THEMES OF DIVERSIFICATION IN NEOTROPICAL FORESTS

K. Kubitzki
Universität Hamburg, Institut für Allgemeine Botanik und Herbarium, D–2000 Hamburg 52, Germany.

Diversification is an adaptive process through which closely related species become sufficiently distinct in order to be able to exploit the same habitat. In tropical forests, which are the most species-diverse communities on Earth, it is possible to perceive various themes of diversification such as growth form, ecophysiological adaptations, several traits of the reproductive system, and secondary chemistry. Drawing on examples from the neotropics it is shown how knowledge of these contributes to a deeper understanding of the diversity of these communities.

THE THREAT TO DIVERSITY

Biological diversity has become a matter of utmost concern not only for biologists but for society as a whole. This is due to the awareness that mankind is responsible for the present mass extinction of biological species, which is one of the most serious extinction events that has afflicted the biosphere in the entire history of life[1]. While up to the present less than 1.5 million kinds of organisms have become known to science, there is still uncertainty among biologists as to whether there exist on Earth 2, 5, or about 50 million species of microorganisms, plants, and animals. This is the background against which the global threat to biodiversity has to be seen.

It is not only the diversity of species living in the wild that is under threat. Modern society and western economy and lifestyle and their spread all over the world have become responsible for an alarming loss in diversity of crop plants and of animals living in domestication as well. As much as 80% of the world food supply may be based on fewer than two dozen species of plants and animals. This reduction in the diversity of food resources is largely related to a loss of cultural and ethnic diversity, which is accompanying the wave of biological extinction. An extreme example for the loss of ethnic diversity are indigenous tribes of humans which are vanishing at an alarming pace. Together with them their cultures are irretrievably lost. These often include precious knowledge about the management of natural resources.

It is bitter to see that all these riches of a biological and cultural heritage are lost at a moment at which we are becoming aware how little we know about them. It is only now that we are beginning to understand such basic issues as the origin and maintenance of biological diversity, let alone its meaning and possible function. These issues require a truly multidisciplinary perspective, and natural compound chemistry is one of the disciplines asked for. It is therefore appropriate to discuss these matters in a volume which is dedicated to Professor O. R. Gottlieb.

SPECIES RICHNESS IN THE TROPICAL RAINFOREST

Species richness abounds in the tropical rainforests, although these cover hardly more than 6% of the terrestrial portion of the surface of the Earth. Of the estimated 250,000 species of flowering plants, about 90.000 are confined to the tropics of the New World, with some 30.000 in the Amazon basin and 18.000 to 20.000 in Central America. The number of species of freshwater fish may amount to up to 3000[2]. Based on sampling by insecticidal fogging of forest canopies, and taking into account the host specificity of the animals in question, Erwin[3] extrapolated a number of 30–50 million or perhaps more species of insects on Earth.

Numbers of tree species in the neotropical humid forest amount to up to 300 per hectare, if only individuals of 10 cm of stem diameter or more are taken into consideration[4]. However, this figure hardly covers the overall richness of the forest; Klinge[5], who included all forest plants of 1.5 m height and more, found 502 species of trees in an area of 0.2 hectare in Central Amazônia. From these data it becomes clear that many tree species in the tropical humid forest are represented by a single individual only per hectare, and that population density is generally low.

In view of this overwhelming species richness in humid tropical forests biologists have been wondering for a long time how so many different kinds of organisms can coexist with each other in the same habitat. Biologists had difficulties in applying the concept of the niche, which elsewhere had proven most useful. This concept implies that each kind of organism living together with other kinds utilizes a specific portion of the resources provided by the environment. A corollary of the niche concept is the competitive exclusion principle which in Hardin's[6] wording reads "Complete competitors cannotcoexist". As long as only the abiotic environment (light, nutrients, humidity) was taken into consideration, the niche concept did not appear applicable to the extremely diverse communities of humid tropical forests. However, the discovery of the intensity of biotic interactions between different species of plants, fungi or animals, so characteristic for the humid tropics, has completely changed our outlook. These countless interactions vary between antagonism and symbiosis; those related to reproductive traits such as pollination and seed dispersal are especially well explored. They provide a large number of opportunities for niche separation for closely related species growing side by side in the same habitat. Although often acting only during a short phase of the life cycle, these differences in lifestyle satisfy the ardent desire of ecologists for substantiating the concept of niche differentiation. Clearly the validity of the competitive exclusion principle cannot be proven by such studies; Hardin[6] has demonstrated that this is theoretically impossible. However, the continued search for niche differentiation helps to better understand the pathways of diversification of patristically closely related species.

THEMES OF DIVERSIFICATION

In groups of closely related species often one characteristic is systematically altered, while other traits may or may not remain unchanged. These elements of the adaptive system of the plant include growth form, ecophysiology, habitat preference, reproductive traits such as floral structure, pollination, seed and fruit structure and dispersal, and the breeding system, chromosomal traits, secondary chemistry including chemically mediated interactions, and many other traits. Their variation represents what can be called themes of diversification. While Stebbins[7] has dealt with them for angiosperms as a whole, I here want to specify them for humid tropical forests with special emphasis on the Amazon forest.

Besides species diversty, richness in life forms is the most obvious feature of humid tropical forests. Different combinations of a limited number of morphological traits have first been used in a consistent way by Hallé and Oldeman[8] in order to describe and classify tree morphology. Besides trees, the spectrum of life forms of the humid tropical forest is represented by shrubs, lianas, stranglers, epiphytes, epiphyllous bryophytes and lichens, various kinds of parasites, and others. As regards growth form, closely related species are mostly relatively uniform. This also applies to the position they occupy in the vertical structure of the forest, which is often described as stratified and is considered an important trait of the forest. Within this vertical gradation, dependent on light intensity, most species are confined to a certain level. While the tallest forest trees are often Leguminosae, families such as the Lauraceae, Burseraceae, Myristicaceae, Rubiaceae and Annonaceae are well represented in the understorey, and the numerous species of Piper are shrubs or half-shrubs living on the ground. The ranking of a specific tree species is mainly determined by its demand for light, more explicitly by its point of light compensation, although this may vary between different branches of the same individual or during its life history.

Among reproductive traits the pollination system is a major theme of diversification. Pollination by bees searching for nectar and/or pollen seems to be a very generalized condition. Many plant genera or species have proceeded in adapting to pollination by birds, bats, or even rodents. In different lineages common traits have been acquired in adaptation to the same pollinator or group of pollinators, which allows to identify recurrent syndromes of pollination. These include also temporal traits such as nocturnal activity in nectar secretion in the case of a dependence on nocturnal animals. Pollination by specific vertebrates often occurs erratically in isolated species in different families and genera and is an evolutionarily more recent development.

Adaptations to seed dispersal are also highly diversified. While vertebrates – bats excepted – operate preferentially in the understorey, dispersal in the uppermost strata of the forest is predominantly by wind. Riverine forests exhibit most conspicuous adaptations to dispersal of their diaspores by floating in the water and by fish. Their fruiting season coincides with the period of high water level of the rivers. Ducke[9] was the first to point to the evolutionary relationships of tree species with water dispersed diaspores with their congeners growing on firm land. Numerous plant taxa give evidence of a broad diversification with respect to dispersing agents. in the Lecythidaceae, e. g., wind, water, monkeys, bats and rodents are instrumental.

Although diversification of birds and bats started as early as in the Lower Tertiary, it seems that the switch to bird and bat dispersal is evolutionarily more recent, indeed, no pre-Pleistocene evidence of frugivorous bats seems to be available[10].

Some very strange specialisations, once acquired, seem to impede further diversification. For example, major plant groups often rely on a single method of pollination or dispersal. As regards pollination, this is true of buzz pollination, which is predominant in families such as the Melastomataceae[11] and the Ochnaceae[12]. It is also true of bat pollination in the genus *Parkia*[13] and pollination by hummingbirds in *Fuchsia* and the Andine species of *Passiflora* which have elongated floral tubes. The entire evolutionary history of *Fuchsia* and these Passifloras may have been linked to that of the hummingbirds whose origin and major evolution took place in the Andes. Also, the replacement of nectar by fatty oil as an indemnity for flower-visiting insects and the consequent dependence on anthophorid bees in the neotropical Malpighiaceae[14] can be named as an example. Obviously, the adaptative shifts that stood at the beginning of the evolutionary history of these lineages became so fixed that further changes were hardly possible. The dependence on bats as dispersing agents of larger genera such as *Piper* and *Vismia* less easily can be understood.

Diversification may follow the line of least resistance. In the buzz pollinated Melastomataceae diversification proceeds via phenology: Sympatric species of *Miconia* were found to flower and fruit successively with little overlap, covering nearly the entire year[15]. This kind of staggered flowering does not only act as a reproductive barrier between the species, but also contributes to support over much of the year the pool of pollinators and dispersers common to these species.

Secondary metabolism (or "special metabolism", Gottlieb[16]), has only recently come into focus as a major theme of variation. For neotropical foresta, this is mainly the result of the work of O.R. Gottlieb (for summaries, see Gottlieb[16,17]). This work has provided a wealth of data concerning the chemical diversification of numerous plant taxa of neotropical forests, notably the Lauraceae, Leguminosae, Myristicaceae, and Guttiferae.

Natural compound chemistry has the advantage that its characters can be described very accurately and put into biogenetic sequences. Distinct levels of chemical change can be distinguished, beginning with variation in substitution, and proceeding over changes in constitution to those of skeletal structure, and finally leading to blocking or switching of entire biogenetic pathways. In the work of O. R. Gottlieb these changes have been correlated with taxonomic data derived from morphological traits, and have provided systematic criteria that are most valuable because they are independent of conventional classifications. The observed chemical changes have also been found to have spatial directionalities. This is indirect proof of the adaptive nature of chemical change, which seems to be part of the mechanisms of differentiation of populations and speciation[18,19]. The variation of secondary metabolites within and between individuals, populations, and communities has become a novel area of research, denoted as defense theory. Waterman and McKey[20] have given an overview of this interesting field, in which chemical change usually is interpreted as following selective pressure by herbivores. However, Gottlieb[16] has pointed to the primacy of internal factors of the plant for biosynthetic diversification, while external factors such as herbivory according to him play only an additional role.

THE MEANING OF DIVERSITY

Biological diversity, such overwhelming a phenomenon, clearly requires an explanation. How it has come into being and what are the mechanisms for its maintenance are questions that are much debated. Another question is that for the meaning of diversity, to which only vague answers are available. Starting from the observation of extreme scarcity of nutrients in most parts of Amazonia, one might interpret the diversity of consumers as implying longer nutrient chains, which may be more efficient in the retention of nutrients in the system than shorter ones. This would permit to assign a function to the enormous diversity of tiny animals living in the soil, the litter and in the streams crossing the forest. Moreover, the diversity of life forms and growth forms of plants in the forest could act as a filter system scavenging nutrients from rainfall, as has been hypothesized by Klinge[5] and Fittkau[21]. Indeed, precipitation is the major source of nutrient input for the forest and by and large outweighs the loss of nutrients by leaching. After raindrops reach the canopy, they drip over several strata of trees, shrubs and epiphytes, whose leaves are supposed to take up nutrients from them, before arriving at the ground. Jordan et al.[22] found nutrients to be adsorbed by algae and lichens that live on the surface of the leaves. Thus diversity in life forms both of animals and plants could be envisioned as having a stabilizing effect on an ecosystem under heavy nutrient stress.

We can not fully appreciate the scientific and economic (not to speak of the aesthetic) value of tropical forests as long as we know little more than the scientific names of their component species. Tropical forests have very appropriately been compared with libraries and books, whose value is not measured by the sheer number of words they contain or by the number of kinds of words[23]. Society would hardly support the maintenance of libraries which have enormous holdings but for which no library services exist and which cannot be used. The same is true for tropical forests, when the biological traits of their components are largely unknown, and when their preservation will impose a marked burden on society. We only now are beginning to be able to read in this grand book of nature. O.R. Gottlieb's work has contributed to make it fascinating reading.

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