INSTITUTE OF CURRENT WORLD AFFAIRS

GSH-8 The Biological Model of Diversification in the Tropics

Apartado 8-3870
San Jose, Costa Rica
3 March, 1979

Mr. Peter B. Martin
Executive Director
Institute of Current World Affairs
Wheelock House
4 West Wheelock Street
Hanover, New Hampshire 03755

Dear Peter:

The fifth international symposium of the Association for Tropical Biology (ATB) was held February 8-13, 1979, in Macuto Beach, Venezuela. The symposium had been scheduled for Manaus, but on December 21, 1978, the Brazilian Defense Council decided the symposium could not be held anywhere in Brazil. Although the official reasons were not known, it is generally assumed by symposium participants that Brazil did not want a group of foreign scientists meeting in Brazil to discuss the Amazon basin.

Organizers of the symposium in collaboration with the Venezuelan Ministry of the Environment and Renewable Natural Resources did a remarkable job with the symposium change of venue. It was an excellent symposium, very well organized, with many quality papers that allowed little time for the 134 registered participants from 18 countries to bask in the warm tropical sun or leisurely enjoy the swimming pool.

Although titled "The Biological Model of Diversification in the Tropics," the symposium served as a forum for critically assessing the tropical forest refugia theory. It is theorized that the climatic fluctuations causing cold glacial and warm interglacial periods in temperate latitudes during the past two million years also had profound effects upon the organisms living in tropical latitudes. Cooler, drier climates are believed to have caused drastic geographic reductions in the extent of tropical forests, particularly in South America and Africa. At issue in this symposium was the role of tropical forest refugia as evolutionary source areas for the great species richness present in today's tropical forests. To the credit of the symposium organizers, critics of the forest refugia theory were invited, as were scientists knowledgeable of the Old World Tropics. I include here the speakers and topics as a ready reference to my discussion of the symposium.

Opening Address: Jürgen Haffer (Essen, W. Germany) "General Aspects of the Refuge Theory"

Sessions 1 & 2: Geomorphology, Palynology and Paleoclimatology

Aziz N. Ab'Sáber (Institute of Geography, São Paulo, Brazil) "Geomorphological Data and its Relationship to the Refugia Model in Amazonia"
Tomas van der Hammen (University of Amsterdam, the Netherlands) "Paleoecology of Tropical South America"
Maria Lucia Absy (National Institute of Amazon Resources, Manaus, Brazil) "Quaternary Palynological Studies in the Amazon Basin"

Georg Irion (Senckenberg Institute, Wilhelmshaven, W. Germany) "Quaternary Geology of Central Amazonia"
Alan Graham (Kent State University, Kent, Ohio) "Tertiary History and Paleoenvironments of the Neotropical Rain Forest Near its Northern Limits"
Keith S. Brown, Jr. (Campinas State University, Campinas, São Paulo, Brazil) "Ice Age Refuges, Soils, and Modern Endemism in Neotropical Forests: Correlation and Examination of Some Details in the Patterns of Evolution"
David Gifford (University of Brasilia, Brasilia, D.F., Brazil) "Biogeography of Butterflies on the Brazilian Planalto"

Session 3: Humid Vegetation

Alwyn H. Gentry (Missouri Botanical Garden, St. Louis, Missouri) "Phytogeographical Patterns in Northwestern South America Interpreted in the Light of Pleistocene Climatic Oscillations"
V. Manuel Toledo (Autonomous National University of Mexico, Mexico) "Pleistocene Refuges in Tropical Mexico and Adjacent Areas: Phytogeographic Evidences"
Ghillean T. Prance (New York Botanical Garden, Bronx, New York) "Diversity of Habitats, Long-Distance Dispersal, and/or Forest Refugia? Evidences from Woody Angiosperms"

Session 4: Arid Vegetation

Julian A. Steyermark (Botanical Institute, Caracas, Venezuela) "Relationships of some Venezuelan Forest Refuges with Lowland Tropical Floras"
Otto Huber (Ministry of the Environment and Renewable Natural Resources, Caracas, Venezuela) "The Ecological and Phytogeographical Significance of the Actual Savanna Vegetation in the Amazon Territory of Venezuela"
Jean-Jacques de Granville (Botanical Institute, Montpellier, France) "Probable Location of the Forest Refuges in French Guyane During the Late Pleistocene and Holocene"

Session 5: Insects

John R.G. Turner (Rothamsted Experimental Station, Harpenden, Herts, England) "Disorderly Extinction in the Amazonian Refuges: A Model for the Evolution of Parallel Mimicry in *Heliconius*"
Donald R. Strong (Florida State University, Tallahassee, Florida) "Hispid Beetle Communities in Rolled *Heliconia* Leaves"
Gerardo Lamas (National Major University of San Marcos, Lima, Peru) "A Preliminary Zoogeographical Division of Peru Based on Butterfly Distributions"
Terry L. Irwin (Smithsonian Institution, Washington, DC) "Amazonian Inundation Forest Canopies: Short-Term Refugia and Long-Term Evolutionary Centers"

Session 6: Vertebrates

W. Ronald Heyer (Smithsonian Institution, Washington, DC) and Linda R. Maxson (University of Illinois, Urbana, Illinois) "Distribution, Relationships, and Zoogeography of the Lowland Frogs of the *Leptodactylus*-Complex in South America, with Special Reference to Amazonia"

William E. Duellman (University of Kansas, Lawrence, Kansas) "Pleistocene Forest Refugia and Patterns of Distribution and Speciation in Anuran Amphibians in the Amazon Basin"

Stanley H. Weitzman (Smithsonian Institution, Washington, DC) "Small and Pygmy Characoid Fishes as Evidence for Testing Forest Refugia Hypotheses in the Amazon and Orinoco River Basins of South America"

Kenneth E. Campbell (George C. Page Museum, Los Angeles, California) "Pleistocene Climatology and the Origin and Evolution of the Fauna of Northwestern South America"

Paul Müller (University of Saarlandes, West Germany) "Centers of Dispersal in the Neotropical Region"

Session 7: Miscellanea (Primates, Anthropology)

Warren G. Kinsey (City University of New York, New York) "Distribution of the Neotropical Primates in Light of the Pleistocene Refugia Model"

Betty J. Meggers (Smithsonian Institution, Washington, DC) "Archeological and Ethnographic Evidence Compatible with the Model of Forest Fragmentation in Amazonia"

Ernest C. Migliazza (Cornell University, Ithaca, New York) "Recent Linguistic Realignments and the Amazonia Forest Refuges Model"

Session 8: Evidence of Refuges in Old World Tropics

Donald Walker (The Australian National University, Canberra, Australia) "Speculations on the Origins of Rainforest in Tropical Australasia"

Peter Grubb (University of Ghana, Legon, Accra, Ghana) "Refuges and Dispersal in the Speciation of African Forest Mammals"

Willem Meijer (University of Kentucky, Lexington, Kentucky) "Plant Refugia in Indo-Malesia"

Daniel A. Livingstone (Duke University, Durham, North Carolina) "Quaternary Geography of Africa and the Theory of Rainforest Refugia"

Session 9: Theoretical Perspectives

David L. Pearson (Pennsylvania State University, University Park, Pennsylvania) "Effect of Tropical Forest Refugia on Lowland Bird Community Structure in Western Amazonia, West Africa, Borneo and New Guinea"

John Terborgh (Princeton University, Princeton, New Jersey) "Distribution of Endemic Bird Species in Colombia and Ecuador"

John Endler (Princeton University, Princeton, New Jersey) "Biological Diversification in the Tropics, Clines or Refugia?"
Woodruff W. Benson (Campinas State University, Campinas, Sao Paulo, Brazil) "Alternative Models for Infrageneric Diversification in the Humid Tropics"

Session 10: Refuges and Conservation

Stefan J. Gorzula (Ministry of the Environment and Renewable Natural Resources, Caracas, Venezuela) "Contributions to the Zoogeography of the Herpetofauna of Northeastern Venezuela"
Norman Myers (Nairobi, Kenya) "Conservation and Refugia in Africa"

David Oren (Harvard University, Cambridge, Massachusetts) "Testing the Refugia Model for South America: An Hypothesis for the Discrepancies in the Number of Refugia"
Thomas Lovejoy (World Wildlife Fund, Washington, DC) "Panel Discussion on Conservation and Refugia in the Amazon Basin"

Unfortunately, some Brazilian scientists were unable to attend the symposium. It is hoped that their invited papers will be included in the book, "The Biological Model of Diversification in the Tropics," to be edited by Ghillean T. Prance and published by Columbia University Press.

Before highlighting several of the papers, a brief review of geological time may be in order.

Years Before Present	Epoch	Period	Era
10,000	Holocene / Pleistocene	Quaternary	Cenozoic
2 million	Pliocene	Tertiary	Cenozoic
12 million	Miocene	Tertiary	Cenozoic
25 million	Oligocene	Tertiary	Cenozoic
36 million	Eocene	Tertiary	Cenozoic
58 million	Paleocene	Tertiary	Cenozoic
63 million	Cretaceous		Mesozoic
135 million	Jurassic		Mesozoic
181 million	Triassic		Mesozoic
230 million			

Many of the symposium papers were concerned with Pleistocene expansions and contractions of tropical forests. A few papers dealt only with the Holocene and a few discussed flora and fauna of the Tertiary.

Tropical forests as we know them today were well-developed by mid-Eocene, with the occurrence of many families and genera of present-day plants. The Tropical Tertiary Flora is known from Eocene fossil records in England, Tennessee and Alaska. Starting in the Miocene and continuing into the Pliocene was a long period of mountain building, continentality, and increasing aridity that pushed the Tropical Tertiary Flora back to lower latitudes.

The Pleistocene was characterized by repetitive advances and retreats of glaciers. Cold, usually dry glacials (the Ice Ages) were periods of active glacier formation and lower sea levels. Warmer interglacials (which we are in now) were generally moist with higher sea levels. Pleistocene glacials have been studied by geologists for more than a century, but it wasn't until 1969 that Jürgen Haffer suggested Pleistocene forest refugia contributed to the species richness of birds in the Amazon Basin. Haffer's seminal paper stimulated considerable scienfific interest in tropical forest refugia as evolutionary source areas of new species. Partial concordance of postulated refugia from independent studies of lizards, butterflies and trees further whetted the scientific appetite.

Fittingly, Jürgen Haffer presented the opening address on "General Aspects of the Refuge Theory." In discussing the evolutionary significance of Quaternary forest refugia, Haffer noted that the three main outcomes are: a) extinction, b) survival without differentiation, and c) survival with genetic-morphologic differentiation to subspecies or species level. Haffer stressed the importance of active dispersal of organisms during ecologically favorable conditions (e.g. continuous forest) and range fragmentation (vicariance) of the population during ecologically adverse conditions (e.g. forest refugia). Haffer stated that the severe and repetitive climatic changes during the Quaternary caused cool-dry periods to alternate with warm-moist periods.

Geomorphological evidence was presented in two papers. The first, by Ab' Sáber, dealt with the widespread occurrence of stone lines in Amazonia as strong support for arid climates during the Quaternary. Ab'Saber's interpretation of stone lines near Manaus was strongly challenged by Irion, who said the stone lines are layers of plinthite--a type of laterite. By definition, a plinthitic layer is formed *in situ*, hence it cannot be a sedimentary deposit of stones. The important question concerning the geomorphological interpretation of stone lines or plinthite layers was not resolved. Irion's studies of riverine lakes adjacent to present rivers led him to conclude that riverine lake sedimentation took place under continuous humid climatic conditions, over a period of at least 100,000 years B.P.

Probably the best paleoecological evidence of differing climates comes from the scientific field of palynology, the study of pollen preserved in sediments. Wind-transported pollen deposited in lakes is thought to give a fairly accurate historical record of the dominant plants growing near the lake. Carbon-fourteen (C^{14}) dating of organic matter in the sediments provides an accurate age up to about 50,000 years B.P. Van der Hammen has been studying the palynology of the northern Andes, especially in Colombia, for more than two decades. He pointed out that the Sabana de Bogotá, now at 2560 m, was approximately at present sea level in the late Pliocene. It was lifted to its present elevation by the general uplifting of the Andes at the close of the Tertiary. Van der Hammen drew the following conclusions for the Andes: (1) Important changes in vegetation took place not only in the Quaternary, but in the Tertiary as well, particularly in the Miocene and Pliocene. (2) Palynological evidence suggests 20-30 climatic changes during the past three million years. (3) The last glacial (ending about 10,000 B.P.) was wet, despite general agreement worldwide of a major dry period between 20,000 and 12,500 B.P. (4) The driest periods in the Tropics occurred during the second half of a glacial period, that is, from the maximum onwards. (5) The Holocene has been characterized by lower effective rainfall, with recognizable dry periods in 5000-3500 B.C., 2700-2100 B.C. and 500-1300 A.D.

Absy's palynological studies in Rondonia (western Amazonia) show several alternations of forest and savanna vegetation. The Rondonia dry periods conform with comparable dry periods in the Magdalena Valley of Colombia. She suggests that Holocene vegetation changes were probably caused by water level fluctuations.

Graham's studies in Veracruz State, Mexico, indicate that the disruption of the extensive Neotropical Tertiary Flora began near the end of Miocene times. Graham's results conform with the general evidence of fluctuating environmental conditions (climate and sea level/water table changes) during the Cenozoic. He suggests that the specific rainforest evident today in eastern Mexico may represent a combination of genera in existence for only a few thousand years since the end of the last glaciation. Toledo cautioned that the absence of pollen of present-day genera does not necessarily mean they were absent from the tropical forests of earlier times, because modern sedimentation under tropical forest shows practically no pollen of the forest dominants.

In the tropical lowlands of Mexico, Toledo found evidence for three distinct phases in the past 40,000 years: a) from 40,000 to 25,000 years B.P. existed a cool-humid climate with deciduous oak forest; b) from 20,000 to 14,000 B.P. occurred a cool-dry climate with oak-pine predominating; and c) from 8,000 to 2,000 B.P. was a warm-dry period with subdeciduous tropical forest (no oak or pine). Toledo suggests five Pleistocene refugia: the regions of Lacandona and Soconusco in Chiapas, Mexico; the Maya mountains of Belize; and the Peten and Lake Izabal regions of Guatemala.

Keith Brown has worked several years on the evolutionary biogeography of forest refugia in the Amazon Basin. He reviewed his recent interests and findings on the correlation of paleoclimates and soils with known centers of endemism. Brown's major points were: a) the existence of a number of usually morphologically primitive "doughnut" species on the periphery of endemic centers; b) the occurrence of high endemic values near to present-day ecological barriers; c) the relatively greater effectiveness of genetic or ecological barriers in retarding dispersal; d) the importance of gallery and remnant forests in the preservation, differentiation and dispersal of small organisms; e) the identification of areas that received more rainfall during the late Pleistocene than today, that show high endemic values, no hybridization and no "doughnut" species; f) different biological groups may not have responded similarly to changing climatic regimes; g) paleoclimate has been the prime factor in the restructuring of Amazonian ecological systems.

Gentry's phytogeographic analysis of the extremely wet Chocó region of northwestern Colombia shows 20% of the poorly known flora is endemic, whereas the mid-elevation flora has considerably less endemism. Gentry offered an intriguing speculation that the species rich Pacific coast mangrove community probably persisted in the moist life zone of the Chocó during dry phases, while the much less rich Atlantic coast mangrove community may have lacked a major refugium during dry phases.

Prance's work with the tree families Chrysobalanaceae, Lecythidaceae, Caryocaraceae, and Dichapetalaceae is the only published information for forest refugia based on plants. He urged that only lowland forest species lacking long-range dispersal be used to locate refugia. Prance believes that gallery forests are important dispersal corridors during dry phases.

Steyermark proposed three principal forest refugia in Venezuela: the coastal Cordillera, Imataca and Pantepui. Although the sandstone tablelands of the Guayana Highland have generally been considered a strong center of endemism, Steyermark states that species endemism on individual summits ranges from 5 to 55% of the local flora. Generic endemism is only 8%, hence there has been repetitive centripetal migration of floristic elements to the tablelands.

According to Huber, 12% of the Amazon Territory of Venezuela is covered by savanna; however, it is a savanna dominated by herbaceous plants, in contrast to the grass-dominated Llanos to the north. Huber believes these herbaceous savannas are of pre-Quaternary origin caused by edaphic (soil) and hydrological factors, and have been largely unaffected by Quaternary climatic fluctuations. In contrast the grass savannas of the Venezuelan and Colombian Llanos are of Pleistocene or post-Pleistocene origin.

Switching now to evidence from invertebrates, Turner pointed out that in the butterfly genus *Heliconius*, hybrid zones are kept very narrow in central Amazonia by normalizing selection. Lamas described 48 biogeographic zones in Peru based on Rhopalocera butterfly distributions and centers of endemism, thought to have been shaped by Quaternary climatic changes. Irwin stresses the importance of forest canopies as a refuge for the arthropod fauna during annual river flooding. He suggests that the intense over-packing of arthropods in the canopy during annual inundation may help to explain the diversity of arthropods in Amazonia.

The symposium also included evidence from vertebrates. Heyer and Maxson, working with the frog genus *Leptodactylus*, show that the Amazon distributions of species are fairly homogeneous. By using sequence similarities of serum albumin proteins as "evolutionary clocks", the authors found that most *Leptodactylus* speciation occurred in the Tertiary, but some intraspecific differences are Plio-Pleistocene. Heyer and Maxson indicate that the "albumin clocks" are similar in amphibians and mammals.

Duellman stated that Pleistocene climatic fluctuations and concomitant expansions and reductions of forest were the primary paleo-ecological factors in the differentiation and the determination of patterns of distribution of Amazonian frogs and toads. He emphasized that most amphibian reproductive specialists have restricted ranges, usually involving a proposed forest refugium.

Weitzman showed that certain species of small characoid fishes have distributional patterns corresponding to proposed forest refugia.

Campbell's studies of the fossil bird fauna in the Talara Tar Seeps in northwestern Peruvian desert indicate a more humid climate about 14,000 B.P. Bird fauna relationships suggest a linkage of moist habitats, such as gallery forest and open marsh, with Central America during glacial periods. Campbell explained the proposed climatic changes were similar to the modern climatic anomaly known as "El Nino" that brings rain to the virtually rainless coastal desert of northern Peru. During glacial periods the greater energy gradient between polar regions and the equator resulted in an intensification of the atmospheric winds, causing the northeastern tradewinds to shift farther south during the northern hemispheric winter than they presently do. After crossing the Central American isthmus, the northeasterly tradewinds were deflected to

the southeast, bringing seasonal rain to the coasts of southwestern Ecuador and northwestern Peru. Due to a cooler ocean during a glacial, the rainfall would decrease along the west coast of Colombia, allowing for a moist corridor to Central America.

In an analysis of terrestrial vertebrates and some invertebrate groups, Müller found at least 40 centers of dispersal in the Neotropics.

Kinsey described subspecific distribution patterns for the callithrichid monkeys in Brazil. Each of the ten subspecies of *Callicebus torquatus* and *C. moloch* occurs in one of the Amazonian refugia proposed by Brown based on *Heliconius* butterflies. Kinsey does not believe that rivers are effective barriers to dispersal of Neotropical monkeys.

Meggers stated that the dates of introduction and routes of dispersal of several kinds of archeological traits of Amazonian Indian tribes seem to coincide with the estimated durations and locations of corridors of non-forest vegetation during the past 15,000 years.

Migliazza pointed out the significant correspondence between indigenous linguistic groups in the Amazon and the biogeographic model of forest refugia.

Moving to the Old World Tropics, Walker concentrated on the probable origins of the rainforest flora of the Sahul Shelf islands (east of Wallace's Line--between Java and Bali). Approximately 90% of New Guinea's flora is estimated to be endemic, with substantial generic endemism. Walker suggested that the high generic endemism of the Sahul Shelf islands resulted from physical selection pressures. In contrast, the generically poor but very species rich Sunda Shelf region (Malaysia, Borneo) has had strong biotic selection pressures due to continental continuity and environmental stability since the late Miocene. Walker was the only speaker who did not once use the word refugia.

Meijer's presentation was poorly organized and incoherent, which is unfortunate because he is very knowledgeable about the flora of the tropical Far East.

Grubb presented an informative analysis of the present-day distribution patterns of African forest mammals. Discontinuous distributions, suggesting both recent and more ancient dispersal routes, are related to probable forest refugia in Central and West Africa. He gave several examples of eastward migration, including transcontinental migration, from West Africa. Grubb believes that dispersal is at least as important as isolation in accounting for present-day distributions.

Livingstone reviewed his considerable paleo-ecological work in the East African mountains and offered several African-American comparisons of the forest refugia model. He suggests that Pleistocene dry periods caused a maximum 50-60% reduction in African forests. However, Livingstone stressed that dynamic change is the most significant feature of African Quaternary geography, with no climatic regime prevailing for more than a few thousand years. Such dynamic changes in climate are not consistent with the relative climatic stability of American forest refugia in which evolutionary differentiation is proposed to have occurred.

Pearson analyzed bird community structure in the context of proximity to proposed forest refugia. He found that the different patterns of bird community structure were not satisfactorily explained by current ecological theories of convergent evolution, species packing, foliage complexity, resource abundance or non-avian competition. Location in a refugium, or proximity thereto, provides a more satisfactory explanation of the differences Pearson encountered in the structuring of bird communities. He suggested that the ideal organism for testing the forest refugia model of biological diversification should have the following traits: limited to primary forest, short-range dispersal, viable population in a small area, readily observed and manipulated, and be well-known taxonomically.

Terborgh analyzed the distributions of 156 bird species in Colombia and Ecuador with known ranges less than 50,000 km^2 in order to locate centers of endemism. He found only a minority of the species studied to be presently limited by physical barriers. About one-third of the species appear to be limited in range by closely related congeneric species. The major centers of endemism coincide with presumed forest refugia.

Endler presented an alternative hypothesis of biological diversification--the observed geographic patterns of morphological variation of a species result from present-day environmental gradients. He believes the evolutionary effects of Pleistocene climatic fluctuations have been diluted by present ecological conditions.

Benson stated that the forest refugia model has been more of a biogeographic classification system than a true theory with predictive value. He proposed an alternative population biology model based on the inferences that wide-spread Quaternary climatic variations were not extreme, that race and species formation can be largely independent of past isolation by physical barriers, and that local species richness and differentiation are more sensitive to within community ecological characteristics and proximity of communities than on macrospatial factors. Benson's studies with *Heliconius* butterflies support the population model over the refugia model.

In the symposium session on conservation and refugia, Myers presented an informative overview of the present situation in Africa. He stated that the rate of deforestation is fairly low in Central Africa, but the conservation situation is much more serious in West Africa and East Africa. Unfortunately, conservation efforts in Africa have ignored the location of centers of species richness and endemism in the selection of new national parks. Based on his current study of tropical deforestation, Myers predicts that unprotected virgin forest will be gone by 1990 in southeast Asia, Central America and West Africa.

Oren presented a preliminary report on his study of bird communities in "campina"--low scrubby vegetation on white sand soil. As campina size increases, the avifauna includes higher proportions of habitat and feeding specialists, while dispersal ability decreases. Oren predicts that the smaller the minimum critical area of refugium required for a species to survive, the greater the number of refugia there should be. This is supported by the number of refugia proposed for butterflies, birds and trees.

Lovejoy chaired a panel discussion on conservation and refugia. Dr. Harald Sioli, German ecologist recently retired after 39 years in Amazonia, eloquently criticized the export of nutrient capital from tropical countries in order to feed the "infectious mental disease" of consumption spread by developed countries. Sioli insisted that highly technical agribusiness will not be successful on the non-flooded soils of Amazonia. He proposed modest openings in the forest for local communities of intermediate technology as the only means of rationally developing Amazonia. Panel participants agreed that conservationists should insist on the inclusion in national parks of representative ecosystems on fertile soils because such areas may be most important for species conservation due to great species richness and long environmental stability. In other words, conservationists should not be satisfied with the "crumbs"--vast expanses of vacant land some governments are quite willing to set aside as national parks.

In summary, the ATB symposium on "The Biological Model of Diversification in the Tropics" was most successful in providing a stimulating forum for discussing the forest refugia model. It is amply evident that forest refugia existed during numerous dry periods of the Quaternary. Additional research is required to more precisely determine the locale and size of refugia and the concordance for major groups of organisms. I noticed that proposed refugia tended to be smaller and more precisely defined in relation to the heterogeneity of the taxonomic group studied. For example, the studies of *Heliconius* butterflies and small families of birds and of trees tend to result in small, reasonably well-defined refugia, whereas biogeographic analyses of larger taxonomic groups, such as butterfly families and frogs and toads, do not show such precisely delimited refugia. This is not to say forest refugia were unimportant to the evolutionary diversification of these major groups; rather, it suggests caution in using narrow taxonomic groupings for locating and defining forest refugia.

I was impressed by the strong evidence presented in several papers of the very striking species richness in the Andean foothills of the upper Amazon. Centers of species richness of birds, amphibians, butterflies and plants certainly point to the lower Andean slopes of the upper Amazon Basin in Colombia, Ecuador and Peru as critical areas for conservation. I am concerned that these more heterogeneous and species rich regions of the upper Amazon are being ignored in the worldwide concern about deforestation in Brazilian Amazonia.

Several papers emphasized the absence of tests of the forest refugia model. I am sure that this symposium stimulated several researchers to return to tropical forests to obtain the necessary data for testing not only the forest refugia model but also some of the proposed alternative models of biological diversification in the tropics. I believe the next few years will see a flurry of research interest in tropical refugia that should greatly increase our knowledge and understanding of the role of tropical forest refugia in the spectacular diversity of tropical species.

Sincerely,

Gary

Gary S. Hartshorn
Forest & Man Fellow