

CHAPTER 1

BIODIVERSITY SURVEY AND PRINCIPLES

BIODIVERSITY IN ECOSYSTEMS: SOME PRINCIPLES

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Abstract

A scientific treatment of biodiversity must aim at the development of a generally valid theory, for only in this way, the scientific foundations for pragmatic approaches to the preservation of biodiversity can be worked out. This is also embodied in the "International Convention" on the protection and conservation of biodiversity, which was passed at the United Nations' conference "Environment and Development" at Rio de Janeiro in 1992, and has meanwhile been ratified by numerous nations. In this article, a definition of the concept "biodiversity" will be given, and partly synonymously used terms, like "variation", "differentiation", "diversification", "heterogeneity", "variety", "variability", "complexity", and "richness" be differentiated. As matter and energy occur in very different organization forms and on varying hierarchy levels, it is necessary to delimit first those areas in which biodiversity phenomena appear.

An essential prerequisite for a scientific investigation of the diversity of biocoenoses and ecosystems is the theoretical examination of opposing positions: holistic approach versus individualistic approach, deterministic approach versus stochastic approach. Central questions are studied, concerning also ecology in general.

The varying forms of biodiversity can basically be assigned to four different groups: diversity of elements (element pattern of biodiversity), diversity of interactions (dynamic pattern of biodiversity), mechanisms causing diversity (causing pattern of biodiversity), and process of functioning (functional pattern of biodiversity). Examples will be given for each group. "Intrabiocoenotic diversity" includes the diversity of phytocoenoses, zoocoenoses, and synusia. A classification into synusia should

follow stratotope, choriotope, and merotope patterns. "Interbiocoenotic diversity", on the other hand, refers to the diversity of landscape parts (vegetation complexes) and landscapes (vegetation complexes occurring together). Some fundamental relations will be outlined.

On the basis of the comprehensive discussion of biodiversity criteria in the literature, 30 hypotheses on biodiversity will be presented and explained. A final chapter deals with the importance of the theory of biodiversity in applied nature protection. The preservation of biodiversity is a basic component of the survival programme "sustainable development".

Introduction

Experts, but also the general public, agree that the preservation of biodiversity is of paramount importance. Accordingly, on the United Nations' conference "Environment and Development", held at Rio de Janeiro in 1992, an official "International Convention" on the protection and conservation of biodiversity was drawn up and, within two years, ratified by the majority of the undersigning nations. This official declaration of intent obliges the international "scientific community" to work out the scientific principles of a "theory of biodiversity" (Solbrig 1991); an important contribution to this has to be made by ecologists and biocoenologists/community ecologists (Raustiala & Victor 1996; Haber in this volume). Numerous, partly voluminous treatises give evidence of the particular relevance of biodiversity, and of the general efforts to do justice to its complexity (Wilson 1988, 1992; During *et al.* 1988; Stearns 1990; McNeely *et al.* 1990; Solbrig 1991, 1994; Solbrig *et al.* 1992; Courrier 1992; Groombridge 1992; World Resources Institute 1992; Schulze & Mooney 1993; Ricklefs & Schluter 1993; UNEP 1993, 1995; Huston 1994; Krattinger *et al.* 1994; Heywood & Watson 1995; Kim & Weaver 1995; Rosenzweig 1995; Haeupler 1997; Reaka-Kudla *et al.* 1997).

The objective of a scientific study of biodiversity is the development of a general theory (Fig. 1).

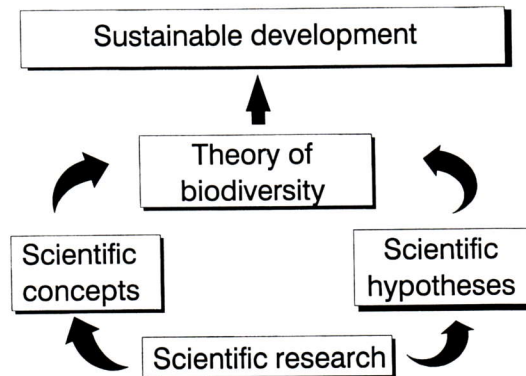


Figure 1. Ways to the formulation of a "theory of biodiversity", to be incorporated into the concept of a "sustainable development".

To this end, scientific data are gathered from which natural laws shall be deduced. The formation of a theory requires the formulation of scientific concepts and hypotheses. If there is evidence for general principles, it is possible to make prognoses and to create scenarios. In order to successfully cope with future tasks in accordance with the programme “sustainable development”, predictions on the consequences of altered environmental conditions and the development of scenarios are of considerable significance (Kratochwil 1996). One of the key issues is the importance of the preservation of biodiversity for the maintenance of the global natural balance. Apart from the question to what degree it should be preserved, it has first and foremost to be studied to what extent it can be preserved (Blab *et al.* 1995).

To find out whether biodiversity is governed by certain natural laws is only one component of the analysis. Since the historicity of life is one of the fundamental characteristics of biology and thus also of ecology (Whittaker 1972; Osche 1975), evolution-biological and evolution-ecological aspects have to be considered in concepts and hypotheses, and have to be incorporated into a general theory of biodiversity. Hence follows that not all forms of biodiversity are repeatable at any time and any place. Dollo’s law on the irreversibility of evolution-historical processes implies that a plant or animal species can only originate once. Structures lost in the course of evolution can never be regained in their original form (see *e.g.* Osche 1966). What is lost, is irretrievably lost, since evolution - as genealogical process - takes a linear course, not a cyclic one.

When investigating biodiversity, man has to be considered as biological and ecological factor, too. A study of biodiversity thus allows not only a more detailed understanding of life processes in general, but also of human life; moreover it is, as component of the survival programme “sustainable development”, important for the future of man (Fig. 2).

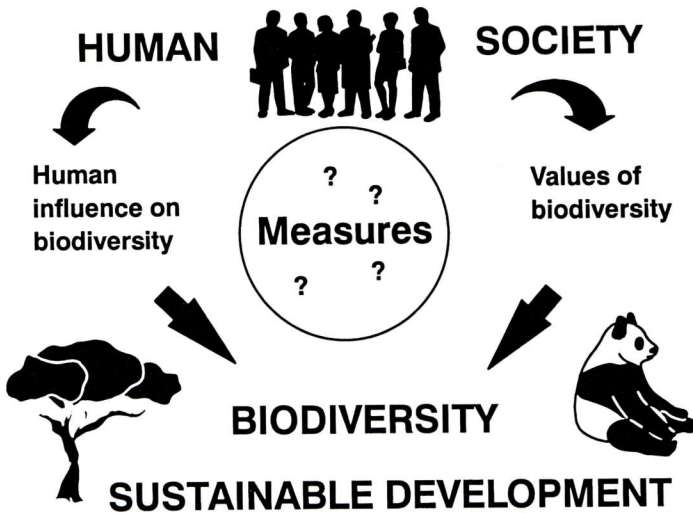


Figure 2. The interaction between human society and biodiversity (based on Heywood & Baste 1995).

Like biodiversity is closely linked with biological evolution, cultural diversity and the cultural and historical development of mankind (cultural evolution) go hand in hand (Gadgil 1987). For both, the many and diverse processes are system-inherent. Losses of their material and non-material values are always irrecoverable. The question which biological and cultural “achievements” should be preserved can only be answered by individual assessments.

Two central issues have to be investigated first:

- What is biodiversity? (see Akeroyd 1996)
- How can biodiversity be measured? (see *e.g.* Whittaker 1972; Magurran 1988; Hawksworth 1995).

What is biodiversity?

In its original sense, diversity means “variation” and “differentiation”, “diversification”, in contrast to “uniformity”. Diversity may be understood as something static: “heterogeneity” then denotes irregularities, “variety” differences. “Variability” covers dynamic aspects. Diverse systems may be simple, but also very complicated. As a rule, complexity is a sure sign of diverse systems: it is defined as something very intricate or complicated. Complexity covers the profundity of system structures, diversity their width. When assessing biological systems, diversity may also be seen as “richness”.

By biodiversity, biological diversity is understood: the total differentiation, variation, variability, complexity, and richness of life on earth.

These definitions show already the catch in such “condensed” terms: their ambiguity, which may help a layman to associate a number of things with a term (when being given the relevant information), but may of course also lead to misinterpretations; that is why experts avoid using merely the terms, but attempt to more closely define and differentiate the concepts behind (Akeroyd 1996; Haber in this volume). Many biological and ecological terms (and concepts) have been subject to a similar development: the concept “ecology” itself, the “island theory”, and the “metapopulation concept” (Kratochwil 1998). The problem of the complexity and ambiguity of concepts can hardly be solved; they have always been renamed and redefined, and will also be in future. All the same, concepts must be defined as “tools” and as means to exchange information, in accordance with a general convention.

The following definition of biodiversity is proposed (based on art. 2 of the “Convention on Biological Diversity” of the IUCN, Rio de Janeiro 1992, altered after Bisby 1995): “ ‘Biological diversity’ means diversity (according to differentiation, variation, variability, complexity and richness) among living organisms from all sources, including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part, this includes diversity within species, between species and of ecosystems”.

Ranges of validity of biodiversity

Diversity is a fundamental quality, manifesting itself in the different organization levels of matter and energy (Haber 1978; Odum 1983). It is a characteristic feature of all levels of the non-biological and the biological hierarchy (hierarchical diversities) (Fig. 3); there is diversity on every single level. The levels of life are particularly diverse, here we generally distinguish between structural diversities and functional diversities (Solbrig 1991).

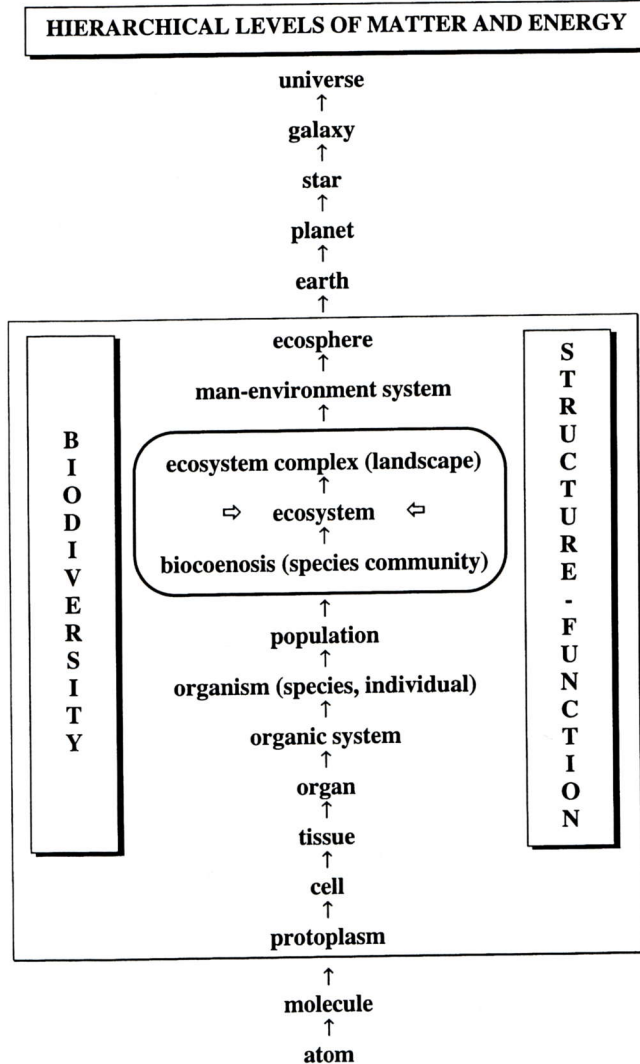


Figure 3. The hierarchical order of certain organization forms of organisms or parts thereof, of matter and energy (altered after Haber 1978), and the rank of biocoenology within the different organization levels.

Data on diversity may be studied at each level of the hierarchical structure, using two different approaches:

- a descriptive approach (*e.g.* identification, determination, description and differentiation of elements and their components);
- a functional approach (*e.g.* a causal analysis of the combination of the elements and their components, as well as of absorption, transformation, and processing of energy and matter).

Subject of this analysis is the level of ecosystems in the broader sense: their biotic components (biocoenoses) and their habitats (biotopes). Moreover the level of ecosystem complexes (landscape units) will be dealt with. Such complexes are formed by several ecosystems, the correlations of which follow certain rules. Since the Neolithic Period and increasingly in the past 150 years, man has considerably influenced ecosystems and ecosystem complexes in many parts of the world. A study of biodiversity therefore must include "man-environment systems". An increase in, but also a reduction of biodiversity may be anthropogenically caused.

On most organization levels of matter and energy (Fig. 3), the objects are supposed to represent entities. This, however, is not generally accepted for the levels of biocoenoses and ecosystems.

On the scientific treatment of biodiversity at the level of biocoenoses, ecosystems, and ecosystem complexes

An essential prerequisite for a scientific investigation of biocoenoses and ecosystems is the intensive theoretical examination of several, widely diverging approaches. The discussion focuses on two different viewpoints (Fig. 4) (after Trepl 1988, 1994):

- a) holistic approach versus individualistic approach
- b) deterministic approach versus stochastic approach.

There are gradual transitions between those widely diverging viewpoints. The two extreme views "ecosystems as super-organisms" or "as mere by-products" (the latter designated as "Gleasonian approach", Gleason 1926) are not endorsed by many. The majority of scientists rather follows deterministic or functionally based approaches (after Elton 1933). Opinion is divided as to the assessment of random events as system component. A deterministic principle does not necessarily exclude such events in a certain phase. In the course of succession of vegetation, an early stage may largely depend on random colonization, a latter one to a lesser extent. It seems pointless to analyze the importance of determinism, of stochastics, or of probability without examples and without relation to concrete objects, since in nature there is less an "either - or" than rather a "both - and" of phenomena.

It is agreed that biodiversity must not be seen as purely static, but that life on the different hierarchy and complexity levels always implies a dynamic component.

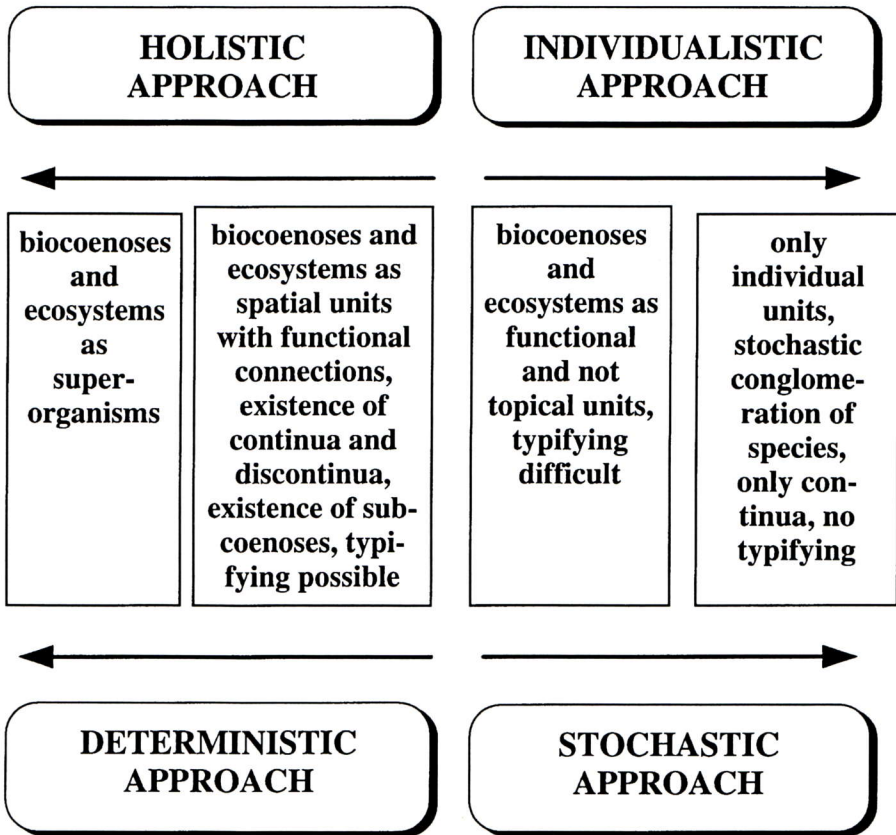


Figure 4. Differences in scientific approaches to the investigation of biocoenoses and ecosystems: a) holistic and individualistic approach, b) deterministic and stochastic approach.

Forms of diversity

The different forms of biodiversity may basically be assigned to four types:

- diversity of elements (element pattern of biodiversity)
- diversity of interactions (dynamic pattern of biodiversity)
- mechanisms causing diversity (causing pattern of biodiversity)
- process of functioning (functional pattern of biodiversity).

Diversity of elements (element pattern of biodiversity)

Taxonomic and syntaxonomic diversity, species and coenosis diversity. Following Whittaker (1972, 1975, 1977) various species and coenosis diversity levels can be distinguished in different spatial units: α -diversity, β -diversity and γ -diversity,

complemented by another category, δ -diversity (for definition see also Schwabe in this volume).

α -diversity refers to the species diversity of a certain area. It is for instance described by several calculation methods and the determination of indices (see *e.g.* Krebs 1989). One problem is how to delimit a specific area. It may be characterized according to the different spatial structure types. In this case, however, a "quasi-homogeneity" of the habitat must be presupposed, provoked by the physiognomy of a specific plant community or by certain synusia, of which this community is composed. Following v.d. Maarel (1988) α -diversity is defined as "diversity within a community"; it could also be described as "intra-biocoenotic diversity".

Gradients between different biotopes (habitats) can be analyzed by β -diversity. This procedure is especially suitable for regions with ecological gradients (ecoclines), *e.g.* forest/open land areas, zonation complexes at water banks etc., less however for areas with pronounced discontinuities. V.d. Maarel (1988) defines this diversity type as "diversity between communities", although it would certainly be more precise to describe it as "gradient diversity between communities".

γ -diversity characterizes the diversity of landscapes, in which case a landscape is defined as landscape part (= physiotope, see Schwabe in this volume). Such a landscape part consists of several communities, the entirety of which makes up a vegetation complex. In a physiotope certain uniform factor combinations can be found (geological substratum, soil conditions, nutrient balance, water balance etc.). Units relevant for the investigation of γ -diversities would be ecosystems and ecosystem complexes. Following v.d. Maarel (1988) one might speak of a "diversity of complex communities" ("interbiocoenotic diversity").

As suggested by Goetze & Schwabe (1997), γ -diversity may again be divided into γ_1 -diversity and γ_2 -diversity. γ_1 -diversity characterizes the number of vegetation types in a vegetation complex, γ_2 -diversity the number of vegetation complexes in a landscape part.

δ -diversity characterizes (analogously to β -diversity, where changes in the number of species along an ecological gradient are analyzed) changes in the number of vegetation types along an ecological gradient (Goetze & Schwabe 1997).

Sigmasociological methods are used to register and analyze vegetation complexes, and to characterize γ -diversity and δ -diversity (Schwabe 1990, 1991a, 1991b; Schwabe in this volume; Goetze & Schwabe 1997).

Diversity of life-forms. The concept "life-form" comprises the whole complex of species-specific qualities of an organism, which developed in adaptation to the particular conditions of a certain habitat (morphological, physiological, and ethological characteristics). Such life-forms can be typified. A "life-form type" belongs to a group of species, which often have different systematic ranks, but have acquired, adapting to the conditions within a habitat, analogous morphological, physiological, and ethological characteristics and modes of life in the course of evolution, and thus have the same life-form. For animals, life-form types can be classified according to feeding habit (*e.g.* phytophagous, zoophagous, parasitic, detritophagous; filter feeders, substrate eaters, grazing animals, sap feeders, stinging suckers, gatherers, predators, trappers, parasites), according to mode of locomotion (*e.g.* burrowing, crawling, climbing,

jumping, flying and running animals), and according to place of residence (edaphon, atmobios, herbicolous organisms = living on or in plants; phyllobios, lignicolous organisms = living on or in wood, epizoa, endozoa, and others) (see *e.g.* Tischler 1949).

For plants, different life-forms can be distinguished according to the way of surviving the unfavourable season (classification after Raunkiaer 1907/1937), according to adaptations of the water balance (xerophilous, mesophilous, hygrophilous, hydrophilous), according to light requirement (heliophytes, skiophytes), according to soil factors, and according to diet (see *e.g.* Strasburger 1991).

A very comprehensive system of different life-form types was presented by Koepcke (1971, 1973, 1974).

Diversity of spatial structures. After Tischler (1949) a habitat can be divided into three different spatial structure types: stratotope, choriotope, and merotope. Such a differentiation is essential for the recording and analysis of synusia within a biocoenosis. A detailed characterization of the different spatial structure types will be given in the chapter "Intrabiocoenotic diversity".

Trophic diversity. Classification into producer, consumer and decomposer levels with further subtypes (see *e.g.* also Cohen 1978).

Phenological diversity. Characterization of time structures, diurnal and seasonal changes, periodic phenomena within a year (*e.g.* different flowering phenologies, see Kratochwil 1983, 1984).

Genetic and population-specific diversity. Characterization of genetic variability and of the genotype spectrum, phenomena of homo- and heterozygosis and of gene drift, mutation rate of individual populations, and others (see *e.g.* Stearns *et al.* 1990; Vida 1994; Frankel *et al.* 1995); on population-specific diversity see *e.g.* Matthies *et al.* (1995).

Biochemical diversity. Characterization of different plant ingredients (*e.g.* alkaloids), partly important as "biochemical defence" against phytophages (see *e.g.* Feeny 1976) or scents as attractant for flower-visiting animals (Kugler 1970).

Diversity of interactions (dynamic pattern of biodiversity)

Among themselves, species create bi- and polysystems and thus form so-called biocoenotic links. These interactions between the organisms induce the emergence of characteristics which may contribute to stabilizing the system (quasi-stability in the species composition). Such interaction patterns can be divided into probioses (mutualism, symbiosis, commensalism) and antibioses (predation, parasitism etc.).

Mechanisms causing diversity (causing pattern of biodiversity)

Basically two different processes causing biodiversity can be distinguished:

- effects in evolutionary times (separation, speciation, and radiation)
- effects in ecological times.

Effects in evolutionary times. In evolutionary time periods, biodiversity is attained by speciation (allopatric, sympatric). Of great importance are in this case the separation of originally linked populations, the subsequent differentiation of the separated populations, the development of isolation mechanisms, and the formation of different ecological niches. A decisive factor for high diversity rates is an only slight extinction.

An especially high species diversity is elicited by radiation. Examples for this are Darwin's Finches (Geospizinae) on the Galapagos Islands (Lack 1947), or the honey-creepers (Drepanididae) and fruit flies (Drosophilidae) of Hawaii (Mayr 1943; Carson & Kaneshiro 1976; Carson *et al.* 1970).

Effects in ecological times. In ecological time periods, a biocoenosis rich in species can only develop when communities immigrate and are newly formed. In this context, the number of ecological niches to be realized plays a decisive part. The concept "ecological niche" is used in the sense of Günther (1950). According to his definition, the ecological niche is no spatial unit, but the dynamic relation system of a species with its environment. It is composed of an autophytic/autozoic and an environmental dimension. The autophytic/autozoic dimension comprises the phylogenetically acquired morphological and physiological (for animals also ethological) characteristics of the species, the environmental dimension the sum of all effective ecological factors. Where both dimensions overlap, the ecological niche of a species is realized. The breadth of the niche depends on the degree of specialization of the ecological niches which realize it. Niche overlaps can only be tolerated by species with a greater niche breadth.

Process of functioning (functional pattern of biodiversity)

The question to what extent biodiversity contributes to the functioning of biocoenoses is controversially discussed. There is no doubt that many organism species are constantly linked by certain interactions, and that these interactions may be obligatory. Such an interaction structure has only system character when it can be differentiated from other systems and when an independent matter flow is ascertainable. The differentiation of biocoenoses and ecosystems, however, has first a merely hypothetical character. Therefore only theories can be developed in reply to the questions how much redundancy a biocoenosis or an ecosystem may tolerate without being impaired in the maintenance of their functional balance, or whether there are upper and lower limits of biodiversity. The "theory of biodiversity" is closely linked with the "ecosystem theory".

The more diverse the system, the more diverse must be its functional structure to stabilize the system. The element pattern (see chapter "Diversity of elements") and

the diversity of interactions (chapter “Diversity of interactions”) primarily contribute to this stabilization.

Matter (nutrient) and energy flow are required to keep up the system and attain a quasi-stability. The stabilization processes include matter and nutrient absorption, transformation, and transfer (as input-output reaction).

Intrabiocoenotic diversity

A biocoenosis is composed of the plant community (phytocoenosis) colonizing a phytotope, and the animal community (zooconosis) inhabiting a zootope. Owing to the physiognomically dominating higher plants, plant communities can be more easily analyzed and typified. The number of associations is remarkably high: in Germany, there are approximately 700 plant communities (Pott 1995) and more than 3,200 higher plant species (Oberdorfer 1994).

All the same, phytocoenoses can be more easily recorded in their diversity than zooconoses. In Germany alone, more than 45,000 animal species occur. The animal species number of a beech forest roughly corresponds to the total number of Germany’s plant species. How can this wide variety of animal taxa possibly be registered?

There are different pragmatic approaches to the study of biocoenoses and their diversity:

- investigation of taxonomic groups (zootaxocoenoses): classifying biodiversity
- investigation of functional groups or guilds, respectively (“subsystems”, smaller units, functional groups of co-existing species which use the same resources in a similar manner): functional biodiversity
- investigation of certain relations (*e.g.* plant-insect complexes, food chains, food webs): interaction biodiversity
- investigation of microhabitats (= synusia): classifying microhabitat biodiversity.

More than 90 % of all terrestrial animal species are bound to habitats characterized by their vegetation. The first step in the recording of an animal community must be a phytosociological characterization of the habitat, for plant communities or vegetation complexes characterized by plant communities constitute typifiable units under ecological, structural, dynamic, chorological, and syngenetic aspects (Kratochwil 1987, 1991a). Such a characterization of a habitat via its plant communities and plant community complexes is the starting-point for a registration and analysis of biocoenological (community-ecological) diversity.

The second step is a classification into microhabitats (= synusia); this classification should be based on three different spatial structure types (Tischler 1949): stratotope, choriotope, and merotope (Fig. 5).

The different strata, *e.g.* of a forest, are designated as stratotopes; here it can be distinguished between tree stratum, trunk stratum, herb stratum etc., each colonized by its own stratocoenosis. Choriotopes, on the other hand, are independent vertical structures of the entire spatial unit or of parts of the stratotope, so-called choriocoenoses, like the insect community of a tree or a shrub. Finally, in a habitat rich in structures, merotopes can be found, *i.e.* structure elements within a stratotope or a choriotope, like organisms living on leaves or on bark, or flower visitors.

STRATOTOP	STRATOCOENOSIS	EXAMPLES
horizontal structures	subcommunity belonging to the stratotope	litter layer herb layer shrub layer treetop layer

CHORIOTOPE	CHORIOCOENOSIS	EXAMPLES
typical vertical structures of the whole spatial unit or parts of the stratotope	subcommunity belonging to the choriotope	tree tree stump shrub carcase excreta anthills bird's nest

MEROTOPE	MEROCOENOSIS	EXAMPLES
structure element within a stratotope or choriotope	subcommunity belonging to the merotope	leaf residents wood residents bark residents flower residents flower visitors

Figure 5. The three different spatial structure types (stratotope, choriotope, and merotope), the coenoses they comprise (stratocoenoses, choriocoenoses, and merocoenoses), and examples for these types (based on Tischler 1949).

Stratocoenoses. Analyses of taxonomic biodiversity demonstrate that each of these strata has its own animal species inventory, e.g. own spider stratocoenoses in Central European oak-birch forests (Fig. 6); see Rabeler (1957). Comparisons of the strata of various plant communities, of the leaf and soil strata of a melic grass-beech forest (Melico-Fagetum), and of an oak-hornbeam forest (Querco-Carpinetum) show distinct differences in the species composition of earthworms in the stratocoenoses, especially in the leaf litter stratum (Rabeler 1960; see also Kratochwil 1987).

Choriocoenoses. Other structural elements include special, clearly differentiable elements, so-called choriotoxes: a tree, a shrub, or a single plant, e.g., each with its community of phytophagous insects (phytophage complex). The diversity of a choriotope will be demonstrated at the example of a bird's nest (Fig. 7); ABmann & Kratochwil (1995); Kratochwil & ABmann (1996a). Bird species utilize very specific requisites to build their nests. The Long-Tailed Titmouse (*Aegithalos caudatus*) builds highly characteristic nests in juniper (*Juniperus communis*) in northern Germany.

An analysis of the nesting material shows that it consists of specific materials: certain moss species, lichen species, algae etc. The composition depends on the plant community, in which the nest is built. It is an orderly, habitat-typical structural diversity. The nest of a Great Tit (*Parus major*) is built in another way, moreover this bird species is mainly found in quite different habitats. The diversity of species entails a diversity of the small structures created by them.

Spiders of an oak-birch forest (*Betulo-Quercetum*)

STRATOTOP	STRATOCOENOSIS	EXAMPLES
horizontal structures	subcommunity belonging to the stratotope	treetop layer shrub layer herb layer litter layer

- Crustulina guttata*
- Drassodes silvestris*
- Wideria cucullata*
- Robertus lividus*
- Microneta viaria*
- Trochosa terricola*
- Pardosa lugubris*
- Zora spinimana*
- Linyphia clathrata*
- Linyphia triangularis*
- Meta segmentata*
- Theridium ovatum*
- Xysticus lanio*
- Anyphaena accentuata*
- Philodromus aureolus*
- Theridium tinctum*
- Araneus sturmi*

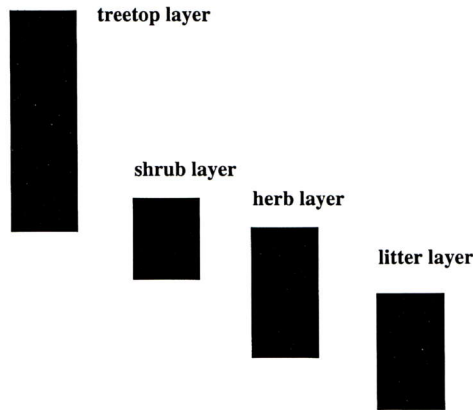


Figure 6. Dominant spider species from different strata in a Central European oak-birch forest (based on Rabeler 1957).

Merocoenoses. The merotopes, parts of strato- and choriotopes, represent the third, final element. Strato-, chorio- and merotopes combine to a special degree structural and functional diversity. Here we particularly investigate ecological niches, interaction levels, and relation structures between organisms.

The community of flower visitors corresponds to a merocoenosis, with the flowers representing merotopes. First we find a “systematic biodiversity” of very different animal groups: Hymenoptera Apoidea, Hymenoptera Aculeata, Lepidoptera, Coleoptera etc. (Kratochwil 1984). Within this flower/flower visitor system, there is a “functional diversity” introduced by the visitor: e.g. food relations (pollen, nectar, oil), or certain other resource relations, like the use of the flowers as warming-up places, due to their parabolic mirror-like forms (Hocking & Sharplin 1965; Kevan 1975), as “rendezvous” places (Eickwort & Ginsberg 1980), as food source for predators and parasites (Mayer & Johansen 1978; Morse 1984), as overnight accommodation e.g. of bees (Dafni *et al.* 1981), or as provider of nesting materials (Benno 1941). Flowers even supply scents, used to mark swarming paths, as done by the neotropic, scent-gathering euglossine bees (Euglossinae); see Evoy & Jones (1971). Alone for oil-producing plants,

about 1,400 plant species (belonging to ten families) are known world-wide, and approximately 300 wild bee species specialized on them (Vogel 1988).

	Longtailed titmouse (<i>Aegithalos caudatus</i>)		Longtailed titmouse (<i>Aegithalos caudatus</i>)		Great tit (<i>Parus major</i>)
	JUNIPER PLANT COMMUNITY (DICRANO-JUNIPERETUM)		JUNIPER PLANT COMMUNITY (ROSO-JUNIPERETUM)		BEECH FOREST (PERICLY-MENO-FA-GETUM)
NESTING MATERIAL	NEST 1	NEST 2	NEST 3	NEST 4	NEST 5
BRYOPHYTES, LIVERWORTS					
<i>Hypnum mamillatum</i>	8,9 %	23 %	12,8 %	38 %	+
<i>Dicranum scoparium</i>	++	++	-	-	-
<i>Campylopus introflexus</i>	+	+	-	-	-
<i>Lophocolea bidentata</i>	+	-	-	-	-
cf. <i>Dicranoweisia</i>	+	-	-	-	-
<i>Hypnum mamillatum</i>	-	-	+++	-	-
<i>Eurhynchium swartzii</i>	-	-	++	-	-
<i>Dicranoweisia cirrata</i>	-	-	-	+	-
<i>Rhytidiadelphus squarr.</i>	-	-	-	-	50 %
<i>Scleropodium purum</i>	-	-	-	-	40 %
<i>Brachythecium rutab.</i>	-	-	-	-	+++
<i>Eurhynchium praelong.</i>	-	-	-	-	+
<i>Pleurozium schreberi</i>	-	-	-	-	+
LICHENS					
	11,5 %	13,1 %	14,6 %	9,8 %	-
<i>Hypogymnia physodes</i>	x	x	x	x	-
<i>Parmelia sulcata</i>	x	x	x	x	-
<i>Physcia tenella</i>	-	-	x	x	-
<i>Physcia adscendens</i>	-	-	x	x	-
ALGAE					
<i>Ulothrix spec.</i>	+	-	-	++	-
<i>Pleurococcus vulgaris</i>	+	-	-	++	-
MISCELLANEOUS					
feathers	15,8	19,4	35,5 %	11,6 %	-
juniper bark	64 %	12,6 %	9,7 %	4,7 %	-
juniper berries	++	+	+	+++	-
juniper needles	++	+	+	+++	-
spiders threads	+	+++	+++	++	-
insect cocoons	-	++	-	-	-
heather	-	+	-	-	-
indefinable	-	32 %	32 %	-	-
leaf remains	-	-	-	+	-

Figure 7. Structural diversities of nests of Long-Tailed Titmice (*Aegithalos caudatus*) and a comparison with the nest of a Great Tit (*Parus major*); based on Aßmann & Kratochwil (1995) and Kratochwil & Aßmann (1996).

Moreover also plants show different degrees of functionality (functional diversity). For the plant, the margin ranges from symbiotic relations, in which case the pollen-transferring insects are rewarded with food, to parasitism, which can be found in its most

distinctive form in specimens of the genus *Ophrys*: the flowers imitate female bees and “sneak” by optical, olfactory, and tactile stimuli into the instinctive behaviour of male bees to ensure a transfer of pollinia (Kullenberg 1961; Paulus 1988).

Species diversity and functional diversity always correlate with structural diversity. One example for this is the correlation between the structure of the pollen-gathering device of a bee and certain pollen grain structures (Paulus 1978). The bee *Lasioglossum lineare* (Halictidae), main pollinator of the pasque-flower *Pulsatilla vulgaris* (Ranunculaceae), has a specific gathering device at its hind legs, composed of particularly fine hairs. These hairs exactly fit into the sutures of the pollen grains of *Pulsatilla vulgaris* (Kratochwil 1988a); a coevolution between specific flowering plant and pollinator.

How much structures determine functions, and vice versa, is shown by the next example. There are hairs on the *Ophrys* flowers. The position of a male bee landing on such a flower depends on their orientation. In this way it is also determined whether the pollinia are attached to the head or to the abdomen (Paulus 1988).

The structural diversity of a flower/flower visitor merocoenosis is immense:

- optical diversity: the colours of the flowers in the visible, but also in the ultraviolet wave range (literature in Kratochwil 1988b, 1991b)
- olfactory diversity: the multitude of different flower scents (Kugler 1970)
- ethological diversity: the behavioural variety of flower visitors (Westrich 1989)
- phenological diversity: the diurnal and seasonal variation of the occurrence of flowers and their pollinators (see *e.g.* Kratochwil 1983).

Each plant community has its own animal community or synusia of different animal communities. On ecosystem level, the structural and functional diversity levels of different organism groups correlate with their specific abiotic environment. The biocoenoses or biocoenosis complexes are characterized by certain character species. However, each biocoenosis has its own range of diversity types and patterns. The greater the species diversity, the more varied are other diversity types: genetic diversity, space-structural and physiognomic diversity, biochemical diversity, phenological diversity etc.

Interbiocoenotic diversity

As a rule, landscapes are not composed of single biocoenoses, but of biocoenosis complexes and a mosaic of different ecosystems. The development *e.g.* of individual vegetation units into associations is not arbitrary, but follows certain rules (for a detailed depiction see Schwabe 1990, 1991a, 1991b; Schwabe in this volume). Especially ecosystems with a distinct microgeomorphology, *e.g.* inner-alpine dry slopes (Schwabe 1995; Schwabe *et al.* 1992) or steppe heaths in Central Europe (Köppler 1995; Köppler & Schwabe 1996) are perfect examples of habitats with very high species and coenosis diversities in Central Europe.

It is interesting that regularities on the species/biocoenoses and biocoenoses/biocoenosis complex levels follow the same natural laws (Schwabe & Kratochwil 1994). At the example of the rock and moraine physiotopes in central alpine dry areas it

could be shown that "Thienemann's 2nd basic principle" may also be formulated as coenological and landscape-ecological principle: "The more variable the environmental conditions of a habitat complex, the larger the number of its coenoses/synusia." and: "The more the environmental conditions of a habitat complex deviate from the normal and for most coenoses/synusia optimum conditions, the poorer in coenoses/synusia the complex will become, the larger and the more characteristic are the occurring coenoses/synusia."

On the other hand it is just these areas characterized by vegetation complexes which represent habitats for certain animal species (Schwabe & Mann 1990; Schwabe *et al.* 1992) and for special zoocoenoses (Kratochwil 1984, 1989; Kratochwil & Klatt 1989a, 1989b; Aßmann & Kratochwil 1995; Kratochwil & Aßmann 1996a, 1996b), and thus allow a biocoenological analysis of landscape units.

Now ecosystems are not static structures, but dynamic units, be it in the scope of succession or of spatial and temporal cyclic processes. Particularly in Central and southern Europe, man has played an important part as "landscape architect", for he created, by extensive and long-lasting agricultural management, a great biodiversity. This positive influence was diminishing in the course of the past century, when intensive management forms were introduced and mechanization set in.

A good example for habitats created by man are the pasture-woodlands, *e.g.* in northern Germany (Aßmann & Kratochwil 1995; Kratochwil & Aßmann 1996a, 1996b; Pott in this volume). Despite intensive interventions of agriculture and forestry, primarily in the past fifty years, there are still some habitats in the north-west German lowlands which reflect in a special way the long-lasting and extensive anthropogenic utilization of the land: the "pasture-woodlands". They arose due to range management (pasture farming) that was first restricted to woodland sites (wood-pasture), but then increasingly led to an opening of the woodland and to the development of numerous open land sites, also as a consequence of further utilizations (*e.g.* cultivation by sod). What is particularly striking for visitors still today is the impression of a "parkland", a mosaic of sand dunes free of or poor in vegetation, extensively managed open pastures with grass, tall herb communities ("hem communities"), richly structured edges of woodlands, the occasional individual tree, clusters of shrubs and trees of varying sizes and woodland communities with open stands, and a large share of especially characteristic tree individuals, which often still show signs of the former wood-pasture: pollard forms, trimming and pruning marks, as well as distinct traces of the damage caused by browsing animals (see *e.g.* Burrichter 1984).

The high biological diversity of such a landscape is due to its richness in structures, both on the species (α -diversity) and on the coenosis level (γ -diversity), and to its gradients (β -diversity, δ -diversity). These structures arose as a consequence of anthropo-zoogenic landscape dynamics. The landscape genesis follows the principle of "variety in space" (a high degree of constant spatial changes of the factor combinations, van Leeuwen 1966) and is characterized by a continuous preservation of its mosaic structure. The stabilizing and system-preserving factors are in this case not the natural factors, as asserted by Remmert (1991) for woodland ecosystems, but the anthropo-zoogenic influences which have affected the biocoenoses since the Neolithic Period. Judging by pollen-analytical findings, the areas were being used as pasture-woodlands for about 5,000 years (Pott & Hüppe 1991).

Hypotheses on diversity

There are a number of different hypotheses on biodiversity (see *e.g.* Solbrig 1991, 1994; Schaefer in this volume, and others). They constitute the basis for the development of a general "theory of biodiversity". In the following 30 hypotheses will be presented (formulated as questions), some of which correlate as to their contents. Except for the first one, all hypotheses refer to the ecosystem and the ecosystem complex level. Their order is arbitrary and does not reflect an evaluation. It should also be stressed that none of the hypotheses is absolutely valid; they apply as a rule, but allow for exceptions.

1 *Is the entire biodiversity (holodiversity) increasing with higher levels of hierarchy in a system?*

If a systemary approach is taken as basis and the respective elements of a hierarchy level can be integrated into the next higher level (see Fig. 3), the degree of complexity is increasing on higher levels of hierarchy, since on every new level further new system characteristics (emergent characteristics) appear ("principle of functional integration" after Odum 1971). The entirety of the elements of one level is more than merely the sum of its components. However, in the framework of our examination, this principle only applies to the level of biodiversity. The biochemical, genetic, or structural diversity of a landscape part is always much greater than that of an individual organism or of a cell. The principle is moreover not wholly applicable to compensation phenomena. The physiological constitution of a single organism, for instance, is as a rule always greater than its ecological constitution (restriction of the physiological constitution, *e.g.* under prevailing competitive conditions).

2 *Is the species and ecosystem diversity increasing with advancing age of the ecosystem?*

Ecosystems like the tropical rain forest, the coral-reefs, old lakes (*e.g.* Lake Tanganyika, Lake Baikal) have, owing to their advanced age, created ecosystem complexes with a particularly high diversity. According to this "time hypothesis" (Latham & Ricklefs 1993) older ecosystems have more species than younger ones. This is on the one hand due to evolutive reasons (speciation), on the other to ecological reasons (immigration and colonization). Prerequisites for an augmentation of the species number are that, with growing succession of a habitat and its microhabitats, its habitat diversity increases, that a species pool exists, from which species can immigrate and realize ecological niches, and that the new "inhabitants" are compatible with the others and may be incorporated into their interaction structure (Cornell 1993).

With advancing age of an ecosystem, the share of organisms following a K strategy is increasing, the share of the so-called r strategists is decreasing (see hypotheses 14 and 17). It is undisputed that a certain "species set" is essential for the maintenance of the homeostasis of an ecosystem, but also for the genesis of a biocoenosis. Whether the entire species diversity of such systems necessarily has a system-preserving character, is controversially discussed. It may however be assumed that *e.g.*

a historically caused high diversity often has redundancy character (see hypothesis 16). Individual relic biocoenoses may be very rich in species, too (see hypothesis 12).

However, there are also examples to the contrary, showing that in the course of succession biodiversity must not necessarily increase towards a climax stage ("intermediate disturbance" hypothesis) (Connell & Slatyer 1977; Connell 1978; Huston 1985); see hypothesis 27. So Pignatti & Pignatti (in this volume) could demonstrate for Mediterranean ecosystems that the species diversity is not necessarily increasing in the course of succession, that the man-made habitats are richer in plant species than the natural vegetation without any anthropogenic influence. The same may apply to individual zootaxocoenoses (Kratochwil & Klatt 1989a, 1989b).

In a beech forest, the diversity of plant species is also decreasing with succession; this is however not true for its fauna.

3 *Is biodiversity increasing with the degree of biocoenotic progression?*

Analogous to the degree of sociological progression of a plant community or of a vegetation complex in phytosociology (Dierschke 1994), there are also different degrees of biocoenotic or ecosystemary progression between different biocoenoses. The concept "degree of sociological progression" involves:

- attachment of the majority of the individuals from one community, of stands and communities, to a certain site
- interrelations between the individuals of different species and communities
- diversity of the structure of strata, diversity of life-forms
- longevity of the stands.

An augmentation of the degree of biocoenotic progression should entail an increase in biodiversity.

4 *Is ecosystem diversity increasing with growing radiation energy and humidity?*

Although very little energy is needed for the photosynthesis rate of autotrophic organisms (often less than 1 % of the global radiation), the "operation temperature" must be favourable for the constructive and the energy metabolism throughout the year, to provide advantageous environmental conditions, especially for ectothermic organisms. That is why it is not surprising that particularly the tropics, as regions with a diurnal and not a seasonal climate, with high temperatures and a high amount of precipitation, are the centres of greatest biodiversity on earth. This also reflects thermodynamic natural laws. A very high degree of systemary order (neg entropy) presupposes the supply of a large quantity of free enthalpy. Accordingly Pignatti & Pignatti (in this volume) could, when assessing the biodiversity of Mediterranean ecosystems, prove that there is a relation between the number of plant species and temperature and water availability. The amount of precipitation alone is not significant, the rate of evaporation is the decisive factor (Pignatti & Pignatti in this volume). Thus the overall productivity of an ecosystem is causally related to its richness in species (Currie 1991; Latham & Ricklefs 1993). The degree of quantity and quality of primary production determines biodiversity.

5 *Is ecosystem diversity increasing with relief intensity?*

An increase in biodiversity may be related to a higher relief intensity, since in the temperate zones the angle of incident radiation is getting more favourable with higher inclination (see also hypothesis 4). In the northern hemisphere, southern slopes are richer in species than northern ones. The same is true for Mediterranean ecosystems, as shown by Pignatti & Pignatti (in this volume). With varying relief intensity, different meso- and microclimate conditions, as well as different soil conditions (soil types) alternate on a small scale; thus different site conditions and subsequently a differentiated vegetation develop. The water factor has a modifying effect.

6 *Is ecosystem diversity dependent on the geological set-up and its diversity?*

The distribution of numerous plant species depends on certain geological and pedological conditions. Consequently they are, according to their respective, geologically determined life-form type, designated as calcicolous plants, silicate plants, chalkophytes etc. In an area where geological and pedological patterns intensely change, more different plant species grow than in a region with a smaller diversity of geological and pedological site factors.

As many molluscs and arthropods need CaCO_3 , they are richer in species in calcareous than in siliceous regions.

In connection with the different geological, but also pedological characteristics of an area, the respective pH-value determines its diversity, too. As a rule, higher species numbers are attained in a neutral or slightly alkaline milieu than in an acid environment or one extremely rich in bases.

7 *Are species and ecosystem diversity increasing with the possibility of a post-glacial recolonization?*

Many areas in the northern temperate zones could, owing to a glaciation in the Pleistocene, not be colonized by plant and animal species. The ice ages moreover led to the local extinction of numerous species. This is especially true for Europe, where the Alps - as a kind of crossbar - prevented the escape of these species to more southern regions (refuge areas). In northern America, where the great mountain ranges run from north to south, this was not the case. That is why - so many scientists assume - the diversity of a number of tree species is higher in northern America (Walter & Straka 1970). In addition, the conditions for a recolonization were more favourable in northern America than in Central Europe.

8 *Is diversity increasing with the probability of allopolyploid and autopolyploid processes?*

The fact that in the course of the ice ages numerous populations were divided into subpopulations led to gene drift and other processes (different selection pressures, random selection) and, in consequence, to a greater variation of genotypes. In extreme

cases, the formation of new species was only made possible by allo- and autopolyploid processes (species and subspecies level); see *e.g.* Ehrendorfer (1962). Man has also considerably influenced this development (Pignatti 1983).

9 *Is biodiversity increasing with the size of an area?*

Inspired by the studies of Arrhenius (1921) and Palmgreen (1925) of terrestrial plants, species-area relations have long since been described for highly different organism groups from numerous islands in the sea, but also from continental islands of varying sizes. So Darlington (1957) could show that on the West Indies the species number of reptiles and amphibians is rising with increasing island size; similar phenomena were observed for the birds on the Solomon Islands (Diamond & Mayr 1976) or for the higher plant species of the Azores (Eriksson *et al.* 1974). A number of further examples substantiating this thesis can be given (Diamond 1972; Lassen 1975; Galli *et al.* 1976; Aho 1978; Jurvik & Austring 1979 *etc.*).

This species-area relation may be expressed by the simple formula $S = C \cdot A^z$, with S being the species number, A the size of the island, and C a constant which depends on the respective biogeographical region of the investigated taxon. Another parameter, the exponent z , ranges, according to empirically gathered data, as a rule between 0.20 and 0.35, independent of the studied taxocoenosis, be it ground beetles, ants, birds, mammals, or plants (Connor & McCoy 1979). The exponent indicates the inclination of the regression line $\log S$ to $\log A$ (Preston 1962), which is also influenced by the constant C . Within a terrestrial area, the species number is also rising with increasing area size, however, the z -value is far lower in this case. This is *e.g.* proven by a comparison of the relation of area and number of ant species (Ponerinae and Cerapachyinae) from different-sized Molucca and Melanesian islands with the species-area curve under non-separated conditions, *e.g.* on New Guinea (Wilson 1961). The z -values of the species-area curves on the continent amount to merely 0.12-0.17; see also compilations of the z -values of different taxonomic groups in MacArthur & Wilson (1967) and May (1975), quoting original literature.

Preston (1962) could mathematically derive the z -value, on the hypothetical assumption that both the species and the individual numbers are lognormally distributed in a site. Studies of birds by Preston (1962) and of moths by Williams (1953), as well as of many other animal groups, support this assumption, but there are also exceptions. Preston (1962) calculated, via a canonical distribution, a z -value of 0.263 for insular relations, which is in good agreement with many values ascertained in nature. All these examples prove that biodiversity is increasing with growing size of an area (but see also Haeupler 1997).

10 *Is habitat diversity increasing with the size of an area?*

The relation between species number, growing size of an area, and increase in habitat diversity has often been discussed in the literature, however, there are considerable differences in the assessment of the importance and weight of the main factors. Some authors consider area size and habitat diversity to be exchangeable (Hamilton

et al. 1964; Johnson & Raven 1973; Simberloff 1974). Others see them as extremely correlating factors, with one giving rise to the other. In this case, there are different views as to their importance: Johnson & Simberloff (1974), Simberloff (1974), Reed (1981), Lynch & Whigham (1984) consider the habitat diversity to be of greater relevance, whereas Hamilton *et al.* (1964), Johnson & Raven (1973), Brown (1971) argue that the area size is more important.

Based on the ideas of Dean & Connell (1987a, 1987b), O'Connor (1991) developed two alternative hypotheses which may explain the relation between species diversity and area size. The "sampling phenomenon hypothesis" purports that the relation between the increase in habitat diversity and the increase in species diversity is alone determined by the size of the investigated area and the consequently higher number of available resources (Douglas & Lake 1994). The "resource availability hypothesis" argues that the new resource qualities bring about the increase ("niche availability hypothesis" in the sense of Dean & Connell 1987a, 1987b). Buckley (1982, 1985) also points out that not the diversity of the whole area is decisive, but the quality of single habitat types.

The species number (plant and animal species) of an area with homogeneous environmental conditions is not or only slightly increasing, even if a considerably larger area of the same quality is investigated (Vestal & Heermans 1945; Vestal 1949; Goodall 1952; Greig-Smith 1964; Forman *et al.* 1976; Dierschke 1994). Therefore it is essential to know the minimum area of a plant community or biocoenosis, beyond whose limits the number of typical, characterizing species is no longer rising. The same applies to communities which form typifiable vegetation complexes: their number varies merely slightly in a specific landscape (Schwabe & Kratochwil 1994).

11 *Have separated ecosystems lower species numbers than less separated ones?*

At the same area size, less separated islands have higher species numbers than those which are far away from a colonization source (the same is partly true for continental islands). This was *e.g.* shown by Lack (1969) for the avifaunas of different islands off New Guinea. Islands lying more than 3,200 km away from the mainland had a much lower species number than those less than 800 km away. A different "reachability" of islands for immigrating ground beetles (Carabidae) was already shown by Lindroth (1960); this has meanwhile been described in many cases and for many taxa. Rosenzweig (1995) however points out that not the distance from the mainland can be regarded as a generally comparable measure for the respective species number of an island in the sea, but the different immigration probabilities. They are indirectly linked to the distance, however, they depend on the "quality" of the "source".

12 *May the species oversaturation of an area be one reason for an especially high species number?*

In accordance with the island theory (equilibrium theory) by MacArthur & Wilson (1967), many cases are meanwhile known in which, due to an increase in the sea-level, land bridges sank in the course of the past 10,000 years, or islands were reduced in their size. The biocoenoses there are at present still species-oversaturated, since extinction

exceeds colonization and an equilibrium has not yet been reached. Diamond (1972, 1973) studied 32 of such former "land bridge islands" off the shore of New Guinea, which were linked to the mainland only 10,000 years ago. The changes in the sea-level in the continental shelf zone are quite well documented; considering several analyses made by different authors, it varied by at least 60 m in the last 10,000 years. An avifaunistic investigation performed by Diamond (l.c.) only showed a relation between species number and area size; the z-value amounts to more than 0.35. By increase in the sea-level, destruction of the former land bridge and an entailing reduction in size of the area, these islands which previously belonged to the mainland are for the moment species-oversaturated. Owing to the now lower area size and in accordance with the species-area relation, a lower species diversity is to be expected. Until a new equilibrium is attained, extinction prevails; a further colonization is restricted by the barrier effect. Terborgh (1974) who studied the avifauna of five neotropical land bridge islands obtained the same results (see also Karr 1981).

This phenomenon was also observed in some relic biocoenoses. From the Great Basin in western USA, 17 mountain ranges rise with heights of over 3,000 m. The boreo-alpine habitats on the summits of these mountain islands are today surrounded by dry and hot sites. A link to the extensive Rocky Mountains and the Sierra Nevada was only present in the Pleistocene. The reduction in size of the area, and the lack of colonization possibilities and colonization ability of the species led to a high number of small mammals (after Brown 1971).

13 *Is species diversity increasing with habitat and structure diversity?*

According to the "habitat diversity hypothesis", set up by Lack (1969), species diversity is increasing with habitat and structure diversity (see in this context also Hamilton *et al.* 1964; Simberloff 1974, 1976; Tangney *et al.* 1990; Hart & Horwitz 1991; Kohn & Walsh 1994). This hypothesis correlates with the "niche theory" (see hypothesis 14).

14 *Is the number of ecological niches related to the number and composition of the species present in a biocoenosis?*

A high diversity of ecological niches may be due to a (historical) competitive situation. After niche differentiation, competition among the species is reduced, and a coexistence of different species is possible. This however only happens in localities where the immigration of species plays no dominant part in establishing a species community. Processes of niche differentiation take a longer time.

A high species number in a habitat is as a rule based on a niche differentiation (niche partitioning, see Schoener 1986). The degree of the ecological occupation of a niche always depends on specialization and a reduction of the competitive pressure between the species. According to the "competitive exclusion principle", an increase in diversity should be accompanied by a decrease in interspecific competition. In a "mature" ecosystem, the share of stenoecious species should be higher than that of euryoecious ones. Likewise a lower number of individuals of numerous stenoecious species correlates with a higher number of individuals of few euryoecious species

(see Thienemann 1920, 1956); see also hypothesis 15. At an early succession stage, however, euryoecious species prevail as a rule, consequently the probability of a first colonization by such r strategists is higher.

The diversity of niches in a biocoenosis is determined by the following factor groups (Diamond 1988):

- quantity of the available resources and requisites
- quality of the available resources and requisites
- interactions between the species
- dynamics of the biocoenosis

Species diversity always correlates with resource and requisite diversity.

15 Is the number of individuals of certain species decreasing with growing species diversity?

If it is assumed that the carrying capacity (total number of individuals) of a habitat is limited, only a lower number of individuals of single species can occur when the species number is increasing. The respective population size is to a certain extent species-specific ("minimal viable population size").

This hypothesis reflects Thienemann's basic principles. In his summarizing work (1956) he formulated (p. 44): "There are sites of optimum favourable development for organisms... Here the conditions for life are stable, harmonic, no excess to any side; thus life possibilities for many species. But when a vital factor occurs in a lower amount or with less intensity, or when another one gains a superior position; when the optimum is shifting, ..., via a 'pejus', towards a 'pessimum': then the species number of the biocoenosis is more and more decreasing, and finally only few species remain. These may however, provided that the conditions for life are favourable, develop in enormous individual numbers, since they have no food competitors..."

Thus two biocoenotic basic principles apply (Thienemann 1920): 1): "The more variable the conditions for life of a site, the larger the species number of the respective community." 2): "The more the conditions for life of a biotope deviate from the normal and for most organisms optimum conditions, the poorer in species the biocoenosis will become, the more characteristic it gets, the more individuals of the single species will occur."

16 Do redundancy phenomena occur more frequently with growing species diversity?

According to the redundancy hypothesis also such species exist in an ecosystem that are not directly important for the maintenance of the system and do not influence the species structure to a great extent. The number of these redundant species should increase with growing biodiversity (on redundancy see Lawton & Brown 1993; Walker 1992).

17 *Is with increasing biodiversity the share of r strategists decreasing, while analogously that of K strategists is growing?*

With increasing niche differentiation, the share of K strategists is growing, that of r strategists decreasing. This hypothesis coincides with hypothesis 2 and hypothesis 14.

18 *Is the extinction probability of individual species growing with increasing degree of ecological niche differentiation?*

The increasing specialization of a species may in particular cases become a selection disadvantage. This can e.g. be shown at the phenomenon of the so-called "taxon cycle", in which colonizers on islands (as a rule r strategists and wide-spread, ecologically not differentiated species) develop into geographical subspecies, then more and more differentiate and specialize (are K-selected), and thus provoke an evolution which may lead to an endemism (Wilson 1961; Ricklefs & Cox 1972). Finally the highly specialized forms are extinguished by the competitive pressure of newly colonizing species (generally r-selected). With a new colonizer this cycle starts afresh. Examples for a "taxon cycle" can be found for birds (West Indies) (Ricklefs & Cox 1972) and ants (Melanesia) (Wilson 1961). The theory of the "taxon cycle" demonstrates how dangerous wide-spread and highly competitive "generalists" can be when they, after having overcome special barriers, "attack" extremely evolutionized systems. Simberloff & Cox (1987) and Simberloff *et al.* (1992) cite, among others, the following disadvantages of corridors facilitating the access to habitats rich in species: dispersal of pests and diseases, immigration of strong competitors, immigration of predators. A separation of single habitats is often an important protective mechanism to maintain a higher species diversity.

19 *Is the trophic structural diversity within an ecosystem (phytophages, carnivores, parasites, hyperparasites, parasitoids etc.) growing with increasing species richness?*

By trophic structural diversity, the diversity of different trophic levels is understood. Trophic diversity involves phytophages (feeders on living plant material), saprophages (utilizers of dead organic matter), microphytophages (feeders on bacteria, fungal hyphae and/or algae), and zoophages (predators, parasites and parasitoids). Especially the category of zoophages is further differentiated (zoophages of first, second, third and higher orders, parasites and hyperparasites etc.). The greater the species richness, the higher the trophic structural diversity of an ecosystem.

20 *Is biodiversity increasing in the course of the food chain?*

Within an ecosystem, the flow of energy and matter can only occur via different trophic levels. The distribution of biomass is larger for producers than for consumers, and it is further decreasing with each higher consumer level. For the species diversity, however,

the reverse is true. The highest species numbers are attained by parasites and parasitoids (see also Schaefer in this volume). Zoophages are richer in species than phytophages, saprophages or microphytophages. The diversity of parasites by far exceeds that of predators. The extent of diversity on the lowest level (consumers of first order) positively correlates with the one on higher levels (consumers of higher order, parasites, hyperparasites).

21 *Is biodiversity increasing with the species richness of the respective immigration pool?*

As biocoenoses - unless they are very old, in which case evolutive reasons may be given for their original biodiversity - develop as a consequence of the immigration of species that colonize a habitat by realizing ecological niches, their composition depends on the potential immigration pool of the environment. Positive correlations between local and regional species pool could be demonstrated by numerous authors (see Eriksson 1993; Ricklefs 1987; Lawton 1990; Rosenzweig 1995). A prerequisite for a colonization is the existence of "open niches"; see hypotheses 13 and 14.

22 *Of what importance is the separation of single geographical areas for the diversity of convergent developments?*

The distribution of plant and animal species is restricted to certain geographical areas. Independent of their natural relationships, organisms may show, because of a similar mode of life and in adaptation to a similar habitat, many identical features in the form and morphology of their bodies (convergence). In the respective ecosystems, they have a similar "ecological and functional rank". The biocoenoses to which they belong are therefore also called isocoenoses. The diversity of convergent developments is due to similar ecological selection pressures on different species sets.

23 *Does an increase in species diversity correlate with an increase in the variability of the micro- and the mesoclimate?*

An increase in the structural diversity of a habitat entails a diversity of microcoenoses (synusia). Their existence is frequently due to a small-scale alternation of meso- and microclimate conditions. Different microclimate phenomena are also dependent on the soil substrate, especially in the temperate zones. Needle ice, *e.g.*, leads to a loosening of the upper soil material and to the formation of synusia of annual plant species (therophyte communities).

24 *What effect does an increase in the extensive human influence have on biodiversity?*

Pignatti & Pignatti (in this volume) could show that because of the human impact the biodiversity of the Mediterranean vegetation is far greater as under natural conditions (without anthropogenic influence), contrary to tropical regions, where highest

species diversity is only attained at the climax stage. Thus a general connection between high biodiversity (α - and γ -diversity) and primary vegetation cannot be made. The increase in biodiversity by extensive human influence is due to the fact that, over different stages of succession, a climax vegetation may possess a multitude of different man-made plant communities (see also hypothesis 27: “intermediate disturbance” hypothesis; Connell & Slatyer 1977; Connell 1978; Huston 1985). The manifold anthropo-zoogenic influences (kind, point in time and extent of soil cultivation, mowing, grazing etc.) are reflected by the wide variety of vegetation selected due to these measures. The impact has a multiplicative effect and induces the origin of a number of possible vegetation types (progressive development). One important prerequisite is however that the factors do not become extreme factors with a levelling effect (recessive development); within the past fifty years, this has frequently led to a significant decrease in species in landscapes intensively used by agriculture and forestry.

25 Is the share of species of smaller body size increasing with growing species number?

As a rule, species of small body size dominate in a habitat (May 1978; Rosenzweig 1995). This is partly due to the fact that there is a much greater habitat diversity for small species than for bigger ones, and that thus smaller species have much better niche differentiation possibilities in the spatial and temporal axis. This ratio of small to big species is especially characteristic for sites with a great spatial heterogeneity. In addition, smaller species often have a higher mobility and thus a better immigration potential. Schaefer (in this volume) has formulated the following hypothesis: Diversity is higher for taxa containing more mobile species (see also Blackburn & Gaston 1994). Investigations of carabids (Carabidae) showed that small macropterous species are first colonizers; the share of brachypterous species, as well as that of bigger ones, is only increasing in the course of time.

Among the arthropods, particularly the relic communities have a higher share of bigger species. K strategists are usually bigger than r strategists. There are more brachypterous forms in relic communities.

26 Is the share of species with a shorter life cycle increasing with growing species number?

A habitat is usually dominated by species of small body size (see hypothesis 25) and short life cycles (May 1978; Rosenzweig 1995). The small body size often correlates with a short generation time (see Schaefer in this volume). This principle, which was originally applied to animal species, is also true for plant species. In a plant community, e.g., the duration of the flowering stages correlates with the species richness (see also Kratochwil 1984). A niche differentiation in the time axis is thus better possible.

Spatial heterogeneity is generally favourable for organisms of small body size, however, it does not imply that all these organisms are also short-lived. If the habitat quality remains stable in the time axis, longevity or - with insects - polyvoltinism may occur. For insects, however, a high species diversity within a site can rather be attained by monovoltinism than by polyvoltinism.

27 *Do extensive disturbances by spatial and temporal heterogeneities increase the species number?*

The phenomenon that extensive disturbances by spatial and temporal heterogeneities increase the species number has been formulated as “intermediate disturbance” hypothesis (Connell & Slatyer 1977; Connell 1978; Huston 1985). A similar connection is made by the principle of “variety in time and space” (van Leeuwen 1966; see in this context also Pickett & White 1985).

28 *Are degree of disturbance and body size linked to species diversity?*

An increase in the extensive disturbance (see hypothesis 26) favours smaller species and such with shorter life cycles. This also applies to anthropo-zoogenically extensively influenced sites. In stable habitats, on the other hand, long-lived (example: lichens) and big species (example: many tree species) prevail.

29 *Do life-form diversity and species diversity correlate?*

As shown in the chapter “Diversity forms”, an increasing species diversity must be accompanied by a greater variation of life-form types, since these are essentially different as to their diet and mobility. This hypothesis correlates with the hypotheses 19 and 20.

30 *Is there a correlation between plant species diversity and animal species diversity?*

As a rule there is a positive correlation between plant diversity and variety in animal species (Andon 1991; Gaston 1992). This relation is basically due to the close linkage of a number of phytophages to certain plant taxa and to predators and parasites, which occupy higher trophic levels. However, a plant stand poor in species (*e.g.* reeds with *Phragmites communis*) may cause a great animal species diversity. This can mainly be put down to the high structural diversity of the key species *Phragmites communis*, but also to environmental factors changing clinally and on a small scale (open/light and dense stands, young and old reeds, a changing reed structure [in dependence on the depth of the water, on abiotic factors, like wave action, and on biotic factors, like the influence of bird species, mammals etc.]). In beech forests, the great variety of animal species does not correlate with a high plant diversity, either.

Applied aspects of biodiversity

At present, about 1.5 million of the earth’s animal and plant species have been described (Wilson 1989; Heywood & Watson 1995). Their actual number maybe varies between 5 and 30 million (see in this context also May 1988). For the last quarter of this century, scientists have predicted the extinction of approximately 1 million species

(Myers 1985). Also here an exponential tendency can be ascertained: from 1600 to 1900, every four years a species was eradicated by man, after 1900 every year; currently more than one species disappear per day. Wilson (1989) has assumed that every hour one species is extinguished; today already up to three species. According to Lugo (1992), 20-50 % of all species will have disappeared by the end of this century.

Under natural conditions, the net growth rate of the species number is 0.37 % in 1 million years, that is to say 0.00000037 %; an extremely low value. The natural extinction rate has thus been increased by 10,000-fold by man; the decrease is at least 100 times higher than the loss of species in the past 65 million years (Wissenschaftlicher Beirat der Bundesregierung "Globale Umweltveränderungen" ¹ 1993; see in this context also Smith *et al.* 1993), and the rate of loss of genetic diversity on the level of populations yet extends this value by far.

The centres of especially high biodiversity lie in the tropics, mainly in the tropical mountainous areas. On few hectares of forest in south-eastern Asia or in the Amazon region, more tree species can be found than in the whole of Europe. In Venezuela's "evergreen rain forest" there are at least 90 tree species per hectare (Walter & Breckle 1984). In special regions, the loss of biodiversity is significant: world-wide, numerous ecosystem types are particularly endangered, among them the "tropical rain forests", certain marine ecosystems, islands in the sea, high mountain ranges, arctic and subarctic habitats, savannahs, steppes, and semideserts, large river systems, mangrove forests, and many lakes, but also the landscapes in the countries we live in.

A loss of biodiversity cannot be tolerated for ecological, ethical, religious, aesthetic, and cultural reasons, all the more as the destruction of biodiversity is irreversible (Arrow & Fisher 1974; Bishop 1978). To maintain biodiversity, to work out theoretical principles and translate them into practical measures is one of the major tasks of the next years. The maintenance of biodiversity is closely linked to the survival of man on earth, and has thus been incorporated into the concept of a "sustainable development".

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