, which have occurred on the order of 10^8 years, are consistent with astronomical cycles of the solar system against the Galaxy (Clube & Napier, 1986), suggesting potential propagation of astrophysical influences on plate motion.

The Earth is a very particular planet in this cosmic world, because ours has abundant living things in advanced form, and at present we have no evidence that the extraterrestrial equivalents ever exist. Life on the Earth has undergone evolution in response to changing global circumstances since its birth. In the course of biological evolution, diverse and complicated faunal and floral assemblages came into existence. Biological crises of mass extinction in the geologic past may have played an important role in promoting biological diversity. Diversification, when interpreted in the context of geological settings, is a consequence of terrestrial processes subjected to astronomical catastrophes. In this sense, the Earth is not a solitary planet.

References

- Alvarez, L., Alvarez, W., Asaro, W. F. & Michel, H. V. (1980). Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* 208: 1095-1108.
- Berner, R. A. (1991). A model for atmospheric CO₂ over Phanerozoic time. *Am. Jour. Sci.* 291: 339-376.
- Berner, R. A. & Canfield, D. E. (1989). A new model for atmospheric oxygen over Phanerozoic time. *Am. Jour. Sci.* 289: 333-361.
- Clube, S. V. M. & Napier, W. M. (1986). Galactic cycles and the terrestrial record. In: *The Galaxy and the Solar System*. R. Smoluchowski, J.N. Bahcall & M.S. Matthews (Eds.) pp. 260-285. University of Arizona Press, Tucson.
- Chumakov, N. M. (1985). Glacial events of the past and their geological significance. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 51: 319-346.
- Frakes, L. A., Francis, J. E. & Syktus, J. I. (1992). *Climate Modes of the Phanerozoic*. Cambridge University Press, Cambridge.
- Gaffin, S. (1987). Ridge volume dependence on seafloor generation rate and inversion using long term sealevel change. *Am. Jour. Sci.* 287: 596-611.
- Grieve, R. A. F., Sharpton, V. L., Rupert, J. D. & Goodacre, A. K. (1987). Detecting a periodic signal in the terrestrial cratering record. *Proc. Lunar Planet. Sci. Conf. 18th*: 375-382.
- Minoura, K. (1991). Biological extinction and radiation in the geologic past: Global environment of Permian and Triassic ages. In: *Papers in Honor of Professor H. Nakagawa upon His Retirement*. K. Minoura & S. Osozawa (Eds.) pp. 151-159. Tohoku University, Sendai. (in Japanese with English abstract)
- Parrish J. T. & Curtis, R. L. (1982). Atmospheric circulation, upwelling, and organic-rich rocks in the Mesozoic and Cenozoic eras. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 40: 31-66.
- Raup, D. M. & Sepkoski, J. J., Jr. (1984) Periodicity of extinctions in the geologic past. *Proc. Natl. Acad. Sci. USA* 81: 801-805.
- Sepkoski, J. J., Jr. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7: 36-53.

Smith, A. G., Hurley, A. M. & Briden, J. C. (1981). *Phanerozoic Paleontological World Maps*. Cambridge University Press, Cambridge.

Thayer, C. W. (1979). Biological bulldozers and the evolution of marine benthic communities. *Science* 203: 458-461.

Evaluation of Biodiversity of Soil Microbial Community

Kazunari Yokoyama

Laboratory of Soil Microbial Ecology
National Institute of Agro-Environmental Sciences
3-1-1 Kan-non dai, Tsukuba, Ibaraki 305 Japan

Key words: *soil bacteria, community structure, diversity index, microbial ecology, biological control.*

Introduction

Everyone realizes that the whole ecosystem, including human society, cannot maintain its material and energy cycles without the functioning of microbes in the environment. Microbes in the soil, for instance, are considered to be a key player in the circulation of almost every substance functioning in the agro-ecosystem.

Two factors important in evaluating a certain soil are its fertility and its resistance to soilborne diseases in agriculture. Fertility of the soil is estimated by its productivity, and its disease suppressiveness is evaluated by the intensity of diseases occurring. The various functions of soil microbes utilizing and supplying many kinds of inorganic materials to plants are already well documented, and the role of the diverse soil microbe community surrounding the host-pathogen complex as a limiting factor of disease development is well known (Schroth & Becker, 1990). Thus, both fertility and disease resistibility are considered to be greatly dependent on the soil microbes. This is why farmers usually concentrate on improving the soil microbes by introduction of organic materials, *e.g.*, composts, in their fields. In the field of agronomy, the importance of studying those microbes and their functions as a total community has been discussed for more than a half century, and many researchers tried to fully understand the interrelating function. And they all faced to the same question: "how to realize the biological function of the soil microbial community", compared to that chemical function of the soil was detectable and measurable by chemical analysis.

Many of them, perhaps including us, believed that investigating the individuals in detail and reconstructing the information could answer the questions, relating to the understanding of soil microbial function as the total community. However, the complexity of the community and variability of the microbes composing the community gave most of

them a different answer. This has been disappointing and has shown the difficulty of scientific elucidation of soil microbes.

A new trial

Until recently, elucidating a very complex subject, through isolation, investigation of individuals and reconstruction of information was thought to be an effective strategy. But, when the subject of observation is directly affected to isolate and observe, this method may not always be good. This is why we focused on complexity to describe the complex soil ecosystem, and furthermore on the biological diversity of the soil microbial community to characterize its complexity. The biodiversity of any life forms other than microorganisms in an ecosystem has been based on the diversity of taxonomic species. This means that the biodiversity and study of it is also absolutely dependent on its taxonomy. For microorganism, on the contrary, time consuming work to determine the taxonomic species of an individual is a barrier to studying diversity in the field of ecology. This is why we can only get the information of soil microbial community by counting the number of units forming colonies on culture media. Recently, the taxonomical methodology for microorganisms based upon their patterns of response to given chemicals, for example, utilization of various forms of carbon sources, has been developed and has helped to make drastically the time for taxonomical classification shorter. We tried to use this method and numerical data characterizing each individual microbe to analyze the structure of a soil microbial community.

A new concept constructed

Now, we come to the necessity of having a new concept for estimating the diversity of the community without the conventional classification representing "the species diversity." A diversity of community based on the function of each individual component is an answer to the problem of how to understand the microbial ecosystem as a whole. To estimate functional diversity based on, for example, the ability to utilize carbon sources, soil bacteria isolated from soils were put into a bacteria identification system based on carbon utilization. Patterns of utilization of carbon sources supplied were expressed as numerical values using a binary number, 1 or 0 representing could utilize/could not utilize. The isolated organisms composing a community were clustered according to the numerical characteristics and then a mathematical multi-dimensional space with distances calculated between the components was constructed. We considered that the complexity itself of the spatial structure represents the functional diversity of the community and level of the functional complexity of

the community at the same time. We made a formula to get a diversity index using the total aggregate distance within the multidimensional space and the average distance of each component. Analysis was carried out of soil bacterial communities collected from soils under different conditions of fertilizing, physical condition, concentration of carbon dioxide and temperature and/or crop culturing. Results from this method were compared with the other conventional indices, *e.g.*, Shannon's index and/or Simpson's index, to evaluate diversity of plant and/or animal communities in this study.

Examples of practical use of this analysis

Effect of soil amendment on diversity of soil bacterial community

Soil amendment as a management of arable land is considered to affect dramatically the soil microbial community. However, we do not yet know the effect precisely, because the change in the community was only detectable when the number of viable colonies was changed drastically. Recently, we conducted an experiment to make clear even small changes in bacterial communities in soils differently amended, by using the diversity analysis.

Soils were newly cultivated for this experiment from a virgin forest and continuously amended with only chemical fertilizer, pig manure, or rice straw compost for three years, respectively. The result was that no significant difference was detected in the number of each soil bacteria using conventional colony counting or even the conventional diversity analysis. The analysis of the soil bacterial diversity, however, realized a significant difference between them. The bacterial communities from the soils amended with organic matters possessed significantly higher diversity than that from the soil only chemically amended. Furthermore, we detected that the community of antagonistic bacteria from the soil amended with the rice straw compost had the most diverse structure.

Effect of CO₂ and temperature rise on soil bacterial community

We have evaluated the ecological complexity of a soil under the probable future conditions, temperature and CO₂ concentration rises. The soil was collected from the ECOTRON, which is a green house facility creating the temperature(2°C rise) and CO₂ concentration (650ppm) of the near future climate. The number of soil bacteria from the ECOTRON was rather rich compared to that from the soil conditioned naturally. However, the diversity of the community was getting poor after only 6 months. This may be the first datum

revealing the possible change in the soil microbial community under future condition as a reduction of diversity.

Conclusion

We all are hypothesizing that a more complex environment could develop more diverse biosphere, including the microorganism community. A main reason why scientific understanding of the microorganism community is still behind that of other major fields, animal and plant, is undoubtedly the boring labor necessary to identify the millions of individuals. There used to be no way to skip that to start further scientific research. Recently, however, some leading trials for estimating the soil microbial community, with focus on genetic and/or phenotypic diversity, have been started (Batzli *et al.*, 1992; Leach *et al.*, 1992; Garland & Mills, 1991; Torsvik *et al.*, 1990a, b). Furthermore, their communities are unfortunately always wobbling and keeping their dynamic balance in the mass community. This is because the microorganism community is very resistant to scientific elucidation. On the other hand, the diverse microbes could be a potential for the innovation of future technology (Bull *et al.*, 1992). Moreover, this changeable, wobbling and, highly balanced community might become the most sensitive sensor to detect any kind of environmental change and to evaluate the ecological complexity of the environment. I believe that we need to keep the diverse community, and that the diversity itself is the best way to evaluate the complexity of a complex world.

References

- Batzli, J. M., Graves, W. R. & Van Berkum, P. (1992). Diversity among rhizobia effective with *Robinia pseudoacacia* L. *Appl. Environ. Microbiol.* 58: 2137-2143.
- Bull, A.T., Goodfellow, M. & Slater, J.H. (1992). Biodiversity as a source of innovation in biotechnology. *Annu. Rev. Microbiol.* 46: 219-252.
- Garland, J.L. & Mills, A.L. (1991). Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization. *Appl. Environ. Microbiol.* 57: 2351-2359.
- Leach, J.E., Rhoads, M.L., Vera Cruz, C.M., White, F.F., Mew, T.W. & Leung, H. (1992). Assessment of genetic diversity and population structure of *Xanthomonas oryzae* pv. *oryzae* with a repetitive DNA element. *Appl. Environ. Microbiol.* 58: 2188-2195.

- Schroth, M.N. and Becker, J.O. (1990). Concepts of ecological and physiological activities of rhizobacteria related to biological control and plant growth promotion. In: *Biological Control of Soil-borne Plant Pathogens*. D. Hornby (Ed.) pp. 389-414. CAB International, Wallingford, UK.
- Torsvik, V., Salte, K., Sorheim, R. & Goksoyr J. (1990a). Comparison of phenotypic diversity and DNA heterogeneity in a population of soil bacteria. *Appl. Environ. Microbiol.* 56: 776-781.
- Torsvik, V., Goksoyr, J. & Daae, F.L. (1990b). High diversity in DNA of soil bacteria. *Appl. Environ. Microbiol.* 56: 782-787.

**Molecular Genetic Approach to Microbial Diversity
(5S rRNA, replication origin, RNA polymerase,
two component system)**

Hiroshi Yoshikawa

Advanced Institute of Science and Technology, Nara
8916-5, Takayama-Cho, Ikoma city, Nara 630-01 Japan

Key words: genetic regulatory system, phylogenetic tree, initiation of replication, origin of chromosome, sigma factor of RNA polymerase, promoter of transcription, environmental stimuli.

Introduction

Molecular genetics, since the discovery of DNA as a universal carrier of genetic information from bacteria to man, has been devoted to elucidate basic principles underlying various biological phenomena. Obviously individual species have not been the target of research: thus, the *Escherichia coli* genetic system has been regarded as the standard for all prokaryotes and a model for eukaryotic systems. Development of recombinant DNA technology however has changed the basic concept of "from bacteria to elephant" through the discovery of the complex structure and expression of eukaryotic genes. Since then, more attention has been paid for the genetic system of individual species using the *E. coli* system as a reference, to identify similarity and difference between various species among microorganisms.

The second development in molecular genetics was the study of the complex genetic systems rather than structure and function of individual genes. Such studies made it possible to understand complex cellular functions such as cell growth regulation, differentiation (spore formation and germination and adaptation to environmental stimuli). Through these developments in molecular genetics together with technical advancements in DNA technology, it is now possible to conduct comparative studies of several complex genetic systems among many bacterial species. Such studies should open a new road towards understanding bacterial diversity of ecological significance in molecular terms. The aim of this report is to present examples of possible molecular genetic approaches to the study of the diversity of complex functions in bacteria.

Diversity based on phylogenetic relations

One of the major achievements in Molecular Biology is to determine evolutionary relationship between organisms for which no fossil records are known by measuring base changes in a given gene universally conserved in all organisms (Hori & Osawa, 1987). A gene for a small ribosomal RNA, 5S rRNA, is ideal for such analysis because of its small size, GC content and structure which allow sizable changes in base sequence without altering the essential function of the RNA.

The molecular clock hypothesis is based on the assumption that the rate of base substitution in a given gene is dependent solely on time and not on the generation time of each species carrying the same gene. The validity of this theory has not been tested in microorganisms and should be examined as the mechanism of spontaneous mutation in microorganisms becomes clearer. At the moment there is no crucial discrepancy between molecular and taxonomic measurements. Molecular phylogenetic relationship of 5S rRNA or 16S rRNA genes are therefore used as a quantitative measure of the microbial diversity.

The phylogenetic analyses of the 5S rRNA gene have disclosed when given two bacterial species have undergone evolutionary divergence. However functional diversity between the two species cannot be revealed by comparing the base sequence of the conserved genes. In general, the functional products from conserved genes used for phylogenetic analysis are too conserved to study diversity in function as well as in structure. From the view point of the molecular genetic approach it is essential to have a gene or group of genes in which both function and structural diversity can be studied at the molecular level. It is now possible to use complex genetic systems rather than single genes as a probe for determining their conservation and diversity in bacteria.

Replication origins of bacterial chromosome as a probe for biodiversity

This is a case where one can study conservation of diversity of structure and function by the combination of the coding sequence of an essential gene and a regulatory sequence recognized by its gene product. We found that both the "initiator protein", a protein required for the first step in the initiation of replication of bacterial chromosomes, and a signal sequence, the binding site of the initiator on the chromosome, are conserved in most of the eubacteria (Ogasawara *et al.*, 1985). Accordingly they are named as DnaA protein and DnaA-box, respectively. The "replicator" or the origin of chromosomal replication (*oriC*) is composed of 1-3 sets of regions containing several

DnaA-boxes (DnaA-box region). Both numbers and locations of DnaA-boxes in the DnaA-box regions are essential for the origin function. Although the DnaA-box sequence is conserved in bacteria, the number and location in each of the box-regions and the number of the DnaA-box region sets are variable among bacteria. Basic function of the binding of DnaA protein to DnaA-box is conserved in all cases. However variations in the organization of DnaA-boxes in the "replicator" results in a diversity of modes of DnaA function both in activation of *oriC* and the negative control of *dnaA* gene itself.

As expected for conserved genes, variations in DnaA protein structure are closely related to phylogenetic relationship of bacteria. Variations in structure of "replicator" are also phylogenetically related. Replicators are widely different between Gram positive and Gram negative bacteria, while they are well conserved between *E. coli* and *Pseudomonas putida*. The organization of two DnaA-box regions flanking the *dnaA* gene is characteristic to Gram positive bacteria. Detailed comparison can also be made within various Bacilli species. From these comparative studies we could propose an evolutionary relationship of the origin of chromosomal replication in eubacteria (Yoshikawa & Ogasawara, 1991).

In summary, DnaA-replicator interactions provide a good model system to study functional diversity based on variations in structures conserved in eubacteria. The next problem is how to correlate the changes in replicator functions with diversity of growth regulation of bacteria in various environments.

Diversity in RNA polymerase sigma subunit-promoter in bacteria

The second intriguing case in bacteria is the diversity in sigma factors of RNA polymerase and their recognition sequences, the promoters of transcription. The multiple sigma species were discovered first in *Bacillus subtilis* in connection with spore formation (Stragier & Losick, 1990). Later, the presence of minor sigma was found in *E. coli* in relation with stress responses (Grossman, *et al.*, 1984, Fujita & Ishihama, 1987). Now it is commonly believed that 10 or more different sigma factors are present in bacterial cells.

Comparison of structure of various sigmas shows clearly that they are related and evolved from an ancestral form as a gene family by gene duplication and mutation. Comparison between *E. coli* and *B. subtilis* has revealed that the multiplication had occurred before the two species were evolutionary diverged. After the multiplication, some sigma species seem to be conserved in structure and function. For

instance, major sigma factors, which play an essential role in vegetative growth both in *E. coli* and *B. subtilis*, are invariable not only in protein structure but also in their promoter sequences. As for the role of minor sigma factors, however, remarkable diversities can be observed. In *B. subtilis* some of them constitute a sigma cascade through which sequential biochemical events leading to spore formation are temporally regulated (Strager, 1991). No comparable roles have been identified for minor sigmas in *E. coli* except for cell's response to environmental stimuli, such as heat. However, recent studies seem to reveal the role of sigmas in the physiology of stationary phase *E. coli* cells (Tormo *et al.*, 1990; Ozaki *et al.*, 1991).

From the ecological point of view, the physiology of stationary phase is as important as spore formation because most bacterial cells undergo the physiological states similar to those of stationary phase cells in natural environment. It is important to study the diversity of sigma factors in structure and function systematically in order to understand their roles in the physiology of various cells. In this system one can study functional diversities that are highly relevant to ecological problems at the molecular level.

The two component regulatory system for bacteria signal transduction

The two component system is a device through which environmental stimuli, chemical and physical, are transmitted into cellular biochemical processes (Stock *et al.*, 1989). This is the third example of functional diversity in genetic systems that can be studied in molecular details. Many two component systems have been discovered in bacteria in relation to a cell's diverse responses to environmental stimuli such as osmotic pressure, nutrients, and chemotaxis (Stock *et al.*, 1990). Although more systematic comparative studies are needed to understand the molecular basis of the diversity, the possibility that the two component system constitutes a large gene family originating from an ancestral gene has been clearly suggested (Ronson *et al.*, 1987).

Obviously, diversity in cellular responses to environmental factors is a basis for understanding the ecological diversity of bacteria. Here is another case where a molecular genetic approach may be able to contribute to solution of some ecological problems.

The development of DNA technology such as the polymerase chain reaction and automatic DNA sequencing made it possible to analyze multiple gene systems described above and others. Investigation of the diversity of such complex systems, however, requires systematic

efforts by many workers. One should therefore choose proper organisms of ecological importance for such studies. It is therefore essential to have a tight and extensive cooperation between molecular geneticists and microbial ecologists to achieve this type of new approach to understand biodiversity at the molecular level.

References

- Fujita, N. & Ishihama, A. (1987). Heat-shock induction of RNA polymerase sigma32 synthesis in *Escherichia coli*: Transcriptional control and multiple promoter system. *Mol. Gen. Genet.* 210: 10-15.
- Grossman, A. D., Erickson, J. W. & Gross C. A. (1984). The *htpR* gene product of *E. coli* is a sigma factor for heat shock promoters. *Cell* 38: 383-387.
- Hori, H. & Osawa, S. (1987). Origin and evolution of organisms as deduced from 5S ribosomal RNA sequences. *Mol. Biol. Evol.* 4: 445-472.
- Ogasawara, N., Moriya, S., von Meyenburg, K., Hansen, F. G. & Yoshikawa, H. (1985). Conservation of genes and their organization in the chromosomal replication origin region of *Bacillus subtilis* and *Escherichia coli*. *EMBO J.* 4: 3345-3350.
- Ozaki, M., Wada, A., Fujita N. & Ishihama A. (1991) Growth phase-dependent modification of RNA polymerase in *Escherichia coli*. *Mol. Gen. Genet.* 230: 17-23.
- Ronson, C. W., Nixon, B. T. & Ausubel, F. M. (1987). Conserved domains in bacterial regulatory proteins that respond to environmental stimuli. *Cell* 49: 579-581.
- Stock, J. B., Ninfa, A. J. & Stock, A. H. (1989). Protein phosphorylation and regulation of adaptive response in bacteria. *Microbiol. Rev.* 53: 450-471.
- Stock, J. B., Stock, A. M. & Mottonen, J. M. (1990). Signal transduction in bacteria. *Nature* 344: 395-400.
- Stragier, P. (1991). Dances with sigmas. *EMBO J.* 10: 3559-3566.
- Stragier, P. & Losick, R. (1990). Cascades of sigma factors revisited. *Mol. Microbiol.* 4: 1801-1806.

- Tormo, A., Almiron, M. & Kolter, R. (1990). *surA*, an *Escherichia coli* gene essential for survival in stationary phase. *J. Bacteriol.* 172: 4339-4347.
- Yoshikawa, H. & Ogasawara, N. (1991). Structure and function of DnaA and the DnaA-box in eubacteria: Evolutionary relationships of bacterial replication origins. *Mol. Microbiol.* 5: 2589-2597.

Providing a Scientific Backbone to Biodiversity

Francesco di Castri

Assistant Director General for Environment UNESCO
7 Place de Fontenoy 75700 Paris, France

Key words: *biodiversity, Diversitas, ecosystem function, conservation.*

The emerging public interest in issues related to biological diversity - as well as the media coverage - is often of an emotional nature with little scientific backing. Statements such as: "we know how much biodiversity exists", "It is all in the tropics", "People have always reduced it", "We can save every species" or "A hands-off approach is the best protection" are much too common myths. Accordingly, management of biodiversity is sometimes biased or unrealistic. Even the newly launched "Convention on Biodiversity" lacks, admittedly, straight facts on relevant topics.

Biodiversity in several countries is therefore considered as being "a soft science" with confused research hypotheses. To remedy this situation, IUBS (International Union of Biological Sciences) in cooperation with SCOPE (Scientific Committee on Problems of the Environment) and UNESCO have launched a new international research programme called: "Diversitas".

The main research emphasis of Diversitas focuses on three key aspects: function, that is to say, the ecosystem function of biodiversity, where redundancy and thresholds are main processes; *mechanisms* regulating the origin, maintenance and loss of biodiversity, and mostly determining local and global extinctions; *change*, by inventorying biodiversity through space and monitoring biodiversity through time. Two very important transversal issues, often neglected in the past, deal with micro-organism biodiversity and marine biodiversity.

The research foundation of Diversitas is a hierarchical approach covering different levels of organization and different scales of space and time. Its operational foundation is mostly provided by the UNESCO International Network of Biosphere Reserves.

Diversitas is not exclusively a research programme. Its added values imply revitalizing and enhancing taxonomy; providing a continuum from molecular biology to landscape ecology, with a cross-cutting and integrated view of diversity by most biological sciences; ensuring sites

for long-term ecological research and training; committing local populations to biodiversity conservation through opening options for sustainable development; and facilitating a more rigorous public information on biodiversity.

The fact that so many uncertainties on biodiversity are to be reduced, does not mean at all that we can not act until we know more. It would be an almost suicidal and irreversible attitude to even more delay action for the conservation and the use of biodiversity. The "unknown" can be managed in as far as a precautionary approach is adopted. This implies, among others, that a strict control should be kept as regards the release of genetically bioengineered species and varieties, that the protected areas should be more effectively selected and managed for biodiversity conservation, that national and international interacting networks of research sites for biodiversity be established, and, above all, that biodiversity as well as sustainable development should be considered as an integral part of the overall landscape planning.

The forthcoming global climate change is likely to modify the current configuration of the conservation measures. In particular, if national parks remain closed zones of isolation for protection, the rate of species extinction may be higher there than anywhere else. For the isolated and often "low-population" species of parks, it would be impossible to shift their habitat or to undertake long migrations in order to find conditions in harmony with their adaptive potential.

Biology International
is the News Magazine of the
INTERNATIONAL UNION
of
BIOLOGICAL SCIENCES

President: F. di CASTRI (Italy) Past-President: J. SALANKI (Hungary)
Vice-Presidents: T. OKADA (Japan) Secretary General: D. STONE (U.S.A.)
V.SOKOLOV (Russia) Treasurer: D.F. ROBERTS (U.K.)

Executive Director: T. YOUNES

IUBS SECRETARIAT

51, Boulevard de Montmorency, 75016 Paris, France.
Tel: 33 (1) 45.25.00.09 - Telefax: 33 (1) 45.25.20.29
Telex: c/o ICSU 645 554 F

The International Union of Biological Sciences is a non-governmental, non-profit organization, established in 1919. Its objectives are to promote the study of biological sciences, to initiate, facilitate, and coordinate research and other scientific activities that require international cooperation, to ensure the discussion and dissemination of the results of cooperative research, to promote the organization of international conferences and to assist in the publication of their reports.

The membership of the IUBS presently consists of 43 Ordinary Members, adhering through Academies of Science, National Research Councils, national science associations or similar organizations, and of 75 Scientific Members, all of which are international scientific associations, societies or commissions in the various biological disciplines.

National Adhering Organizations

ARGENTINA- Consejo Nacional de Investigaciones Cientificas y Tecnicas
AUSTRALIA- Australian Academy of Science
AUSTRIA- Osterreichische Akademie der Wissenschaften
BELGIUM- Royal Academy of Science, Letters & Arts
BRAZIL- Conselho Nacional de Desenvolvimento Cientico e Tecnologico
BULGARIA- Bulgarian Academy of Sciences
CANADA- National Research Council
CHILE- Sociedad de Biologia de Chile
CHINA- Association for Science and Technology, Beijing
CHINA- Academia Sinica, Taipei
CUBA- Academia de Ciencias
CZECHOSLOVAKIA- Czechoslovak Academy of Sciences
DENMARK- Det Kongelige Danske Videnskabernes Selskab
EGYPT- Academy of Scientific Research and Technology
FINLAND- Delegation of Finnish Academies of Science & Letters
FRANCE- Académie des Sciences
GERMANY- Deutsche Forschungsgemeinschaft
HUNGARY- Academy of Sciences
INDIA- Indian National Science Academy
IRAQ- Scientific Research Council
IRELAND- Royal Irish Academy
ISRAEL- Academy of Sciences and Humanities

ITALY- Consiglio Nazionale delle Ricerche
JAPAN- Science Council of Japan
JORDAN- Yarmuk University, Irbid, Jordan
MEXICO- Consejo Nacional de Ciencia y Tecnologia
MONACO- Centre Scientifique de Monaco
NETHERLANDS- Koninklijke Nederlandse Akademie van Wetenschappen
NEW ZEALAND- Royal Society of New Zealand
NORWAY- Det Norske Videnskaps-Akademi
PHILIPPINES- National Science Society
POLAND- Academy of Sciences
ROMANIA- Academy of Sciences
RUSSIA- Russian Academy of Sciences
SAUDI ARABIA- King Abdulaziz City for Science & Technology
SOUTH AFRICA- Foundation for Research Development
SPAIN- Comision Interministerial de Ciencia y Tecnologia
SWEDEN- Kungl. Vetenskapsakademien
SWITZERLAND- Swiss Academy of Sciences
UNITED KINGDOM- Royal Society
U.S.A.- National Academy of Sciences- National Research Council
VENEZUELA- Consejo Nacional de Investigaciones Cientificas y Tecnologicas
YUGOSLAVIA- Union of Biological Sciences