Biodiversity
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Contents

Summary

Diversity is the most striking feature of the living world. It may be seen on many levels of the hierarchical organization of life - from genes to the whole biosphere - but is perhaps most apparent in the diversity of species. There are many interesting patterns of species diversity, ranging from the patterns of community diversity generated by the dynamics of colonization and local extinction driven by interspecific interactions, to the patterns of regional or global diversity attributable to the dynamics of species origination and extinction. Although the diversity of organisms has been studied by biologists for several hundred years, the total species richness of the Earth is still unknown. Contemporary human-induced changes lead to the loss of both local and global biodiversity, with unpredictable ecological consequences.

Keywords

Species diversity, interspecific interactions, communities, evolution, speciation, extinction, global species richness, biosphere, loss of biodiversity

1.1.6.3.1. Introduction

The term „biodiversity“ refers to the richness of living forms in the natural world. In the widest sense, it comprises the diversity of species living on the Earth, as well as the diversity of molecular mechanisms in the cell, the genetic diversity of populations, and, for instance, the diversity of habitats on a continent-wide scale. However, in a common (and stricter) sense, biodiversity refers especially to species diversity and to the diversity revealed at the higher levels of the organization of the living world (functional units of ecosystems, taxa, communities, habitats, landscapes), which is supposed to be partially derived from species diversity. Biodiversity is therefore not a single thing or a single „quantity“: although it is possible to measure diversity from a particular point of view, the term refers especially to the fact that the biota consists of many things (individuals, species, processes, communities, environments) and these individualities together are not easily reduced to a common denominator. Therefore, it refers also to the multidimensionality of the living world.

The scientific study of biodiversity started in the early 1960s, when ecologists recognized species diversity as an important feature of ecological communities. There were two main questions concerning the diversity of communities: (1) How is local diversity maintained? and (2) What is the effect of diversity on the stability of a community? The first question is closely related to the old problem of species coexistence: why, within one locality, do species coexist for a long time, without the competitively subordinate species being excluded from the community by one or more dominant species. The second question concerns the intuition that more diverse communities are also more stable. Although that hypothesis was not confirmed, it stimulated intensive research into the diversity of communities during the 1970s. However, during the next decade, ecologists abandoned this field of research, because ecological thinking had substantially changed during that time toward the study of variability, heterogeneity and nonlinearity. An individualistic approach to communities had prevailed, and communities were considered more or less random assemblages of mutually independent species. In the last decade of the twentieth century, however, the study of biodiversity began to flourish again. The revival of biodiversity studies has been connected to an appreciation of the loss of global biodiversity and of the evolutionary aspects of biodiversity dynamics. For these reasons, particular attention has been paid to large-scale biodiversity patterns and processes.

Importantly, although biodiversity as a specific theme appeared in ecology in the second half of the twentieth century, related phenomena had, of course, been studied much earlier by taxonomists and evolutionary biologists. The origins of the diversity of organisms, as well as the patterns of diversity within and between taxa, were studied intensively at least since Darwin, but on a much broader scale than the diversity of communities. Evolutionary biology and systematics incorporated the study of diversity of whole taxa on a continent-wide scale, and, for example, paleontology included the study of changes in diversity on a scale of millions of years. Ecologists recognized that diversity patterns are scale-dependent: whereas ecological processes play a primary role within smaller scales of time and space, evolutionary processes are more important within larger scales. However, it has only recently been recognized that both major scales of biodiversity are closely interconnected. On the one hand, ecology (relatively local relationships between organisms) depends on evolution which forms the properties of organisms involved in these relationships and, on the other hand, evolution is shaped by ecology which sets up constraints on the processes driving the evolution of living forms.

1.1.6.3.2. Scale dependence of species diversity

According to the processes that contribute to generating and maintaining diversity, three main levels of species diversity can be discerned. **Local diversity** is the diversity of a single locality, e.g. one wood, meadow or lake. This level depends on the local abiotic conditions, the interspecific interactions, the number of species that are able to successfully colonize the locality, and so on. **Regional diversity** concerns larger regions, the size of which is comparable to the size of species ranges. In contrast to local diversity, which depends on colonization from adjacent areas, regional diversity depends on the rate of the origination of species within particular regions. Regional diversity is thus governed by evolutionary processes of speciation and extinction. **Global diversity** is the species diversity of the entire globe, and is influenced also by speciation and extinction dynamics driven by large-scale geological and/or climatic changes (and, at least sometimes, by internal dynamics, including the activity of one dominant species, e.g. *Homo sapiens*).

These levels of biodiversity are not, of course, strictly separated. We can easily imagine intermediate situations, such as a large island where some species originated on the spot, while others colonized the island from the adjacent mainland. Moreover, even within large areas, local ecological conditions and interspecific interactions play a role in maintaining diversity. Therefore, there exists a gradual transition from local to regional diversity, following a simple rule that larger areas contain more species. This so-called species-area relationship is highly regular: when the number of species within a set of study plots is plotted against the area of the study plots on a log-log scale (i.e. both axes are log-transformed), the relationship obtained is approximately linear (see Fig. 1). **The relationship between an area and its number of species is regarded as the major and most robust biodiversity pattern**. The pattern has no simple explanation, however, and the processes responsible for the pattern differ according to the character of the study plots compared. The slope of the regression line is higher when the species numbers of isolated study plots (i.e. islands) are compared, and much higher when different provinces (e.g. continents) are compared (Fig. 1).

1.1.6.3.3. Factors affecting local diversity

The problem of the diversity of local ecological communities has attracted the attention of ecologists for several decades. Individual communities differ greatly in their species diversity. Whereas some communities are composed of only a few species, other communities are extremely diverse: several hundred tree species may occupy one hectare of tropical rain forest, and up to 25 species of plants may be found on a 10x10 cm square of temperate meadow. Community diversity may be affected by several factors. **Interspecific competition** may limit species diversity, because the dominant species may outcompete the subordinate ones in the local community. The intensity of interspecific competition is affected by the **productivity** of a given environment – when productivity is low, the competition between

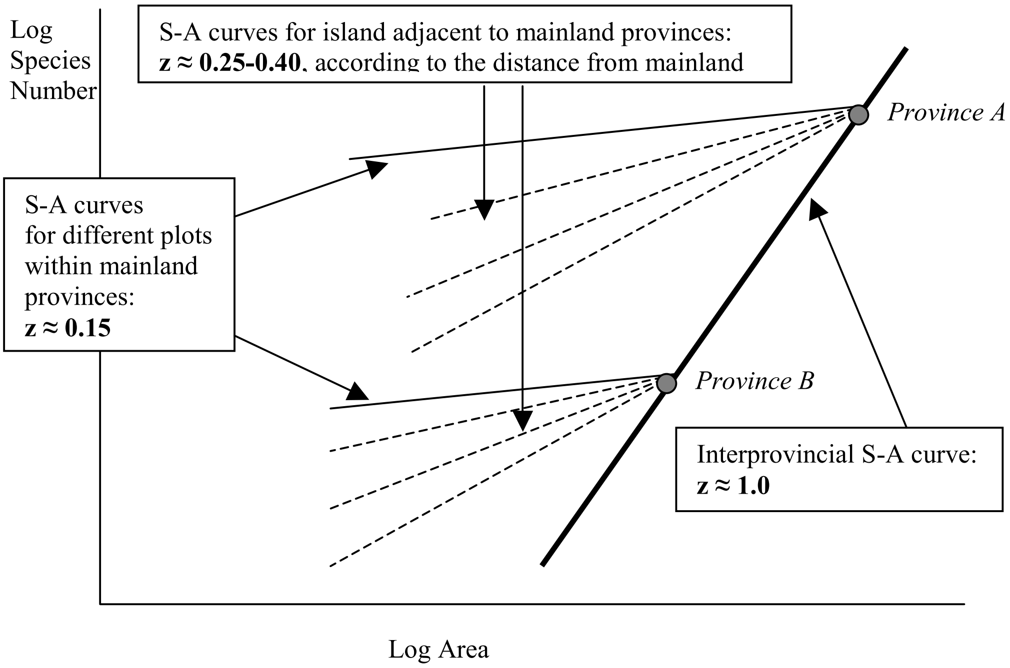

Fig. 1. Species-Area (S-A) curves. They are linear in a log-log scale, and they therefore could be expressed as a power law equation $S=c*A^z$, where S = number of species, A = area, c = constant representing species diversity per unit area, z = slope of the curve. The slope of the curve is the most steep for comparison between different provinces, less steep for comparison between isolated islands and the least steep for comparison of different plots within one continuous mainland area. See text for explanation.

species is stronger, because the amount of resources shared by the species is more limited. Interestingly, very high productivity may also promote competition, because the very productive environment aids in the proliferation of only the best adapted species, which outcompete many less adapted species. Therefore, intermediate levels of productivity generally promote the greatest diversity, because there are sufficient resources, but interspecific competition is relatively symmetrical (that is, its effect is not so unidirectional, fast and predictable).

Some factors substantially limit the effects of interspecific competition and therefore promote species diversity. The most important are **disturbances** – unpredictable events that kill individuals and thus reduce population numbers. As in the case of productivity, intermediate levels of intensity and/or frequency of disturbances promote greater species diversity. When the disturbances are too intense or frequent, they have fatal consequences for population persistence. When the intensity and/or frequency of disturbances is, on the other hand, too low, their effect is not strong enough to have any substantial effect. But when their intensity and/or frequency is appropriate (in relation to many factors and local conditions, such as productivity, the life histories of respective organisms, and so on), disturbances may reduce the population sizes of the dominant competitors, enabling the subordinate competitors to survive, and thus promoting species coexistence. **Predation** could have effects similar to those of disturbance, especially if the predator is opportunistic, i.e. when its prey forms the dominant species. In the case of an appropriate balance of both predation and disturbance, the populations of competitively dominant species are prevented from increasing in size to a level where they outcompete the subordinate species.

One of the major factors affecting biodiversity is **environmental heterogeneity**. It promotes the coexistence of species, because each species may be better adapted to some particular habitat, where it can outcompete other species. **Habitat fragmentation** may have a similar effect to that of heterogeneity in the strict sense, because it may limit dispersal of the dominant competitor (or predator, for example) and allow a subordinate competitor (or prey, respectively) to persist in local refuges, at least for some time. (On the other hand, habitat fragmentation may lead to population extinction, because small isolated populations are often unable to resist crises.) Environmental heterogeneity is often generated by disturbances, because disturbances are mostly local, creating mosaics of different habitat patches in different stages of recruitment. Environmental heterogeneity is a primary factor in the species-area relationship revealed within one continuous landscape (see above):

a larger area can comprise more habitat types and thus harbor more species.

Local diversity is affected not only by local conditions and interspecific interactions, but also by the opportunity and ability of individual organisms to colonize a given locality. This opportunity is greatly limited by the **isolation** of the locality from other „source“ localities. This effect is responsible for the lower diversity of island communities. Species impoverishment on islands is caused by the combined effect of isolation, which limits the colonization rate, and limited **area**, because limited areas harbor fewer habitat types (see above) and smaller populations of individual species which are therefore more prone to extinction (see chapter 1.1.6.3.4.2.). Therefore, smaller and/or more distant islands generally contain fewer species. These so-called „island effects“ are also responsible for the steeper regression line in the species-area relationship in the case of isolated areas (Fig. 1), because immigration does not compensate for species extinction on the smaller islands. However, the presence and strength of island effects depends on the organisms involved, because „isolation“ itself is recognized differently by different species. For some good dispersers (e.g. albatrosses or plants with light spores) even remote oceanic islands are not in fact „isolated“, whereas for poor dispersers (e.g. some plants) individual patches of forest within a deforested area could represent true islands.

The **size of the species pool** (i.e. the set of the species able to colonize any given locality) seems to be even more important for local species diversity than the other factors. Some areas are species-poor simply because there are no more species in the entire region that could occupy the area. One hectare of temperate forest in Southeast Asia contains several times more tree species than one hectare of the same forest in Europe. This is not because of any of the factors mentioned above, but simply because the regional tree diversity of Europe is six times lower than the tree diversity of Southeast Asia (due to the geographical constraint of south-north migration in Europe and the devastating effect of ice ages). Therefore, local diversity could be largely affected by regional diversity. The most extreme formulation of this statement, the so-called „species pool hypothesis“, states that the effects of local factors on local species diversity are mostly minor in comparison with the effects of the species pool, i.e. the regional diversity.

1.1.6.3.4. Regional diversity and its origins: speciation and extinction

Regional diversity is the diversity of regions that are large enough to contain whole species’ geographical ranges. Therefore, it is supposed that the species originated in these regions (rather than colonizing these areas from outside), and the processes responsible for their origin and maintenance are regarded as important within that scale of diversity. Regional diversity is thus affected by the dynamics of speciation (the origination of species) and extinction. The factors influencing the rate of speciation and extinction affect the resulting regional diversity.

1.1.6.3.4.1. Speciation

Speciation is the process of one ancestral species dividing into two or more new species. A species represents a distinct evolutionary line (i.e. a group of organisms sharing a common evolutionary path), and in sexually reproducing organisms this common path (i.e. species individuality) is ensured by interbreeding (i.e. the flow of genetic information between individuals within a population). Therefore, speciation in sexually reproducing organisms is caused by the division of ancestral species into two or more populations in which individuals can interbreed with each other, but cannot interbreed with individuals from the other population(s). The populations may be divided initially by any geographical barrier (e.g. a mountain ridge, a sea) and subsequently may evolve separately. Due to their independent evolution, whenever the populations meet again, they may be reproductively incompatible, thus forming new species. Alternatively, they might interbreed, but due to their differences, the hybrids might be less fit and natural selection could lead (after generations) to the avoidance of mating of individuals from the different populations (species). This type of speciation, caused primarily by geographic separation of populations, is termed **allopatric speciation** (allopatric = inhabiting different areas). By contrast, in so-called **sympatric speciation** (sympatric = inhabiting a common area), the species divide without a preceding geographical division of populations. Especially in plants, but also in some fishes and amphibians, the species division may be caused by interspecific hybridization that is often accompanied by the multiplication of chromosomes (polyploidy). The individuals differing in chromosome number may be unable to mate successfully with individuals of the ancestral species, thus forming a new species. Another form of sympatric speciation is sometimes called **competitive speciation** and occurs when the ancestral species can specialize ecologically in several alternative ways. When, for instance, the ancestral species is able effectively to exploit either one resource type or another, but not both types simultaneously, some individuals specialize for one type and some for the other type. Hybrids of the two ecological specialists would not be able effectively to exploit either resource type, and hybridization between the two types of specialist would therefore not be advantageous. Natural selection in that case would lead to the avoidance of interbreeding between the two types of specialists, and thus (after generations) these specialists could form new, ecologically distinct species.

It was supposed for a long time that allopatric speciation was the major speciation mode. The main pieces of evidence came from the fact that isolated areas, such as islands, carry plenty of endemic species, i.e. distinct species that are restricted to the isolated area. Therefore, isolation almost always led to speciation within evolutionary time scales. Sympatric speciation appeared to be only a minor speciation mode – interspecific hybridization and polyploidisation were too rare and competitive speciation seemed rather improbable for genetic reasons (there was the theoretical problem of how genetic mechanisms could lead to the avoidance of interbreeding between differently specialized individuals). Contemporary evidence suggests, however, that sympatric speciation is much more prevalent than was previously thought. There are some groups of closely related species inhabiting common places whose preceding geographical subdivision is highly improbable. In addition, there are some species that are ecologically subdivided although the subpopulations still interbreed. One important factor promoting (or even enabling) this type of speciation is assortative mating, i.e. preferential mating between partners ecologically similar to each other. Sometimes assortative mating may lead to speciation even without complementary ecological specialization.

1.1.6.3.4.2. Extinction

Extinction of species and populations may be caused by many factors – rapid environmental change, introduction of an over-efficient predator or competitor, epidemics, and so on. Therefore, each extinction is an unique event and it is hardly possible to generalize. However, different populations (or species) are at different risk of extinction. It was once thought that, for instance, physically larger species are more vulnerable to extinction than smaller ones or that species with longer generation times have a different probability of extinction from short-lived species. Nevertheless, there is only one general correlate of extinction probability: population size. **Smaller populations are generally more prone to extinction than large populations**. There are several reasons for this. The most popular explanation used to be one based on population genetics. According to this theory, smaller populations have **lower genetic variability**, which increases the danger of accumulation of lethal mutations due to mating between related individuals. However, this explanation has only limited validity; it is applicable only to very small populations, up to several tens of individuals. Also of limited application, the second explanation assumes that the lowering of population size or density could lead to the **breaking of behavioral, social and ecological mechanisms** that enable successful reproduction. Although this may be true in some social animals, it is surely not applicable to most species. Statistical reasons are probably more important. There is a larger probability in small populations that **random fluctuations** in population number will be fatal (simply put, small numbers are closer to zero). Even more important is the fact that small populations also occupy limited space. Therefore, even **small disturbances or local changes of environment** could lead to the extinction of small populations. Large disturbances and environmental changes are generally less common than small ones, and thus, large populations become extinct less often than small ones. Almost all documented population extinctions are due to fatal change in a local environment (including the local introduction of a natural enemy of the respective species).

1.1.6.3.4.3. Factors affecting regional diversity

Factors affecting speciation and extinction rates consequently affect the regional diversity of particular taxa. There are several factors that could affect speciation. One of the most important is geographical configuration. If, for example, several islands are sufficiently close to each other to enable colonization, but at the same time too far apart to allow continuous interbreeding, subsequent speciation events could lead to enormous biodiversity. A typical example is the extraordinary diversity of Hawaiian fruitflies (*Drosophila*), where each species inhabiting the islands within the archipelago acted as a potential source of colonists that, at the time they successfully colonized a neighboring island, gave rise to other new species. On the other hand, if it is true that sympatric speciation is a common speciation mode, environmental heterogeneity could promote diversity as well, since it may lead to the ecological specialization of species subpopulations. However, this possible large-scale effect of heterogeneity is still obscure and ecological specialization is generally regarded as a consequence of a different process – the ecological diversification of already established competing species. Speciation may also be promoted by particular features of the taxa concerned. African cichlids, for instance, recognize their mate according to his or her color. Fine changes in color accompanied by changes in mating preference probably led to the rapid establishment of new species.

Different taxa generally differ in their ability to produce new species. These inherent differences lead to the phenomenon called **species selection**, i.e. competition between individual evolutionary lineages for their ability to produce new species. Species selection is in principle similar to natural selection, where individuals compete for reproductive success, but species selection acts on a higher hierarchical level and within larger time scales.

The rate of extinction could also be affected by several factors. As probability of extinction is closely related to population size, the main factors affecting extinction rate are probably related to the constraints on population size: resource quantity and area. For this reason, larger provinces harbor many more species than smaller ones (the regression line of the species-area curve is steepest when whole provinces are compared – see Fig. 1) because within larger areas species are able to reach larger population sizes. Other extinction-related factors include the presence of predators and competitors. For example, the diversity of Madagascarian lemurs as well as Australian marsupials was maintained mainly because of the absence of predators and/or competitors.

The evolution of individual taxa is often characterized by a relatively short period of rapid diversification, i.e. rapid production of many species. This rapid diversification is termed **radiation** (or **adaptive radiation**, when accompanied by the acquisition of some specific adaptation) and is often enhanced if the range of resources for the taxa broadens. For instance, the radiation of many taxa occurred after global extinction in which ecological space was vacated. Similarly, the evolution of plants and plant-eating (phytophagous) insects was characterized by a series of radiations within each group of organisms, each radiation following the acquisition of important adaptations which helped to overcome constraints imposed by another group. It is impossible to determine whether the cases of radiation following vacation of ecological space are affected by a reduction in extinction rate because population sizes increase, or whether the broadening of the range of resources is accompanied by increased environmental heterogeneity, thus affecting the rate of sympatric speciation.

1.1.6.3.5. Large-scale biodiversity patterns

There are several interesting large-scale diversity patterns, most of them still rather poorly understood. However, the key to comprehending them must lie in the understanding of factors influencing differences in speciation and extinction rate. One example of a large-scale pattern, mentioned above, is the higher diversity of larger provinces. In this case, it is relatively easy to explain the pattern by reference to speciation or extinction rates: populations can reach higher sizes in larger areas and thus lower their extinction probability within these areas. The other diversity patterns, however, are more enigmatic.

1.1.6.3.5.1. Individual taxa differ greatly in their diversity

Some taxa are extremely species-rich, whereas others comprise only a few species (Fig. 2). A trivial explanation lies in their different ages: the younger taxa have had, of course, less time to diversify. However, taxa of a similar age differ greatly in their diversity as well. These diversity differences among taxa are produced by species selection (see chapter 1.1.6.3.4.3.), which could be simply characterized as unequal chances of producing new species and evolutionary lineages, whether this be due to the inequality of speciation rates or extinction rates between particular taxa. The factors promoting or limiting speciation and extinction rates, respectively, are highly diverse (see chapter 1.1.6.3.4.3.). There are, however, some general correlates of taxonomic diversity, at least for animals. The two main life-history correlates of taxonomic diversity are (1) generation time and (2) ability to colonize and utilize new resources. The ability to colonize is thought to increase speciation rate, since speciation often operates by means of colonization of new areas and subsequent creation of population isolates. Generation time may be related to the ability to recover rapidly from population crises. Nevertheless, exact relationships between these correlates of diversity and speciation or extinction rates remain obscure to date. Moreover, the exact relationships may be masked by complicated relationships between different life-history characteristics. Generation time could be, for instance, closely related to body weight, which is also related to species diversity (see below).

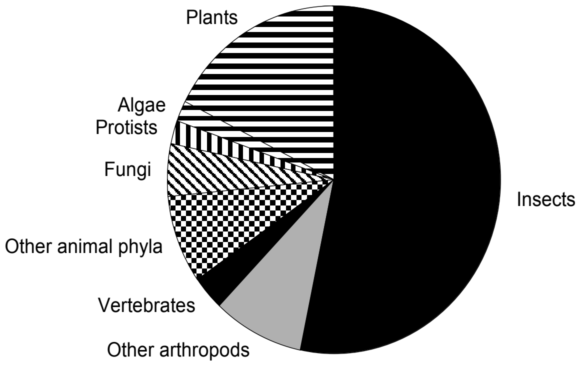

Fig. 2. Comparison of known species diversities of different taxa of eukaryotic organisms (i.e. not including bacteria and viruses). Note that the unknown, but probably extraordinary diversity of nematods is not included.

Within the animal kingdom, the species diversity of taxa is apparently related to their ability to fly: the most diverse animal class generally is insects, while birds are the most diverse class of land vertebrates. This pattern can also be observed within different hierarchical levels of systematic classification: only one order of mammals, bats, has the capacity for active flight, and this order contains 20 per cent of all mammalian species (bats are, after rodents, the most species-rich mammalian order). However, although the ability to fly is clearly related to the colonization ability mentioned above, hasty conclusions may be misleading. Insects, birds and bats are in fact the only three taxa truly able to fly actively, and this number is too low for any convincing conclusions to be drawn. There are also many diverse flightless taxa (e.g. amphibians), and moreover, even among insects, there are flightless families (especially beetles) which are extremely diverse. Therefore, we can conclude only that flight is probably somehow related to species diversity, but other characteristics are surely also important. Similar conclusions may be reached in the case of other apparently important life-history characteristics of animals and plants.

It should be noted that the species diversity of unicellular organisms (protists and bacteria) represents a great enigma. There is, of course, a general problem concerning the relevance of the concept of „species" in these organisms, because many of them are asexual and there are thus no criteria for establishing species membership. However, even if we accept some ad hoc criterion for species membership, the problem of diversity of unicellular organisms remains. These organisms generally have a short generation time together with a very good ability to disperse by air. Therefore, they have the life-history characteristics generally related to high diversity, as described above. However, there are some pieces of evidence to show that notwithstanding their colonization ability, protists (and perhaps also bacteria) do not form endemic species, i.e. they have no ability to form isolates which could potentially give rise to new species. The colonization ability may be so high in these organisms that all their local populations are in fact interconnected by continuous migration, preventing them from forming new species. Bacteria are even more problematic for technical reasons: only a tiny fragment of the total richness of the bacterial world is known, because most bacteria are simply undetectable using contemporary techniques. The diversity of bacteria is absolutely unknown.

1.1.6.3.5.2. There are more species of smaller organisms

Most animals, as well as most plants, are small. This pattern holds for the plant and animal kingdoms in general, but also for almost all higher taxa, up to the level of classes (insects, mammals, fish, birds, and so on). The pattern could be caused by a multiplicative speciation process: the sizes of new species are likely to differ from that of the ancestral species by a larger value in large than in small species. A new species of whale could differ in size by several kilograms, but this will be unlikely in a mouse. Therefore, whereas small species will produce similarly small species, large species could produce similarly large species as well as larger or, alternatively, smaller species. However, there exist even more small species than could be explained by this random multiplicative process alone. One possible explanation is that smaller species can specialize better and thus avoid interspecific competition. Smaller species may perceive their environment as a diversified mosaic of different habitat patches more easily than large species could, since larger species have larger territories and „perceptual ranges", i.e. the range that they perceive as their own environment. During a five-minute walk, an elephant would go through many habitat patches from a mouse's point of view. A second explanation is based on the extinction rates of larger species, which should be higher than for smaller species, because larger species cannot reach such high population densities, assuming that they utilize similarly abundant resources. These explanations are not mutually exclusive: larger species might not specialize to particular resources or habitats because extinction probability would increase due to the consequent lowering of population size of these specialized large animals. From the evolutionary point of view, there are few large species because the species that specialized became extinct due to the increased extinction rate, while those that did not specialize competed fiercely for resources.

A third explanation of the distribution of body sizes between animals (this explanation is hardly applicable to plants) is based on the assumption that within particular taxa there is an optimal body size: animals smaller than the optimum have to invest too much energy into self-maintenance, whereas larger animals have to invest too much energy into growth and reproduction. According to the theory, most animals of a particular taxon are of approximately optimal size, i.e. relatively small, but many species are either smaller or larger to avoid competition with these „optimal" animals. This theory has been confirmed by some bioenergetic calculations and, more importantly, by the evolution of body sizes in those situations where overall species richness was impoverished, namely on islands. Island animals have a tendency to change their body size over evolutionary time scales; smaller animals tend to increase their size, whereas large animals are smaller after generations than their ancestors were. Animals whose body size is optimal do not change their size. Moreover, the tendency is stronger the more the initial body size differs from the optimal body size. Perhaps there is a selection force which pushes all species within particular taxa towards the optimal size, but which is normally balanced by interspecific competition that leads to ecological diversification of species and consequent diversification of body weights.

1.1.6.3.5.3. Areas with intermediate levels of productivity have maximum diversity

This pattern has been recognized in a variety of taxa and communities, ranging from bottom-dwelling marine taxa (where productivity is directly related to the depth of the ocean floor, which determines the availability of light for photosynthesis) to tropical vertebrates (bird and mammal diversities are higher in tropical highlands than in lowland forests, if area is factored out). On local scales, a similar pattern is found, which is attributed to stronger interspecific competition in places with both low and very high levels of productivity (see chapter 1.1.6.3.3.). On regional spatial scales, however, the situation is more complicated, because any explanation must be related to the speciation and/or extinction rates. The lower diversity of less productive areas presents no theoretical problem: lower resource abundance will lead to lower population sizes and consequently higher extinction probabilities. But the decreasing diversity in more productive areas is not yet satisfactorily explained. There exist at least nine competing hypotheses, only two of which appear relatively convincing. One hypothesis is based on the assumption of lower perceived heterogeneity on more productive patches. Simply put, in very productive environments the relative differences between habitat patches seem rather unimportant, because all patches carry a multitude of all resources. Consequently, species do not specialize in the productive environments and they therefore suffer much stronger interspecific competition leading from time to time to species extinction. Alternatively, if speciation is promoted by environmental heterogeneity (which is still questioned, as discussed in chapter 1.1.6.3.4.1.), the absence of perceived heterogeneity could lower the speciation rate.

The second hypothesis claims that each type of organism competes best at a restricted set of productivity levels and at higher levels of productivity is replaced by other types of organism. This hypothesis is thus framed in terms of intertaxonomic competition, i.e. competition between distantly related taxa. The lower diversity of particular taxa in more productive areas is, according to the hypothesis, caused by inability to compete successfully with taxa that can better utilize higher productivity. For instance, reptiles are most successful at lower levels of productivity (because they need not invest energy into thermoregulation), but when productivity increases, they are replaced by competitively superior mammals. Intertaxonomic competition undoubtedly exists, but its contribution to the observed pattern remains unclear.

1.1.6.3.5.4. Diversity is highest in the tropics

The most striking pattern of diversity is known as the latitudinal gradient of biodiversity; that is, a gradient of diversity decreasing with latitude. Most taxa are most diverse in the tropics. The most diverse habitat on the Earth is the tropical rain forest, but other habitat types in the tropics (savannas, coastal zones, rivers) also harbor an enormous richness of species. There exist several hypotheses explaining the pattern, which differ as to the factor considered to be the most important. Some hypotheses have failed in their explanation of the pattern because they assign importance to some factor produced by or tightly connected to diversity itself. For example, some hypotheses related high species richness to higher environmental heterogeneity or to the greater importance of interspecific interactions. There is, however, no evidence that the tropics are more heterogeneous *per se*, i.e. that the heterogeneity of tropical ecosystems is generated in a manner not directly connected to the diversity of living forms. Similarly, if interspecific interactions are more important in the tropics, this may be a consequence of the higher species richness, i.e. the causality is reversed. However, whereas the general phenomenon of the latitudinal gradient of diversity cannot, of course, be explained by some aspects of the diversity, the diversity of some taxa might be causally related to the diversity of other taxa (e.g. animal diversity could be a byproduct of plant diversity). Nevertheless, if we want to explain the latitudinal gradient in general, we must look for the factors that influence major differences between the tropics and the other climatic zones.

Two candidates for the factors responsible for the high tropical diversity are thought to be directly related to the lower extinction rate in the tropics. One of them is **productivity**: the tropical climatic zone is clearly the most productive due to its high precipitation and solar energy supply. The second factor is **area**: the tropics represent the largest climatic zone. Both high productivity and large area could promote higher population and species range sizes, lowering extinction probability. However, both these explanations seem insufficient. The relationship between productivity and diversity is complicated (see above) and, more importantly, population sizes and species range sizes are generally smaller in the tropics (which should lead to higher extinction probability). Therefore, the factors responsible for higher diversity in the tropics cannot operate via a lowering of extinction probability by increasing the population or range sizes of individual species.

A very popular explanation of the latitudinal gradient is based on the **geological and climatic history** of the Earth. The tropical climatic zone was presumably not impoverished by severe climatic oscillations during the Quaternary Period, whereas temperate zones suffered from the alternation of Glacial and Interglacial periods, because species ranges and all vegetation types shifted northward and southward and many species had to repeatedly reduce their ranges, eventually becoming extinct. The tropical zone was, on the other hand, repeatedly fragmented during the Glacial Era and such fragmentation might have promoted speciation. However, the consequences of the Glacial fragmentation of the tropical ecosystems are not well understood; fragmentation could plausibly also lead to extinction. Generally, the nature of the tropics is regarded as ancestral, because the tropical zone was much wider during the Tertiary (when most recent life forms originated), covering most of the globe surface. The nature of other climatic zones is considered, according to this hypothesis, as highly derived and continually impoverished by severe climatic changes. The hypothesis seems highly convincing, although some paleontological data suggest that the latitudinal gradient is much more general and had existed during all the preceding geological eras. However, it might be hypothesized that during those eras the higher latitudes were impoverished (by unknown climatic events) as well:

any climatic change is probably more severe in higher latitudes for purely geophysical reasons.

The greater **climatic stability** of the tropics may explain the latitudinal gradient not only because of the large-scale climatic oscillations in higher latitudes, but also because of regular annual oscillations. These oscillations are much more pronounced in higher latitudes, which imposes a selection pressure upon all the species inhabiting those zones – these species must be adapted both to the summer heat and to the winter frosts and consequent lack of food. Therefore, they might be prevented from specializing much. The tropics, on the other hand, are climatically very stable so tropical species could in principle specialize for a narrow range of conditions, preventing interspecific competition and subsequent potential extinction. However, there is no evidence of higher specialization in the tropics, although it is known that tropical species have narrower geographical ranges. The phenomenon of smaller species ranges in the tropics is known as the Rapoport rule and is traditionally attributed simply to the effect of differences in the amplitude of climatic oscillations between the tropics and the temperate zone.

No existing explanation of the latitudinal gradient of species diversity can be considered absolutely satisfactory. However, although both area and productivity may contribute to the high diversity of the tropics, climatic stability is probably the most important factor.

1.1.6.3.6. Global biodiversity and its changes

There is no consensus concerning the total species richness of the Earth. There are about two million species described, but the actual species richness is undoubtedly much higher. Different attempts to estimate total species richness range from a few million to about one hundred million species. The total biodiversity is distributed highly unequally on the Earth's surface as well as between individual taxa (see chapter 1.1.6.3.5.): most biodiversity is concentrated in the tropics and most species belong to only a few higher taxa. It has been believed for a long time that arthropods (mainly insects) are the most species rich, but some contemporary findings suggest that nematods may be even more diverse. Whatever the case, the biosphere remains to a great extent unexplored. Moreover, even the diversity of well-known taxa is often unknown, because of problems of species discrimination. The diversity of birds, for instance, was recently estimated to be twice the traditional estimate, thanks to detailed studies of bird genetics and ecology.

1.1.6.3.6.1. Maintaining global biodiversity

It is thought that recent species diversity represents 0.1 per cent of the total diversity of all species that ever lived on the Earth. 99.9 per cent of the total species richness is therefore represented by extinct species and 1000 speciation events have been on average balanced by 999 extinction events. The similarity between the numbers of speciation and extinction events may be interpreted as evidence that biodiversity on the Earth is rather stable. If the numbers of speciation events exceeded the number of extinction events by a larger figure, there should be a much higher proportion of recent species; conversely, if the extinction rate were higher than the speciation rate, there should be no species at all. There are also some other pieces of evidence showing that global species diversity is really surprisingly stable. However, some findings indicate, on the contrary, that global biodiversity is continually increasing. Certain evolutionary steps were almost certainly accompanied by an increase in diversity (e.g. colonization of land or fragmentation of the former Pangaea continent). Moreover, younger fossil assemblages are generally more species rich than older assemblages, although this may be attributed to the better preservation ability of the younger fossils. There is a lack of consensus concerning whether global biodiversity is stable or continually increasing. If it is not stable, however, global biodiversity is undoubtedly increasing only very slightly.

The apparent stability of global diversity was probably ensured by the fact that extinction rates are regulated by the limited total amount of resources available for living organisms. Assume that total amount of resources is approximately stable, as is rather probable considering that the main source of energy (solar radiation) did not change substantially during most of the Phanerozoic Era, an era of apparently diverse multicellular life. A limited amount of resources could support a limited number of individuals or, more precisely, a limited amount of overall biomass (assuming stable distribution of body sizes, biomass can be directly related to the number of individuals). This stable number of individuals could be represented by any number of species, but the more species there are, the smaller their population sizes will be. Therefore, an increase in diversity could result in the lowering of average population sizes, and thus to an increase in extinction probability. The stability of global diversity is maintained by a feedback loop between diversity and extinction rates, which is due to the limited total amount of life-supporting resources.

1.1.6.3.6.2. Rapid changes in global biodiversity

Although global diversity is stable in general, it has suffered brief periods of sharp decrease, familiar to us as mass extinctions. Five large mass extinctions have been recognized in the fossil record, but there have also been many smaller extinction events that differ from the large ones only quantitatively. Generally, following the general rule governing most catastrophic events including local disturbances (see chapter 1.1.6.3.4.2.), large extinction events have been rarer than smaller ones – the large mass extinctions follow one another after approximately one hundred million years (although there is no apparent regularity in their occurrence), while the smaller ones repeat more often. Complicated cascades of environmental effects with a global impact have characterized the large extinctions (oscillations in sea level, changes in atmospheric composition, climatic changes – see chapter 1.1.6.4.), which thus often affect very different (and geographically distant) taxa. The immediate effect of a mass extinction on diversity was often severe: it is estimated that up to 96 per cent of animal species became extinct during the largest mass extinction, at the end of the Permian Period. However, the contribution of mass extinctions to biodiversity dynamics is – perhaps paradoxically - relatively small, due to the low frequency of these extinctions. The species turnover on the Earth's surface is rather high in relation to that frequency: one species persists for approximately four million years, and thus the entire diversity will have changed approximately 25 times between two large mass extinctions. Moreover, diversity increased rapidly to the initial levels after any mass extinction (probably due to the vacation of resources; see chapter 1.1.6.3.4.3.).

Although mass extinctions have had a relatively small impact on overall biodiversity dynamics, their impact on macroevolution has been substantial. Individual higher taxa were differently vulnerable to extinctions during these events (their vulnerability was well related to the overall range size of the whole taxon) and thus the mass extinctions provide a strong species selection effect substantially changing the Earth's biota. Extinction of some higher taxa promotes (adaptive) radiation of other taxa. It has been assumed that these mass extinctions alone are responsible for the changes of taxa dominating the Earth during large-scale evolutionary time. For instance, the transition from land communities dominated by dinosaurs toward communities dominated by mammals has traditionally been attributed to the mass extinction event at the Cretaceous-Tertiary boundary. On the other hand, there have been some significant transitions during evolutionary history (e.g. the change of dominance of large plant taxa) which were apparently unrelated to any mass extinction events.

There exist many theories concerning the reasons for mass extinction. Extreme positions claim that all extinctions were caused by purely extraterrestrial forces (i.e. meteoric impact) or, on the other hand, by the internal dynamics of plant and animal communities. Other hypotheses include volcanism, continental drift, atmospheric changes, and so on (see chapter 1.1.6.4.). There is no general consensus concerning the causes of mass extinctions.

1.1.6.3.6.3. Contemporary biodiversity changes

Contemporary human impact on the biosphere has led to a substantial reduction of biodiversity. This effect is thought to be comparable to the effects of the five major fossil mass extinctions that led to the extinction of at least 50 per cent of species. However, estimating contemporary biodiversity loss is very problematic. One estimate comes from the known rate of deforestation in tropical forests. As the forests harbor much of global diversity (see chapter 1.1.6.3.5.4.), the loss of diversity in the forests represents a major contribution to the global diversity loss. As the total area of tropical forests is reduced by a known rate, the remaining species richness and the rate of its loss can be derived from the well-known relationship between area and species number (see Fig. 1). These estimates suggest that the contemporary rate of lowering of the tropical forest area is accompanied by a loss of 0.5 per cent of forest species per year.

Other estimates of biodiversity loss are based on the known proportion of threatened species. However, that proportion differs greatly between individual lists of endangered species, according to the criteria used to identify endangered species. There are no hard criteria for this - after all, almost all species are somehow endangered. Some further estimates are based on the proportion of species whose population sizes are declining. That proportion is apparently high – perhaps over 50 per cent. However, the estimate is probably strongly biased by the fact that almost all species populations are, on any particular time scale, either increasing or decreasing. Therefore, there will almost inevitably be nearly 50 per cent of decreasing species. Data from the long-term study of population changes in North American birds, for example, suggest that the proportion of decreasing species is almost equal to the proportion of increasing species and that the rate of decrease in some species is closely proportional to the rate of increase in some other species. There is no convincing evidence of a contemporary prevalence of population decrease in the majority of species.

Generally, estimates of contemporary biodiversity loss are largely unreliable and, moreover, produce numbers that are hard to interpret. If, for instance, we know that 0.5 per cent of species become extinct per year, we still do not know whether this is really „too many". Nature is constantly changing and nobody knows how frequent species extinctions were before the modern human impact. The oscillation cycles in the Quaternary Period, for instance, led repeatedly to even more drastic reductions of the tropical forest area, and the Pleistocene-Holocene transition 10,000 years ago was accompanied by a vast reduction in the diversity of large mammals (although this was probably caused by Paleolithic human impact). The contemporary extinction rate is hardly comparable to „normal" extinction rates, because „normal" extinction rates were never stable and, moreover, are not known. It is possible to estimate an average extinction rate from the fossil record, but comparability to the recent extinction rate is very low. The fossil record involves mainly widespread, marine species, whereas contemporary changes particularly affect tropical species with small ranges, which generally rarely fossilize.

Although the reduction of global biodiversity is perhaps drastic and comparable to the previous global mass extinctions, there exists a phenomenon that is probably more important and certainly better documented. This is the „biotic homogenization“ of the biosphere, i.e. local extinctions of endemic species accompanied by the replacement of local biota with non-indigenous species. Biotic homogenization has two causes: environmental modification and transportation of exotic species by man. The homogenization could lead to a (perhaps ephemeral) increase of local species richness, but to a decrease of regional and global diversity. A large number of geographically restricted native species with sensitive requirements is replaced by a small number of widespread, broadly tolerant forms that can live with humans.

1.1.6.3.7. The value of biodiversity

Biodiversity seems to be valuable for many reasons, ranging from the purely cultural to the purely economic. Four reasons to undertake biodiversity conservation are generally acknowledged. The first reason is **cultural**: the diversity of living forms represents a cultural and aesthetic value important for all human societies, for their culture, mythology and so on. The second reason is much more problematic and is based on the assumption that we have no justification for destroying or even influencing biodiversity. This reason for biodiversity conservation is therefore **ethical**. The third reason relates to the **economic** value of biodiversity: the diversity of nature, and especially the nature of tropical forests (the most diverse and probably most endangered habitat on the Earth), provides an invaluable source of possible new drugs and chemicals that may be used by pharmacy, medicine etc. The fourth reason is **ecological**: biodiversity is thought to play an invaluable role in maintaining basal ecosystem processes such as nutrient cycling, production of biomass etc. All these reasons are legitimate and all are at least partially problematic. The cultural and economical value of diversity, for instance, apparently refers not to diversity as a whole (i.e. all the animals, plants and microbes), but only to some specific animals, plants etc. Most species surely have no value for the satiation of human cultural or economic demands – remember that insects and nematods form the absolute majority of species. The problem with the ethical reason for biodiversity conservation is, on the other hand, that ethics is too relative and too subject to cultural consensus. Moreover, according to our contemporary cultural consensus, it is unethical to impose our consensus concerning the value of biodiversity upon other cultures. Finally, the ecological value of biodiversity is still questioned.

The ecological value of biodiversity was supposed to be related to the stability of communities and ecosystems. More diverse communities were regarded as more stable because in these communities many species play a similar ecological role, and thus each species could replace another species with a similar ecological role if necessary. This intuition seemed to be supported by several pieces of evidence, especially by the fact that artificially impoverished communities (e.g. agricultural monocultures) are more vulnerable to any changes than natural communities are. However, such arguments supporting a diversity-stability hypothesis were later shown to be false. The reason for the lower stability of artificially impoverished communities probably lies in the artificiality of the communities, not in the lower diversity itself – these communities are artificially kept out of any equilibrium. Moreover, there are some natural monocultures (e.g. reeds or salines) that are very stable. These and similar findings led to the conclusion that there is no direct relationship between stability and diversity. The only relationship exists for purely statistical reasons: the population of one species may fluctuate considerably, but the fluctuation of several species’ populations with independent dynamics could „average“, because as one population decreases, another may increase.

The original intuition concerning „ecological roles“ of species and the possible replaceability of species within these roles seems nevertheless not only still alive, but also very productive. No community could be impoverished up to the point where some important ecological role (e.g. production of living matter by plants or plant pollination by insects) does not continue to be performed. From that point of view, all species are not equally important for community stability and functioning: some roles are performed by only a few species and these species are therefore more important than species which share their role with many other species. Some vital roles may even be performed by only one species. Unfortunately (or, perhaps, fortunately), it is not easy to discriminate individual species roles: they are, in fact, often complicated and may not be stable. Some of them are seemingly simple: plants are primary producers (i.e. they produce organic matter), microorganisms and fungi are decomposers (i.e. they utilize organic matter, reducing it into inorganic molecules which serve, in turn, as a resource for plants), animals are consumers which regulate the population densities of other organisms or act as dispersers or pollinators. However, there are much more complex interconnections between individual species, which complicate the resolution of the roles. For instance, certain particular species of plants may support some species of animals or fungi which affect (positively or negatively) populations of other plants which in turn affect the presence of particular pollinators indispensable for reproduction of some plant species etc. In this case, therefore, although all individual species of plants perform the role of organic matter production, they are not interchangeable due to the differences in their ability to influence other species in a community.

It is generally possible to distinguish several types of organisms according to their importance. **Dominants** contribute to the majority of the biomass of a community: they include trees in forests, grasses in savannas or corals in coral reefs. The dominants substantially affect the structure and functioning of communities. However, other species also substantially affect community dynamics, without reaching high population densities. Such species are known as **keystone species**. These species could act, for example, as pollinators or seed dispersers, but classic examples of keystone species include predators which control the populations of species that represent some danger for the dominant species. Some mammal carnivores are able, for instance, effectively to control the populations of herbivores grazing on the dominant plants. Some keystone species may act as **ecosystem engineers**, i.e. organisms that directly influence the physical properties of their environments (such as beavers, elephants, or earthworms which substantially affect physical properties of the soil). However, determining that a particular species acts as a keystone species is often problematic, and almost any species could become a keystone species in a particular situation.

Ecosystems and communities are sometimes compared to an airplane, with individual species representing rivets. Some rivets could be removed without any effects, while removing some more rivets would lead to a catastrophe, but we are unable to say exactly how many species (rivets) are sufficient for maintaining a system. However, it appears that rather than diversity itself (which is, after all, only a quantity), it is the individual species and individual processes which are important: ecological attributes of species can influence ecosystem processes more than species richness *per se*. The goal of thinking profoundly about biodiversity is not to discover a general principle, but rather to develop respect for all individualities such as species, life forms and individual processes in particular environments. These individualities are the keystones of the living world.

Glossary

Biodiversity: In its most general sense, this word refers to all aspects of variety in the living world: the richness of living forms ranging from genes and molecules to whole ecosystems or, for example, body plans.

Biomass: The total weight of living organisms in a community.

Community: The set of populations of different species that occur together in space and time.

Competition: An interaction between two or more organisms that share common resources, the utilization of which leads to lowering of the individual fitness (and the reproductive rate) of at least some of the organisms.

Disturbance: A more or less unpredictable event that removes organisms from a community.

Ecosystem: A community associated by all the physical and chemical components of the immediate environment and characterized by energy flow and nutrient cycling.

Extinction: The loss of a species or population that arises from the death of the last surviving individual of that population.

Global diversity: Total species diversity of the Earth.

Local diversity: Species diversity of a particular community inhabiting a particular habitat.

Population: A group of individuals of one species in an area.

Population density: The number of individuals of a population per unit area.

Productivity: The rate at which biomass is produced per unit area, determined by the total amount of utilizable resources (i.e. energy input into an ecosystem).

Regional diversity: The diversity of regions which are so large that most species present presumably originated within them and did not colonize them from outside (the size of these regions is comparable to the size of species ranges).

Speciation: Origination of species by dividing an ancestral species into two or more new species.

Species: A group of organisms that share a common evolutionary path, ensured by interbreeding in sexually reproducing organisms.

Species diversity: A quantity referring to species richness; typically, the number of species in the respective community, region or taxon.

Species pool: The set of all species in a region that could potentially colonize a given locality.

Species range: The geographic area where a species lives.

Species selection: The process leading to differences in diversity among taxa due to their unequal chances of producing new species (unequal speciation/extinction ratio).

Taxon: A group of evolutionarily related organisms, i.e. a group of organisms that have a common ancestor. More rigorously, all the descendants of one ancestral species.