I **General part**

**Part B - Ecological basis (synecology)**

1. Environment and competition
2. Pollination and fertilization (flowers, seeds and fruits)
3. Dispersal and distribution
4. Ecotypes and biotope change
5. Historical dimension
6. Coevolution and symbioses
7. Population ecology
8. Biodiversity
9. Zonal, azonal and extrazonal vegetation
10. Literature

[IMAGE]

Tundra with dwarf shrubs like Vaccinium myrtillus, V. vitis-idaea and Loiseleuria procumbens at snow-poor parts of the tundra (zonobiome IX) in northern Finland (Photo: Breckle)

**1 Environment and competition**

The climate of a site determines its vegetation. But the assumption often made that the distribution of plant species is directly caused by site conditions is almost never correct. These are only of indirect importance by altering the competitiveness of species. Only at the absolute limits of distribution in the arid and cold desert, at the edge of the salt desert, i.e. where the individual plants are isolated, are the site factors (usually a certain extreme factor) directly determining. If we disregard these exceptional cases, plant species can still grow far outside their range if they are protected from competition from other species. For example, the northeastern distribution boundary of beech runs through the Vistula region (river in Poland), but beech still grows in the botanical gardens of Kiev and Helsinki. The Mediterranean evergreen holm oak (Quercus ilex) reaches its range northern limit in the southern Rhône valley, cultivated trees still hold out in the botanical gardens of Bonn, Leipzig or Copenhagen.

The natural range limit of a species is reached where changing environmental conditions reduce its competitiveness or competitive strength to such an extent that it can be displaced by other species. It therefore depends above all on the presence of certain competitors (or a certain fauna). For beech, these are hornbeam on the eastern border, oak on the northern border and spruce in the mountains. European beech (*Fagus sylvatica*) is the dominant species of Central Europe’s natural forests. It spans a rather broad spectrum of thermal (6.6 – 13.5 °C mean annual temperature; 16.9 – 23.0 °C mean temperature of the warmest mont), hygric (470 – 2000 mm annual precipitation) and edaphic site conditions (pH, CEC etc.). Of all the beech species it is the one advanced furthest toward dry climates (Leuschner 2020).

If the northeastern border of beech shows a similar course as the January isotherm of -2°C, or the northern border of oak coincides with the temperature line of four months above +10°C, or the northern border of spruce coincides with the July isotherm of +10°C, there need be no direct causal connections. At the most, one could conclude that for beech the increasingly colder winter towards the east and for oak and spruce the shorter summer towards the north probably strongly reduces the competitiveness of these species. In future it might be increasingly threatened by climate change related heat waves and longer drought periods in parts of its distribution range.

If we designate as the ecological optimum the conditions under which a species occurs most frequently in nature and as the physiological optimum the conditions under which it thrives best in the laboratory (climate chamber) or in individual culture, these optima often do not correspond (◘ Fig. B-1).

From the distribution of a species, therefore, one cannot readily determine its physiological requirements. If, for example, pine is found in the temperate zone under natural conditions only on dry limestone slopes, but also on very dry, acidic sandy slopes or even on very wet acidic moorland soils (◘ Fig. B-2), this is because it is displaced from the sites more favourable to it by stronger competitors. On the other hand, knowledge of the physiological requirements and adaptations of a species determined in climatic chambers does not yet give us the possibility of predicting or explaining in detail its distribution in nature. Whether the species occupies the site that can be colonized according to its physiological requirements, or only partially, is decided not only by the historical factor, but also by its competitors. In the ecogram, it can be shown for certain ecological factor combinations which species occur dominantly and where their respective ecological optima lie. This is shown for Central European tree species in ► Fig. B-2.

Competition is not a direct dependency relationship between species. It can be recognized by the fact that isolated plants develop more luxuriantly than those in a plant community. Inhibition in competition is mostly due to deprivation of light by above-ground organs or of water or nutrients in root competition. Whether certain inhibitors secreted by the plants also play an important role in the competition (allelopathy) is difficult to prove under natural conditions. Only in some cases this seems to be the case. In other cases, there is probably also mutual promotion, in particular through substance exchange via the fungal hyphae network in the soil, which can connect the mycorrhiza of different trees and supply additional nutrients to young seedlings (nursing system). In ecosystems, however, the processes of competition outweigh those of such cooperation.

◘ Fig. B-2 Ecogram of the most important forest tree species of Central Europe of the submontane stage in a temperate-suboceanic climate. The font size expresses approximately the proportion of the tree layer that would be expected as a result of natural competition (modified after Ellenberg 1996).

In competition, a distinction is made between intraspecific, which takes place among individuals of the same species, and interspecific between different species. The first promotes the survival of the most vigorous individuals and serves to preserve the species. In interspecific competition, one species may gain dominance and displace the other, or an equilibrium may develop in mixed stands, depending on the competitive strength of each partner. In the mountains of Central Europe, for example, it can be observed on the beech-spruce border that beech predominates on southern slopes, spruce on northern slopes, while on eastern and western slopes both more or less balance each other out and form mixed stands. These will also form if the seedlings of one species develop better under alien species than under individuals of the same species, which seems to be true in the tropical virgin forest, perhaps because herbivore and parasite pressure or other inhibiting factors are graded accordingly.

The competitive vigor of a species is a very complicated and difficult phenomenon to measure, especially considering that it can vary greatly with the stage of development. It is weakest in seedlings and young plants and increases with age, especially in trees. It always applies only to very specific environmental conditions. The totality of all morphological and physiological characteristics of a species is important. Biennial species are more competitive than annuals because they begin growth in the second year with greater reserves accumulated during the first year. For the same reason, from the third year onwards, perennial herbs are superior to biennials. Woody species are victorious over perennial herbs if they are not suppressed in the first years of life, i.e. if they succeed in forming woody axillary organs that rise above the herb layer.

As a result of competition, similar combinations of plant species occur again and again at similar sites in a limited area, which are referred to as plant communities (phytozonoses). In Central Europe, for example: Beech forests on calcareous soils with their herbaceous flora or alluvial forests, certain types of bogs or reed beds, etc.

In a stable plant community, the species are in a certain ecological balance with each other and with their environment. Together with the animal organisms they form a biocoenosis. The following are decisive for this balance (if one disregards the herbivoral influence of the animals):

1. Interspecific competition
2. The dependence of each species on the presence of others (for example, shade species)
3. The occurrence of complementary species that complement each other spatially or temporally so that almost each ecological niche is filled.

The natural community is thus to a certain extent "saturated" and foreign, introduced species can hardly invade, whereas they have much more of a chance to do so if the equilibrium is disturbed. For this reason, the long-distance transport of seeds plays a significant role in the spread of plants only in the case of areas that have not yet been colonized, for example in the case of young volcanic islands.

The balance of a plant community is not a static but a dynamic phenomenon. Individuals die, others germinate and grow. In the process, there is usually a constant change of place between the individual species. Especially in uninfluenced stands, in moors, and even more so in primeval forests, a constantly changing mosaic of different developmental phases occurs side by side. In primeval forests these processes are obviously very long-term; they lead to the fact that on larger areas all phases are represented. The phases that can be distinguished in this process are interdependent and can merge in different ways with specific cycles (◘ Fig. B-3).

In terms of quantity, the species composition shows certain or even considerable fluctuations. The species composition does not remain the same either, especially when the external conditions change from year to year, e.g. rainy years are followed by dry periods, etc. As a result, some species are favoured in the competition, then the others are favoured. If the site conditions change permanently in a certain direction, for example if the groundwater level rises slowly over many years, the species combination will also change: Certain species will disappear, others will invade from outside, until finally a new plant community emerges.

Fig. B-3 Scheme of the different phases and their transitions in primeval forests, derived from surveys in the Roth forest near Lunz am See (Lower Austria, modified after Zukrigl et al. 1963). Accordingly, the phases and mosaic stands observed in Bialowiecz (primeval forests in eastern Poland and Bielorussia) can also be classified in such a cyclic scheme.

If human interventions are carried out in the same way over a long period of time, an anthropogenically induced equilibrium develops and plant communities emerge which are referred to as cultural formations in the case of intensive use or as semi-cultural formations in the case of more extensive use. They make up the vegetation of areas densely populated by humans. The essential cultural formations are maintained by certain measures, and the succession sequence is always restarted when there is a change of use (◘ Fig. B-4).

The sequence of succession is mostly random, depending on which seeds (diaspores) arrive first or in larger quantities on the surface and on the germination conditions of the seeds and the establishment possibilities of the seedlings and their competitive success.

2 **Pollination and fertilization (flowers, seeds, fruits)**

Since the establishment and maintenance of species depends on their reproduction and this on the pollination and fertilization processes, as well as on the dispersal possibilities of seeds and fruits, it is necessary to briefly discuss their biological basis. However, this does not yet explain the respective distribution of a species, i.e. its current geographical area, because this is the result of a long historical process.

Flowering plants are characterized by zoogamous or anemogamous flowers. The mostly coloured flowers of zoogamous species serve to attract insects (entomogamous species), sometimes these are mainly beetles (coleopterogamy) or butterflies (lepidopterogamy), species flowering in the evening especially attract hawkmoths (sphingophilous species), but hymenopterans (bees, bumblebees, wasps) are particularly important as pollinators, also for important crops. In tropical regions, there are some species adapted to bat pollination (chiropterogamous species), whose flowers are usually drooping, pale yellow, and open at night, as well as species with often bright red flowers pollinated by birds (ornithogamous), e.g., by hummingbirds in the New World and nectar birds in the Old World (◘ Fig. B-5). In the subtropical thorny savannah spots in SE Afghanistan, such species just reach the border of Afghanistan from the Indian subcontinent.

Pollination is the transfer of pollen from one flower to the stigma of another flower. This transfer can take place by wind (anemogamous species): Their flowers are very rich in pollen but inconspicuous and small (grasses) . The zoogamous species, as mentioned above, are much more conspicuous. They are sometimes extremely adapted to pollinators as part of coevolution. In the case of orchids, only individual pollinia are formed, which are specifically transferred by certain bees or wasps ("registered mail"), conversely, the number of seeds is huge, the dusty seeds are transported by the wind in an untargeted manner ("mail shot").

Pollination is a prerequisite for fertilization. It occurs when the pollen tube on the stigma grows out to the ovules in the ovary of the pollinated flower. There, nuclear fusion takes place and a diploid zygote is formed, which divides and then continues to grow, ultimately forming an embryo, which is surrounded by more or less nutritive tissue in the seed and protected by the seed coat. From the ovary the fruit grows. But just like the huge number of different structures in the flowers, the range of variation in fruits and the seeds they contain, is immense.

3 **Dispersal and distribution**

The mature seeds must be shipped into the environment to maintain the species. This can be done by releasing the seeds from the fruit or by using the fruit itself as a dispersal unit.

Dispersal can take place by wind (anemochorous species), for which the seeds are either fine as dust or they or the fruits develop flight organs (wings, umbrellas). The dispersal can also be done by animals (zoochorous species). In these cases, there are also different ways of attracting animals. Fruits can be eaten, but many seeds are indigestible and after intestinal passage (in birds or also mammals) are even better germinable (endozoochorous species). Other species have adhesive appendages on the fruits, which then remain attached to the fur and are thus spread further (exozoochorous species).

The success of propagation depends on several factors. The number of seeds formed by the plants each year plays a major role. Many seeds that are shipped far compensate for a high loss rate. Few seeds that are targeted to good locations are also a successful strategy; for example, some nuts are purposefully collected and stashed by rodents, where some are then allowed to germinate. However, the rate of loss is generally huge. In old beech forests (Fagus sylvatica) in Central Europe, up to or more than 100 million beechnuts fall on 1 ha in mast years in autumn. Depending on winter and herbivore pressure, 10-20% of these germinate. This results in a dense carpet of seedlings. At the end of the first vegetation period only 1-10% are left. In the second and third year more than half of them die due to lack of water, feeding and shading. This still leaves about 5-10 young trees per m2, which can form a dense stand of shrubby young beeches as soon as they receive a little more light. In the coming years, however, the strong competition will lead to a situation where only a few young trees will be able to grow up to the approximately 300-700 old trees on one hectare (there is no room for more with their broad crowns). These are then every few years a few dozen young trees, this is quite sufficient to maintain the stock.

Fig. B-5 Hummingbird pollination of the flower of a Stachytarpheta plant (Verbenaceae) (a, photo: H. Breckle) in the New World and of a *Strelitzia* by a nectar bird in the Old World (b, photo: Rafiqpoor, S-Africa). The red colour of the flower is an adaptation to the pollination of this plant by animals.

The distribution of a species is the geographical area that the species colonizes. The distribution is very similar for some species, which are then referred to as geo-element to which these species belong (e.g. Mediterranean species, Central Asian species). The range size can be very different. At one extreme are cosmopolitan species; they occur worldwide on all continents. At the other extreme are narrowly restricted occurrences, e.g. only in one valley or only in one mountainous region; these are called **endemics**. However, one must always precisely identify the geographical region one is referring to. One often speaks of country endemics, although of course country borders are usually political and do not represent natural borders. Thus, one speaks of endemics of Afghanistan. Of the approximately 5000 species of higher plants in Afghanistan, about 25% are endemics (Breckle et al. 2013). However, directly neighbouring regions (with the same climate, etc., Chitral, Kurram Valley) should be included here (subendemic species).

Most species in Afghanistan have an Irano-Turanian distribution. But also species with an Eastern range (Himalayan, Sino-Japanese) occur in Eastern Afghanistan. In the high mountains, species of the boreal and even arctic region of Euro-Siberia reach into Afghanistan. In the basin of Jalalabad or near Khost even some Saharo-Sindian and Sudanese distributed (subtropical-tropical) species occur, as well as in Southern Afghanistan some Saharo-Sindian desert species.

4 **Ecotypes and biotope change**

Many plant species or phytocenoses (plant communities) have a very wide distribution and, if you look at their areas (residential districts) on a map, apparently grow under quite different climatic conditions. This fact may be due to two reasons.

1. The species as a taxonomic unit is often strongly differentiated eco-physiologically, for example with regard to its resistance to cold or drought or its climatic rhythm. Thus, the pine, Pinus sylvestris, occurs from Lapland to Spain and eastward to Mongolia, with at most its growth habit showing taxonomically insignificant differences. But the Spanish pine cannot grow in Lapland because it is too sensitive to cold, and the Lapland pine cannot grow in Spain because it needs a long winter dormancy. Therefore, the forester must always pay very close attention to the provenance (origin) of the seed. Most taxonomically uniform species consist of many such ecotypes (races, varieties).
2. The second possibility of a wide distribution is based on a biotope change of the species or phytocenosis, when its range extends into a climatically different area. If, for example, the climate at the northern edge of the range becomes colder, the species is no longer found on the plain, but on the microclimatically warmer southern slopes, i.e. a biotope change occurs which compensates for the climate change, so that the site or environmental conditions for the plants hardly change, i.e. remain relatively constant. This regularity (law of relative site constancy) can be observed everywhere: In the southern part of the range, plants move more and more to the northern slopes, into deep moist canyons, or up into the mountains. If the climate becomes wetter, the plants seek out dry limestone or sandy soils. In the dry climate, on the other hand, they are found accordingly on heavy, wet soils or on those with a high groundwater level.

Of course, one must take into account that in the southern hemisphere the northern slopes are warm, and on the equator - the east and west. Similarly, in arid regions, the sandy soils have the most favorable water supply for plants.

This applies not only to water conditions in arid regions, but more generally to all factors that are influenced by climate.

The law of biotope change must also be taken into account in the mountains when determining the elevational levels: Already the differences in elevational limits at different exposures indicate this law. Much more extreme are special niches with intensive irradiation and cold runoff, which allow small stands of trees to grow above the timberline already within the alpine belt. Individual trees were found in the West Pamir in blown-through gorges without cold air dams even at 4000 m NN, and shrubs in the wild terrain even at 5000 m NN; in the Hindu Kush we found such at 5100 m in very sheltered niches on southern flanks. On the other hand, in cold-air dolines of the Eastern Alps, forest vegetation is already absent at 1270 m NN, the lowest temperature in Western Europe being measured at -51°C near Lunz (Lower Austria).

Soil factors also play a role. Fragments of alpine vegetation in the Eastern Alps can be found in the middle of the beech belt on dolomite, rocks that are difficult to weather. Special niches are also the avalanche ranges, where the competition of tree species is eliminated, so that the krummholz species of the subalpine level are able to assert themselves at low altitudes of the forest level. On such special biotopes one often finds relicts of species that formerly had a wider range under different climatic conditions. However, historical evidence for the relict nature of an occurrence should be provided if possible.

5 **The historical dimension**

Today's geo-biosphere is closely linked to the history of the Earth. It is the result of a long development of the plant and animal kingdom on the one hand, and of a long geotectonic history of the earth's solid surface on the other. Therefore, in ecology one must always take into account the historical development. The continents did not exist in today's form in former times, also they took a different position to the poles and the equator. This theory of Wegener's continental drift has been further developed today as the theory of plate tectonics. The movements of the land masses are explained by large-scale plate tectonics and convection currents in the Earth's mantle. The movement of the plates of a few centimeters per year leads to very slow changes of the plates in relation to each other. The present position of the plates is shown in ◘ Fig. B-6. Due to the magmatic upwelling areas (for example, opening, extension of the Atlantic Ocean), "submergence" of plate material must occur elsewhere; this occurs in the area of the subduction zones. In their vicinity are usually particularly active volcanic areas, which are important for the evolutionary processes of flora and fauna.

Compared to the shifting continental plates, the atmospheric wind system with the climate zones appears to be relatively a very stable system, which in this form, at least in a comparable form, probably goes back far into the Mesozoic. The climate system as such appears as the more stable, the continents as lithosphere swim under it and are the more variable part in the very long-term overall system of the biosphere (Krutzsch 1992).

Life began in the water. The first land plants are known as fossils since the turn of the Silurian/Devonian. From the fact that NaCl, the main component of sea salt, is not needed by cormophytes and is toxic to all plants except halophytes, one must probably conclude that the ancestors of land plants were freshwater algae, perhaps living in coastal lagoons under humid tropical climates. The halophytes among the angiosperms are young secondary adaptations to saline soils in coastal areas or salt deserts.

The conquest of the land was made possible by large cell vacuoles, which in their entirety, the vacuome, form an inner aqueous medium for the cytoplasm. Around the plasma, the cell wall forms a water-saturated, spongy outer medium that envelops the cell. Toward the outside world, land plants have protected themselves from desiccation by forming a cuticle. The invention of stomata allows controlled CO2 uptakefor photosynthesis, and the root and conduit system provides compensation for transpiration losses (Walter 1967), while also serving as a transport system for mineral nutrients.

Due to the greater isolation of the continents after the formation of the angiosperms in the late Mesozoic, their development took different paths, which led to the formation of six floral kingdoms (◘ Fig. B-7), which essentially also more or less correspond to the faunal kingdoms.

In the phylogenetically relatively old group of conifers it is evident that the Podocarpaceae and especially the *Araucaria* are found only in the Southern hemisphere, while the large family of Pinaceae and almost all Taxodiaceae have a Northern hemispheric distribution, while the Cupressaceae are found scattered over all continents.

A much stronger differentiation shows the distribution of the flowering plants (angiosperms), the youngest branch of the plant kingdom. Original forms, partly relicts, are still found mainly in Southeast Asia (e.g. New Caledonia). The oldest families of this group of plants are only known from the early Cretaceous, but the flowering plants experienced their main development in the Tertiary, when the Gondwana land mass had already split into the individual continents. In the northern hemisphere this was only the case to a lesser extent; only in the Pleistocene did a final separation between N America with Greenland and Eurasia occur. Therefore, the floristic differences in this area are small, so that these continents are combined into one floral kingdom, the Holarctic. The tropical floras of the so-called New and Old World differ much more. Therefore, they belong to two different floral kingdoms, the Neotropics on the one hand and the Palaeotropics on the other hand. Even less in common are the floras of the southernmost parts of S America and Africa, and of Australia and New Zealand, which lie very isolated. The differentiation led to the formation of three floral kingdoms: Antarctica, which includes the southern tip of South America and the subantarctic islands, Australis, which is spatially identical with the continent of Australia, and Capensis, the smallest but particularly species-rich floral kingdom at the extreme southwestern corner of Africa (► Fig. B-7).

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| **Box B-1** Plate tectonics |
| Plate tectonics: From a geotectonic point of view, the current position of the plates is only a specific snapshot. For the understanding of today's distribution of organisms, the former position of the plates to each other and the course of evolution is an important basis |

Fig. B-6 Overview of the main tectonic plates of the Earth's crust. The direction of movement of the plates (arrows) and the mid-ocean ridges along which material is transported from the Earth's mantle to the surface are also indicated.

◘ Fig. B-7 The floral kingdoms of the Earth. On New Zealand and Tasmania, Antarctic as well as Palaeotropical and Australian floral elements occur, respectively.

These six floral kingdoms are not sharply demarcated. Individual floral elements from one floral kingdom can radiate far into the neighbouring one. On New Zealand, one finds both Palaeotropical-Melanesian elements and Antarctic elements, which often interpenetrate like a mosaic. Therefore, the attribution of these islands to one of the two floral kingdoms is a matter of judgement.

The animal regions of the zoologists agree to a large extent with the floral kingdoms, only the Capensis is not distinguished by a special fauna.

The floras provide the building blocks, i.e. the plant species determine the structure of the plant communities that make up the vegetation of the individual areas. If these building blocks are different, similar life forms can nevertheless arise under certain extreme external conditions; this is known as **convergence**. However, these are more the exceptions. As a well-known example, we cite the stem succulents, which in the arid, i.e. dry regions of America belong predominantly to the family Cactaceae, but in Africa mainly to the genus Euphorbia (spurge) (◘ Fig. B-8). In Australia, on the other hand, there are no succulents at all in climatically similar arid regions, although Australia is otherwise particularly rich in other convergences not known from the other continents. New Zealand's temperate climate lacks deciduous forests, which are widespread in the Holarctic. The total genetic stock of each flora, determined by historical evolution, is limited, so that the same life forms did not form everywhere. This is particularly true of the Australian floral kingdom, whose vegetation is physiognomically very different from that of other continents; the original mammalian fauna there is also very peculiar.

**◘ Fig. B-8** Convergent life forms from the Old World a: Euphorbia resinifera, from Morocco (photo: Rafiqpoor); b: Trichocaulon pedicellatum (Asclepiadaceae) from SW Africa, (photo: Breckle); c: Didierea madagascariensis from Madagascar (photo: E. Fischer) and from the New World: d: Cacti (Cereus macrostibas) from the Atacama Desert S-Peru (photo: Rafiqpoor).

Tab. B-1 Endemism on islands (percentage of endemic species of the native flora)

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| Islands | Degree of endemism (%) |
| Hawaii | 97.5 |
| New Zealand | 72 |
| Fiji Islands | 70 |
| Juan Fernandez | 68 |
| Madagascar | 66 |
| Galapagos Islands: in the dry areas | 64 |
| Galapagos Islands: in the humid mountain zone only | Only 8-27 |
| Galapagos Islands: in coastal areas | 12 |
| New Caledonia | 76 |
| Canary Islands | 50-55 |
| Offshore islands | 0-12 |

The Pleistocene left strong traces due to the multiple ice ages, especially in the Northern hemisphere. The flora in Europe became impoverished. Many genera died out, while they are still found in North America and East Asia. There, N-S escape was easier. In Europe, on the other hand, the W-E course of the Alps blocked escape and return.

In parts of the Sahara, the ice ages were temporarily noticeable as rainy, i.e. as pluvial periods, whereas in the tropics they were more noticeable as dry periods.

For this reason, it is essential to consider the historical factor when dealing with the vegetation of zonobiomes that span several floral kingdoms. This is particularly true for zonobiome IV with winter rainfall, which consists of sub-areas in Holarctic, Neotropical, Australis and Capensis. It is convenient to divide this into five vegetation-historical biome groups (Mediterranean, Californian, Middle Chilean, Australis, and Capensis, which differ greatly by floral stock despite similar life forms).

Due to their isolation, islands are also often characterized by strong endemism, i.e. by many species that occur only on them and nowhere else. In percentages of the total flora, the figures given in ◘ Table B-1 are given for the individual islands or island groups.

Endemism is more pronounced the further the islands are from the mainland and the longer they have been isolated, but ocean currents also play a role. Recently many species had been introduced to most of the islands, thus a mixed vegetation is now present.

6 **Coevolution and symbioses**

Biological systems interact with each other with the result of the evolution of the organisms involved in them (coevolution). The expression of the various ecosystems is not understandable without the processes of coevolution in the course of historical development. In many ecosystems the interlocking, i.e. the mutual dependence between certain plants and animals is so close that one must speak of an obligate relationship. It is now certain that in the long evolution of living things, interaction with other organisms has been much more important than with the inanimate world for many radiative events. In ◘ Fig. B-9, the evolution of flowering plants and pollinators is demonstrated.

The radiation of Diptera and Hymenoptera took place simultaneously with the radiation of angiosperms. A.O. Wallace already suspected from the observations of long spurs of tropical orchids (e.g. Angraecum sesquipedale) on Madagascar (◘ Fig. B-10) that butterflies with similarly long proboscises must exist for their pollination. In 1987, the appropriate species (Xanthopan morgani-praedicta) was finally found and described for the Malagasy Angraecum (Nilsson et al. 1987). This is a result of coevolution, with the long spur evolving through the interaction of nectar predators and pollinators. Thus, coevolution is one of the keys to the origin of new species. Coevolution not infrequently involves linkages between pollinators, herbivores, and certain plant species that change over the course of the year, but this can only be maintained in a large-scale population. In the course of evolution, such close interdependencies have come about through the reinforcement of mutual mechanisms of action. This applies in the same way to numerous relationships between the most diverse organisms. Such a close network of relationships is particularly diverse in those ecosystems that have undergone a particularly long period of evolution (in and since the Tertiary), such as the tropical rainforest. Close functional links between organisms make it more difficult to clearly distinguish the functional compartments in an ecosystem analysis.

◘ Fig. B-9 Evolution of flowering plants and their pollinators. Diversity of fossilized insect orders across geologic epochs. A small fraction of fossil insects is documented in Paleozoic deposits. However, the majority evolved with the advent of flowering plants, two-thirds of the fossils of which are documented in deposits from the Mesozoic onwards (below) (modified after Labandeira et al. 1993 and Niklas et al. 1983).

◘ Fig. B-10 Angraecum sesquipedale (right) with the long spur. On the left Xanthopan morgani-praedicta with the long proboscis (photo: Barthlott).

The various symbioses (a close coexistence in which two partners "parasitize" each other, so to speak: In equilibrium, each provides the other with something vital) are to be emphasized above all. Symbioses that occur ubiquitously are, for example, the various forms of mycorrhiza, to which we will refer in more detail. But also the nitrogen-fixing symbionts, which occur not only on legumes in the form of nodules with Rhizobium, but also on a number of other species (for example, Frankia on alder roots), improve the competitiveness of the species, or the symbioses even make possible the conquest of certain spaces that are actually hostile to life, as in the case of lichens, which are thus the dominant primary-producing organisms in Antarctica (◘ Fig. B-11) or in the nival altitudinal zone of the mountains.

The particularly close interlocking of an extraordinarily large number of different organisms with each other led, in the course of long evolutionary times, to an incredibly diverse network of relationships and to a functional structure in the case of the tropical rainforest, which is in itself very stable under the uniform climatic conditions at the equator. After destruction, however, this feedback network cannot be regenerated within a foreseeable period of time. The secondary forest, which usually has fewer species, therefore has a much wider, looser functional network.

◘ Fig. B-11 In Antarctica, lichens grow on rocks and open ground that protrude from the snow cover in summer (photo: http://is.gd/Oe5qIj).

7 **Population ecology**

A population is a group of individuals of a species that occur simultaneously in the same space and are capable of interbreeding. Population ecology is concerned with the study of the size (and distribution) of populations and the processes (primarily biological) that determine these parameters (Begon et al. 1996). In particular, the dynamics of populations - i.e. the changes over time in the absolute numbers of individuals and relative proportions of different age or developmental stages in the population - are of great interest, as an understanding of population dynamics facilitates predictions of future population trends.

In highly diverse systems, the question of regeneration of the numerous species is usually difficult or impossible to answer. The fluctuations in the population sizes of the many species involved (seed bank→germinating seed→seedling→sapling→young growth→adult plant; or egg→ larva→pupa→imago→etc.) are often not detectable, birth and death rates are only known for a few organisms in their temporal sequence, and even less so are the influencing variables that control population sizes. This is also due to the fact that the input and output of seeds (or diaspores) can be highly variable spatially and temporally, and that, moreover, in some ecosystems some species have a very large seed bank that can be rapidly reactivated years later under changing conditions (for example, meadow becomes fallow land that has been plowed). This is reflected in the general scheme in ◘ Fig. B-12 for reproduction in plants. Not infrequently, certain drastic events lead to new developmental impulses of species. The steady development of populations is thus repeatedly interrupted and stimulated anew not so much by periodic as by episodic damaging events (fire, storm, flood).

◘ Fig. B-12 Individual components for the regeneration of a plant species or the maintenance of its population at a given site (modified after Burrows 1990).

Periodic events are predictable, occurring regularly (→ winter in ZB VII; the tides on the coast, etc.). Episodic events are not predictable, they occur at irregular, usually longer intervals (→ thunderstorms in ZB III, El Niño, tsunamis, frosts in Brazil's coffee cultivation, etc.).

This is particularly striking in tropical evergreen rainforests, where the stand structure is very heterogeneous, and where gaps of different sizes ("gaps"; ► Fig. D-16) are repeatedly torn by branch or tree fall, which are quickly filled by fast-growing species, but where the stand species also rejuvenate. Probably in many more ecosystems than we have thought so far, such episodic events are prerequisites for their long-term maintenance through successive renewal of their structures. However, this then also leads to cyclic renewal of different lengths, which is predominantly stochastic (random) rather than deterministic; individual parts of a biome are younger, others older; the mosaic character and temporal dynamics of natural ecosystems was already characterized decades ago by Aubreville (1938). It is an important principle of maintaining high numbers of species in a dynamic side by side and coexistence.

8 **Biodiversity**

Biodiversity encompasses the different forms of life (plant and animal species, fungi, bacteria), the different habitats in which these species live (e.g. ecosystems such as forests or standing and flowing waters, etc.) and the genetic diversity within the species (e.g. subspecies, varieties, and breeds) (http://is.gd/iirae3). In this way, biodiversity encompasses life existing on earth in all its diversity and is thus also the basis and potential of all life processes and ecosystem services on our planet (Lozan et al. 2016). Biodiversity is the result of "trial and error" in millions of years of evolution, recently additionally shaped by the influence of centuries to millennia of human use (hunting, gathering, clearing, agriculture, settlement, etc.). Biodiversity can be a measure of the originality and naturalness of ecosystems. Under extreme ecological conditions, however, a completely intact and pristine ecosystem can be species-poor, mainly if only specially adapted specialists can survive (Breckle 2000, 2006). In the case of very high diversity, the question of the regeneration of numerous species can usually not be answered.

Life with its immense biodiversity is the only specific quality of our planet. All the more surprising is the fact that our knowledge of this biodiversity is shockingly low (Barthlott & Rafiqpoor 2016). About 1.8 million different living organisms have been scientifically recorded - but all projections show that at least 8 million, but probably far more than 10 million different species exist on Earth (Mora et al. 2011).

Based on a rather conservative estimate of 10 million species, ◘ Fig. B-13 shows that the various large groups of organisms account for highly unequal shares of global biodiversity. The arthropods, shown in red, account for the largest proportion, with an estimated five million species. In addition to the approximately 1.8 million species, about 90% of all species are unknown. The most species-rich group within the arthropods are the insects (e.g. beetles, hymenopteres, butterflies). Scientifically described ones alone are about 350,000 beetle species from 179 families: What a contrast to the conspicuous vertebrates (e.g. mammals, birds, reptiles), which comprise only about 62,000 species, but are quite well known already because of their body size (knowledge level over 83%) (Barthlott et al. 2014).

Terrestrial plants (higher plants or vascular plants, i.e. flowering plants, gymnosperms and ferns) are a relatively species-poor group, with an estimated 370,000 (Pim et al. 2014) species. But compared to insects, they are also large and conspicuous creatures that are also "sessile", i.e. do not run away: the trivial reason why the level of knowledge is very high at around 90% (► Fig. B-13).

But anyone concerned with global biodiversity in a constantly changing environment should be largely concerned with arthropods, which after all account for more than half of global biodiversity? Ecosystem-wise, this would be a fatal flaw. Arthropods and the other animals are the consumers within the system. They are all based on the producers, the massive global powerhouse that covers the planet as a worldwide green solar collector: the higher plants.

◘ Fig. B-14 illustrates the ratios in the representation as pyramids, based on the number of species (left, assumption 10 million) and estimated mass (right). Consumers, with their high diversity, comprise about 69% of the species, whereas plants comprise only about 5%. However, the latter are the most important structural elements in all terrestrial communities. Our own food, clothing and medical care also rely to a considerable extent on plants (Barthlott et al. 2014).

The most important normative instrument in the field of biodiversity is the Convention on Biological Diversity (CBD), which was adopted at the UN Conference on Environment and Development in Rio de Janeiro in 1992. Currently, 192 countries (including Afghanistan and the European Union) are members of this convention. All UN member states, with the exception of the USA, Somalia and North Korea, have ratified the Convention in an internationally binding manner. The Convention contains three main objectives: a) protection of biodiversity, b) sustainable use of its components, c) equitable sharing of benefits arising from access to genetic resources: The so-called "Access and Benefit-Sharing (ABS)". Biodiversity faces a constant threat despite global efforts, such as the 2002 global treaty to reduce biodiversity loss by 2010 (the so-called '2010 Target'), which was not achieved; or the Nagoya Summit of the CBD Convention in 2010, which also included a strategic plan, and the so-called '20 Aichi Target' (for more details see Erdelen 2014). Great hopes are currently linked to the establishment of the IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) in 2012, which, like the IPCC (Intergovernmental Panel on Climate Change), coordinates global activities in the field of biodiversity. In addition, a paradigm shift in the Green Global Agenda could accelerate our efforts to reduce biodiversity loss (Barthlott & Rafiqpoor 2016).

As regards the protection of biodiversity, the EESC (European Economic and Social Committee) recently stressed that there is no shortage of laws, regulations, political declarations and recommendations in the EU. The problem is the lack of implementation. This whole judicial framework is not worth the paper on which it is written as long as it is not transformed into real action, it was concluded. The Commission has the tools and means, to encourage the Member States to stick to their obligations. This failure is a sign of the Commission's and Member States' lack of political willingness and cooperation (www.eesc.europa.eu). But this can be observed worldwide.

◘ Fig. B-13 Estimated species numbers. 10 million different species are estimated to exist on Earth, but only 1.8 million of these have been scientifically recorded and described: (80% of the species on our planet are unknown (from Barthlott & Rafiqpoor 2016).

◘ Fig. B-14 Percentages of producers, consumers and decomposers in terms of their biomass and biodiversity (from Barthlott & Rafiqpoor 2016).

**8.1 The uneven global distribution of biodiversity**

The extraordinary differences in the number of species per unit area in the different geographical regions of the earth are astonishing. On one hectare of a Siberian taiga, the forest may be formed by only one tree species. On the same area of a rainforest in Amazonian Ecuador, up to more than 300 tree species with BHD >10 cm may grow (Valencia & Balslev 1994) (► Fig. B-36). For comparison, it should be noted that only 40 tree species are native to the entire Federal Republic of Germany (area 375,121 km2).

In our considerations, we always refer to the relatively well known land plants. But we would find similar relationships in animals and in marine ecosystems: Comparing a North Atlantic rocky reef with a tropical coral reef leads to similar results (Barthlott et al. 2014). Maps of global terrestrial diversity are best constructed based on plants only. For animals, the state of knowledge is too low (e.g. arthropods), and only a few non-representative groups (e.g. birds or butterflies) have been sufficiently studied; i.e. in general, the determination of biodiversity often encounters great difficulties. It can only be stated for specific groups of organisms, and there are also many different methods and indices etc. (Humphries et al. 1995, Barthlott et al. 2005). The large-scale biodiversity of each region of the world was first compiled in a world map with diversity levels by Barthlott et al. (1996). This map has been continuously refined and updated by increasing the size of the data base and improving analytical methods (Barthlott et al. 2005, 2007, 2014).

The world map of global biodiversity used here by Barthlott et al. (2014) (◘ Fig. B-15) is based on analysis of several thousand floras, checklists, and databases (for the method of generating the map, see Barthlott et al. 1996, 1999, 2005, 2007, 2014).

◘ Fig. B-15 The uneven distribution of global biodiversity: Species numbers of plants per 10,000 km2 (from Barthlott et al. 2014).

The map shows the spatial global distribution of biodiversity with the best currently achievable high resolution. On this map, areas of high biodiversity are shown in red and those with low biodiversity in light colours (blue→green→ yellow). Areas of high biodiversity with more than 3,000 species per 10,000 km2 are concentrated in the tropics and subtropics, especially in mountainous regions. Regions of low diversity are the warm (Sahara, Arabian desert, Atacama desert, etc.) and cold (polar regions, Tibetan plateau, etc.) deserts of the Earth with <100 species per 10,000 km2. This latitudinal gradient has been known for a long time. The reason is the increasing favourability of hygrothermal parameters towards the equator. A water temperature of more than 26°C of the sea surface shows a surprisingly good correlation with the highly diverse tropical areas. Where there is too little water (e.g. Sahara) or where edaphic conditions are unfavourable (e.g. nutrient-poor Gran Sabana in Venezuela), species-poor systems can also exist in tropical and subtropical areas. Obviously, however, soil nutrients are not responsible for the development of high biodiversity.On the contrary, ancient, very nutrient-poor areas in Southwest Australia or in the Cape region with extremely poor quartz sands often have an incredible biodiversity.

In the search for causal dependencies for the diversity patterns, a number of principal relationships can be identified. It becomes clear that high biodiversity is by no means linked only to tropical regions: The Caucasus is comparatively richer in species than parts of the Congo lowland rainforest. Here, a second fundamental factor plays the decisive role: The biodiversity of a given space is strongly dependent on habitat heterogeneity (Kreft & Jetz 2007, Kreft et al. 2008), i.e. the diversity of abiotic factors (climate, geology, geomorphology, soils, water availability) within this space, which we subsume under the term 'geodiversity' (Mutke & Barthlott 2005) in contrast to Gray (2004), who subsumes only geological-geomorphological structures and processes under geodiversity. Highest diversities are almost always found in mountainous areas (Agakhanjanz & Breckle 2002). This suggests that higher attention should be paid to the mountainous regions of the world when considering conservation measures on a global scale. They may represent refuges and gene pools for species, especially in the course of global climate change.

If we now combine areas with more than 3,000 species per 10,000 km2 on a map, we obtain a total of 20 centres of biodiversity on Earth (◘ Fig. B-16). These centres clearly coincide with the mountainous areas of the tropics and subtropics in the Earth's so-called megadiversity countries, which are primarily developing and newly industrializing countries. Afghanistan, with its location in the "Caucasian-SW-Asian" centre of diversity, is one of these megadiversity countries (Barthlott et al. 2014).

◘ Fig. B-16 Global centres of biodiversity, each hosting over 3000 species per 10,000 km2, largely coincide with mountainous areas of the tropics and subtropics (from Barthlott et al. 2014).

Another dimension of biodiversity is the degree of endemism that must be considered for a country or a specific area. Kier et al. (2009) were able to show that, in addition to quantitative aspects, qualitative aspects of biodiversity such as the degree of endemism, i.e. the "specific quality" of an area, play a significant role. A comparison between Hawaii and the federal state of Thuringia in the east of the Federal Republic of Germany would make this clear: The federal state of Thuringia harbors a total of 1,570 plant species on an area of 16,200 km2, not a single one of which is endemic to this federal state. Hawaii, on the other hand, with the same area as Thuringia (16,600 km2), is home to 1,140 native species, 977 of which are endemic to this island. If, in the event of a catastrophe, the entire flora of Thuringia were to be destroyed, there would be no disadvantage for global genetic resources. Such a disaster in Hawaii, on the other hand, would irretrievably destroy a significant part of the genetic resources for mankind. At the same time, this reflects the special role of island systems, but they are not shown on the biodiversity map. Kier et al. (2009) and Weigelt et al. (2013) have shown elsewhere that oceanic islands comprise only 3% of the land surface but harbor 25% of the known plant species. Among the 10 most endemic areas on Earth, six are islands: New Caledonia, Polynesia-Micronesia, Atlantic Islands, Caribbean Islands, East Melanesian Islands, Madagascar, and Taiwan (Barthlott et al. 2005, 2014).

An interesting but by no means surprising aspect is the contrast between the mega-diversity centres of the tropics and subtropics and the "mega-research centres" of the industrialised nations in predominantly temperate regions. In ◘ Fig. B-17, without claiming to be exhaustive, large research institutions dealing with biodiversity are projected onto the biodiversity map (Barthlott et al. 2014). A North-South gradient is evident.

Afghanistan is not represented in the field of biodiversity research (no red dot). The unequal North-South gradient in research intensity and biodiversity gives rise to a major responsibility for the industrialized nations in terms of "capacity building" to raise awareness of the sustainable use of biodiversity in the megadiversity countries and to protect natural resources for future generations in a sustainable and responsible manner.

Brazil holds the biodiversity record of all countries. The Brazilian rainforest is a determining factor for the world climate. Though Brazil has pledged to stop illegal logging, however, the rainforest in 2020 has shrunk as much as it has not since 2008. Lumberjacks, cattle breeders, soil speculators - and an unrepentant government is responsible. The deforestation curve rises and rises. Deforestation in Brazil has been increasing almost steadily for the last eight years. Now it has reached its highest value in twelve years. Between August 2019 and July 2020, the deforested area in the Brazilian Amazon rainforest was 11,088 km2 - more than the area of Jamaica. The increase compared to the same period of the previous year was 9.5 %. The destruction of the rainforests represents a global environmental problem for all of mankind. Burning down the tropical forests not only contributes significantly to the emission of the greenhouse gases CO2, but also to the irreversible loss of many, quite often still unknown species. Brazil, which has the largest tropical forests in the world, is increasingly the focus of global attention.

**8.2 On the value of threatened diversity**

The loss of biodiversity since the beginning of the industrial age, but probably only in full force since the 1960s, is alarming (Hammond 1995, Perrings et al. 1997, Duffy 2003). Like the growth of the world population, it appears to be exponential. Despite all international conventions since "Rio 1992" and all political declarations of intent, nothing has fundamentally changed, as the results of "Rio 2012" shockingly showed (Barthlott et al. 2014). The destruction of habitats, including the clearing of tropical rainforests, continues at an unchanged or even increased rate. At the same time, as a globalization phenomenon, species numbers are increasing locally. The Federal Republic of Germany and the USA have higher diversity than ever before due to invasive species, but globally they are decreasing. Bio-globalization is becoming a central issue. Competitive invasive species also play a major role in studies on the reasons for species extinction (Essl et al. 2008; Klingenstein & Otto 2008; Nehring et al. 2010). A prominent example of the threat and extinction of biodiversity is the extinction of bird roc (◘ Fig. B-18) in Madagascar (http://t1p.de/uqk1).

The conservation of global biodiversity is only possible with a change in our economic system, and this does not meet with acceptance, especially in industrialized nations, but also in many emerging economies. It is also extremely difficult to convey why we want to maintain a high level of biodiversity (Barthlott et al. 2014). The important ethical aspects should not even be considered here - it is primarily utilitarian considerations that must be brought into the field for conservation (overview in TEEB 2010): Two topics play a role here:

1. The ecosystem value of biodiversity (stability of ecosystems, ecosystems services, for climate, soils, etc.), which can be indirectly expressed in figures and as economic benefits.
2. The direct use of plants and animals: as food (e.g. rice), medicines, building materials (e.g. wood) or fibre suppliers (e.g. cotton, hemp).

◘ Fig. B-18 Example of the threat to biodiversity on islands: A fossil egg of the elephant bird (Aepyornis maximus), which was native to Madagascar until a few hundred years ago. The elephant birds, which can grow up to 3 m tall and weigh 400 kg, were wiped out after human settlement of Madagascar and survived as the bird Roc in "1000 and One Nights" and many other Arabian fairy tales (Photo: Barthlott).

Over 20,000 plant species are used directly by humans. From 100,000 different marine organisms alone, 200,000 extracts are obtained, the pharmaceutical use of which is currently being investigated (http://is.gd/vgiCZ7). Yet over 50% of the diet of billions of people depends on just four grass species: Wheat (predominantly Near East), Rice (predominantly Southeast Asia), Maize (predominantly New World) and Millet (predominantly Africa). The diversity of different species and varieties is an important basis for human life. Only one of over 6,200 rice varieties studied was resistant to a virus that threatened Southeast Asia's entire rice crop in the 1970s. If all such delicate but also unique apple varieties were replaced in Afghanistan by a slightly higher yielding - introduced in the early 1970s by Dr. Abdul Wakil - and currently very widespread "Red Delicious" variety, a single virus attack of the newly introduced variety would irretrievably destroy the entire apple crop in Afghanistan. One would then have to look for the resistant native varieties in the remote valleys of Afghanistan to make up for this loss to some extent. The preservation of biodiversity is of high "utilitarian" value for human existence alone.

Every year, new active medical active substances are discovered in plants and animals. For example, drugs against leukaemia and testicular cancer are extracted from the Madagascarian Catharanthus roseus. Cultivated and escaped, this plant is also known from eastern Afghanistan (Breckle et al. 2013). Similarly, almost 80% of the new antibacterial agents introduced today are natural products or ingredients derived from them. The same applies to about 60% of the new ingredients introduced in the field of cancer therapeutics during the same period.

2010 was the UN Year of Biodiversity. The countless institutions active in research in the field of biodiversity used this occasion to disseminate information on the protection and sustainable use of biodiversity. Many organizations, institutions, companies and individuals were invited by the UN Secretariat for Biodiversity Conservation (UN-CBD) to participate in this important cause to raise public awareness about the continuing loss of global biodiversity. This key year also saw the publication of the "Field Guide Afghanistan - Flora and Vegetation" with a foreword by the Secretary General of the UN-CBD Dr. Ahmed Djoghlaf (Breckle & Rafiqpoor 2010, p. 7) on the importance and value of this work as a small contribution to Afghanistan as a partner in the association of States Parties that have signed the Convention on Biological Diversity.

The flora of Afghanistan is very diverse due to the high geodiversity of the country. The desert and semi-desert regions of northern and SW Afghanistan fall into diversity level DZ-3 of the world map (► Fig. B-15), with 200-500 species per 10,000 km2. There is a strong gradient from the lowlands towards the mountains to diversity level DZ-7 (with 3000-4000 species per 10,000 km2) in the species-rich humid mountain canopies of the Hindu Kush, Kohe Baba and Safed-Koh in Eastern Afghanistan.

Groombridge (1992) has listed species numbers by country. According to this, Brazil hosts about 55,000 species followed by Colombia (35,000 species) and China (30,000 species). India (15,000 species) and Turkey (8,000 species) are ranked 12th and 13th respectively. Groombridge (1992) gives an estimated 3,500 species for Afghanistan, of which about 30-35% are endemic, i.e. occur only in Afghanistan. About 5-10% await rediscovery according to Groombridge. According to our earlier estimate (Breckle & Rafiqpoor 2010), about 4,100 species should occur in Afghanistan, of which about 30% should be endemic. After elaboration of all plant species described to date for Afghanistan (Breckle et al. 2013), about 5,000 species now occur in Afghanistan, of which about 25% are endemic. Many parts of Afghanistan have not been targeted for collection. We estimate that a substantial number of plant species could still be newly discovered. According to our findings, Afghanistan with about 5,000 species is considered an important hotspot of biodiversity in the Near East after the Mediterranean countries Italy with 5,600 species (Pignatti 1982) and Greece with 5,700 species (Strid & Kit Tan 1997).

9 **Zonal, azonal and extrazonal vegetation**

Zonal vegetation corresponding to the climate is found only on areas where the typical regional climate is fully effective. Such biotopes are called euclimatopes (Russian: plakor areas). They are flat, slightly elevated areas with deep soils that are neither too permeable (like sand) nor prone to waterlogging.

If we call the vegetation on the euclimatopes zonal vegetation, then, after the biotope change has taken place, it is extrazonal vegetation for which the large-scale climate is no longer decisive, but the local conditions. For example, if forests along rivers extend far into an arid climatic region as gallery forests, these gallery forests are extrazonal vegetation; they are often the basis for irrigated cultivated land (◘ Fig. B-19). Similarly, the floodplains of rivers and streams (◘ Fig. B-20) are equally azonal vegetation in forest areas but also in steppes or semi-deserts. The extrazonal vegetation can provide information about the zonal vegetation of a humid or colder zone or of an arid or warmer zone, if the zonal vegetation has been destroyed there.

◘ Fig. B-19: Gallery forest strip along the broadly meandering (Tajik) Pamir River shortly before the confluence with the (Afghan) Wakhan River (in the background) as an example of azonal vegetation (photo: C. Naumann).

◘ Fig. B-20: Stream floodplain with dense azonal meadow vegetation north of Almaty (Kazakhstan), surrounded by open forest and steppe (photo: Breckle).

The term zonal vegetation should only be used in large-scale considerations for the subdivision of the natural vegetation of large areas or entire continents. Only then does the influence of climate become clearly noticeable, and the local differences caused by soil, relief and exposure are less prominent.

On the other hand, under natural conditions, zonal vegetation may be largely absent even over large areas, for example, when groundwater is so high that swamps and bogs cover everything (W Siberia, Sudd swamps in Sudan, tropical swamps in Congo) or in the alluvions of major rivers. A mosaic of vegetation unlike zonal vegetation also grows on extensive lava blankets (Idaho) or on saline soils of wide drainless basins (Aral Sea). In these cases, we are dealing with pedobiomes, or azonal vegetation, which is much more strongly influenced by the specific soil properties and on which climate has only a weak effect. This does not mean that azonal biotopes would look the same all over the world; they are also influenced by climate, as shown by the very different zonations, for example on seashores.

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