BIODIVERSITY: STRUCTURE AND FUNCTION

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Contents

Summary

The earth is unique among the planets of our solar system in bearing life, and has an extraordinary richness of living organisms. The species inventory of the earth is far from being completed, and it only can be estimated that the global number of extant species lies between 12 and 100 million. Biodiversity is not evenly distributed on earth but shows considerable differences between biogeographic zones. The species richness of most groups of organisms peaks in the tropics, with rainforests being particularly diverse. The maximum richness of plant species is mostly to be found near the equator, for example in the northern Andes and in the Malaysian region.

Biodiversity forms a still largely unexplored treasure that is severely endangered due to a multitude of destructive human actions. The current rate of species extinctions due to anthropogenic impacts will result in the irreversible loss of genetic diversity, and likewise of metabolical construction plans. It can be easily predicted that the losses for agriculture, for medicine, and many other fields of basic and applied sciences will be severe: there will be a failure to gain further knowledge about species lost, and the losses will hamper the development of future research strategies and technological innovations.

Changes in land-use, habitat diminution and fragmentation, nutrient enrichment, and environmental stress, caused by human beings in the form of pollutants, for example, lead to reduced biological diversity on all levels (genes, species, and communities) and for all functional roles. At the moment in many cases it is not yet sufficiently clear how severely these changes in diversity will affect processes such as energy flow and nutrient cycling in ecosystems. The conversion of natural landscapes and the fragmentation of natural habitats (that is, the breaking up of ecosystems into smaller, more or less isolated pieces) due to anthropogenic impacts are the greatest threats to biodiversity. Habitat fragmentation affects species diversity mainly by reducing total ecosystem size in a region, reducing the size of particular habitats, and increasing isolation between habitat fragments. The effects of fragmentation are species-specific, with species possessing low dispersal potential and establishment (or recruiting capacity) effectiveness, and species requiring especially large home ranges, being particularly prone to local extinction. These losses lead to a simplification of fragmented ecosystems which could result in reduced ecosystem stability and in the loss of ecosystem functions. Today invasive species form a significant component of global change, in particular in anthropogenically modified ecosystems. Invasive species have a severe economic impact and the costs of these species are estimated to reach billions of US dollars annually.

Global biodiversity is still rich, though it has already been considerably reduced. However it cannot be conserved at its current level on an earth that is increasingly being modified by human beings. Most biomes will, if human pressure is not very quickly and fundamentally reduced, increasingly suffer from species extinctions as well as from reductions in population size which create a loss of genetic diversity. They will also suffer from weaker connectivity, with the probable consequence of impaired functionality. Very difficult and unavoidably controversial decisions will have to be made concerning the extent of biodiversity that should be protected in the long run.

It will be of decisive importance to convince the broad public of the economic relevance of services rendered by the biosphere, and to demonstrate the important part biological diversity plays in sustaining the biosphere's vital life support system. To gain a better awareness of the irreplaceable and vital services of the biosphere is to access arguments that might help in setting priorities for future political decisions. It is important that people should recognize that conserving high biological diversity on all levels is in the longer run a prerequisite for humanity's survival. Therefore it is not an obstacle to further socio-economic development, but a precondition for its success.

There is widespread agreement that species have considerable economic, amenity, and moral values. At present, however, our knowledge is not sufficient to enable us to calculate the value of most species. Economists calculate an option value for species of unknown worth: that is, the potential value of a currently useless species after future discoveries have detected its possible interesting attributes. Calculations of option values for economic reasoning depend on our knowledge of species and on estimates of the money value of their uses. For the long-term protection of the biosphere as a well-balanced and self-sustained system, according to the educated guesses of many experts it will be necessary to finance a system of protected sites that cover at least from 10 to 20 percent of the terrestrial land surface. Moreover, biodiversity-related research activities should be enhanced, with particular focus on capacity building in those regions of the earth that harbor extraordinarily high shares of biodiversity.

1. The Biosphere at Risk

Only twenty-five years ago it seemed that, after centuries of collecting and describing plants and animals, the organismic inventory of the Earth could be completed soon. It thus came as a big surprise when Erwin (1982) published the results of his studies of canopy fogging (that is, spraying the forest canopy with an insecticide) from a rainforest site in Peru. Erwin provided data and theoretical extrapolations about beetles living in the canopy, on the basis of an assumed degree of host-specificity.

His findings and his upscaled assumptions indicated that the number of species living on Earth had hitherto been substantially underestimated. Some time after its publication, this material gained considerable importance in stimulating new estimates of global species numbers, and a very lively discussion about the overall dimension of biological diversity on our planet. In addition, May (1990), working on the basis of theoretical assumptions about the body size distribution of organisms, suggested that the global number of terrestrial species reaches about 10 million.

Since this research was undertaken it has become very obvious that the species inventory of the earth is far from being completed, and that for groups such as arthropods, nematodes, fungi, and microbes, our knowledge is extremely limited. It can only be estimated that the global number of extant species lies somewhere between 12 and 100 million. Biodiversity thus forms a still largely unexplored treasure for basic science and applications in many fields—but a treasure that is severely endangered due to a wide spectrum of destructive human actions.

The current rate of anthropogenic species extinctions represents the sixth severe mass extinction on Earth during the last 500 million years. This will result in the irreversible loss of a large part of genetic diversity, and likewise of many highly specialized and unique metabolical construction plans. It can be easily predicted that the losses will have a severe impact on the acquisition of further knowledge in agriculture, medicine, and many other fields of basic and applied sciences. Along with other factors, this will hamper the development of future research strategies and technological innovations.

2. Characterization of Biodiversity

The earth is unique among the planets of our solar system in bearing life, and it has developed an extraordinary richness of living organisms and different communities. During the last decades, in which the negative anthropogenic impact has become very apparent, biodiversity has become a focal point of different natural and social sciences. The term “biodiversity” itself was coined in 1986 on the occasion of the National Forum on BioDiversity, held in Washington, D.C.

The results of this meeting were published by Wilson and Peter (1988) under the title *Biodiversity*. The current usage of the term can be traced back to (for example) Lovejoy (1980), who equated biodiversity with species richness: that is, the number of species in a community. Today, the concept of biodiversity is relatively broad: it comprises the total complexity of life and includes a wide spectrum of variations from the molecular to the ecosystem level. Frequently, biodiversity is considered to consist of three principal levels: genes, species, and ecosystems.

Biodiversity-related phenomena have been the subject of study for a long time, but the foundations of modern biodiversity research were laid in the 1960s and 1970s. A number of highly influential works developed the tools of theoretical ecology for analyzing central challenges of this field, such as the correlation between diversity and area and the mechanisms behind it (MacArthur and Wilson, 1967), and the relation between diversity and stability (May, 1973).

The central question why there are so many species still cannot be answered. A large number of explanations have been suggested for the origin and maintenance of species richness. According to Crawley (1997), the proposed explanations of species richness hinge on whether or not the communities are in equilibrium. In the first case a number of hypotheses suggest that niche specialization prevents interspecific competition and allows the coexistence of many species, including subordinate ones, with very similar ecological requirements.

In contrast to this, stochastic assumptions predict that most communities exist in a state of non-equilibrium, where species richness is promoted by periodic environmental disturbances which prevent the dominance of a few highly competitive species.

Apart from species richness, biodiversity considers spatial patterns of diversity in an ecological context. According to Whittaker (1977) the following components of diversity can be defined:

- **Alpha diversity:** that is, within-area diversity, the number of species occurring within a defined area.
- **Beta diversity:** measures the degree of species change along a physiographic gradient or between habitats.
- **Gamma diversity:** that is, landscape diversity. It describes the overall diversity within a large region. Gamma diversity has no upper limit and it often refers to large regions or countries.

The concept of diversity takes into account two factors: species richness, that is the number of species, and evenness, that is how equally abundant the species are. The species diversity in a sampling unit can be measured by species richness indices (for a survey see Magurran, 1988).

Species form the basic units of biodiversity, and taxonomy provides a reference system which differentiates between individual species and classifies them in an evolutionary context. There is much debate about an exact definition of what constitutes a species, resulting in different classification systems and species numbers.

Today taxonomists have described about 1. 75 million species out of the possible 12 to 100 million (Hawksworth and Kalin-Arroyo 1995; see Figure 1).

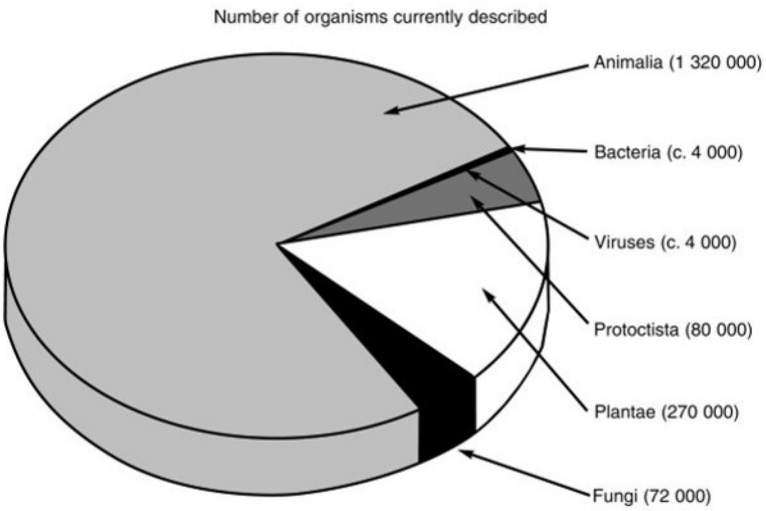

Figure 1. Approximately 1.75 million species are currently recognized. However, for most groups the precision of the species counts is highly variable
Source: Data based on Hawksworth and Kalin-Arroyo (1995).

Our knowledge of the biology of most of the species that have been described to date is very poor. Evidence from the fossil record (mainly of a limited number of marine, well fossilizing taxa) suggests that among many groups of organisms the number of species has increased almost continuously since the origin of the group (Figure 2). However, the fossil record indicates large variations in extinction rates, with periodic episodes of mass extinction which were possibly caused by meteorite impacts (Alvarez et al., 1980) and by large-scale tectonic processes. In total five major mass extinction events were recorded, the last at the end of the Cretaceous (66 million years ago) leading to the demise of the dinosaurs. Whether meteorite impacts were really responsible for all these periodic episodes of mass extinction is still a matter of debate, and it is possible that plate tectonics and drastic climatic changes played a bigger role.

Concerning the number of extant species, our knowledge of certain taxonomic groups, such as vascular plants and most vertebrate classes, is relatively good. However, this "relatively" is underlined by the fact that even for most of the well-known groups of organisms, such as vascular plants, the number of species had until recently been considerably underestimated (Prance, 2001). This demonstrates that, even for the best investigated groups, a full inventory of the earth has not nearly been completed. For the really diverse taxonomic groups, such as arthropods, fungi, and bacteria, it will hardly be possible to provide reliable data about their species richness in the near future, unless far more emphasis is put into their recording, and taxonomic as well as systematic categorization.

Our ignorance is not only due to the vast diversity of these organisms, but is also a consequence of the rapidly decreasing number of taxonomists. With the tasks of identifying and naming species, taxonomy and systematics provide important services for the conservation of many ecosystems. In addition to a count of the number of species, the systematic position and sometimes the uniqueness of species are considered important for assessing the value of certain regions. In this case taxic diversity and systematic particularity become additional criteria for setting priorities among conservation options. Moreover, the rarity of a species is an additional criterion that is frequently considered in this context, but cannot be even roughly guessed at in most of the very diverse taxa.

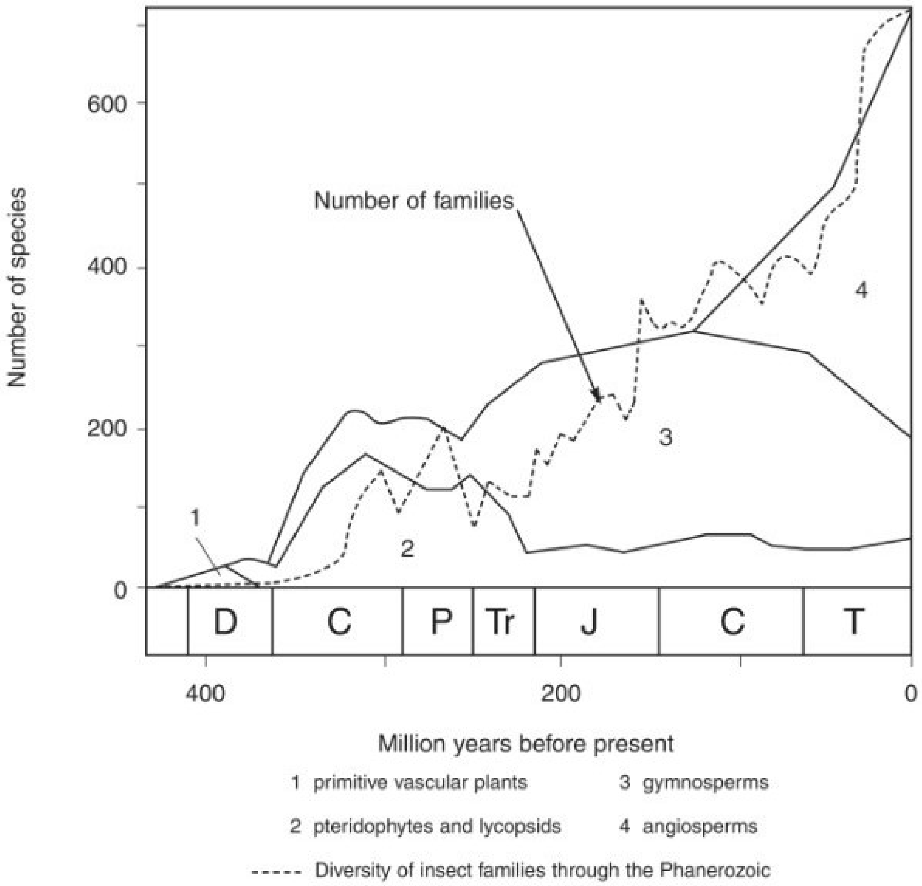

Figure 2. Among most groups of organisms for which data are available, the total number of species has increased almost continuously. The fossil record indicates that rates of extinction varied greatly, with increased numbers of extinctions occurring during relatively short time periods.
Sources: Data for land plant diversity after Niklas et al. (1985); diversity of insect families according to Labandeira and Sepkoski (1993).

Endemic taxa form important units for identifying and prioritizing protected areas. “Endemics” are those taxa restricted to a specified geographical area. The occupation with quantifying patterns of endemism dates back to de Candolle (1820). Frequently the number of endemics is correlated with the species richness of a certain area; however, relatively species-poor island communities may also contain large numbers of endemics. Endemics can be categorized in different ways (see the survey in Hawksworth and Kalin-Arroyo, 1995), and often a differentiation is made with regard to evolutionary age between neoendemics and palaeoendemics. “Neoendemics” belong to clusters of closely related species groups that have evolved relatively recently (such as the cichlid fishes in Lake Victoria and Lake Malawi or the Canarian species of the plant genus *Sonchus*). “Palaeoendemics” are ancient isolated taxa that are considered to represent evolutionary relicts (for example, the maidenhair tree *Gingko biloba* and *Welwitschia mirabilis* of the

Namib Desert).

Degrees of endemism depend on environmental variables such as precipitation, temperature, and productivity. Plant endemism increases with increasing altitude and with higher rainfall (Gentry, 1992; Cowling, 1983). Islands have been much studied in terms of plant endemism (Carlquist, 1974; Bramwell, 1979).

Continental islands (such as Madagascar and New Caledonia) are characterized by large numbers of ancient, taxonomically isolated endemics. Younger oceanic islands such as the Canaries and Hawaii are rich in plant groups which underwent extensive adaptive radiation.

There is a well-known concentration of endemic plants in localities offering edaphic particularities (such as outcrops of serpentine, limestone, or quartzite). According to Kruckeberg (1986) there is evidence that these nutritionally unusual substrates provided strong selective forces for the evolution of endemics.

Both the Convention on Biological Diversity and *Agenda 21* have called for the earth's biodiversity to be inventoried and monitored. Inventorying is the naming, surveying, sorting, cataloguing, quantifying, and mapping of biological entities (from genes to ecosystems).

Repeated inventorying over time is needed for monitoring changes in biodiversity. Today only a few countries have programs to make inventories of their own biota, and mostly the tools to identify the organisms present are inadequately developed.

Our knowledge about the species diversity and species composition of many ecosystems is as poor as for the earth as a whole. This is illustrated by the fact that despite considerable efforts of generations of biologists to inventory the temperate and boreal forests of the northern hemisphere, we are still not able to present comprehensive lists of all organisms present in these forests. Our knowledge of species numbers in most tropical ecosystems, such as rainforests, is much worse.

Occasionally whole ecosystems have been ignored up to now from an ecological point of view. This is the case for a number of marine habitats as well as for terrestrial communities, for example white sand savannahs and rock outcrops. The latter are widespread throughout the tropics where they occur in the form of limestone hills, sandstone table mountains, and as granitic or gneissic monoliths (Porembski and Barthlott, 2000).

Rock outcrops are characterized by harsh environmental conditions and thus harbor a unique vegetation, with many species showing particular adaptations to withstand water shortage (such as succulence and desiccation tolerance). Up to now the remarkable richness of ecosystems that are characterized by environmental extremes in hosting organisms well adapted to them has been barely regarded as worthy of consideration in terms of searching for new solutions for future applications.

From an ecological point of view it is important that species play different roles in ecosystems and that they possess different adaptive traits. Species that possess ecologically important attributes (for example, plants which contribute to nitrogen enrichment in soils) or have a disproportionately large effect on other species or on the function of ecosystems (animals acting as "ecosystem engineers" by regulating, for example, the flow of certain nutrients) are called "keystone" species (Bond, 1993). The term "functional diversity" describes the richness in functional types and features, as well as the diversity of keystone species present in certain ecosystems and geographical units.

In most ecosystems certain functional types are represented by a number of species, which leads to the question, are all those species absolutely essential for the function of the ecosystem, or is there a certain amount of redundancy within plant and animal communities?

The differences between individual species concerning ecosystem processes, such as nutrient cycling, can be large. This is illustrated by a comparison of the 20,000 to 25,000 species of orchids and the 200 species of the largest conifer family, the Pinaceae.

The relatively low number of genera and species of the latter family, which largely dominate the northern boreal forests, are of outstanding importance on a global scale, for example with respect to the role of these forests in climate change (in acting as sinks or sources for carbon dioxide).

Despite their huge species number, however, orchids generally are rarely relevant (for example, in the canopy of tropical forests) for the regulation of ecosystem characteristics and processes. According to the "redundant species hypothesis" (as in Lawton and Brown, 1993), species-rich ecosystems are characterized by a number of species that are functionally non-relevant and thus do not form essential ecosystem constituents. The term "redundant species" is, however, problematic since our knowledge about most species is too limited to allow prediction of their role in ecosystems over prolonged periods.

Biodiversity is not evenly distributed on earth, but shows considerable differences between biogeographic zones. The definition of biogeographic zones is based on their flora and fauna. The species richness of most groups of organisms peaks in the tropics, with rainforests being particularly diverse. The underlying reasons for the latitudinal gradient in species richness from the polar to the equatorial regions are still not clearly identified (Gaston, 2000).

In addition, there are large gaps in our ability to exactly circumscribe the regions that are characterized by high numbers of species and endemics. Being able to define accurately these so-called "hot spot" regions (Myers et al., 2000) would be of outstanding importance in the prioritization of regions for conservation purposes. According to Barthlott et al. (2005; Mutke et al. 2005), plant diversity is not statistically distributed on earth, with regions of maximum plant species richness mostly situated near the equator, for example the northern Andes and the Indonesian archipelago (see Plate 11.1–1). The South African floristic kingdom Capensis is an example of a species-rich region outside the tropical latitudes.

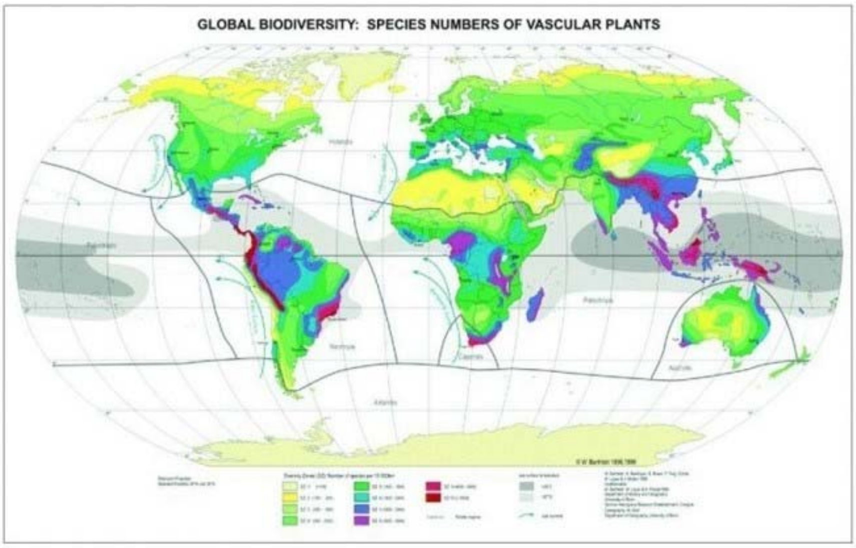

Plate 11.1–1. According to the plant diversity map produced by Barthlott et al. (2005; Mutke et al. 2005), most areas with the maximum number of plant species are in the equatorial regions. In particular, regions characterized by a highly variable topography and small-scale climatic variations (such as mountain ranges) harbor high numbers of species. The South African floristic kingdom Capensis is an example of a species-rich region outside the tropical latitudes.

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Biographical Sketches

Professor Wilhelm Barthlott was born in 1946, in Forst (Baden-Württemberg, Germany). He studied

Biology with Chemistry, Physics and Geography at the University of Heidelberg, and his dissertation subject was the contribution to taxonomy and biogeography of the palaeotropic Rhipsalis and to the general micromorphology of Cactaceae.

He was Scientific Assistant at the Institute of Systematic Botany and Plant Geography, University of Heidelberg, and Associate Professor at the Institute of Systematic Botany and Plant Geography of the Freie Universität, Berlin. Since 1985 he has been Professor and head of department at the Botanical Institute and director of the Botanical Garden of the University of Bonn.

His main fields of research are tropical ecology and biodiversity (epiphytes, vegetation of inselbergs, mapping of biodiversity by use of geographical information systems, and carnivorous plants), and the systematics of angiosperms; high resolution scanning electron microscopy of cuticular surfaces and systematic applicability of epicuticular wax ultrastructure; ecological aspects of contamination and effects of tensides; and the technical development of artificial "intelligent" surfaces with self-cleaning effects (the "lotus-effect"). He has researched mainly in South America (Brazil, Ecuador, and Venezuela), West Africa (Ivory Coast), and Madagascar. He has been awarded numerous grants by for example the DFG, BMBF, Volkswagen Stiftung. He received the Karl-Heinz-Beckurts-Award in 1997; he was nominated for the Deutschen Zukunftspreis des Bundespräsidenten, and awarded the Order of Andrès Bello of the Republic of Venezuela in 1998. He has also received the Philip-Morris Science Award and the German Environmental Award (1999), the Treviranus-Medal of the Association of German Biologists and the Austrian GLOBArt Innovation Award (2001). He was awarded the Cactus d'Or on behalf of the International Organization of Succulent Plant Study in 2002. He is a member of the Academy of Science and Literature in Mainz, the Academy of Science of North Rhine Westphalia, the German Academy of Naturalists (Leopoldina), and was appointed a Foreign Member of the Linnean Society in London.

Professor K. Eduard Linsenmair was born in 1940 in Munich (Bavaria, Germany). He majored in Zoology with Botany, Chemistry, Anthropology and Psychology at the Universities of Heidelberg, Freiburg im Breisgau and Frankfurt am Main. His dissertation was an etho-ecological investigation on semiterrestrial crabs at the Red Sea.

He was Scientific Assistant in the Faculty of Biology and Pre-clinical Medicine, University of Regensburg, and "Privatdozent" and Professor for Zoology, University of Regensburg. Since 1976 he has held the Chair of Animal Ecology at the Zoological Institute; and is now Chair of Animal Ecology and Tropical Biology at the Theodor-Boveri-Institute for Biological Sciences at the University of Würzburg.

His main fields of research are behavioral ecology, sociobiology, and eco-physiology, and as his main subject in recent years tropical biology with a major emphasis on community ecology, biodiversity questions, and life history studies. He has researched mainly in West Africa (Ivory Coast) and South-East Asia (Malaysia and Indonesia), and also in South America (Ecuador, French Guyana), and formerly North Africa, Sahara.

He has received financial support from the DFG, and subsequently from DAAD, the Volkswagen Stiftung, the Fritz Thyssen Stiftung (for construction of a permanent research station in the Comoé National Park in the Ivory Coast), Körber-Stiftung 1996 (for the construction of a canopy access system in French Guyana), Volkswagen Stiftung 1988 for "Wettbewerb Biowissenschaften" and the Fritz Thyssen Foundation. He received the European science award in 1996, and is a Member of the German Academy of Naturalists (Leopoldina), and the Academia Europea. He is the initiator and co-ordinator of the priority program of the DFG: "Mechanisms of the maintenance of tropical diversity," and has been co-organizer of two other main emphasis programs of the DFG ("Biochemical and physiological mechanisms of ecological adaptations in animals" and "Chemical ecology: natural compounds as behavioral modificators"). He is also the initiator and chairman of an ESF (European Science Foundation) program on "Tropical canopy research," and co-initiator of the "Flanking program for tropical ecology" of the GTZ and member of the program and evaluating board. He is the co-ordinator of the BIOTA-West ("BIOdiversity Monitoring Transect Analysis in Africa") program in the framework of the large BIOLOG program of the German Ministry for Education and Research (BMBF).

He is President of the "Gesellschaft für Tropenökologie" (Tropical Ecology Society), and a member of the National Committee for Global Change Research (Speaker DIVERSITAS Program Germany).

Professor Stefan Porembski was born in 1960, in Berlin (Germany). He studied Biology with Chemistry and Physics at the Freie Universität Berlin and at the University of Bonn, and his dissertation subject was functional aspects of the morphology and anatomy of succulent plants with particular emphasis on Cactaceae.

He was a Postdoctoral and Scientific Assistant at the Botanical Institute of the University of Bonn, and since 1998 has been Professor and head of department at the Botanical Institute and director of the Botanical Garden of the University of Rostock, where he created a working group on terrestrial habitat fragments (inselbergs, miniature dunes, forest islands, and temporary pools).

His main fields of research are tropical ecology and biodiversity (the vegetation of inselbergs, forest fragments, desiccation-tolerant vascular plants, carnivorous plants, succulents, and epiphytes), and systematics of angiosperms. He has concentrated especially on the analysis of spatial and temporal dynamics of plant communities by using permanent plots placed in different tropical ecosystems. Several of his projects are concerned with the consequences of changing land-use activities for the species diversity of tropical ecosystems. He has researched mostly in South America (Brazil), West Africa (Ivory Coast, Benin), and India, and has received grants from, among others, the DFG, BMBF, and DAAD. He is Vice-President of the International Organization for Succulent Plant Study (IOS).