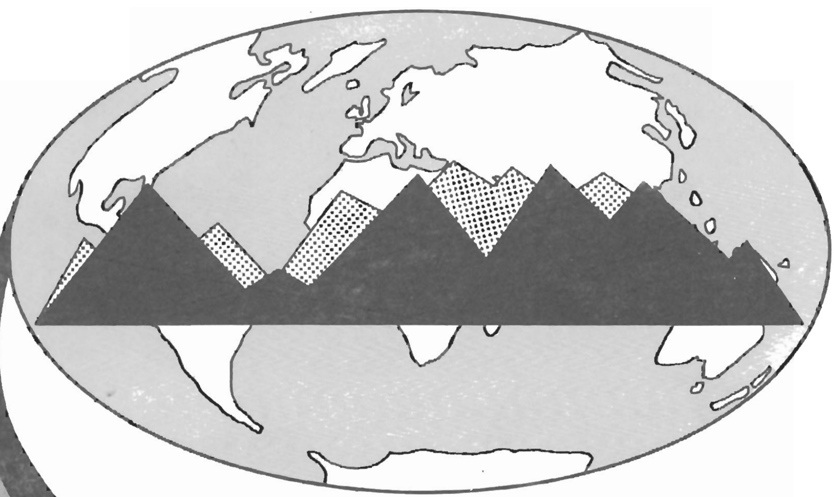
SPECIAL ISSUE - 8

Biology International

The News Magazine of the International Union of Biological Sciences (IUBS)



COMPARATIVE STUDIES ON TROPICAL MOUNTAIN ECOSYSTEMS

A PROPOSAL FOR A COLLABORATIVE PROGRAMME OF RESEARCH

Edited by

Dr. M. Monasterio - Dr. G. Sarmiento - Prof. O. Solbrig

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A Proposal for a Collaborative Programme of Research

Report of the meeting of the IUBS Working Group on
Tropical Mountain Ecosystems/Decade of the Tropics Programme
co-sponsored with
the UNESCO Man and Biosphere (MAB) Programme and
the Spanish National Committee to IUBS

2-4 May, 1984
Barcelona, Cataluna, Spain

Edited by

Dr. Maximina Monasterio and Dr. Guillermo Sarmiento
Universidad de Los Andes
Facultad de Ciencias
Apartado 246
Merida 5101, Venezuela

Professor Otto T. Solbrig
Department of Organismic and Evolutionary Biology
Harvard University Herbaria
22 Divinity Avenue
Cambridge, MA 02138, U.S.A.

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News Magazine

INTRODUCTION

This document represents a proposal for a programme of collaborative research on tropical mountain ecosystems. The objectives of the programme are as follows:

> *to gain an understanding of tropical mountain ecosystems; and the interrelationships of the natural ecosystems with prevailing patterns of land use.*

It is unlikely that in the short period of ten years, whatever the scientific input, a thorough and complete understanding of these systems will be reached. Then a second, more realistic goal, on the basis of available resources is a comparative, intercontinental analysis of some selected aspects of tropical mountains, to identify and validate general principles, particularly those that might be useful in giving scientific support to developmental programmes and associated technologies.

We envision an interdisciplinary approach involving a diversity of biological inputs such as physiology, genetics, ecology, biogeography, evolution, and anthropology, as well as inputs from the environmental sciences and agronomy, and even sociology and economy.

A number of research teams concerned with various aspects of tropical mountain biology and ecology are already in existence. Some of these were represented at the Barcelona conference; we hope all of them will be represented in the future. One aim of the Mountain Programme of the Decade of the Tropics is to assist every interested working team in the pursuit of their research, to foster a greater degree of communication between all these groups, and especially to strengthen local research centers, through a variety of means, including interchange of scholars and students; seminars and workshops; literature exchange; and publication outlets, in accordance with the general principles of the Decade of the Tropics (Solbrig and Golley, 1983).

BACKGROUND

Within the world mountain areas, tropical mountains deserve particular attention since, besides the fact of being quite complex and interesting natural systems, most of them are also heavily populated. Human and social pressures on the natural environment reach levels presently unknown outside the tropics. The fragility of the human environment is thus greatly increased, making still more urgent the search for alternative models of development. These models should be directed towards the increasing satisfaction of human needs in a framework of preservation or sometimes of restoration of the natural equilibria.

Any successful developmental programme has to be based on scientifically sound technologies which take into account all relevant features of the physical, biological, and human systems. Unfortunately, our knowldege of the ecosystems is still quite fragmentary, both in relation to the often relictual primary ecosystems or to the more widespread secondary formations, or even to the principal types of agroecosystems.

From a scientific viewpoint, tropical mountains appear as a promising research subject for a series of different reasons. Some of these are:

1. As with all mountain systems, tropical mountains appear as particularly fragile ecosystems.

2. In contrast to most temperate mountain areas, tropical and subtropical mountains have been subjected to increasing demographic pressures. In other instances, the problems stem from a loss of population.

3. Tropical mountains appear as one of the most diversified ecological areas of the world. In fact, over surprisingly short distances, the three dimensional array of their ecosystems and their patterns of human settlement conform a rich and complex mosaic of biological types, ecological situations and socio-cultural problems from tropical rain-forests and savannas in the basal areas to extreme deserts in the uppermost belts, with many kinds of intermediate situations.

4. The high altitude zones of tropical mountains are a unique environment found nowhere else. This is due to the overwhelming importance of the daily temperature cycle (cold night, warm days) within an area of very low seasonal variation, and the hypobaric conditions that produce decreased amounts of available oxygen (hypoxia). Consequently, in these zones we expect novel adaptations to have evolved.

5. In tropical countries, mountains represent alternatives in land use that complement the economy of adjacent lowlands.

6. Several of the most important food and agricultural resources of tropical countries are produced mostly or totally in mountain areas. This is the case, for instance, of tubers like potatoes and sweet potatoes; grains such as corn, wheat, and rice; most vegetables, a significant part of the milk and wool production; as well as some of the most valuable export crops like coffee and tea.

7. Many vertical and horizontal exchanges and connections take place between mountains and lowlands, giving rise to complex, and reciprocal, physical, biological, and cultural influences.

METHODOLOGICAL APPROACH

A basic property of mountains is verticality. By this we mean that along altitudinal gradients and over very short distances, there is an ecological zonation as well as a zonation in land use and human occupation. Verticality leads to a high rate of abiotic, biotic, and cultural exchanges among zones, with this exchange being unique to mountains.

Because the degree of zonation and contrast between lowlands and highlands is most pronounced in tropical mountains, they are the best sites to study verticality and associated phenomena.

The basic analytical tool will be the analysis of altitudinal gradients through transects. This will be complemented with an experimental approach whenever possible.

Through a comparative analysis we hope to detect repetitive patterns that will lead to the formulation of general theories to explain the processes involved. We also hope to detect cultivars, management practices and technologies that are amenable to being transferred between tropical mountain regions.

The investigation will consist of a comparative study of transects in the Andes, East African mountains, the Himalayas, the mountains of New Guinea, and those of Hawaii. Each of these areas has been studied by various research teams, and consequently, we have some basic information on each region. Moreover, each area has distinctive environmental, biological, and cultural features, but together they form a representative sample of the tropical mountains of the world.

In addition, when necessary, intracontinental comparisons of tropical mountain systems, as well as comparisons of mountain and non-mountain systems will be undertaken.

We suggest an analogy with an experimental situation where one variable is maintained constant. In the intercontinental comparisons ideally, we can choose areas with similar environments acting on dissimilar phylogenetic stocks and cultural traditions, while in the intracontinental comparisons we will keep as constant as possible the phylogenetic and cultural component. The intracontinental comparisons focus on the evolutionary divergence while the intercontinental comparisons emphasize the possibility and the degree of convergence.

1. Intercontinental comparisons.

To maximize the comparability of gradients among continents and islands, in other words to obtain gradients that are as well matched as possible (and knowing that perfect matching is not possible), we have to insure that both remote sensing analyses and climatological comparisons are carried out.

We are aware that the degree of matching of various components is not necessarily equally precise, e.g., climatic and soil conditions, geological history, plant architecture, etc. The factors which make up the differences that exist among gradients from different continents and islands include geological, age, and other features, the phylogenetic origins of the component taxa of the ecosystems, and the history of human occupation from the earliest to the most recent trends of land use.

The degree of convergence can be evaluated on the basis of information from one or more of the following: morphological characters of species, physiognomy of vegetation, resource partitioning in guilds, ecophysiological processes in plants and animals, organic decomposition processes, and patterns of human occupation and use of resources.

2. Intracontinental comparisons.

Three to five altitudinal gradients should be selected within each continent or island group. Within continental masses (South America, Africa, and Asia) these gradients should encompass a range of variations measured mostly by the relative amount of precipitation. For instance, in South America, they could range from the humid conditions of the Venezuelan-Colombian Andes to the more arid conditions of Peru-Bolivia and of northern Chile-northern Argentina.

In island groups, these gradients should represent different degrees of insularity. Islands such as Hawaii and New Guinea are suitable locales for the selection of such gradients.

3. Comparisons of tropical mountains and other systems.

The divergence/convergence hypotheses can be tested further by studying patterns and processes in closely related taxa that occur both in mountain gradients and in other non-mountainous areas that are either near (i.e., in nearby lowlands), or distant (i.e., in the arctic tundra for comparisons with paramo-puna birds or plants; or in subantarctic ecosystems for comparisons with the soil arthropods of the high tropical mountain formations). Also for functional processes like production and decomposition such comparisons will be very useful.

RESEARCH PROPOSAL

We have identified the following four aspects as being characteristic of, or even unique to tropical mountain systems: **verticality, spatial diversity, temporal variation,** and the **high altitude environments.** We propose to study the following aspects of the natural and cultural systems:

1. environmental relations, temporal dynamics, and spatial diversity;

2. ecological and economic rationality of land use patterns and cultural adaptations;

3. basic evolutionary processes at high altitudes;

4. the process of organic production at high altitudes, including primary production, consumption, and decomposition.

1. Environmental relations, temporal dynamics, and spatial diversity.

For the analysis of the spatial and temporal diversity we recommend as a basic approach the use of transects (Van der Hammen, et al., 1983). By a transect we understand the systematic sampling across an altitudinal gradient of representative variables. The transect does not necessarily have to be on a straight line because it must sample without bias the existing local variation and the vertical zonation which is not always possible when sampling is along a line. A transect is a sampling device to increase the efficiency of data gathering.

The principal conceptual items are: a) the sampling design; b) the properties and attributes to be recorded or measured; and c) the analysis of the data.

a.) Sampling design. A first phase is a reconnaissance survey. It consists of the elaboration of pre-existing knowledge of the geology, soils, climate, vegetation, and land use. Wherever available, this information will be gathered from topographic and geological maps, aerial photographs, and satellite imagery, climate records, vegetation studies, agricultural and land tenure records, etc. It will be complemented when necessary by preliminary field surveys.

The second phase consists of the design of the sampling procedure and the laying of the transect which must be done on the basis of information gathered in phase one.

In some areas, phase one has already been completed; in other areas, available information is sufficiently comprehensive to complete phase one in a short time, while sometimes much information is still missing and will have to be obtained as part of the project.

We recommend that field data be collected in the season most favorable for vegetation development. When there are contrasting seasons we recommend additional sampling of attributes that show seasonality at appropriate times during the year.

b) Properties to be recorded (data collecting). This consists of sampling in the field by means of relevés or sampling stations whose position and altitudinal intervals will have been determined by the sampling design.

We suggest that data be collected regarding vegetation, soils, and land use and when possible on microclimate. Among vegetation attributes to be sampled we suggest i) a description of the vegetation structure and plant life forms; ii) a checklist of the plant species (or at least the dominant species); iii) an estimate of each species quantity or density. Soil data: i) a soil profile description; ii) sampling for mechanical and chemical analysis. Among data relating to human use: i) type of use, such as grazing, agriculture, forestry, recreation, etc.; ii) estimation of the intensity of use; iii) landscape modification; and iv) special management practices such as use of fire, irrigation, grazing, etc.

When resources and logistic support are available, we suggest that automatic mircoclimatic sampling stations be installed to record temperature, humidity, precipitation, and radiation on a continous basis. The exact location of these stations should be carefully planned near the sites where the studies on production and decomposition will be performed.

These items refer to the baseline data needs of any given transect. A more comprehensive programme of data collection is optional and recommended wherever possible. This expanded data base could include quantified information on climate, soil fauna, and other soil characteristics, plant species composition and life form spectra (or profile diagrams for each relevé) and local human land use. The optional programme of data collection will be described in a manual of recommended methods to be published later.

c) Data processing and data display. This third work phase relates to the analysis and synthesis of the collected data and to the methods of display. For analysis and synthesis of such relevé data, there are well established and proven methods relating to cluster analysis in form of dendrograms, ordination displays, and two-way tabulation techniques.

In addition to cluster analysis of the elevational components making up the transect ecosystems, individual species and selected individual parameters can be diagrammatically displayed over the topographic transect profile (Mueller-Dombois et al., 1981; Van der Hammen et al., 1983; Van der Hammen, 1984).

Each local transect should be analyzed individually. In addition, the information from all the transects can be pooled and analyzed collectively in order to disclose universal patterns of the variability of tropical mountains.

This approach will result in the identification and preliminary characterization of the ecosystems, their environmental constraints and successional status, as well as the nature of the human impact. This will further lead to a structural framework and a sound basis for the generation of research hypotheses. These hypotheses will be concerned with the interpretation of patterns and processes that operate in the altitudinal, lateral, and temporal dimensions of the world's tropical mountain systems.

2. Ecological and economic rationality of land use patterns and cultural adaptations.

The objective is to explain changes in the zonation of human production activities characterizing each main zone in terms of its origin, evolution, past changes, and predictable trends in the near future. A major interest here is to understand the distribution of human populations and their economic and cultural organization over altitudinal gradients.

Tropical mountains have been exploited by human populations for thousands of years, and by a variety of subsistence and productive means. Hunting and gathering dates back to approximately 15,000 to 20,000 years ago in the Andes, and several million years ago in the East African highlands of Ethiopia, Kenya, and Tanzania. Between these times and the present, humans have exploited tropical mountain lands for hunting, pasture, both subsistence and intensive cultivation, logging, and mining.

These patterns of exploitation of mountain ecosystems have led to considerable landscape modification that dates back to antiquity. Deforestation occurred and terracing was practiced in the Andes, for example, long before the Spanish conquest, so mountain ecosystems have a long history of modification, and even degradation (Ellenberg, 1964). Contemporary patterns of land use are then based in part on a long history of landscape modification.

In tropical mountains throughout the world, there are several research areas that should be explored within a comparative framework.

A first problem area concerns the unique character of mountains in which there are vertical ecosystems or environmental belts within a limited horizontal scale. This produces considerable ecosystemic diversity that can be exploited by human populations with much more ease than comparable latitudinal diversity.

Human populations have managed mountain agroecosystems for approximately 5,000 years. This management has created genetic resources of worldwide importance and agricultural landscapes that limit damage in an erosion prone environment. Traditional patterns of land use adapted to the tropical mountain environment are being stressed by a number of factors: rapid population growth, changing expectations and consumption patterns, road and market penetration, and new agricultural technology permitting more intensive land use. The economic organization of agro-pastoral systems in tropical high mountains depends on the use of and exchange between different production zones located in distinct altitudinal belts. Production zones are defined by: a) the inventory of crops and animals; b) the rules governing land use; c) population distribution; and d) the intensity of land use.

<u>a)</u> <u>Crops and animals.</u> Several tropical mountain regions are areas of crop origin and/or crop genetic diversity (e.g., the Andes, insular South East Asia). Mountain environments have promoted the development of genetic diversity, and human culture has reflected this in the selection of crops and animals that produce more efficiently in certain altitudinal belts. An important research topic is the nature and measure of effective limits on crop distribution. How the customary limits affect the introduction of new crops is a related topic. Mountain agriculture in the tropics is distinguished by its emphasis on diversity between and within zones. Research here can contribute to our understanding of polyculture by analyzing the agronomic and economic relationship between crops and crop varieties that are produced in the same zone and within the same field.

b) Land use rules. Production zones are also demarcated according to different rules governing their use. Certain zones are distinguished by communal control, while other zones are under individual control. A common pattern is to have high altitude production zones used communally for forestry and pasture and lower zones controlled individually for crops. In many tropical mountain environments, however, community control is exercised over crop land to determine crop and field rotation cycles and to set the agricultural calendar. Apart from land tenure rules and setting the agricultural calendar, other rules apply to the maintenance and operation of the agricultural infra-structure, such as irrigation and transportation. Important research questions surround the relation between individual and communal control: how control is defined and how conflicts between interests are resolved. The effects on land tenure and other rules of such things as population growth, changing consumption, and the spread of markets into subsistence economies are also important topics.

c) Population distribution. The population density of tropical mountains generally exceeds that of other tropical regions, and some tropical mountain areas have attained relatively high densities (e.g., the Andes). Human population densities, however, differ greatly between and within tropical mountains. Environmental and socio-economic factors have been identified in the maintenance of low densities. Important research topics in the comparison of human demography of different tropical mountain areas include how limiting factors function in different areas and the relation of population growth to ecological and socio-economic variables such as erosion, deforestation, crop inventories, and land use rules. Within tropical mountain regions, different population patterns may be observed. Certain zones are more densely populated, and population changes occur at different rates by zone. Lower zones in several places are being heavily populated for the first time, and some historically dense zones are loosing population. Migration as well as fertility plays a major role in these changes. It is important to describe these demographic patterns and to relate them to the ecological and socio-economic variables mentioned above.

d) Intensification. Intensification refers to the frequency of land use in a particular place and to the amount of labor invested in production. Intensification is measured by the number of fallow/cropping years, number of crops per year, amount of purchased inputs, and rotation sequences. There is a tendency in agriculture to move over time from labor and land extensive systems to more intensive systems. In mountain environments, as stress factors increase in higher zones, land is worked in more extensive ways than in lower areas where climatic conditions are more favorable. Intensification takes place by more careful terracing, construction of irrigation systems, and the use of agricultural subsidies (fertilizers, pesticides, and herbicides). The causes behind intensification include population growth, technological innovation, and socio-economic reorganization. Limits on intensification include the extraction of surplus (e.g., by taxation), technical and environmental limits, and opportunity cost. An important question is the environmental effects of intensification; especially erosion and the loss of genetic resources. How do farmers recognize and weigh these losses? An objective of research on intensification is to estimate its likelihood, in particular mountain agroecosystems and production zones, and to identify ways to limit its damage to agricultural resources.

A second problem area concerns highland migration with movement both to urban centers in the highlands and to rural and urban areas in the lowlands. The downward migration from highlands to lowlands is a result of highland "push" factors due to population pressure on land resources, and "pull" factors due to perceived economic and life-style advantages in cities and rural homesteading zones (Glaser and Celecia, 1981).

A third problem area closely tied to the others, is the effect of population pressure on land resources. Highland ecosystems are fragile and particularly sensitive to human-initiated destructive processes (Billings, 1979). In the Simen Mountains of Ethiopia, population pressure at 3000-4500m is contributing to an accelerated "destabilization of the entire geoecosystem", particularly soil loss (Hurni and Messerli, 1981). In the Papua-New Guinea Highlands, land use intensification is severe at elevations less than 2000m in Enga Province because of shifts to cash cropping combined with downward migration of peoples from higher elevations (Pain and Scott, 1981). Goldstein (1981) has observed an alarming change in cultural values in the Himalayas, where with increasingly limited land resources there has been a "shift in attitude toward the environment from one focused on long-term conservation and adaptation to one focused on short-term exploitation and manipulation". Hence, there is a dangerous positive feedback that can develop where ecosystem perturbation leads to a breakdown in traditional socio-cultural values, which contributes to further ecosystem perturbation. For these and other reasons, the axis of population, ecosystem, and socio-cultural values and practices should be the basis for much of the research to be conducted.

3. Basic evolutionary processes at high altitudes.

The theoretical objective of this subject is to explain and predict evolutionary and successional processes in an environment characterized by a great heterogeneity of biotypes. This heterogeneity is caused primarily by spatial variability in the sense of verticality and climatic changes at the geological and historical scale. These conditions produce insularity. To achieve these objectives, three specific topics will be emphasized:

a) species turnover;
b) process of speciation;
c) altitudinal effects on growth, maturation, and reproductive activity in selected plant species and in humans.

<u>a) Species turnover.</u> According to the present theory (Hutchinson, 1978), every species is supposed to occupy a unique place in the environment. The number of different species in a habitat (species diversity or species richness) is considered to be a measure of the heterogeneity of the habitat. It also may reflect past geological events.

The diversity of species within a community or habitat is referred to as the alpha diversity, and can be measured in a variety of ways (Whittaker, 1972;

Pielou, 1968, 1975). Two habitats may have similar diversities but different species. The measure of the rate and extent of change in species along a gradient is called the beta diversity (Whittaker, 1972; Goodall, 1973; Mueller-Dombois & Ellenberg, 1974; Cody, 1975; van Reenen & Gradstein, 1983). Finally, the richness in species in a range of habitats in a geographical area (such as a mountain range) is termed the gamma diversity, and is a consequence of the alpha diversity of the habitat and the beta diversity between them.

The patterns of alpha, beta, and gamma diversity relate to the way a community is structured, and are important in assessing the role of factors such as competition, niche breath, speciation, migration, and theories about community structure.

The objective of this aspect of the project is to look for patterns in the alpha, beta, and gamma diversity along the various transects. Vascular plants, mosses and birds will be selected as target organisms. The recognition of repeatable patterns can lead to the formulation of predictions about the consequences of manipulating natural communities. Among the questions that will be investigated are: i) how regular is the relative abundance of species along the communities in the transect; ii) how do species correlate with physical factors along the gradient; iii) how often do species with particular morphological combinations occur; iv) how do various management practices alter the patterns of diversity in natural communities.

b) Process of speciation. Patterns of species diversity are related to processes of speciation, competition, and extinction. Mountains are especially good research environments to test the importance of isolation and environmental patchiness as a factor in speciation, because of the occurrence of large physical and biotic changes over short distances (Vuilleumier, 1977; Vuilleumier & Ewert, 1980; Vuilleumier & Simberloff, 1980; Prance, 1982). Climatic and environmental changes in time are also of considerable importance as factors in speciation and extinction (Livingston & Van der Hammen, 1979; Van der Hammen, 1974; Van der Hammen & Cleef, in press).

Analysis of the geographical distribution of species is a technique that can provide much information towards the development of general laws regarding speciation and extinction, and will be the basic tool used in this part of the analysis. The question to be researched is why some species have wide distributions, while others are narrowly restricted. Ecologists, evolutionists, and biogeographers, have long been interested in the distribution of species. Species ranges have been correlated with present and past physical and biological environments (climate, habitat, ecosystem type), or historical events (glaciation, droughts), and causal explanations proposed. This has resulted in a great diversity of ad hoc hypothesis. More recently, some authors (MacArthur & Wilson, 1967; MacArthur, 1972; Diamond, 1975, 1978; Simberloff, 1974) have attempted to develop general theories of wide applicability and predictive power. The keystone of these theories is the role played by interactions between species, especially competition, in shaping the dynamics of local populations, and in placing limits on the spatial dynamics of populations over the entire range of the species.

Using birds and vascular plants as research subjects (which represent extremes of vagility), and the statistical analysis of the geographical distribution as the basic research tool, we propose to test models of speciation and biotic equilibrium, in order to see how best to explain the patterns of species diversity and richness recorded in the transects, taking into account both spatial and temporal diversity. The eventual existence of a series of comparable transects in different continents and latitudes, offers a unique opportunity to test the generality of a number of hypotheses relating to speciation and biotic equilibrium.

c) Altitudinal effects on growth, maturation, and reproduction on selected plant species and in humans. As European biologists explored the world during the nineteenth century, they discovered that structurally similar vegetations were found in regions with similar climates, even though the species belong to unrelated families (Griesebach, 1845; Humboldt, 1849). The striking convergences were explained as the adaptations of plants to the constraints imposed by the physical environments in the areas (Schimper, 1903). Although the descriptive aspects of convergence have been well documented, these natural experiments in community evolution have not been extensively exploited (Orians and Solbrig, 1977). More or less independently-evolved communities in regions with similar climates, but isolated from one another by great expanses of different physical environments that impose barriers to dispersal, provide unique opportunities to develop and test a variety of hypotheses about the evolution of adaptations and the resultant patterns of community organizations.

The length of time required for the evolution of community structure imposes severe restrictions on the ways in which answers can be obtained to the key questions ecologists and evolutionists wish to ask. With rare exceptions, it is not possible or desirable to perturb the environment and to measure meaningful evolutionary responses within a period of the creative activity of a single individual. Therefore, studies of ecosystem evolution rely on a number of indirect approaches which take advantage of the natural experiments (Cody, 1974; Orians and Solbrig, 1977) provided by evolutionary processes in different parts of the earth. The hypotheses tested are of the general form **if natural selection had acted in a given manner for a long period of time, then nature should have a given set of characteristics.** This type of hypothesis ideally predicts processes of natural selection precisely enough that the appropriate ecosystems for study and the aspects of their components that are most important for testing are clearly specified.

The high altitude tropical environment is unique. Nowhere else do we find such great daily variations in temperature within a regime of year round uniformity. These environments are found in the high altitude mountains of America, Africa, Asia, and the island of Hawaii. Each of these mountain systems has evolved a unique biota in isolation from each other, whose members are for the most part totally unrelated. Only rarely do they share species or genera. Among the possible subjects for study we have selected two groups: plants and humans.

Altitudinal effects on selected plant species. Plants are especially constrained at the high altitude on account of their requirement for liquid water for dissipating absorbed heat energy through transpiration, and their dependence on light and appropriate temperatures to maintain a positive carbon balance (greater photosynthate production than consumption through respiration). Consequently frequent nightly frosts, low precipitation, and daily nubosity accompanied by low temperatures produce severe constraints on plant growth. Not surprisingly, high altitude floras show unique life forms such as cushion plants, and caulescent rosettes (Cuatrecasas, 1934; Cabrera, 1958; Hedberg, 1964; Cleef, 1978; Monasterio, 1979). These convergences have been described. Much rarer are studies of the growth and reproduction of these species.

The theory of natural selection as developed by Darwin and subsequently refined by a variety of population biologists is based on the differential survivorship and/or reproduction of individual phenotypes (and underlying genotypes). This sets the boundaries to the kind of models we plan to design and test. We will attempt to guess what features of a species that grows in the high altitude tropics will lead to greater survivorship and/or reproduction. Since a separate study deals specifically with production, we will concentrate in this part on demographic and reproductive aspects.

As to methodology, the hypotheses will be tested through the detailed study of selected populations in different high altitude environments of the same mountain systems (such as northern and southern Andes sites), and different mountain sites (such as Andes, East Africa mountains, and Hawaii). These populations will be carefully monitored demographically with the objective of obtaining detailed life tables. We are particularly interested in studying and comparing two major life forms: the caulescent rosette form (genus *Espeletia* in Venezuela and Colombia, *Senecio*, in East Africa, and *Argyroxiphium* and *Wilkesia* in Hawaii), and the cushion plant (e.g., *Llareta* in the southern Andes). Both of these forms are dominant in high altitude tropical mountains, the former in wet sites, the latter in dry areas.

Altitudinal effects on humans. Human and other mammals living at high altitudes are faced with lowered amounts of oxygen in atmospheric air. This can produce one of the most severe forms of climatic stress experienced by humans. At 3,000 meters above sea level, the partial pressure of oxygen is only 70% of that at sea level, and at 4,000 meters, oxygen partial pressure drops to roughly 60% of sea level values (Frisancho, 1975). The effects of this hypoxia on human development and function are profound (Little, 1981). Despite several decades of research on how humans are able to cope with high altitude hypoxia and other stresses (Baker, 1978a; Baker and Little, 1976; Heath and Williams, 1977; Ward, 1975; Weihe, 1963), there are still several unresolved problems concerning human growth, health, and reproduction at high altitude. The principal difficulty in quantifying the effects of hypoxia on these human functions results from the need to control for covariant stresses of cold, disease, and poor nutrition. Hence, methods of research should exercise care in attempting to control for these variables.

There are at least three major problems concerned with high altitude stress that are appropriate for investigation and inter-continental comparison.

1. Why do high altitude children grow more slowly, achieve smaller adult size, and mature later than their sea level counterparts? This has been observed for Himalayan Tibetan and Sherpa populations

(Pawson, 1977), and Andean Quechua and Aymara populations (Beall et al., 1977; Frisancho, 1975; Mueller et al., 1978), but not for Ethiopian populations (Clegg and Pawson, 1978). An important basis for intercontinental comparison is the pattern of large chest sizes in Andean residents (when compared with sea level residents) that is not present in Himalayan dwellers (Pawson, 1977).

2. Is a lifetime of exposure to high altitude necessary to develop full acclimatization to hypoxia? One of the most important influences of hypoxia on the human body is the limit imposed on performing physical work. Evidence is conflicting (Buskirk, 1978), with some studies suggesting the need to be reared at high altitude from an early age in order to fully acclimatize to hypoxia (Frisancho et al., 1973), while others (Greksa and Haas, 1982) found that a lifetime of exposure was not necessary. Again, there are marked differences in patterns of adaptation between Andean and Himalayan populations that merit intercontinental comparisons.

3. Does residence at high altitude impair reproductive capacity in the permanent resident? One of the most intriguing questions bears on the influence of hypoxia on the ability of individuals to conceive and bring a fœtus to a healthy, full-time birth (Haas, 1980). Clegg (1978) did a thorough review of the literature and concluded that "life at high altitudes impairs reproductive efficiency". The general problem of reproductive capacity (fecundity) is, of course, usually observed and measured as reproductive performance (fertility); hence, socio-cultural practices and behaviours must be controlled very carefully to document impaired reproductive function. The evolutionary implications of human adaptation to hypoxia through variation in reproductive capacity and performance are of considerable interest (Baker, 1978b).

Other research problems that relate directly to high altitude environments are the need to partition the effects of hypoxia and socio-economic conditions on disease and mortality of highland natives. These and other studies can be profitably conducted by a variety of research designs based on naturally occurring circumstances. For example, since there is human population movement in many mountain areas around the world, migrants who travel from one environment to another can be compared with those who remain in the home environment and with those who are native in the new environment (Thomas et al., 1977). By a number of intracontinental and intercontinental comparisons, environments and populations can be controlled to resolve some of the complex problems noted above.

4. Organic production and decomposition in high altitude environments.

The objective of this study is to explain some particularities in productive processes and decomposition that are unique to high altitude biotypes, especially those of cloud forests and paramos.

As in any other ecosystem, the production of organic matter by autotrophic organisms and its consumption and decomposition by heterotrophic living beings, constitue the foundations of energetic functioning of the high altitude ecosystem.

The major characteristics of these environments is a very low mean annual temperature. In temperate zones, the monthly mean temperatures vary in an important and characteristic manner, often with well differentiated seasonal precipitation. In the tropical zones the mean monthly temperature variations are not very important, and only precipitation separates the seasons. On the other hand, daily variations in temperature are significant, especially in the dry season.

Another characteristic related to altitude is the increase in solar radiation, and especially, in the absence of clouds, an increase in ultraviolet radiation. Precipitation can vary considerably according to the geographical situation. When precipitation is low, the physiological effect of drought is augmented by the low temperatures. Such diversity can permit fruitful comparisons. Of special importance is the continued day-time cloudiness and mist in the principle condensation zones (cloud forests). The strongly reduced input of light/radiation should have an important influence on production.

Primary production. Physiological studies have shown that there is an effect of cold on photosynthesis on one side and on respiration on the other. They show the possibility of a non-negligible primary production even at relatively low temperatures. This production depends a lot on the specific morphological, anatomical, and enzymatic adaptations of the plant. The age of the mountain (i.e., the time available for an adaptation to evolve) plays possibly an important role which will be interesting to evaluate in comparing the primary production of a large number of plant species and high mountain ecosystems of different ages. Have species in old mountain systems acquired a more efficient primary production system?

The daily alternation of cold and medium temperatures may have a very different effect on productivity than the alternation of a long period of cold temperatures and one of warm temperatures (as in the temperate zone), or of a long dark period and a long light period (as in the Arctic). The precise comparison of primary production in these different conditions should be of great interest, and has still not been done, in spite of the studies of the IBP.

Consumption. As in many other ecosystems - for example the forests - the consumers of live vegetable matter play only a modest role in the ecosystem. Therefore, it may be convenient to quantify their behavior and to determine whether their low numbers are a consequence of low temperatures or of plant defenses, such as the resin of *Espeletia* in the paramos of the Andes. It is certain that given the growth limitations imposed by the low temperatures, high altitude plants could not support significant predation by homotherm animals whose metabolism is not dependent on the ambient temperature. Therefore, the analysis of the strategies developed by different animals to break the defenses represented by the resins of *Espeletia* is of particular interest.

Other plants defend themselves by producing underground organs and having only cushion and spiny above ground forms, which may also be a way of protection against the cold.

Decomposition. The low consumption rate of living matter has four consequences:

a. A predominant role of microorganisms in decomposition that surpasses 90% of the total. The basic pathway of this decomposition is well known and it will be interesting to compare it under different situations, such as the level of endogenous tissues in cushion plants, at the level of the dead tissue which remains attached to the stem in the case of plants like Espeletia, and in the case of plant parts that fall to the ground (leaves of Polylepis and Hypericum of the high altitude paramos).

The structure in cushions and the persistence of standing dead matter such as the case of Espeletia timotensis in the desert paramo, constitute a very favorable situation to analyze with precision the patterns of decomposition. It is especially favorable for studying the interaction of microorganisms and fungi.

b. The accumulation of carbon in the form of partially decomposed organic matter as a result of a low rate of decomposition that is provoked primarily by anaerobic conditions and low temperatures. This is what happens in the case of peat formations.

c. Extreme air-humidity in cloud forests creates very special conditions, causing a short survival time for individual leaves, reduced soil bio-activity (Van der Hammen et al., 1983) and increased bio-activity in the epiphytic bryophyte layer. Bio-activity and decomposition may in this way partly be moved from the soil to the trees.

c. Relatively slow decomposition in the soil as mentioned in c., might lead to special adaptations like superficial root-mats, related to competition for nutrients (Van der Hammen et al., in press). The role of mycorrhiza in these types of systems is probably important, and should be studied.

IMPLEMENTATION

I. Sites.

Ten research sites have been identified for the initial phase of the study. Additional sites will be added as required if there is local interest and support. Not all sites are known to the same extent; likewise, in some sites active research has been ongoing for a long time, in others, research teams still need to be organized. The sites and the extent of present research are as follows.

1. Andes of Venezuela. For over ten years an interdisciplinary research team from the Universidad de los Andes in Merida, Venezuela, has been investigating the ecology of this region (Monasterio, 1980). These studies have involved research on the physical environment (Schubert, 1979, 1980; Salgado-Labouriau, 1979, 1980); climate (Azocar & Monasterio, 1980); vegetation

(Farinas & Monasterio, 1980), fauna (Vuilleumier, 1979; Vuilleumier & Ewert, 1978), and land use. Transects have been established and ecophysiological and populational studies of selected species are under way.

2. Central Andes of Colombia. Since 1976, the project "Ecoandes" (Investigaciones de Ecosistemas Tropoandinos) has been conducting ecological studies in the Sierra de Santa Marta and particularly in the Andes of central Colombia in the area of the Parque Nacional Natural de los Nevados. This research has been sponsored by INDERENA (Instituto de Ciencias Naturales-Museo de Historia Natural, Departamento de Biologia de la Universidad Nacional); the Instituto Geografico Agustin Codazzi of Colombia; the Hugo de Vries Laboratory of the University of Amsterdam; and the Institute of Systematic Botany of the University of Utrecht in Holland. The objective of the project is to develop comprehensive biological and physical inventories of the Andean ecosystems of Colombia in order to obtain basic information regarding its quantitative composition, functioning, dynamics, and history (Van der Hammen et al., 1983). Knowledge of the ecology of the Colombian Andes will serve as a basis for developmental projects, rational land use, and conservation of natural resources (Van der Hammen et al., 1983).

3. Andes of Central Peru. No research team is working at present in this area along the present lines, but a good data base from past studies is in existence (Baker, 1982; Baker & Little, 1976; Brush, 1982). Contacts have been initiated with Peruvian and United States biologists and anthropologists working in Peru to promote the organization of a research team to collaborate in the present study. A transect in Peru will be highly useful for comparative purposes.

4. Andes of Northern Chile. For a number of years, an interdisciplinary team has been studying the physical environment, the vegetation, the fauna, and the human populations along a transect from Africa on the Pacific to the Bolivian border at lat. 18° 28' S. (Veloso & Bustos, 1982). This research under the sponsorship of the University of Chile and the MAB (Man and Biosphere) programme of UNESCO, aims at a better understanding of the ecology of the region in order to try to resolve pressing land use problems (Fuentes & Castro, 1984).

5. Northern Argentina. A collaborative research programme entitled "The Tropics of North-West Argentina: an ecological and socio-economic analysis as a basis for regional development" has been started under the joint sponsorship of the University of Salta, and INTA (Instituto Nacional de Tecnologia Agropecuaria). As part of the programme, ecological transects going from the Puna plateau to the forests at the foot of the Andes will be established. Research on the preliminary survey phase is underway.

6. Ethopia and 7. Kenya. At present there are no organized research teams working in the mountains of Ethiopia and Kenya along the lines described in this proposal, although a number of individual workers are researching various problems of relevance to this project. There are a number of local and foreign ecologists and anthropologists working in this area that we are trying to interest in setting up one or more transect studies. It is very important for comparative purposes that transects be established in Africa.

8. Himalayas (Nepal). Interdisciplinary studies teams from Nepal, the United States, various European countries, and Japan, have been collaborating in ecological, anthropological, and economic studies of the mountains of Nepal. The aim is to produce a broad data base to help solve some of the conservation and production problems of the area (Ives & Messerli, 1981).

9. Mountains of New Guinea. No organized group exists that is working in New Guinea along the lines described in this proposal. We hope to organize such a team under the leadership of New Guinea ecologists.

10. Hawaii. Much ecological research has been performed in Hawaii including complete and detailed ecological transects (Mueller-Dombois et al., 1981, 1983). Hawaii offers the opportunity to assess tropical mountain phenomena in a very isolated island system, as well as an opportunity to study the impact of a very modern, high-input type of agriculture, on tropical mountain ecosystems.

II. Workshops.

Yearly conferences rotating along the sites are planned. The next meeting is planned for Merida, Venezuela, in May of 1985.

III. Financing.

The organization and financing of the Mountain Programme of the Decade of the Tropics of IUBS will be a decentralized one. Every working group is supposed to adopt its own type of organization and obtain its own financing to suit the needs of each national situation. This type of organization will also avoid the need for any kind of central bureaucratic machinery. It is our goal to devote all available funds for research.

At present only six of the ten research teams are in operation. funds and personnel for the remaining four will have to be obtained, as well as increased funding support for the groups already in existence. The coordinating committee of the Decade will try to aid all working groups in obtaining needed financing. It also will try to obtain support for the workshops and for the comparative analysis of data, when the research reaches that stage.

IV. Administration.

Each research group is expected to have complete independence in the planning and implementation of their phase of the research, as each group will face unique local conditions and problems. It is expected that some individuals and/or research teams will pursue their investigations at more than one site. To help organize the yearly workshops; to facilitate information exchange among groups; help organize new research groups; serve as a liaison with IUBS' Decade of the Tropics Executive Committee and the UNESCO "Man and Biosphere (MAB) Programme", and other relevant research programmes, a

Coordinating Committee has been chosen. The following individuals have agreed to serve on this committee:

Professors
Maximina Monasterio (Chairman), Venezuela
Stephen Brush, U.S.A.
Francesco di Castri, France
Guillermo Sarmiento, Venezuela
Otto T. Solbrig, U.S.A.
Thomas Van der Hammen, Netherlands
Deiter Mueller-Dombois, U.S.A.

In addition, a central office-clearing house has been established to which any questions regarding this programme should be addressed:

Professor Otto T. Solbrig
Tropical Mountain Programme
Department of Organismic and Evolutionary Biology
Harvard University
22 Divinity Avenue
Cambridge, MA 02138, U.S.A.

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