# GLOBAL BIODIVERSITY AND ITS VARIATION IN SPACE AND TIME

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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 biologists have studied the diversity of organisms 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.

## 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, and 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, and environments) and these individualities together are not easily reduced to a common denominator. Therefore, it refers also to the multi-dimensionality of the living world.

The scientific study of biodiversity from the ecological point of view 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? (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 individual species ecologies . 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 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, taxonomists and evolutionary biologists had of course, studied related phenomena much earlier. 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, that 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.

## 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. Evolutionary processes of speciation and extinction thus govern regional diversity. 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*).
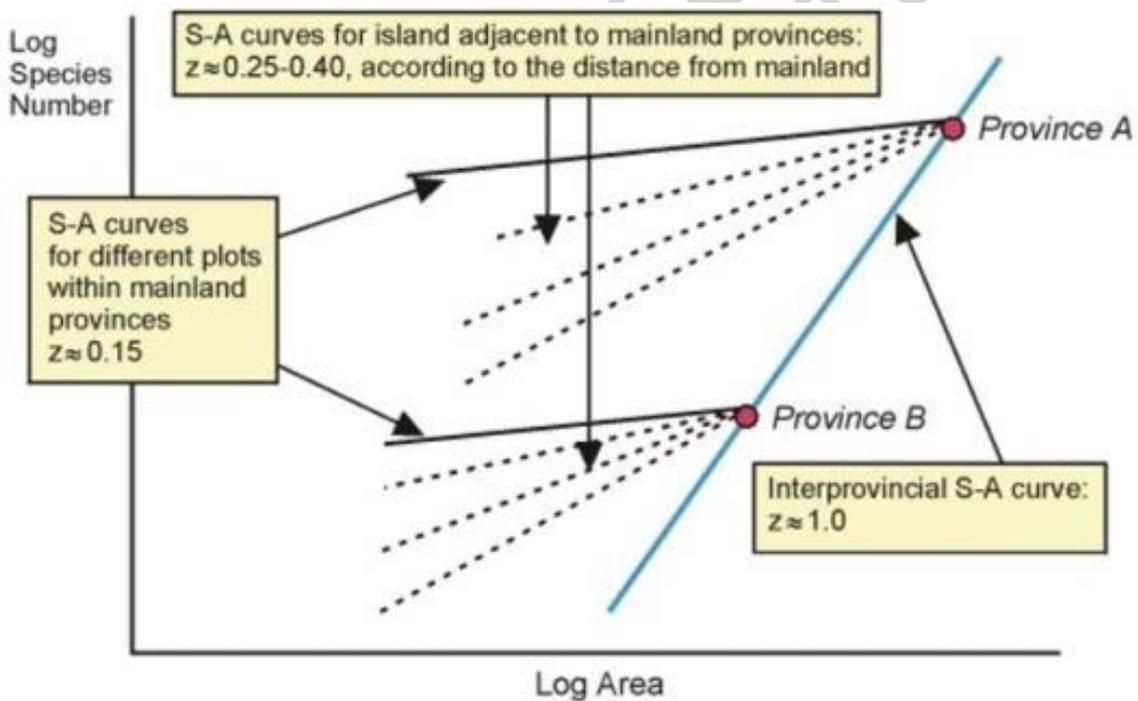


Figure 1. Species–Area curves. They are linear in a log-log scale, and they therefore could be expressed as a power law equation $S = c.A^z$, where $S$ = number of species, $A$ = area, $c$ = constant representing species diversity per unit area, $z$ = slope of the curve. The slope of the curve is the 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.

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 Figure 1).

This relationship 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 often 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 (see Figure 1).

## 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 out-compete 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 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 out-compete 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, 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 out-compete 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 out-compete 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 an important 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. 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 (see Figure 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.

## 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.

### 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, or a sea) and subsequently may evolve separately. Due to their independent evolution, when 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 ecological 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 — inter–specific hybridization and polyploidization 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 probable 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.

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**Biographical Sketch**

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