

# Diversity

**Dr. Tóthmérész Béla**

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## **Diversity**

Dr. Tóthmérész Béla

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# Előszó

A jelen digitális tananyag a TÁMOP-4.1.2.A/1-11/1-2011-0025 számú, "Interdiszciplináris és komplex megközelítésű digitális tananyagfejlesztés a természettudományi képzési terület mesterszakjaihoz" című projekt részeként készült el.

A projekt általános célja a XXI. század igényeinek megfelelő természettudományos felsőoktatás alapjainak a megteremtése. A projekt konkrét célja a természettudományi mesterképzés kompetenciaalapú és módszertani megújítása, mely folyamatosan képes kezelni a társadalmi-gazdasági változásokat, a legújabb tudományos eredményeket, és az info-kommunikációs technológia (IKT) eszköztárát használja.



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# 1. fejezet - Preface

Biodiversity is one of the central topics of ecology and environmental sciences. The biodiversity crisis is a frequent topic in the media nowadays. It forced biologists from many disciplines to interact and exchange data, which generally improves our overall understanding of ecology and evolution. Measuring diversity is a vital topic for the statistical ecologist, as well as the statisticians. This teaching material is a compilation of the most of the recent literature on biodiversity to help the students of ecology, statistical ecologists, and environmental scientists. Major theoretical and practical aspects are covered. The teaching material is mainly based on the following books, monography and encyclopedia, although it also contains a voluminous literature related to diversity.

Gaston, K.J. and Blackburn, T.M. 2000: *Pattern and Process in Macroecology*. Blackwell.

Hubbell, S. P. 2001. *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey, USA.

Jorgensen, S.E. and Fath, B. 2008: *Encyclopedia of Ecology*. Elsevier.

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Levin, S.A. 2000: *Encyclopedia of Biodiversity*. Elsevier

Léveque, C. and Mounolou, J-C. 2004: *Biodiversity*. Wiley.

Maclaurin, J. and Sterelny, K. 2008: *What Is Biodiversity?* University Of Chicago Press

May RM (1975) Patterns of species abundance and diversity. In: Cody M and Diamond J (eds.) *Ecology and Evolution of Communities*, pp. 81–120. Cambridge, MA: Harvard University Press.

May, R. and McLean, A. 2007: *Theoretical Ecology: Principles and Applications*. Blackwell.

McKinney, M.L. and Drake, J.A. 1998: *Biodiversity Dynamics*. Columbia University Press, New York.

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# 2. fejezet - Chapter 1 Diversity in Biology

## 1. A Brief History of Diversity Concept

Diversity is vital in science, as well as in social sciences. The term 'biodiversity' is perceived differently, depending on the scientific disciplines. Taxonomists, economists, agronomists and sociologists each have their own view of the concept. Biologists tend to define biodiversity as the diversity of all living organisms. In agriculture there are interested in exploiting the manifold potential deriving from variations over soils, territories and regions. Industry sees a reservoir of genes useful in biotechnology or a set of exploitable biological resources. These approaches are not independent of one another. They implicitly pursue the same objective, namely the conservation of natural environments and the species which they harbour.

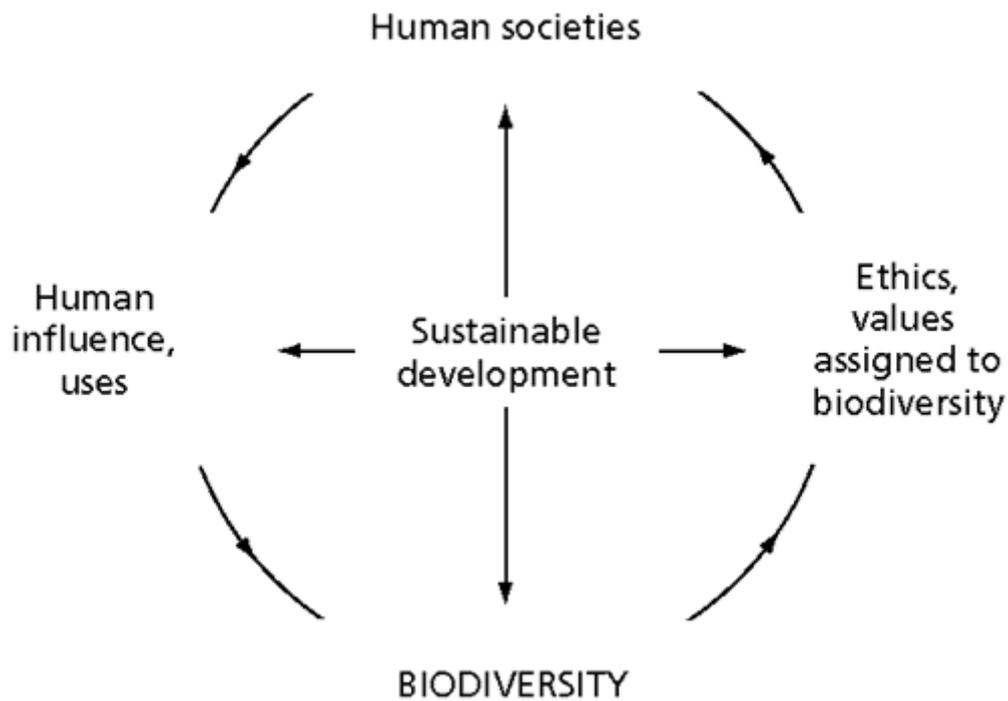
Biodiversity as a buzzword emerged as an environmental issue in the early 1980s, culminating in the Conference on Sustainable Development held in Rio in 1992. Towards the end of the 20th century, humankind grew conscious of its unprecedented impact on natural environments and the danger of exhausting biological resources. At the same time, biological diversity was recognised as an essential parameter in agricultural and industry. This also raised ethical questions about the conservation of biological diversity and patenting of living organisms. Nowadays biodiversity is a framework for considering and discussing the whole range of questions raised by human relationships with other species and natural environments, between ecological systems and social systems.

The concept of biodiversity is at the crossroads of natural sciences and social sciences. The natural sciences are striving to regain public interest; the social sciences are discovering the complexity, but also the richness, of the relationship between humankind and nature. Both sciences approach biodiversity as a field of application for the new relationships that are developing between humans and nature, raising new questions and concerns regarding the living world.

## 2. What does 'Biodiversity' Refer to?

The term 'biodiversity' is a contraction of *biological diversity*. It was introduced in the mid-1980s, and the term was adopted by the political world and popularized by the media during the debates leading up to the ratification of the *Convention on Biological Diversity*. The expression actually covers a number of essentially different approaches, orientated around four major issues.

Due to technological progress and the need to occupy new spaces to meet the demands of a rapidly growing population, humankind is impacting natural environments and the diversity of living resources to an unprecedented degree. The questions raised by this tendency vary considerably, as do the possible responses, depending upon the behaviour and choices of particular societies in their approach to economic development. It is a matter of implementing strategies for conservation so as to preserve the natural patrimony as the heritage of future generations (Figure 1.1).



**Figure 1.1** Interactions between human societies and biological diversity.

To understand the causes and conditions that have led to the diversity of the living world as we know it today, we need a new perspective on evolutionary processes. What are the biological mechanisms that explain species diversity? What are the interactions between changes in the biophysical environment and in the phenomena of speciation? Our knowledge of such matters remains fragmentary. While it is still important to continue with the process of making an inventory of species that was initiated by Linnaeus in the 18th century, we must also exploit modern methodological advances to penetrate the world of the infinitely minute and the molecular mechanisms involved in the diversification of life.

Advances in ecology are also redefining our approach to biological diversity as the product of dynamic interactions among different levels of integration within the living world. We are now aware that the living world acts upon and modifies its physical environment. The functional processes of ecosystems, such as the flows of matter and energy, are subject to the twofold influence of both physical and biological dynamics. This realization constitutes a major paradigm shift, challenging the customary tendency to consider only the influence of the physical context upon the dynamics of the living world, to the exclusion of other interactions. This integrated approach leads to new concepts such as functional ecology and biocomplexity.

Biodiversity is seen as 'useful' nature. The set of species and genes that humankind uses for its own profit, whether they are derived from natural surroundings or through domestication. In this context, biodiversity becomes a natural form of capital, subject to the regulatory forces of the market and a potential source of considerable profit to countries possessing genetic resources. The economic valuation of biodiversity also provides powerful arguments for the cause of natural conservationists.

New fields of research are emerging. The life sciences are seeking to reconcile genetics and ecology to improve our understanding of environmental impacts upon genome expressions and evolutionary mechanisms. We are moreover rediscovering that biodiversity is part of our daily life, that it may represent a considerable economic stake, and that legal experts are called upon to design effective laws for the protection of nature.

Biodiversity has become a social issue. It appeals to new moral values that question the priorities of economic models of development. A certain promise lies in the new, friendly relationship with nature that appears to be evolving in the West. Decision-makers and producers are under pressure to change their relationship with natural science specialists.

Scientists are no longer occupied simply with writing the necrology of species, they no longer stand by as helpless observers when major ecological disasters occur; rather, they are called upon to help degraded environments recover their biological integrity, their functions and ecological services. One instance of this role, the reinstatement of the salmon, has advanced to a symbol and turned into a qualitative standard for the European river ecosystem.

Preservation of the biodiversity that is our heritage requires local management by the populations immediately concerned. Conscious that it is in the nature of international law to lag behind events and that considerable economic interests are involved, it is legitimate to ask what the real implications of potential protective measures are. The shape of the future will necessarily depend upon the ways in which societies and scientists are able to make themselves heard by the policy-makers of today.

### 3. Biological diversity, biodiversity, biocomplexity

Traditionally, the term biodiversity has been used with regard to the depletion of the living world as a result of human activities, or activities undertaken for its protection and conservation. The term biodiversity will be used to refer to the whole range of activities traditionally connected with inventorying and studying living resources. The term biological complexity, or biocomplexity, belongs to the new scientific vocabulary of biodiversity. Biocomplexity is the result of functional interactions between biological entities, at all levels of organization, and their biological, chemical, physical and social environments. It involves all types of organisms from microbes to humans, all kinds of environments from polar spheres to temperate forests to agricultural regions, and all human activities affecting these organisms and environments. Biocomplexity is characterized by nonlinear, chaotic dynamics and interactions on different spatiotemporal scales. Integrating social and economic factors, it deepens our understanding of the living system in its entirety, rather than in bits and pieces.

### 4. Levels of organization in the living world

One of the characteristics of the living world is its complex structure and hierarchy: atoms organise themselves into crystals or molecules, and these molecules, in turn, organise themselves into cells capable of reproduction. Cells can aggregate and cooperate to form multicellular organisms.

The scientific discipline devoted to naming, describing and classifying living beings is called taxonomy. This science is highly formalized and follows the rules of the international codes of nomenclature. Systematics, on the other hand, studies the diversity of organisms and strives to understand the relationships between living organisms and fossils, i.e. the degree to which they share a common heritage. What is now called biosystematics is a modern approach to systematics that draws upon information from different sources: morphology, genetics, biology, behaviour, ecology. Taking into account the environment in which organisms live, increasingly complex entities emerge: ecosystems, landscapes and biosphere. On this hierarchic scale, the elements of one level of organization constitute the basic units for the composition of the next, higher level of organization. At each stage, new structures and properties emerge as a result of interactions among the elements of the level below.

The basic unit of the living world is the individual, each bearing its own genetic heritage. The pool of all genes belonging to one individual constitutes its genotype. A population corresponds to a group of individuals of the same biological species inhabiting the same surroundings. It is at this level of organization that natural selection occurs. A species is often distributed over separate populations. Its existence and dynamics are functions of exchanges and replacements among these fragmented, interactive populations, which are called metapopulations. Multispecific assemblages that are restricted, usually on a taxonomic basis, constitute settlements or communities. A biocenosis is a group of animal and plant populations living in a given place.

The term ecosystem was first introduced by Tansley in 1935 to designate an ecological system combining living organisms with their physical and chemical environment. The Convention on Biological Diversity defines ecosystem as 'a dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit'. This legalistic definition is fundamentally similar to that found in ecological textbooks.

The biosphere refers to all living organisms that inhabit the Earth's surface. However, biosphere may also be defined as the superficial layer of the planet that contains living organisms and in which enduring life is possible. This space also comprehends the lithosphere (terrestrial crust), hydrosphere (including oceans and inland waters) and the atmosphere (the gaseous sheath enveloping the Earth).

The phylogenetic hierarchy is based on the evolutionary relationships of groups descending from common ancestors. The cladistic classification system (sometimes called the Hennigian system) is based on the principle that during the course of evolution, an ancestral species gives birth to two daughter species. If one takes three species and compares them two-by-two, the pair that has the more recent common ancestor is grouped together. A group of species is termed monophyletic if it derives from a single common ancestor, while a polyphyletic group comprises species that manifest similarities but are not all directly descended from a common ancestor.

The methods of molecular phylogeny are also founded upon the hypothesis that resemblances between two organisms will be more numerous if their ancestral relationship is closer. Here, however, genetic sequences are compared rather than morphological traits. Thanks to the methodological advances of molecular biology, phylogenetic classification is currently progressing beyond phenetic classification.

## 5. The concept of species

Until the mid-18th century, systematists had a fixed conception of species: they were such as God had created them and limited in number. Accordingly, the aim of taxonomy was to compile an inventory of all the existing forms of life and describe their specific characteristics. Linnaeus formalized this concept by defining each species in terms of a single type (holotype). A species was constituted by the sum of individuals identical to each other and to its 'type' specimen. In other words, the sample specimen served to describe and characterise the species in morphological terms. Sample specimens were stored in a museum for future reference or as a sort of standard for later comparisons.

This fixed notion could not withstand the discovery of the mechanics of evolution (mutation, selection, genetic drift), and towards the mid-20th century, it gave way to the concept of dynamic biological species, founded not only upon resemblance but also upon the interfecundity among individuals constituting a population and among their descendants. Whilst the donkey and the horse can reproduce, they remain distinct species because their descendants are infertile. It is the reproductive isolation of a group of individuals that defines them as a species; however, demonstrating interfecundity is another matter. Because it is physically impossible to cross the majority of wild organisms so as to establish or refute their potential interfecundity, the concept of biological species is obviously difficult to apply. Besides, this definition can only be strictly applied to species that engage in bisexual reproduction, leaving the question of micro-organisms up in the air. Thus, despite certain reservations, species continue to be identified primarily by morphological descriptions wherever possible, complemented by a biochemical description, such as in the case of bacteria.

Within one species, it is possible to recognize various subunits that are considered as subspecies, races, strains, varieties, etc. There are no precise and universally accepted definitions for these intraspecific categories, which may be based on morphology, geography or genetics. Among the numerous races of domestic animals, we observe forms that are highly differentiated in morphological terms. However, intraspecific variability can also be expressed in other ways, for example in reproductive behaviour or modes of communication.

The new tools of molecular biology are a valuable aid in distinguishing individuals belonging to species that are morphologically very close: this is the case for sister species, which are true biological species that have achieved reproductive isolation but are still difficult to distinguish solely on the basis of their morphological characteristics. It is also now possible to investigate intraspecific genetic variability and the relationships among individuals with a greater degree of precision. Individuals within a population actually have slightly different genotypes. This genetic polymorphism can be quantified in terms of allelic frequencies that vary from one population to another and develop over time. In phylogenetic terms, species may be defined as a single lineage of ancestor-descendent populations, which is distinct from other such lineages within its range and evolves separately from all lineages outside its range.

## 6. Ecosystems

The concept of ecosystem is a rather abstract notion: a chemical and physical environment (biotope) is associated with a community of living organisms (biocenosis), and together they set the stage for a system of interactions among the constitutive elements. In practice, however, ecologists tend to define ecosystems as geographically defined entities such as lakes, watersheds or mountain ranges.

Ecosystem functioning is characterized by flows of energy between organisms such as plants that accumulate solar energy through photosynthesis, herbivorous animals that utilize this energy, and decomposers that recycle organic matter; biogeochemical cycles circulating matter in the form of mineral or organic substances. Such

cycles apply in particular to water, carbon, oxygen, nitrogen, phosphorus, etc.; food chains that impose a trophic structure upon the ecosystem. Trophic interactions are the driving forces for the flows of energy and matter. The concept of ecosystem is intrinsically dynamic: flows, biogeochemical cycles and trophic structures are continuously evolving over time and

## 7. Biocenoses

A core question of ecosystem ecology is whether the whole assemblage of species observed in a particular place is a fortuitous collection of populations that have succeeded in colonizing the ecosystem and maintaining themselves, or else a selection of co-evolved species that established a network of interdependencies over time. Many ecologists currently tend towards the latter theory, but they are having a good deal of difficulty substantiating these different types of interaction.

The time factor plays an important role. When a new habitat is created, it is colonised by opportunistic species, and its settlement is largely fortuitous. With time, there may be a co-evolution of species, and a greater degree of interdependence may develop. A good example to illustrate this phenomenon is the river, with its lowest water level and alluvial plain: in the course of the hydrological cycle, the spatiotemporal dynamics of flooding profoundly modify the landscape as well as the interactions among species. The biosphere is the ultimate ecosystem. Recognition of the importance of global factors (natural and human-induced climate changes, major biogeochemical cycles, globalization of the transfer of species, etc.) has stimulated scientific interest in this level of organization. Research on the global functioning of the ecosystem Earth has become a reality.

## 8. Biomes as ecological units

The distribution of species over the surface of the Earth is not random. It results from a combination of ecological factors, interacting with the preferences and abilities of organisms. On the basis of the combined factors of precipitation and temperature, the Earth can be divided into large morphoclimatic domains. On an extremely macroscopic scale, four ecoclimatic zones can be identified: tropical, hot and humid; temperate humid; polar; and arid. On a more differentiated scale, it appears that different regions with identical climatic conditions are occupied by comparable natural ecosystems. Vegetation has the virtue of being a quite reliable indicator for plotting the interplay of such diverse factors as geomorphogenesis and climate on rather large spatial scales. The boundaries of large vegetation formations mark the discontinuities apparent in the natural world. Homogeneous in climate (temperature and precipitations), biomes are macrosystems on a regional scale.

## 9. Succession

The emergence of the concept of succession at the beginning of the 20th century introduced the dimension of time into what had hitherto been a somewhat static perception of ecology, paving the way for research on the temporal dynamics of communities. The term succession is used to designate the process of colonization of a biotope by living organisms and the changes in floral and faunal composition that gradually take place in a biotope following a disturbance that has destroyed part or all of the pre-existent ecosystem.

Succession may theoretically proceed by the following stages. In a newly created, virgin environment ( juvenile ecosystem) or an environment that has just experienced a disturbance eliminating most of its species, so-called pioneer or opportunistic species will be the first ones to develop. These species are characterized by high fecundity and rapid population growth (demographic strategies of type 'r') and are not very specialized. Their trophic networks are simple. The biocenosis becomes more diversified with the apparition of species characterized by slower growth rates (demographic strategies of type 'K'); food chains become more complex. At the mature stage, species richness reaches a maximum, including lots of slowly growing species with high life expectancies. The web of interactions and trophic network are complex. Productivity is low, and a large proportion of matter is recycled on location. Ecosystems can sometimes be described as ageing, particularly when a small number of species get the upper hand over the others and eliminate them. The process whereby a lake gradually deteriorates and finally disappears, giving way to plant formations, is one particular manifestation of this aging process.

A fundamental characteristic of succession is its reversibility. A disturbance may result in the disappearance of all or part of species from the site. If the disturbance is severe and occurs at a mature stage, the cycle of succession is reinitiated, and the ecosystem is 'rejuvenated.' This process may occur repeatedly. Disturbances may take place either as cyclical or as chance

## 10. The concept of climax

In the early 20th century, Clements, an American ecologist placed the concept of climax at the centre of ecological theory (Clements, 1916). In its original sense, the climax is the ultimate steady-state achieved in the evolution of the vegetation of an ecosystem, following a succession of intermediary stages, and in the absence of natural or man-made disturbances. The climax community for any given region was thought to be determined by climate and soil conditions. The point is not to classify groups of plants as in phytosociology, but rather to understand the ecological factors driving the evolution of terrestrial vegetation towards a steady-state in accordance with the regional climate. In temperate climate zones of western Europe, for example, the climactic climax corresponds to a mixture of different types of central European and Atlantic oak trees, mountain beeches, and sub-Alpine coniferous forests (spruces, larches, mountain pines).

The concept of climax, as applied to ecosystems, reflects the quest for equilibrium that motivated population ecologists for a long time. However, this initial view was later challenged by other ecologists, who interpreted communities as random assemblages of species that would inevitably change in the long run.

## 11. The Dynamic Equilibrium of Ecosystems and the Role of Disturbances

For a long time, for both practical and conceptual reasons, ecologists studied homogeneous ecosystems that were more or less independent of one another. Natural environments, however, are heterogeneous, often fragmented, and they change over time. Long-term studies of ecosystems show that their state at any given time depends upon a combination of their history and the current dynamics of their environment. Over longer periods of time, they tend to oscillate around a median state with varying regularity and amplitude. Rather than remain in a so-called steady-state, an ecosystem is actually an interactive system: a change in the environment triggers a dynamic response throughout the whole system, including numerous positive or negative feedbacks. On the other hand, the ecosystem may also have influence upon its environment, implying a reciprocal relationship; the former is not entirely subordinate to the latter.

The important role that disturbances play in the dynamics of communities and ecosystems is one of the most interesting factors to shed new light on ecological paradigms in the last twenty years. A general definition of disturbance was advanced by Pickett and White (1985) and modified by Resh et al. (1988): 'any relatively discrete event in time that is characterized by a frequency, intensity and severity outside a predictable range, and that disrupts ecosystems, community or population structure, and changes resources, availability of substratum, or the physical environment'. For Townsend (1989), a perturbation is 'any relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species.' As for Sousa (1984), he holds a disturbance to be 'a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established'.

Disturbances can be qualified by different descriptive characteristics: type (physical, biological, etc.), pattern of occurrence (spatial distribution, frequency, intensity, duration, etc.) and regional context. Depending upon their nature and intensity, certain disturbances elicit no response from the ecosystem, while others, for example destroying a habitat and its settlement, may qualify as catastrophes. More generally, a disturbance usually leads to a general restructuring of the ecosystem. In this sense, it can be seen as a rejuvenating process within the phenomenon of ecological succession.

## 12. The intermediate disturbance hypothesis

In a famous paper Hutchinson (1961) describes what he calls the plankton paradox: many more species of phytoplankton have been observed to coexist in a relatively simple environment than are accounted for by the theory of competition and the limitation of resources. He therefore reverses the logic of the question: could the great species richness observed not be the consequence of fluctuations in the environment that prevent it from attaining a state of equilibrium over time? If this were so, then coexistence would be the result of non-equilibrium phenomena, rather than characteristic of a state of equilibrium. In a context where equilibrium theories are the predominant paradigm, such novel ideas have been slow to receive the attention they deserve. But they point the way towards future discoveries about the impact of perturbations upon the specific richness of ecosystems.

Already, many ecological investigations have reached the conclusion that disturbances might actually work in favour of biological diversity by lowering the pressure of dominant species upon other species and allowing the latter to develop. Proposed by Cornell (1978) 'the intermediate disturbance hypothesis predicts that species richness will be greater in communities with moderate levels of perturbation than in communities without any disturbances whatsoever or communities that are subject to overly large and/or frequent disturbances'. The initial objective of this hypothesis was to explain the high specific richness of tropical forests and coral reefs. Where disturbances are infrequent, interspecific competition limits the number of species likely to become established, and the most competitive species occupy the available space. Conversely, when perturbations are frequent and/or intense, the dominant competitive species are eliminated, and only colonizing species with brief life cycles are successfully able to maintain themselves. If the disturbances occur with moderate frequency, intensity and amplitude, resident species will cohabit with pioneer species, resulting in the greatest specific richness.

## **13. Fragmented communities**

In an environment characterized by spatial heterogeneity and/or fragmentation of ecosystems, populations of the same species tend to be fragmented and more or less isolated from one another. Since the 1980s, the theory of island biogeography has prepared the way for the theory of metapopulations, which has been the basis for many theoretical and empirical studies on the effects of habitat fragmentation upon populations. A metapopulation is a group of geographically more or less isolated subpopulations interconnected by individual exchanges that contribute toward maintaining the gene flow between the different subpopulations. A relatively simple instance is that of populations inhabiting oceanic or continental islands with continuous or occasional exchanges among them. In a metapopulation, certain subpopulations where births outnumber deaths act as 'sources' from which individuals disperse towards other areas. Conversely, certain subpopulations live in harsh environments where mortalities exceed births. Such environments constitute 'sinks.' A metapopulation is thus a dynamic system characterized by migration flows and processes of extinction between and within the subgroups of a fragmented habitat. The concept of metapopulation can be extended to multispecific communities, a metacommunity being defined as a group of ecological units sharing certain biotic components and among which exchanges are possible.

## **14. Patch dynamics**

Landscape ecology provides ecologists with a simplified view of heterogeneity by defining space as a mosaic of 'patches' (spatially delimited structures at a given time) arranged over an ecologically neutral matrix. This spatial model grows progressively more complex when the varying characteristics of different patches and their temporal dynamics are taken into account. The patch dynamics concept provides the link between the mosaic distribution of communities (metacommunities) and the spatial/temporal dynamics of the patches. Patches may either disappear or grow over time, as a function of fluctuations in environmental factors. Depending upon the prevailing tendency, associated communities can be either senescent, or pioneers or correspond to a stage in a succession cycle. Moreover, each patch of the matrix and its communities may have completely different dynamics from the others. The seasonal inundations and flood recession of river beds are a good illustration of patch dynamics in that variations in water level create and/or modify the spatial heterogeneity of the river channel.

According to Townsend (1989), the concept of patch dynamics is a major unifying principle in the ecology of running waters, where ecological characteristics such as current speed, substrates and availability of resources tend to manifest considerable spatial heterogeneity. Patch dynamics imply the following principles. Natural or man-made disturbances act upon ecosystems to modify the distribution of habitats over time and space. To give a simple example, river floods create new aquatic habitats as well as modify ecological conditions in already flooded habitats: current speed, depth, etc. The reverse applies equally when the waters recede. In a heterogeneous system, pioneer populations take hold as soon as habitats become available and usually evolve towards a more mature state. Thus, different patches will find themselves at different stages of ecological succession at the same time, as a function of the chronology of inundations. Because they are dynamic over space and time, the assemblages are able to maintain a much greater biological diversity than systems evolving towards a climax in a monotonous way. Such dynamics may allow the co-existence of several species, with different ecological needs, in different patches, that are at different stages of evolution. Thus, spatial heterogeneity and temporal variability are actually key elements in ecosystem functioning and the structuring of communities, and not just a simple 'background noise' that disturbs population dynamics.

Phenomena occurring on large spatial and temporal scales provide a partial explanation for the composition of local communities. The example of river basins provides a good illustration for scales of interaction and the long-term consequences of certain events. The qualitative and quantitative composition of the fish communities inhabiting river basins is actually the result of numerous past events interacting with contemporary ecological factors. Tonn (1990) proposed a theoretical framework based on the principle that the local composition of species is the result of a series of filters acting on different scales of time and space. Species must have passed successfully through these successive filters to be present in the basin under consideration.

The number of fish species in a watershed is thus the result of an equilibrium among: processes of colonization and extinction, depending in part upon the past history (climatic, geological, etc.) of the basin; processes of speciation, resulting from the evolutionary potential of the families present and the duration of their isolation; and competitive phenomena and/or epidemics. The model proposed by Tonn is actually an extension of the concept of patch dynamics on the global level and over very long periods of time.

## 15. Biological Diversity: a Dynamic System

The role of biological diversity in an ecosystem concerns three levels of integration in the living world. Intraspecific diversity, i.e. the genetic variability of populations. It is due to the genetic diversity which is their biological heritage that species are able to respond to changes in the environment. Diversity among species in terms of their ecological functions within the ecosystem. Species exist in a large variety of forms, with different sizes and biological characteristics. Operating individually or in groups within trophic webs, these properties influence the nature and magnitude of the flow of matter and energy within the ecosystem. The different interactions among species, not only competition but also mutualism and symbioses, contribute collectively to the dynamics of an ecosystem. Ecosystem diversity, corresponding to the variety of habitats and their variability over time. Specific richness is usually considered a function of the diversity of habitats and the number of potentially available ecological niches. Owing to their biological diversity, ecosystems play a global role in the regulation of geochemical cycles (fixation, storage, transfer, recycling of nutrients, etc.) and the water cycle.

In the ecological sense of the term, biological diversity results from dynamic interactions within and among the levels of organisation of the living world, as well as with the physical and chemical environment that it contributes towards modifying. The functioning of ecosystems and their flows of matter and energy are thus reciprocally controlled by physical, chemical and biological processes.

## 16. Food Webs and Trophic Chains

The nature and intensity of the trophic relationships between species living in the same ecosystem play a central role in the circulation of matter and energy. Understanding these relationships is crucial to ecological theory. In schematic terms, the chain of dependencies whereby some organisms eat other organisms, before being eaten by yet others in their turn, constitutes a food chain, or trophic chain, and provides a highly simplified description of the circulation of matter or energy through different levels: from autotrophic producers to final consumers. Of course, the reality is far more complex. Trophic webs describe the multiple interactions between species, including relationships of eater to eaten, as well as competitive relationships over the use of the same resources.

## 17. The Diversity of Species and Biological Production

It is not new to postulate the existence of a relationship between species diversity and ecosystem productivity. However, this fact has not yet been conclusively demonstrated. Environments that are poor in species, such as deserts and tundra, are also systems of low productivity, as compared with species-rich tropical forests. Conversely, humid zones or agricultural systems exhibit high biological productivity coupled with a reduced number of species. Thus, high productivity is not necessarily associated with great biological diversity. In fact, numerous observations appear to demonstrate that the flows of energies in ecosystems are not much affected by the number of species present.

In order to learn more about the role of biological diversity in ecosystem functioning, and given the difficulty of studying this question in the natural world, ecologists have carried out numerous experiments in controlled environments. These experimental set-ups enable researchers to test ecological theories and study natural processes under simplified and controlled conditions. At Ecotron (in the UK), natural environments are

simulated in 16 different enclosures, controlling factors such as light, rain, humidity, temperature, etc. These miniature ecosystems may contain up to 30 plant and metazoan species, representing four trophic levels (plants, herbivores, parasitoids and detritivores), interacting over several generations. It is possible to make replicas for statistical analysis.

Experiments have also been carried out in plots in natural situations. The objective of the European BIODEPTH (BIODiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems) project is to confirm or refute the existence of a relationship between specific richness and productivity in grassland ecosystems. The project has eight sites, ranging from Sweden in the north to Greece in the south. Early results indicate a general effect of plant diversity upon biomass production, independent of grassland type and geographic location.

Three general conclusions emerge from different experimental studies investigating the relationship between species richness and ecosystem productivity. Greater specific richness constitutes a form of insurance for long-term ecosystem functioning. Ecosystems where several species fulfill the same functions (redundant species) appear to be better adapted to respond to disturbances than those in which each species fulfills one, unique function. In other words, if several species exploit the same resources, as is the case for generalist herbivores, the gain or loss of one species will have an effect upon the composition of the communities, but it will have little impact upon the ecosystem processes, insofar as the other species will compensate the change. The behaviour of such communities is quite predictable. However, not all ecologists support the idea that biological diversity causes an ecosystem to function better. According to certain studies, ecosystem responses to such changes depend upon the specific composition of the community and its biological or morphological characteristics. In experiments carried out under controlled conditions, the presence or absence of species more able to use the resources than others (so-called dominant species) has emerged as one important explanatory factor. In reality, it is not so much species richness, as such, that is important, but rather the biological characteristics of the species and the diversity of functional types represented. These qualities are much more difficult to quantify than specific richness. Under these circumstances, it is not so easy to predict how a system will behave in the event of a gain or loss of species (cf. the drivers' and passengers' hypothesis).

Interactions among species may generate positive or negative feedback at the ecosystem level that combines with previous effects. Given the complexity and variability of the interactions involved, these effects are usually difficult to establish; nevertheless, the importance of such processes should not be disregarded. Particularly in food chains, changes in one functional group may have important consequences for the dynamics and production of other functional groups (see, for example, the theory of trophic cascades). All these studies point to the conclusion that a greater biological diversity is more favourable to the production and stability of ecosystems and helps to ensure the perpetuation of the cycles of matter and energy.

## 18. Biological Diversity and the 'Stability' of Ecosystems

The term 'stability' is highly contested. It derives from the idea that an ecosystem has a structure and mode of functioning that endure over time, at least on the time scale of human beings. Persistence and permanence are terms sometimes employed to characterize ecological systems that maintain themselves in this fashion without significant modifications. The term resilience (or homeostasis) refers to the capacity of an ecosystem to recover its primitive structure after having been subjected to a disturbance.

The question of the relationship between biological diversity and the resilience or stability of ecosystems has been much debated. One more or less intuitive postulate holds that the more diversified an ecosystem is, the more stable it will be. Based upon the existence of redundant species, this hypothesis expresses a simple presupposition: if the number of linkages in an ecosystem increases, then the disappearance of any one linkage will soon be compensated by the development of another.

Some recent results support this hypothesis. Both laboratory and field experiments have shown that greater specific richness may lead to an increase in the retention of nutrients within the ecosystem. Moreover, modellers have also been able to demonstrate that complexity tends to stabilise ecosystems by dampening the impact of temporary fluctuations in populations. It is similar to a buffer effect. It has been observed that, in the long term, a certain degree of permanence in an ecosystem tends to promote biological diversity. The great lakes of East Africa (Lake Malawi, Lake Tanganyika and Lake Victoria) are a good example: over the course of their several million years of existence, these lakes have acquired a large diversity of endemic species, including communities of fish and invertebrates that are highly specialized on the ecological level. Conversely, in lake environments of more recent origin, such as those of northern Europe or North America that appeared only after

the retreat of the ice caps around 15'000 years ago, communities are not very diversified and are essentially composed of species with a wide distribution range. The evidence that complexity is important to preserve the entirety and stability of natural systems lends weight to ecologists' argument for the necessity of preserving the totality of the species coexisting in these ecosystems.

## 19. List of animation, audio files and movies

animation Adopt a seed, save a species animation.mp4

animation Beer and Biodiversity.mp4

animation Biodiversity begins.mp4

animation Biodiversity Cartoon.flv

animation Launch of the International Year of Biodiversity.flv

voice Biodiversity-Introduction.mp3

video Global Biodiversity Outlook.flv

video International Year of Biodiversity.flv

## 20. Questions

- How to define biodiversity?
- What is the role of biocomplexity in maintaining diversity?
- Why is important to preserv biodiversity?
- What is the relationship of diversity and stability?

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## 3. fejezet - Chapter 2 Bioiversity and Genetics

The conservation of biological diversity, its sustainable use and the equitable sharing of its benefits, are the fundamental objectives of the Convention on Biological Diversity. The reasoning behind this Convention and its ratification by the large majority of nations is relatively simple. It stems from the recognition that the direct impacts like overexploitation, destruction of habitats, and indirect effects of human activities upon natural environments constitute a threat to the future of biological diversity, the renewal of resources and, more generally, to the conditions for life on Earth. Urgent measures are therefore necessary. The declared objectives of the Convention are at the same time highly ambitious and extremely vague: to foster sustainable development, while protecting and using biological resources, without reducing the diversity of species or destroying habitats and major ecosystems.

It seems obvious that if human activities are the immediate cause for the erosion of biological diversity, then the solutions and remedies for the problem must lie in the realm of social behaviour. In other words, the conservation of biological diversity is contingent upon choices made in economic development issues at both national and international levels.

The terms conservation and protection cover a large variety of practices. They may be used interchangeably or with different meanings, depending upon the country and speaker. This adds a certain amount of confusion to the debate. **Conservation** is an approach that considers the long-term viability of ecosystems within the context of resource and environmental management projects. Conservation involves a concept of protection that does not prevent humans from intervening in natural processes; it is rather a philosophy for managing the environment without resultant waste or depletion. The term **protection** is reserved for operations aimed explicitly at safeguarding environments or species endangered by human activities. The emphasis is upon defending specific ecosystems.

### 1. Why Protect Biological Diversity?

For centuries, scientists accumulated knowledge about nature without concerning themselves with the conservation of natural systems and their biological diversity. Nature was a seemingly inexhaustible reservoir, providing humans with everything they needed, whilst at the same time offering vast spaces for the disposal of waste and pollutants. During the

20th century, this attitude underwent considerable change. The European societies of the late 19th century tried to encourage a more rational exploitation of nature's riches. The object was to maintain conditions favourable to the regeneration of living resources so as to ensure their continued exploitation: preservation rhymed with production. This productivist approach led by reaction to the first ecological awareness of nature. Essentially protectionist, its philosophy was to preserve the status quo of certain elements of 'wild' nature. The emphasis was on conserving pristine and inviolable natural domains, sanctuaries valued as landscapes or for their flora or fauna, 'natural monuments.' This is how natural reserves and protected areas were created in many countries. Humans were considered as threats and generally excluded.

Since the 1980's, attention has turned to the economic value of biological diversity, both as a source of genetic resources for agriculture, and for its industrial uses (new molecules for the pharmaceutical industry, biotechnologies, etc.). In this context, biological diversity is seen as a potential source of revenue, in particular for the developing countries, providing an in fine justification for interest in its conservation. If we fail to take the necessary measures, we shall lose the opportunity to derive profit from the potential benefits that biological diversity may bestow upon humanity. Lastly, it is now recognised that biological diversity plays a significant role in maintaining the major equilibriums of the biosphere. Biological diversity is involved in the water cycle and the major geochemical cycles, including the carbon and oxygen cycles. It contributes to the regulation of the physical/chemical composition of the atmosphere, influences the major climate equilibriums, and thus impacts the conditions of life on Earth. All ecological functions are a product of the complex relationships among living species.

The conservation of biological diversity is structured around two distinct but converging traditions. Resource management, which implicitly acknowledges that the protection of 'useful' species is necessary for economic

development. Biological diversity has an economic value; it is considered a treasure to be exploited and turned to profit. It forms the basis for human nutrition. It provides the raw materials for the agricultural and food industries, the pharmaceutical industry, the perfume industry, etc.. From our current perspective, biological diversity offers promising prospects for profit-making in the realm of biotechnology, especially considering the potential of micro-organisms, which still represent a largely unexplored world. Another source of revenue worth mentioning is ecotourism, appealing to urban dwellers keen to experience nature and observe wild species in their natural environment.

An ethical perception of nature, holding that any and all disappearance of species is a loss and demanding maximum protection of biological diversity. The Conference in Rio and its debates on the Conservation of Biological Diversity clearly showed that there is a moral dimension to this question, an extension of the philosophical debate on the relationship between humans and nature. The extinction of species confronts humans with the fundamental moral problem of their relationship with other forms of life and their responsibility for preserving its diversity. As Hans Jonas put it, the question is whether one generation or one people has the right to appropriate and eliminate a large number of species that evolved over hundreds of millions of years and what is the extent of their responsibility. Do we not have the duty to bequeath to our descendents a world equivalent to that which we inherited ourselves?

## **2. The principle of responsibility**

For a long time, Western societies did not think of the environment in ethical terms. Only around the 1980's did we begin to accept that our relationship with nature entails an ethical dimension. Hans Jonas was one of the precursors of this approach; in simplified terms: modern humans have such a powerful technological hold over nature that they are in a position to endanger the future of the world. Scientific and technological progress may dangerously undermine the major equilibriums of the biosphere, compromising the quality of human life and the very survival of future generations. Technology cannot be corrected by technological means. Solutions must be sought beyond the realm of rational science, necessarily invoking an ethical principle, i.e. a general theory of political, moral or legal norms to guide human actions.

Where science fails, ethics intervene. This is what Jonas calls 'the heuristics of fear.' The impending danger tells us that the survival of humanity is at stake, and we are under obligation to protect it by taking appropriate measures to avert catastrophe. Thus, humankind becomes responsible for its own future (the principle of responsibility), vested with the mission to safeguard the survival of humanity, since remaining passive would endanger its survival. Humankind today has a responsibility towards future generations. We must bequeath them a communal patrimony with access to sufficient natural resources in order that they, too, will be able to lead a decent existence.

## **3. In situ and ex situ conservation**

One customary practice is in situ conservation, which consists in maintaining living organisms in their natural environment. To conserve individual species, some effective approaches are: enacting legal protection for the endangered species; improving management plans; and establishing reserves to protect particular species or unique genetic resources. This kind of conservation enables plant and animal communities to pursue their evolution, whilst adapting to changes in their environment, and comprises a large number of species, without requiring preliminary inventorying. However, in situ conservation is not always possible, because many habitats are already seriously disturbed, and some have even disappeared entirely. In such cases, the alternative is ex situ conservation, which consists in preserving species outside their natural habitats. This is one of the roles of botanical and zoological gardens; other methods such as gene banks are also used.

## **4. Species versus ecosystem conservation**

Ever since humans first became interested in nature, their attention has been focused on species, which are generally easier to study than ecosystems. We have inventoried species and compiled lists of extinct species, of disappearing species, or species to be protected. Some of these species have a powerful symbolic or charismatic appeal. The panda, for example, is the emblem of an NGO (the World Wildlife Fund or WWF); the puffin is the emblem of the LPO (League for the Protection of Birds, the French affiliate of Birdlife International), and for a long time, the otter was the emblem of the Council of Europe's conservation department. Generally speaking, the 'species' approach appears firmly established in the world of nature protection and conservation. But new ideas are developing. Many feel that a policy for the conservation of biological diversity must above all strive to

safeguard ecosystems, because it is illusory to protect species without at the same time protecting their natural habitats. It is for this reason that the Convention on Biological Diversity recommends the conservation of ecosystems through policies for protected areas and sustainable management. The ultimate aim is to ensure the preservation of diversity over entire ecosystems, not merely in their components. The European directive 'Habitat' and the network Natura 2000 (see Section 10.3.3) meet these priorities.

## **5. What are the priorities for conservation?**

Is it possible to preserve the entire biosphere? This suggestion is unrealistic, because human activities necessarily involve both predator behaviour and the occupation of territory for agricultural and/or urban purposes. The logical approach, embodied in the concept of sustainable development, is to try to compromise between the economic progress necessary for the well-being of humankind, which is invasive and coercive by nature, and biological diversity, which needs free spaces. In practice, this approach relies on political decisions: which kinds of ecosystems should be protected as a priority? How should they be distributed? What criteria can help us to select which areas or species to protect?

Different propositions have been made for setting priorities. Protect endangered species. This is an extension of the 'species' approach that is applied in protecting e.g. the panda, gorilla, and the great African fauna in general. Assign priority to protecting lines of evolution that are in danger of disappearing from the face of the Earth. It must be noted that sixteen of the designated hotspots are in countries where economic conditions are difficult, prohibiting serious conservation policies, and a large part of the original environment has already been destroyed. This is the case e.g. in Sri Lanka, Madagascar, and the Atlantic forest of Brazil. By no means should the economic vulnerability of these countries be used as a pretext to turn them into expensive 'Indian reservations,' run by international authorities composed mainly of representatives from the rich countries.

## **6. What about the cost?**

Conservation comes at a price. Theoretically, protected areas should be created in zones that are rich in biological diversity, i.e. in developing countries, who often have more pressing economic priorities than to devote their meagre resources to the conservation of species and ecosystems. At the same time, developed countries demand free access to natural resources for use in biotechnology. This causes an economic conflict between the retainers of an economically unexploited, potential treasure vs. industrial users, who have until now enjoyed favourable conditions, including free access to genetic resources. This North-South conflict was clearly apparent while elaborating the details of the Convention on Biological Diversity.

In theory, the Convention on Biological Diversity provides for the transfer of financial resources and technologies from developed countries to developing countries. The Global Environment Facility (GEF) controls this financial mechanism of the Convention. Since its creation in 1991, the GEF has allocated 2.2 billion dollars to activities relating to biological diversity, whilst also encouraging new investments on a national scale in all countries that signed the agreement. This sum may appear large, but it is actually risible compared with what would need to be spent. It is far removed from the annual required investment as evaluated in Rio: 125 billion dollars per year. . .

## **7. Protected areas**

The generic term 'protected areas' is applied in connection with a number of different situations, ranging from large reserves for flora and fauna to small sites dedicated to the conservation of particular species. These may be integral reserves, excluding human intervention, or inhabited zones in which the protection of flora and fauna is ensured by involving local populations in the management of the environment and its species. At present, there are an estimated 4500 protected areas in the world, representing 3.5% of its surface above sea level.

## **8. National parks: nature versus humans**

Toward the end of the 19th century, the general feeling was that conservation and exploitation of natural environments were two incompatible activities. It was therefore deemed necessary to remove entire sections of nature from human contact, which was considered to be the principle factor of disturbance. One of the first national parks in the world was created in this abiding spirit: the United States' Yellowstone Park, inaugurated

in 1872. Although it is now fashionable to criticise it, this approach is not entirely void of common sense if practiced judiciously.

But creating protected areas within inhabited zones poses social problems. In some cases, it has been necessary to resettle local populations and deny them access to zones they previously used. Under such circumstances, they are hardly motivated to respect regulations that the responsible administrations find difficult to apply for lack of sufficient means. This situation encourages poaching and sometimes engenders real social conflicts.

The example of the Galapagos National Park in Ecuador, one of the most prestigious in the world, illustrates the difficulties of reconciling the rationales of different actors: the naturalists who created the park in 1959 as a laboratory to study evolution; the inhabitants of the archipelago, whose territory is currently limited to four islands, while the population (15 600 inhabitants in 1998) is seven times what it was at the time of the park's creation; and the government of Ecuador, interested in developing a global tourist magnet. The attraction (66 000 visitors in 1999) has proved lucrative for enterprises outside the island, but has brought little benefit to the inhabitants of the park itself. The result is rapid deterioration of the natural environment due to over-frequentation, and impoverishment of the inhabitants, who have resorted to intensive fishing for exportation, causing ecological damage.

This is why planners have increasingly encouraged participation of local populations in the conception and management of protected areas towards ensuring the sustainability of such projects. In order to encourage indigenous populations to improve their management of biological diversity, it is necessary to improve their living standard and give them economic incentives for practicing effective conservation. Thus, some projects integrate conservation and development with the object of reconciling the development of new economic activities with conservation activities.

The example of the Biosphere Reserves is interesting in this connection, particularly as the project has an international impetus. The concept of biosphere reserves was first proposed in 1974 by UNESCO's MAB (Man and the Biosphere) programme. What distinguishes it from the traditional perception of reserves is that it tackles the joint objectives of conservation and development simultaneously.

The Biosphere Reserve Network currently comprises 409 reserves distributed over 94 countries. They are conceived in response to the question: how can the conservation of biological diversity and resources be reconciled with their sustainable use? The reserves represent an attempt to act on the principle that local populations constitute one of the driving forces of conservation, and that it is impossible to preserve large regions by excluding them. Local populations, management bodies, conservation movements and scientists must together search for solutions towards reconciling the conservation of biological diversity with economic development.

The effectiveness of conservation in protected areas varies enormously throughout the world. It must be said that many of the regions designated as protected are in reality not protected, due to lack of qualified personnel, financial resources, adequate ecological expertise, or conflicts with local customs. Consequently, they remain menaced by agricultural and urban expansion, as well as poaching.

## **9. Europe and biodiversity: Natura 2000**

The Bern Convention of the Council of Europe on the conservation of wild fauna and natural habitats in Europe was held in 1979. Its objective was to promote cooperation among the nations of Europe in order to ensure the conservation of wild flora and fauna and their natural habitats. Special attention was focused on species (including migratory species) that are vulnerable and threatened by extinction, such as the European white stork, the crane, or the griffon vulture. The 'Bird Directive,' adopted in 1979, was the first step towards ensuring the long-term protection and management of all bird species living in the wild within the communal territory of the Council members, as well as their habitats. The Member States are responsible for safeguarding this communal patrimony of all Europeans, with particular emphasis on protecting the natural habitats of migratory birds.

The Bird Directive inspired the European Union to enact its Directive of 1992 for the conservation of natural habitats (known as the Habitat Directive). Its aim is to ensure the preservation of biological diversity by conserving natural habitats as well as wild flora and fauna, with special emphasis upon species of communal interest. It envisages the implementation of a network of protected areas called Special Areas of Conservation (SACs).

The NATURA 2000 network is an ecological network of protected areas in Europe. Comprising the relevant sites of the European Bird (1979) and Habitat (1992) Directives, its purpose is to preserve biodiversity,

especially in rural and forest areas. The idea is to promote a form of management that is beneficial to the habitats of wild flora and fauna, whilst also taking economic, social and cultural constraints into consideration, as well as the regional and local particularities of each Member State. It is not the intention of the Natura 2000 network to create 'nature sanctuaries'; human activities (including hunting) are incorporated, as in the biosphere reserves.

The Member States proposed a list of sites to the European Commission, and an official list of sites of community importance was compiled in liaison with the 'Nature' theme department of the European Environmental Agency, forming the Natura 2000 network. The Member States committed themselves to establish such sites as special conservation zones and take the necessary measures to ensure their protection.

To apply the directives and implement a coherent conservation policy, it is necessary to draw up a typology of the habitats in question to enable their description and monitoring. An important source of information, the European Nature Information System (EUNIS), was implemented to harmonise the terminology and facilitate the use of data. Habitats were classified on the basis of earlier European initiatives: the CORINE Land Cover and the Classification of Palearctic Habitats of the European Council.

## **10. Sustainable use of Biological Diversity**

The policy of protected areas is a stopgap solution for the short and medium term. Many people believe that the goal of biodiversity conservation must be pursued within the larger context of sustainable development. More generally, conservation should be an integral part of a global vision of land management, defining zones for agriculture, industry or urban living, as well as areas to be protected. So far, this is rarely the case.

The concept of sustainable development is a compromise that acknowledges the validity of development but tries to reconcile the process of economic development with environmental protection. From a long-term perspective, sustainable development is development that meets the needs of the present, whilst at the same time preserving the world's 'natural' heritage for future generations.

Practical application of the concept of sustainable development is founded upon the idea that biological diversity can only be preserved in well-functioning ecosystems. Emphasis is on the need for integrated management of environments and resources. This counterbalances the narrow approach that prevailed for too long and was preoccupied with deriving short-term profits from exploiting certain resources.

The concept of sustainable development breaks with the ideology of 'development' and 'modernisation' that prevailed after the Second World War. Sustainable development has three dimensions:

*An ecological dimension:* Sustainable development asks what limits need to be placed on industrialisation in order to preserve natural resources. The object is to manage and optimise utilisation of natural capital rather than squander it.

*An economic dimension:* With a view towards the present and future impacts of the economy on the environment, this approach considers the choices involved e.g. in financing and improving industrial technologies, as they relate to natural resources.

*A social and political dimension:* Above all, sustainable development is an instrument of social cohesion and a process of political choice. Priority should always be given to equitability – between generations and among States. Any reconciliation of environment and economy must stand up to this double imperative.

World War II. Sustainable development means modifying production methods and improving consumer habits, as well as changing the everyday behaviour of individuals. In theory, if not necessarily in practice, the Western model of development is no longer considered to be the unique and necessary model for social development. Different forms of development correspond to the diversity of situations and cultures in the world.

Sustainable development in agriculture is central to wise biodiversity management. In practice, it is necessarily a compromise between what is economically viable, technically possible, and ecologically acceptable. Thus, in the 1960's, cultivation of high-yield crops with intensive use of fertilisers and pesticides achieved a considerable increase in productivity; however, such progress proved detrimental to the environment and biodiversity in certain regions. From the perspective of general management of renewable resources, the goal is to conceive and implement production systems that are better integrated in their environment and maintain their ecological

viability. This presupposes, among other things, that cultivation systems become more diversified and that farmers devise new technological itineraries: rotations, choice of crop varieties, cultivation methods, etc.

## 11. Ex Situ Conservation

Living collections are found in botanic gardens and zoos, conservatories, and public and private arboreta. They play a fundamental role in the conservation of disappearing species and in programmes for reintroducing them into the natural world. They are an essential tool for the genetic resource management of useful plants and domestic animals. Each Contracting Party shall, as far as possible and as appropriate, and predominantly for the purpose of complementing in situ measures: (a) Adopt measures for the ex situ conservation of components of biological diversity, preferably in the country of origin of such components; (b) Establish and maintain facilities for ex situ conservation of and research on plants, animals and micro-organisms, preferably in the country of origin of genetic resources; (c) Adopt measures for the recovery and rehabilitation of threatened species and for their reintroduction into their natural habitats under appropriate conditions; (d) Regulate and manage collection of biological resources from natural habitats for ex situ conservation purposes so as not to threaten ecosystems and in situ populations of species, except where special temporary ex situ measures are required under subparagraph (c) above; etc.

## 12. Botanic gardens

Around 1600 botanic gardens exist around the world. The earliest collected plants for traditional pharmacology. Later, they served as acclimatisation gardens for tropical species brought back by travellers, which they tried to domesticate or use to develop new cultures for economic or decorative purposes. Botanic gardens assemble flora from conquests, commercial trade and exploratory expeditions. In recent times, their mission has changed once again. New establishments specialise in the flora and fauna of a particular environment (often a local region) with a view towards developing conservation biology and educating the public.

The toromiro (*Sophora toromiro*) is a tree endemic to Easter Island, whence it disappeared around 1960. Several botanic gardens that had preserved seeds networked to create reproductive populations for implantation on Easter Island. Given the growth rate of the tree, it will be another hundred years before we know whether their reintroduction has been successful.

Botanic gardens have always exchanged specimens and information among themselves and with private collectors. While these activities contribute towards enlarging the range of registered plant diversity, the chosen samples tend to over-represent certain groups (orchids, cacti, carnivorous plants, bulb plants, ferns, vegetables, conifers . . .) to the neglect of others. On the other hand, the trade in medicinal plants, decorative plants, fruits and vegetables has developed. The scientific and legal framework for this activity poses difficulties on account of the conflicting interests involved . . . Nevertheless, botanic gardens have developed restricted networks based on acknowledged competencies and charters. These networks are currently developing computer data warehouses, partly accessible to general public through the Internet. Thus, around 350 institutions participate in the BGCI (Botanic Gardens Conservation International) network, compiling more than 250 000 entries on a total of approximately 30 000 species. Botanic gardens are working on refining methods for cultivating, propagating and conserving plant species and communicating this expertise to nurseries and the public. Such practices draw directly upon advances in physiological research on dormancy, cold and drought resistance, vegetative and sexual reproduction, cultivation of cells and tissues. The effects of fashion and trade add to the fascination for certain taxa, whilst more 'humble' species tend to be forgotten, even if they are in danger of extinction.

Botanic gardens play an important role in the biological diversity policy of a country. They provide the public and interested associations with a source of information and a forum for independent debate. They participate in campaigns to restore degraded environments and to reintroduce vanished local species (sensitising the public, providing specimens, assuming co-responsibility for managing indigenous environments: the flora of islands, mountains or wetlands). Together with public institutions and private enterprises, they are active partners in programmes for exploiting plant genetic resources (seed banks, data warehouses, . . .).

Technological and financial investment, the need for daily maintenance and qualified personnel add up to expenses that not all economies can easily bear. The largest botanic gardens are situated in the developed countries. This reflects a flagrant imbalance in relation to the tropical regions, which are richer in natural biodiversity but economically less well endowed.

## 13. Zoological parks

Public and private zoological parks, as well as specialised exhibitions of live animals (often centred around spectacular species: fish, snakes, birds, insects . . . ), have similar missions and activities to those of botanic gardens. Numbering over 2000 around the world, they are mostly organised in networks. Large data bases have been compiled, and in principle, information on approximately 250 000 live specimens, belonging to 6000 species, is freely accessible. In order to keep almost a million tetrapods and as many fish alive under artificial conditions, animal collections must meet high costs that not all economies are able to bear. They require close cooperation with veterinary science and research. Their partnership with animal friends and the general public is very strong, buoyed by considerable goodwill and enthusiasm. Interest is further stimulated by the live animal trade, which is vigorous but difficult to delineate with accuracy.

The environmental dependencies of aquatic species pose a severe constraint. Nevertheless, there is a long history of aquariums and marine stations constructed to house and exhibit creatures of the sea. These institutions enjoy a longstanding relationship with the public. Their mission encompasses information, education, conservation and research. Curiously, considering their cost, they are more evenly distributed around the planet than botanic or zoological gardens and give a fair representation of marine ecosystem diversity. Their maintenance cost is often integrated in government and regional networks for halieutic resource management or comes from basic and applied research programmes.

Marine data banks were coordinated and computerised at an early stage. They are very rich in information and much consulted. Universities use marine stations for teaching purposes; research programmes range from systematics and developmental biology to industrial pharmacology. Marine stations have the infrastructures and means to conduct ecological experiments on a real-life scale. Recently, they started to assume monitoring functions for the environment and biodiversity of littoral and coastal ecosystems that are directly subjected to human pressures (urbanisation, fragmentation, extraction, waste and pollution, etc.). They have also contributed to the follow-up and alleviation of the consequences of marine catastrophes.

## 14. ConservationBiology

Conservation biology was born in the late 1970's. Its object is to ascertain the impact of human activities upon species, communities and ecosystems and to make concrete proposals for averting ecosystem degradations. Whereas environmental protection is essentially an attempt to shield spaces and species from human actions through regulations, conservation biology adapts concepts and theories borrowed from ecology and develops them further to propose appropriate methodologies and implement concrete activities for nature conservation. Like other 'crisis' disciplines combining theory and practice at the cross roads between science and management, conservation biology puts the emphasis on action. Its proponents are working under pressure, since endangered species and habitats may soon disappear, unless effective measures are taken.

Conservation biology finds application in the implementation of the Convention on Biological Diversity. It tackles the task of meshing possible options for conservation with theoretical advances in biology, genetics and biogeography, whilst also taking ethological, physiological and economic inputs into account.

## 15. Reintroduction of species

Ex situ conservation is not only an alternative, but also a complementary approach to in situ conservation. Ex situ conservation provides reservoirs of individuals for infusing and restocking wild populations of endangered species. In reality, there are situations where habitat degradation is such that it is impossible to maintain viable in situ populations. The alternatives are simple: either let the species disappear forever; or try to save endangered populations by preserving them temporarily ex situ. They could be reintroduced into their original environment if and when the threats to the species and their habitats have disappeared. In cases where habitats have been destroyed, there is still the possibility of reintroducing the species into habitats similar to its original ones. This practice is known as translocation.

The practice of preserving endangered species in zoological parks can be evaluated on its achievements: over two centuries, they have preserved over 90% of their initial biological diversity and maintained populations of 250 to 500 individuals with a view towards reintroducing species into their natural environments. A number of zoos collaborate in programmes for breeding over 300 endangered species in captivity. The preserved

populations serve as genetic reservoirs in support of the animals' survival in nature. Zoos have successfully preserved species such as the European and American bison, the Prejwalski horse, etc.

## 16. Ecosystem health, ecosystem integrity

Extending the idea of health to ecosystems is justified by evidence that ecosystem dysfunctioning often results from the impact of human activities. A system in good health is defined as a system that is able to maintain its organisational and functional autonomy over time.

We need criteria and methods to identify dysfunctions, to evaluate their causes and to suggest possible solutions. A gauge for the state of health of ecosystems is provided in part by biotic (cf. below), physical or chemical indicators. But it is also necessary to consider the expectations of the society, which are linked to its value system and perceptions. It is generally accepted that the expression 'ecosystem health' is usually employed subjectively to describe the desirable state of a system as defined by a group of stakeholders. E.g. the main criterion could be the ability to catch certain kinds of fish or to observe certain kinds of birds. Perceptions can also differ according to type of ecosystem and period. Altogether, the notion of health is relative.

The Canadians have developed a related concept called 'ecosystem integrity'. The biotic integrity of ecosystems can be defined as the capacity of an environment to maintain a balanced and well adapted community of organisms with a species composition, diversity and functional organisation comparable to those of local natural habitats (or at any rate, the least disturbed habitats). The concept of integrity, like that of health, relates to social values. In the face of disturbances, the ecosystem must preserve its capacity to react and evolve towards a final stage that is normal or 'good' for that particular ecosystem. In systems that have been modified by human intervention, the question of integrity takes the form: what kind of 'garden' do we want? It is difficult to anticipate the ecosystems of the future, but it is possible to have some idea of what would be desirable.

Concepts of health or integrity are imbued with ethical and moral implications. There are ecosystem states that are 'normal' and others that are 'abnormal,' also described as dysfunctional. This normative approach accords with the notions of variability and heterogeneity that are currently evolving in ecology. For the moment, these concepts as such are accepted by users and help orientate public policies, in the absence of other, more heuristic methods.

## 17. Local and human stakes in biodiversity

The stakes involved in biodiversity are such that at present, there is no true guarantee that it will be conserved for future generations. Large-scale measures on a national or international level are not the whole solution. It is well understood that conflicts of interest are inevitable in the short term, affecting the results of all negotiations, and that fair benefit-sharing is still a distant goal. There is no doubt that to ensure the conservation of biodiversity, compromises must be found. But it is urgent that we ask ourselves whether the present situation, whose legal regulations and institutional frameworks partly reflect our immediate interests, is at all compatible with the long-term objectives of conservation.

Social science research has focused on this question and proposed new practices. Some of these have been tested in the real world, and although they have been unable to break the mould of currently predominant practices, they nevertheless offer interesting perspectives to explore in the future.

## 18. List of animation, audio files and movies

animation Conserving Biodiversity.mp4

## 19. Questions

- Define conservation.
- Define protection.
- Why protect biological diversity?
- What are the priorities for conservation?

## Chapter 2 Bioiversity and Genetics

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- What is the role of botanical gardens in the ex-situ conservation?

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## 4. fejezet - Chapter 3. Biodiversity and Evolution

### 1. The Mechanisms at Work in the Diversification of Life

Hypotheses explaining the origin of biodiversity have developed considerably over the past two centuries. Toward the end of the 18th century, Cuvier was an advocate of creationism, while Buffon defended the theory of spontaneous generation. It was Lamarck, at the beginning of the 19th century, who developed the idea of species transforming into other species. But Lamarck's transformism is tinged with finalism: there exists an 'inner force' which propels organisms to adapt to changes in their surroundings, and these transformations are transmitted to their descendants. In *The Origin of Species*, published in 1859, Darwin borrows certain ideas from Lamarck but rejects his finalism in favour of the principle of natural selection: those individuals who are best adapted are selected through competition. Notwithstanding his advanced insights into evolution, Darwin did not, at the time, provide irrefutable proof to support his ideas on the origin of life.

Toward the end of the 19th century, Pasteur demonstrated that life cannot be generated spontaneously from inanimate matter. Around 1900, the rediscovery of Mendel's laws inspired the study of genetics and accorded an active role to mutations in the process of evolution. Around the mid-20th century, the synthetic theory of evolution integrated natural selection and mutation into one process. The unit of evolution is the population, and natural selection benefits populations that adapt to their life circumstances by favouring the transmission to their descendants of alleles that are advantageous to the species.

### 2. Diversity of living organisms

The present diversity of forms and structures among living things is the expression of a genetic and molecular diversity that is specific to each individual, each population and each species. Understanding the mechanisms that create genetic diversity and the historic processes that enable its perpetuation or, conversely, contribute to its extinction, is important not only to biologists seeking to understand and depict the development of living things, but also for professionals working to maintain and improve the adaptive and productive potential of useful species for their own benefit (conservation and valuation of genetic resources).

The laws that govern processes of mutation and transmission are universal, like the genetic code itself. Their temporal dynamics bring into play chance events, processes of control and environmental filters. As a result, observation of one individual or group of individuals provides no immediate indication of their full genetic potential (genotype). Depending upon the circumstances, the same genotype can express itself in different ways, and conversely, individuals of the same appearance (phenotype) may have different genotypes. The correct interpretation of straightforward observations demands rigorous analysis of the respective roles played by genetic determinism and external factors.

### 3. Mutation

The primary producer of diversity is mutation. Any kind of physical occurrence that modifies the structure of a DNA molecule alters the genetic information carried by that molecule. The term mutation is used to designate both the process and the product of the change. The modified, mutated DNA carries new genetic information, different from that previously contained. Through the study of genetics scientists have discovered and analysed a enormous palette of mutational changes that may affect a DNA molecule: chemical modification of a nucleotide; addition or deletion of one or more pairs of nucleotides; addition or deletion of long sequences spanning the size of one or more genes; etc. Such mutations can be lethal, in which case the story ends there. If, however, the individual with the mutations proves viable, the mutations can be transmitted to its descendants and translate, for example, into physiological, morphological or behavioural modifications. Whatever the chemical mechanisms involved, processes of mutation introduce diversity into a system where the identical reproduction of hereditary patrimony would normally be maintained through the faithful replication of DNA by cellular division. Mutations spontaneously create new alleles. The range of genetic diversity observable at any

given time depends, firstly, on the rate at which mutations appear, and secondly, on the possibilities for the mutated forms to develop and compete successfully with other forms of life.

## **4. Variation and stability**

At any moment in time, each organism is in a balance between its identical replication and the genesis of diversity through mutation. The former enables clonal multiplication of cells, a process by which, for example, bacterial colonies or metazoan tissues are formed. The latter process constantly produces new information. The flux of genetic innovations is modest, and over a limited period of observation (1–10 years), populations generally appear to retain their own identities. Nevertheless, the living world is by nature unstable; moreover, it is continuously subject to external environmental influences that may also trigger mutational processes. However infrequent, mutations have acted as the motor of evolution and have maintained life on the planet despite its transformations.

Direct impacts upon DNA have been recognized for some time. They are not specific to the genes that they affect. However, certain environmental influences may exert a more subtle influence by acting upon the structure and activity of repair enzymes or upon chromatin, thereby rendering a particular gene more or less accessible to the repair system. Thus, while the chemical mechanisms of mutation and repair are not correlated to the nature of the genetic information upon which they operate, the probability of their occurrence may nevertheless vary from one individual to another and from one species to another.

## **5. Hidden genetic diversity and phenotypic identity**

Since the genetic diversity of DNA does not manifest itself systematically at the level of the individual phenotype, two forms of life may appear identical to the observer despite their being genetically very different. A priori, it is usually difficult to spot the genes bearing an allelic diversity and to identify the molecular mechanisms that maintain it. However, this is a reserve of hidden genetic diversity that allows for selection in response to exterior change. Farmers, animal breeders and plant cultivators have exploited this property both implicitly and deliberately. By refining their methods of selection, they have been able to extract new varieties from stocks previously considered to be homogeneous. If practised blindly, selection results in a loss of allelic diversity, as genes of no immediately apparent interest to the selector are eliminated.

As our knowledge of hidden diversity and its applications grows, the importance of genetic resource management is becoming increasingly apparent. Geneticists study the dynamics of hidden genetic diversity by examining the evolution of DNA sequences. The case of microsatellites is especially illustrative: repetitions of short nucleotide motifs are dispersed in the DNA. When they are situated in the non-coding zones of the genome, the number  $n$  of repetitions has no effect upon the phenotype. Observation shows that  $n$  may frequently vary from one individual to another. Their mutability (around  $10^{-2}$ ) is so high that microsatellites are used to expose the genetic diversity between related individuals and establish their lineage. Microsatellites also exist in the coding zones of genes. Here, the possible degree of variation is limited: the motifs must be repeated in triplets to maintain the legibility of the genetic code, and their number is restricted by the extensions or contractions of the primary structure of the protein that are compatible with its function. In this case, changes in  $n$  often have distinctive phenotypic effects upon individuals. The rate of mutation may be so high that  $n$  changes from one generation to the next.

## **6. Spatial organization and dynamics of intraspecific genetic diversity**

Genetic diversity is the fruit of the history of the DNA molecules present on the planet today. It is distributed geographically over all the species inhabiting the different ecosystems. The developmental and reproductive strategies of each species, population and individual mould this genetic diversity both qualitatively, quantitatively and over time. Theoretically, in the absence of any intrinsic or extrinsic constraints, all genes and all DNA molecules are equally prone to replication. Under such conditions, genetic diversity is preserved from one generation to another and, in the absence of mutations, remains identical onto itself. The pattern of diversity observed in a site remains stable, characterized by the frequency of the various alleles present in the area. Thus, for sexually reproductive plant and animal species, mitosis and meiosis are dependable and accurate systems for splitting DNA molecules, independently of the nature and volume of information carried by these molecules.

The laws of genetics revolutionized biology in the 20th century. They are quantitative and predictive and may be tested experimentally by comparing actual observations with the theoretical predictions of a mathematical model. This applies to Mendel's laws on the scale of individuals, as well as to the Hardy–Weinberg law on the scale of populations. (The latter law predicts that for any population, the nature and frequency of genotypes will remain constant from one generation to the next, provided all encounters between gametes of the previous generation are equally probable – a situation known as panmixia.)

Given a large population, its genetic diversity should be preserved over successive generations. However, since associations between gametes are subject to chance encounters, it is likely that certain alleles will not participate in the reproductive process, and therefore, the genetic diversity of the population will decrease over time, even if the probability is low. This effect is known as genetic drift.

In practice, the depletion of diversity predicted by this theory is strongly influenced by the size of the population (the risk is greater in small populations) and by its demographic characteristics (temporarily high mortality and reduced size – constrictive bottlenecks, overlapping generations, consanguinity, fragmentation of the population as a result of the appearance of barriers or parasites, emigration, etc.).

Conversely, the immigration of genetically different individuals or the appearance of new mutants are phenomena that enrich the genetic diversity of populations. Like panmixia, genetic drift can be mathematically formulated and modelled to test the role of these processes within the dynamics of genetic diversity observed in a given place over a given time and for a given population (or species).

In reality, mutations, genetic drift and random demographic circumstances are not the only factors to have shaped the genetic diversity present on the planet. Today, we are only familiar with the individuals who succeeded in reproducing and developing, while in fact they were once in competition with others who inhabited the territory at the same time but disappeared. It was Darwin, in the 19th century, who discovered the essential role of natural selection in the process of evolution.

Mutations are the motor of evolution. They provide the material upon which drift and selection subsequently act. Selection accounts for the difference between the evolution of genetic diversity in reality and such as it would be if a population were subject only to mutation and drift. The selective value (or fitness) of an individual reflects how successfully its genes are transmitted from one generation to the next. There are working theories on how to model genetic diversity under these conditions. They make it possible to compare different populations and species and predict their evolution with respect to the disturbances affecting them.

## **7. Adaptation**

Biological diversity is dynamic by nature. The physical and biotic environment of a species is continuously changing: climates are variable, competitors invade the domain, sources of nutrition change, etc. Within limits, organisms are capable of adapting to changes in the world within which they evolve. Species will always undergo modification in the long term, whether on the genetic, the biological or the behavioural level; some are born, and others die. Adaptation is a functional mechanism that enables species to deal with variability in the conditions of their living quarters. This capacity on the part of living beings is essential to their survival. The term 'biological adaptation' covers many facets: the genetic aptitude of living beings to adjust to different and changing circumstances; the manifestation of this aptitude at any given moment; the mechanisms at work; and the notice that society takes of these different manifestations.

## **8. Individual adaptation: phenotypic plasticity**

Adaptation is based upon the combined use of different aptitudes. At the molecular level, proteins, enzymes and subcellular membrane walls are restructured on a very short-term basis, thereby modulating their catalyst or transportation activities. The environment also intervenes over the long term (the duration of an individual life span, for example), by regulating the expression of the genes that control these molecular actors and influencing such activities as cellular differentiation and proliferation, morphogenetic and physiological plasticity, behaviour and reproduction.

Adaptation may involve modification of a phenotype in response to a specific signal received from its environment. The modification improves biological functions such as growth, reproduction and/or survival. Thus, on the local level, adaptation can be characterised as increasing the frequency of those biological traits

that promote survival or greater reproductive success within the population in question, under the particular conditions provided by its environment.

A basic key to adaptation lies in the plasticity of organisms. The biological characteristics of a phenotype – whether morphological, physiological, behavioural, etc. – are actually the result of an interaction between its genes and the environment. It must exercise flexibility to be able to exploit the resources necessary for the survival of the species. Phenotypic plasticity corresponds to the diversity of adaptive responses produced by a single genome. These responses may then be subjected to natural selection. The basic rule is: the phenotype is the product of the genotype and the environment, but it is also the object of selection!

Behaviour is another phenotypic characteristic that demonstrates great plasticity. For some biologists, the expression of a phenotype first manifests itself through a change in behaviour, particularly when a population has to come to terms with a new habitat or niche. A change in behaviour is almost always the first step towards evolutionary change. Amongst the hypotheses that focus on the interactions between evolution and changes in animal behaviour, a major role is played by the capacity for learning that enables animals to exploit new situations and gain access to new resources. Imitation and learning facilitate the assimilation of ‘evolutionary novelties’ and their transmission within the populations involved.

## **9. Collective adaptation: natural selection**

Thanks to genetic polymorphism, the individuals of a population are able to respond to environmental constraints in slightly different ways. Chance generates variations (mutations), that are then strained through the sieve of selection. This is what Darwin termed natural selection, as opposed to the artificial selection practised by breeders. The principle of natural selection implies two complementary processes: the existence of an hereditary genetic variability, and a phenomenon whereby the best performing individuals of a given environment are selected at the reproductive level. When conditions change, those genotypes that produce the phenotypes best suited to respond to the new constraints enjoy an adaptive advantage and are selected in the course of successive generations. Selection essentially affects the frequency of genes: genes controlling adaptations that reinforce the chances of successful reproduction will be favoured, and their frequency can thus grow over successive generations.

The selected genes may tow along other genes which are not themselves selected, but whose expression is favoured indirectly in this way. Thus, the theory predicts that alongside of progressive transformations, large-scale qualitative leaps may occur when unexpected mutations reshuffle the deck of cards in the game of selection and its consequences. Seen from a different angle, variations in the structure and function of ecosystems are both the cause and effect of natural selection. In this regard, scientists speak of the ‘cycle of biological diversity’: mutations and the biophysical environment are the sources of variability; the product of adaptation and selection is biological diversity; which, in turn, interacts with and modifies the environment.

## **10. The coalescent: population genetic inference using genealogies**

Genealogies contain information about historical demography and the processes that have acted to shape the diversity of populations. Genealogies are family trees which depict the ancestors and descendants of individuals in a population. In a diploid population, each individual has two ancestors in the preceding generation, four in the generation before that, eight in the generation before that, and so on. With haploid populations, each individual’s lineage can be traced back through a single line of ancestors, one in each generation. In the same way that we can construct genealogies of individuals, we can also construct genealogies of genes within individuals. In diploid individuals, each copy of a homologous gene has a different pattern of inheritance and, consequently, a different genealogy. We can think of the genealogies of individual genes as intraspecific gene phylogenies. Imagine selecting two people at random from a large city, and two people from a small town. We would guess that the two individuals from the small town would share a common ancestor only a few generations in the past, whereas the two individuals from the city may have to dig back several generations before finding a common ancestor. The number of generations that separate the two individuals from their common ancestor would depend on the numbers of people that immigrated or emigrated to or from the city or the small town. If there are large numbers of people coming in or leaving the town, we would revise our estimate on the time to common ancestry. Similarly, if we are told that what is now a small town had been a thriving metropolis some 40 or 50 years ago, we would not be so confident that these two individuals have a recent common ancestor.

In these examples, three factors determine the time to common ancestry: the size of the population, rates of migration, and change in population size. Although the examples are simple thought experiments, they capture the essence of how genealogies are used to make inferences about historical population processes and demographies. In the absence of any selective bias that confers differential reproductive success amongst individuals, the numbers of generations that separate individuals from their common ancestors are functions of historical population size and migration between different groups of individuals. In 1982, John Kingman described this process formally in mathematical terms. He called it the coalescent (Kingman, 1982a,b).

## 11. The Kingman coalescent

The simplest formulation of the coalescent begins with a panmictic haploid population where the number of individuals,  $N$ , has remained constant over time, generations are discrete so that at each generation, only the offspring of the preceding generation survive, there are no selective forces acting on the population and all individuals have an equal chance of producing offspring. This is the very well-known Wright–Fisher population model (Fisher, 1930; Wright, 1931).

If we sample two individuals from such a population at the present time, the probability that both will share a common ancestor in the preceding generation is  $1/N$ . To make it a little easier to keep track of time, we number the present generation  $t_0$ , the preceding generation  $t_1$ , the generation before that  $t_2$ , etc., so that  $t_k$  indicates a time  $k$  generations before the present. The probability that two individuals will share a common ancestor at  $t_2$  is the probability that they will not share an ancestor at  $t_1$  (this probability is  $1 - 1/N$ ), multiplied by the probability that their respective parents will share an ancestor at  $t_2$  (this probability is  $1/N$ , since the population size has remained unchanged). This is equal to  $1/N(1 - 1/N)$ . We can generalize this, and calculate the probability that any pair of randomly sampled individuals will have their most recent common ancestor (MRCA) at time  $t_k$ ; this probability is given by:

$$P(t_k) = (1/N) (1 - 1/N)^{(k-1)}. \text{ [eq.1]}$$

Suppose, instead of sampling only two individuals, we sample  $n$  individuals (where  $n$  is larger than or equal to 2, but much smaller than  $N$ ). Now there are  $n(n-1)/2$  possible pairs of individuals in the present generation that may share a common ancestor in the preceding generation, but each of these  $n(n-1)/2$  pairs only has a  $1/N$  chance that both individuals will have the same parent, i.e. the probability that there will be one common ancestor in the preceding generation is

$$P(t_1) = n(n-1)/(2N) \quad \text{[eq.2].}$$

The assumption that  $N$  is large and  $n$  is much smaller than  $N$  allows us to use some quite nice mathematical approximations. The net result is that we can move from talking about time in discrete generations, to continuous time, and we can express it more neatly as:

$$P(t_k) = n(n-1)/(2N) \exp(-n(n-1)/(2N) k) dt. \text{ [eq.3]}$$

Since time is now continuous, the function  $P(t_k)$  is strictly a probability density function; the “ $dt$ ” at the end of the equation indicates that we are calculating the probability of a coalescent event in the infinitesimally small interval  $t_k$  to  $(t_k + dt)$ . This is the density function of the exponential distribution.

The expected time to the MRCA of all  $n$  individuals tends to  $2N$  generations, as  $n$  gets large, and this is the expectation obtained under the Wright-Fisher model. The coalescent, then, is a continuous-time approximation to the Wright-Fisher model when population size,  $N$ , is very large.

Instead of speaking of genealogies of individuals, it is useful from this point forward to focus on the genealogies of gene sequences, because these are likely to be the primary source of data for most biologists. For the moment, we will only consider homologous and non-recombining genes at a single locus. With haploid organisms, there are only as many homologous genes as there are individuals in the population (each individual possesses only a single copy of the gene in question). In contrast, with diploid organisms, in a population of  $N$  individuals, the size of the population of genes is  $2N$ . All this does is change the denominators in [eq.1], so that instead of  $2N$ , we now write  $e4N$ .

## 12. Effective population size

Most biological populations fail to satisfy one or more of the assumptions of the Wright-Fisher model. For instance, it is impossible to find a natural population that remains at a constant size from generation to generation. How then can the coalescent be applied to real-world situations? The elegant solution is to use, in place of  $N$ , an abstract parameter called the effective population size,  $N_e$ . The quantity  $N$  is often called the census population size. The effective size,  $N_e$ , of a real biological population is proportional to the rate at which genetic diversity is lost or gained. If one obtains a measure of this rate in a real biological population, the effective size of that population is equal to the size of an ideal Fisher-Wright population that loses or gains genetic diversity at exactly that rate. There are several ways of calculating effective population size, but for the coalescent, arguably the most appropriate is the “coalescent effective size” proposed by Sjodin et al. (2005).

Essentially, the coalescent effective size of a real population is obtained by finding the value of  $N$  that delivers the same distribution of times-to-ancestry that one would obtain with a sample from the real population in question. This has a certain intuitive appeal: if two independently evolving lineages coalesce into a single ancestral lineage, then we have lost one lineage-worth of genetic diversity.

Effective population size is a useful parameter because it allows biologists to compare populations using a common measure. Lineages in a population with a larger effective size drift more slowly than one with a smaller effective size. Two populations with the same effective size have the same rate of genetic drift. Genetic drift can be quantified by measuring genetic diversity or heterozygosity, under the assumption of neutrality.

The coalescent tells us about historical population processes. Consequently, our ability to relate the rate of genetic drift to the coalescent, via the coalescent effective size, means that we have the opportunity to determine whether the historical dynamics of two or more populations are similar, as these relate to the accumulation or loss of genetic diversity. This is tremendously useful, as one can imagine, and these techniques have been applied in fields as diverse as conservation genetics, the reconstruction of colonization histories of humans and animals, and the epidemiology of infectious diseases.

## 13. The mutation clock

For most phylogenies of gene sequences, we are not able to separate mutation rate from time, except, as we shall see, when we have calibration points or sequences collected at different times. Branch length and the time-to-ancestry of sequences is measured as a composite variable,  $b = \mu t$ , where  $\mu$  is the mutation rate measured as the expected number of mutations per generation, and  $t$  is time in generation time. The branch length, or time-to-ancestry, measures the number of mutations that is expected to have accumulated between any pair of ancestral and descendant nodes. If we can rely on the constancy of  $\mu$  across the genealogy of a sample of sequences, we can rescale time, so that instead of asking, “How many generations have elapsed since these two lineages separated from a common ancestor?” we ask, “How many substitutions have accumulated since these two lineages separated?” Under a molecular clock, each generation is equivalent to  $\mu$  substitutions,  $t$  generations is equivalent to  $b = \mu t$  substitutions, and  $N$  generations is equivalent to  $N\mu$  substitutions. With a little calculus, we can re-derive [eq.3] so that, instead of measuring time in generations ( $t$ ), it is now measured in substitutions ( $t'$ ). By convention, instead of writing  $2N\mu$  (or  $4N\mu$  for diploid populations), population geneticists use  $\theta$  in its place. The parameter  $\theta$  is quite interesting. For one thing, it is equal to the average number of mutational differences between any two randomly sampled pair of sequences from a population with constant effective size. Note that this is not quite the same as saying that  $\theta$  is equal to the average number of observable mutational differences, because there may be hidden mutations, or rather, substitutions.

Amongst its many other uses in population genetics,  $\theta$  also features as a fundamental quantity in Ewens' sampling formula (Ewens, 1972), which tells us about the distribution of the number of allelic haplo-types in a population. Not surprisingly, as a rescaled measure of effective size,  $\theta$  is also a measure of genetic diversity.

## 14. Demographic history and the coalescent

Since the effective size of a population correlates with the expected intervals between coalescent events, changes in population size will result in changes to the distributions of these times. Consider, for example, a population that has grown in size. If we sample a set of genes from the population now, when it has a large effective size (say,  $N_0$ ), we expect to find that the time to the first coalescent event between a pair of sequences will be large. However, after that first coalescent event, some generations in the past, we encounter a population with an effective size,  $N_t$ , that is smaller than  $N_0$ . Two randomly sampled lineages will coalesce at a faster rate, proportional to  $N_t$ . The effect of this process on the genealogy is to produce a tree with long terminal branches and shorter internal branches compared to a genealogy from a constant-sized population.

We can use a similar thought experiment to work out the properties of a gene genealogy from a declining population. In this case, effective size at present,  $N_0$ , is small relative to population sizes in the past. Coalescent events tend to occur with greater rapidity, but as one moves past a series of coalescences backwards in time, population sizes grow ever larger and, concomitantly, coalescent intervals get longer. The rate of growth or decline,  $g$ , of a population where size changes exponentially, is the expected number of offspring per individual per generation. Growth rate is estimated as the composite parameter  $N_0g$  or  $g/\mu$ , since it is not possible to obtain a measure of  $g$  that is not scaled in units of substitutions.

Note the very different timescales, measured in the number of generations: whereas the genealogy on the right has a root only a few hundred generations in the past, the genealogy on the left goes back hundreds of thousands of generations. Up to this point, we have concentrated on describing the coalescent process for panmictic populations. However, most biological populations have some degree of geographical structure, and are not panmictic. The coalescent can be modified to accommodate different types of geographical structure; for instance, the island model of migration breaks the population into subpopulations or demes, with migration of individuals between demes. A special type of island model is the stepping-stone model of migration, where demes are arranged linearly or in a two-dimensional grid, and migration only takes place between neighboring demes. The stepping-stone model is often used to approximate a continuous-space model of migration, where migration rates are a function of distance. For both the island model and the stepping stone model of migration, the distributions of times-to-ancestry depend on the rates of migration between demes and the effective sizes of the population within demes. This is because two lineages can only coalesce if they are in the same deme. If a population is divided into several demes, each with a small effective size, and there are low rates of migration between demes, lineages within demes will coalesce relatively quickly, leaving a single ancestral lineage in each deme. These lineages take a long time to coalesce, because to do so requires a rare migration event to another deme.

## 15. List of animation, audio files and movies

animation Population Growth.flv voice Human Pollution Ecology.mp3 voice Human Water  
Pollution.mp3 voice Symbiotic Relationship Aphids and Ants.mp3 video Why Biodiversity Matters.mp4

## 16. Questions

- What does genealogies mean? - Define the effective population size. - Define the coalescent effective population size. - Explain the Wright-Fisher model. eCh04-SR-of-Communities-10.docx

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# 5. fejezet - Chapter 4. Species Richness

## 1. The Species Richness: Equilibrium and Non-equilibrium Processes

Biodiversity is a dynamic attribute of an ecosystem. Biodiversity results from both past and present selective pressures exerted by the biotic, physical, chemical and spatial characteristics of an environment. The dynamics of biodiversity cannot be understood without also considering the dynamics of assemblages and ecosystems.

Theories of equilibrium play a large role in most fields of science. The concept of the 'balance of nature' has a long history in scientific literature, and most explanations for patterns of biological diversity are based on some sort of equilibrium, defined as a balance between opposing forces operating on different space and time scales. On the other hand, one of the major ecological insights of the 1970s was the discovery of the importance of non-equilibrium processes in the maintenance of species diversity. Since then, the notion of equilibrium has been much criticized in ecology, with new theoretical debates about the regulation of species diversity. Most of the disagreement over the validity of contrasting hypotheses stems from a failure to define the terms equilibrium and non-equilibrium clearly and to consider the spatial and temporal scales at which specific processes are important. Equilibrium and non-equilibrium dynamics are not mutually exclusive, and how observations are interpreted is usually a question of the scales at which investigations have been done.

## 2. Theories of Equilibrium Based on Interspecific Relationships

Ecologists have worked towards identifying factors that explain the composition and structure of biological communities. In particular, they have tried to establish the role of interactions between species in maintaining population equilibriums within communities. Following the Darwinian train of thought, population ecologists of the 1950s focused on competition between species. Only much later did theories arise that stressed the role of mutualism and cooperative relations between species, without completely rejecting the idea of competition. The theory of insular biogeography proposed by MacArthur and Wilson in 1967 has revived ecological debate by demonstrating the importance of history and chance in the composition of animal and plant communities.

## 3. Theories of equilibrium as a result of interspecific competition

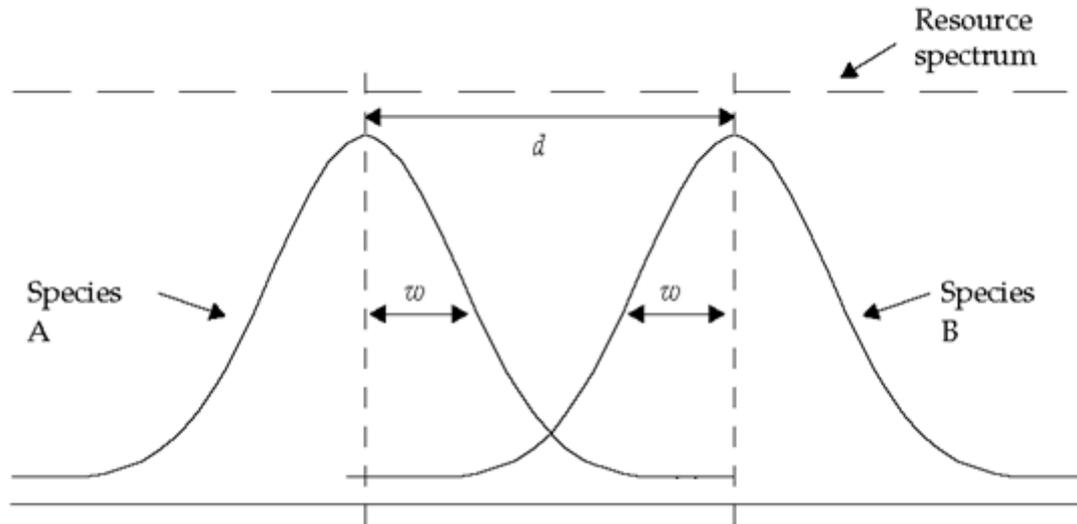
The term 'interspecific competition' describes the competition between individuals belonging to different species over the use of nutritional or territorial resources available in limited quantities. As with intraspecific competition, this may cause a decline in the growth, survival or fertility of the particular species involved.

The principle of competitive exclusion derives from Darwin's Origin of Species. One of the basic axioms of modern ecology, it formulates the intuitive belief that two species with overly similar ecological characteristics cannot coexist over long periods of time. In other words, in a stable environment, whenever two or more species are in competition over the same limited resources, the species that is best adapted will eliminate the other(s).

Hutchinson (1957) basically upheld the idea that competition is the main factor limiting the diversity of species and leads to the emergence of 'patterns' in the structure of communities. He also popularized the notion of 'ecological niches,' which he defined as hypervolumes with  $n$  dimensions, each corresponding to a biological or ecological requirement of the species under study. Competition between species may take place over one or more dimensions of the ecological niche. In theory, the more specialized species are, the less their niches will overlap.

## 4. Ecological niches

For MacFayden (1957), the ecological niche was ‘that set of ecological conditions under which a species can exploit a source of energy effectively enough to be able to reproduce and colonize further such sets of conditions.’ Actually, the term has been used as a generalization of the notion of habitat, which is illustrated as a multidimensional hypervolume of resources axes. Later, Odum (1975) defined the ecological niche of a species as the role that the organism plays in the ecosystem: ‘the habitat is the “address” so to speak, and the niche is the “profession”’. In other words, the niche of a species corresponds not only to its place in the trophic network but also to its role in the recycling of nutrients, its effect on the biophysical environment, etc. Today, there is a tendency to characterize ecological niches with respect to three main axes grouping most of the variables pertinent to the living environment: the habitat axis (climatic, physical and chemical variables); the trophic axis; the temporal axis (use of food resources and occupation of space over time).



**Figure 1.** Demonstration of the classical MacArthur-May theory of niche partitioning by hump-shaped resource utilization functions.

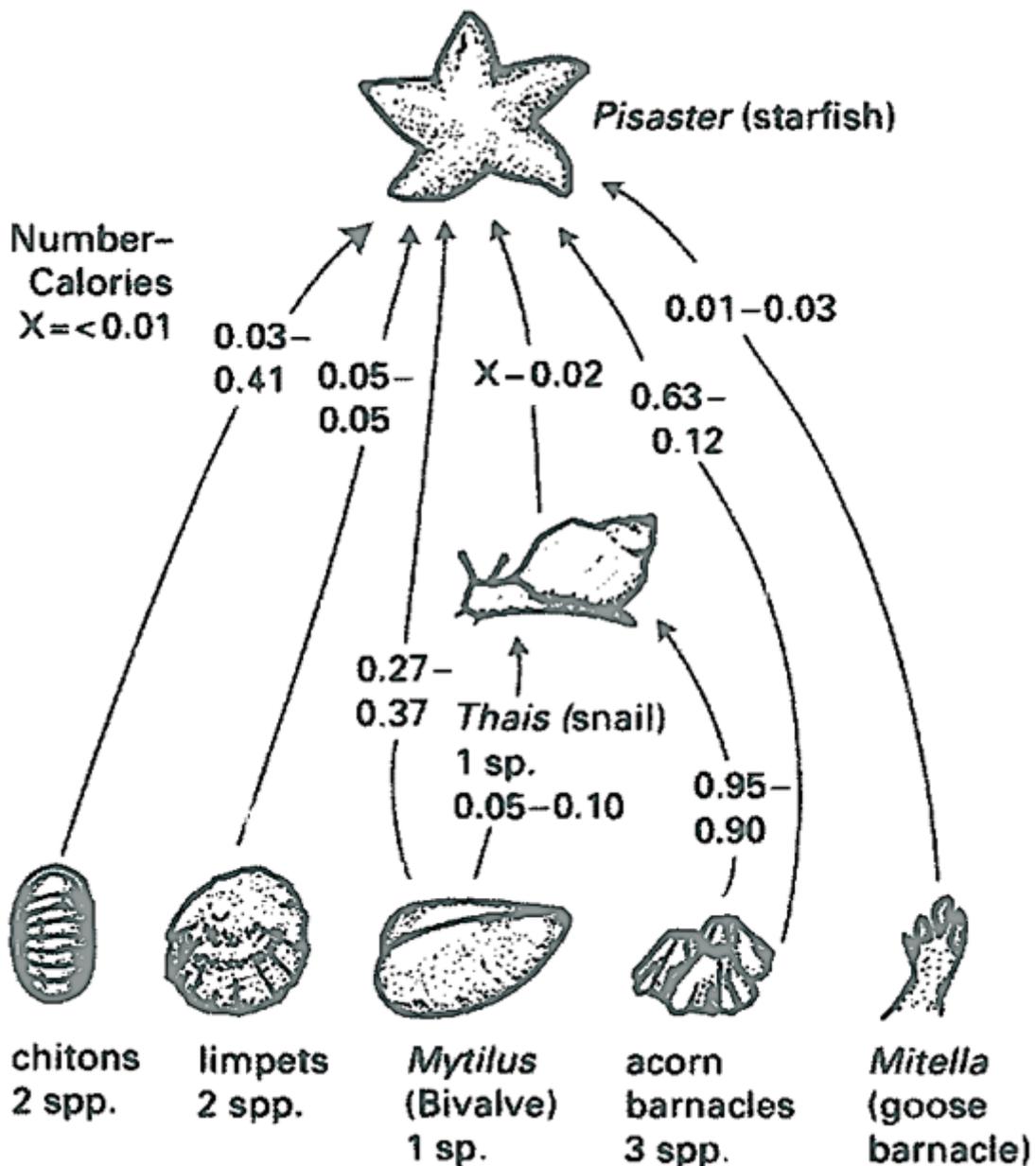
A great many laboratory experiments have been devoted to the model of competitive exclusion; however, it is not very practicable in the field. The methodological difficulties are such that we do not know what roles such interspecific competitive phenomena actually play with respect to other factors in the general dynamics of ecosystems, particularly in ecosystems where disturbances create strong spatiotemporal dynamics. In reality, environments rarely remain constant over long periods, and modifications in ecological conditions modulate the competitive relations among species. Exclusion and coexistence are not straightforward alternatives. Their relationship appears to be subtler. It is more helpful to consider them in terms of trade-offs and evaluate the degree of coexistence possible between species. A dominated species is rarely eliminated entirely, and many observations indicate that the extinction of a species can be a very long process extending over numerous generations.

## 5. The role of predation

One of the ways to limit the growth of a population is to control its development through predation. In a certain sense, the role of predation in the regulation of communities is part of the general theory of competition. However, the dynamics of predator-prey systems are complex and depend upon local conditions – both biotic and abiotic.

A well-known model of prey-predator interaction is the Lotka – Volterra model, which simulates the dynamics of abundance for a single prey species and a single predator species under theoretical conditions where the predator has only one prey and the prey population is not limited by the availability of food. Applied to the North American lynx and the snowshoe hare and based on the number of skins listed in the registers of the Hudson’s Bay Company over almost one century, the model provides an account of the alternating fluctuations in abundance of predator and prey observed in nature: when the predator population increases, the prey population decreases, and vice versa. This mathematical model predicts that the outcome of prolonged competition between species in a confined space always ends with the elimination of one species and the total victory of the other. In reality, the situation is rarely so simple. A predator may consume different varieties of

prey, depending upon their relative availability, without necessarily having a limiting effect on every one of them.



**Figure 2.** The famous *Pisaster* dominated food web at Mukkaw Bay published by Paine (1966).

One hypothesis claims that predators only eat the required number of prey without depleting their ‘capital’ and thus always have enough food at their disposal. This is what Slobodkin (1968) calls the optimal strategy of predation. But such a situation cannot be generalized, because there are a number of cases where predators kill beyond the threshold suggested by the optimal strategy.

Another theory suggests that by limiting the abundance of prey, predators enable the coexistence of a greater number of species. In a famous experiment on the Pacific coast of the USA, Paine (1966) demonstrated that the experimental removal of a superpredator, the starfish (*Pisaster ochraceus*), enabled mussels (*Mytilus californianus*) to spread over the rocky sea-beds and led to a simplification of the biological system. Under normal circumstances, the mussel population is controlled by the starfish. Originally composed of 15 species, sea-bed communities were reduced to eight species by the end of the experiment, because the mussels eliminated several other species competing for the same space.

## 6. Mutualism or co-operative relationships between species

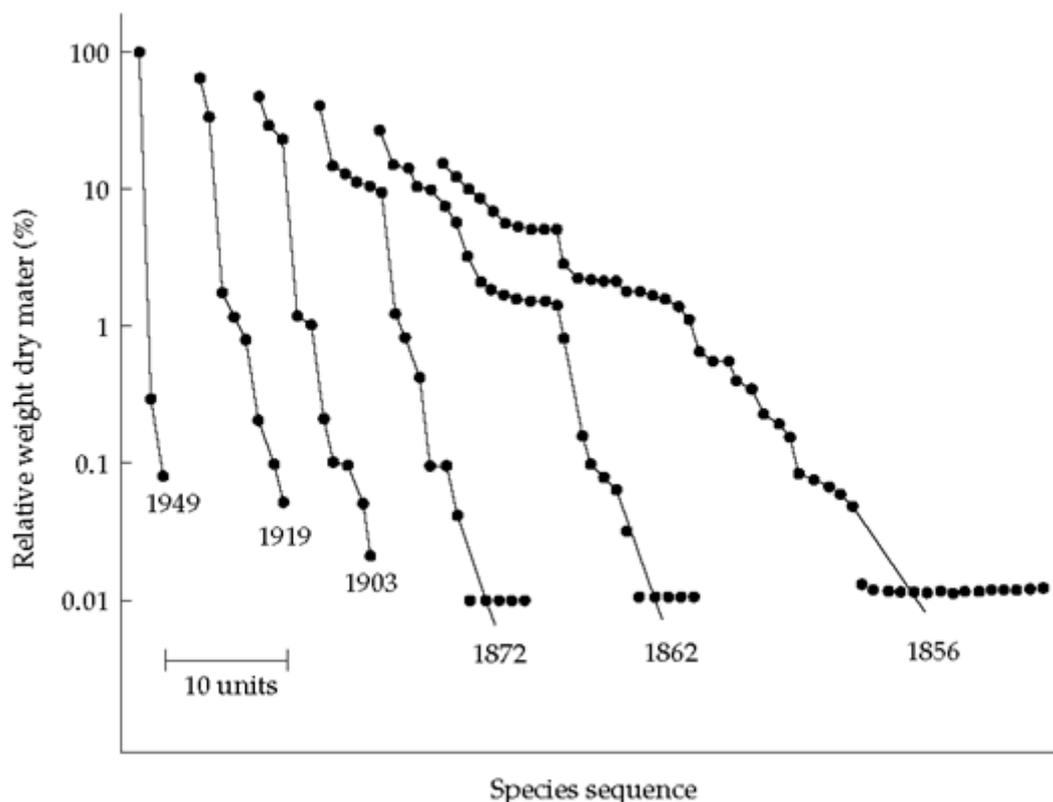
From the 1950s to 1970s, ecological research was largely driven by the idea that competition is the main factor of interaction between species. Since then, the results of many studies have demonstrated that mutualist interactions are far more frequent than previously believed. The concept of mutualism had already been introduced by a Russian, Kropotkin, in a work entitled *Mutual Aid*, first published in 1906. Kropotkin criticizes Darwin for overemphasizing the 'struggle for life', in line with the ideas of Malthus, and overlooking the fact that in nature, living things co-operate towards ensuring their collective survival. They appropriate territories collectively, practising mutualism rather than competition.

Without going into detail, several examples of mutualism are as follows: the relationships between plants and micro-organisms, e.g. mycorrhizae associated with roots, that facilitate the transfer of nutrients to vascular plants; the role of insects in the pollination and dispersal of seeds; the roles of mammals and birds in disseminating fruits and seeds in tropical forests (zoochory); the lichen formed by the association of one alga with one fungus; symbiotic protozoans, able to hydrolyse cellulose, living with social insects (ants) or in the stomachs of ruminants; the association between corals and zooxanthellae (unicellular algae).

## 7. Saturation of communities and biotic interactions

If interspecific competition and other types of interactions really act as structuring forces within biological communities, it should be possible to find situations in which such interactions limit the number of species that can coexist locally in a stable community. In species-rich biogeographic zones, for example, the specific richness of communities could be expected to reach a certain limit or point of saturation on the local level, regardless of how many species are present in the region. In theory, two kinds of actual results are anticipated.

There is a linear relationship between local and regional richness. In other words, local specific richness is independent of biotic interactions occurring at the local level and increases proportionately with the specific richness of the region. This situation is one of unsaturated communities in which the interactions between species are not important enough to limit specific richness at the local level.



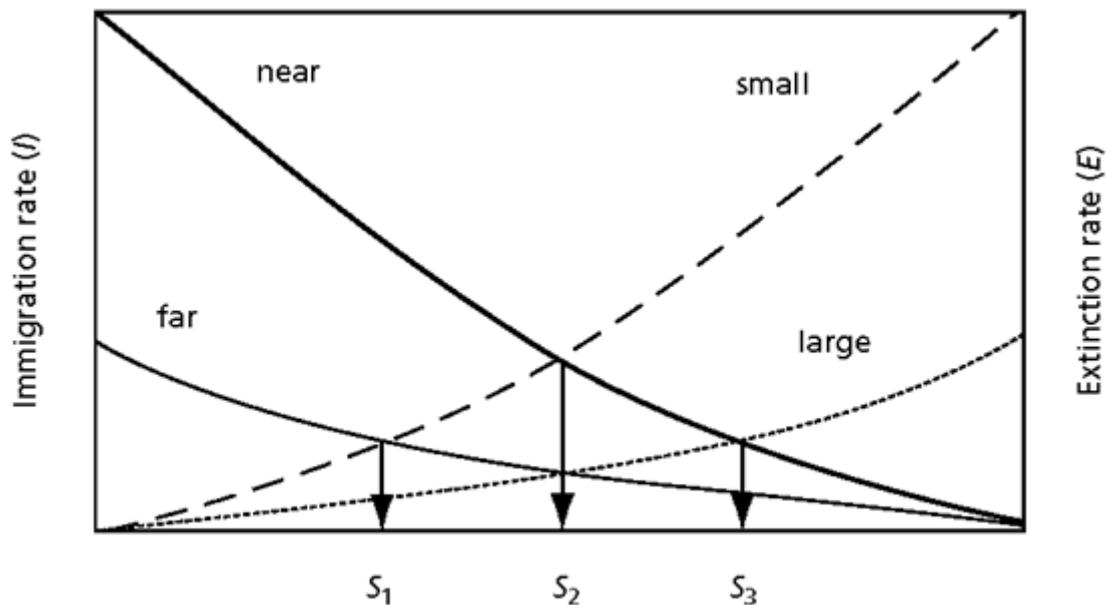
**Figure 3.** Dominance-diversity curves of the Rothamsted park grassland experiment.

There is an upper limit to specific richness at the local level. The number of species may at first increase with the increase in regional specific richness, but will eventually stabilise and become independent of the regional specific richness at a certain level. In this case, the curve is asymptotic, and we have what is called a saturated community, where it becomes difficult to add species without eliminating others.

Since it is difficult to test these hypotheses under natural conditions, ecologists use indirect methods. A relatively simple test to verify the hypothesis of saturation consists in comparing local specific richness with regional specific richness in similar habitats belonging to different geographic zones and inhabited by different pools of species. The hypothesis of non-saturation has been tested on fish communities in west African rivers belonging to the same biogeographic zone. There is a clear relationship between the surface area of the river catchments and their specific richness, varying between 18 and 95 species. The analysis of local richness of fish species observed in different tributaries of these rivers reveals a close relationship between local specific richness and the specific richness of the river, thus demonstrating that the communities are not saturated. In other words, the factors controlling specific richness on the local species

## 8. The MacArthur–Wilson Model

The theory of dynamic equilibrium developed by MacArthur and Wilson (1963, 1967) was first applied to insular environments. The basic hypothesis is simple: the species richness of insular communities depends upon the balance between the rate of immigration and the rate of extinction, expressed as number of species per unit of time. The immigration rate for new species decreases as the number of species settled on the island increases. On the other hand, as the number of species present increases, competitive interactions on the island tend to increase the number of extinctions. The interaction between these two dynamic processes provides an explanation for the specific richness of insular communities (Figure 4.3). One speaks of dynamic equilibrium, because the community is not fixed a priori, and species may be replaced over time. More precisely, the MacArthur–Wilson Model predicts: that islands close to continental sources will have more species than islands farther out; moreover, certain species have a greater capacity for colonization than others; and species richness is higher on large islands than on small islands, given equivalent positions with respect to the source of invasion.



**Figure 4.** Equilibrium on islands depending on the immigration and extinction of species.

The existence of such a relationship between area/number of species is an empirical fact. There is nothing to tell us why this should be so. However, some scientists believe that the low number of species on small islands is the result of a higher rate of extinction due to the small population size. But an equally plausible explanation is that the diversity of habitats increases with the catchment area, and that communities are richer where habitats are more diversified.

This theory on insular biogeography has a number of weak points. For one, it ignores the fact that not all species have the same biological characteristics and that therefore, they do not have the same opportunities for colonization, at least not in the short term. In the original theory, all species were considered identical, without differentiating how individual species contribute towards balancing immigration and extinction rates on any given island. Moreover, the theory can only be strictly applied to species that can move easily from one place to another, whether on their own (birds, insects, etc.) or else borne by the wind or other species. It should also be added that the theory leaves no room for in situ speciation and ignores relationships between species and characteristics of the environment, nor does it take into account the size of the populations present. In spite of all these reservations, this simplified theory has considerable heuristic value and has had significant impact upon research on the organization and dynamics of communities. It has also been applied to continental situations: a mountain summit, a forest grove, a river or lacustrine basin can be treated as 'continental islands.'

## 9. Continental islands

An in situ experiment, carried out by Wilson and Simberloff (1969), corroborated the theory of insular biogeography to a certain extent. After compiling an exhaustive inventory of the arthropods inhabiting the small islets of mangroves along the coasts of Florida, the fauna of these islets was exterminated. Recolonization occurred rapidly, and after 200 days, the number of species stabilized at values close to those registered at the onset of the experiment. However, the taxonomic composition of the new communities differed from the original, indicating that there is an element of chance in colonizations, with early colonizers enjoying an advantage over latecomers. Despite these taxonomic changes, the trophic structures of the new communities were similar to those of the original communities, with the various trophic groups (herbivores, decomposers, predators) represented in the same proportions as before. This is a point in favour of the hypothesis that there may be redundant species fulfilling similar functions within a community.

## 10. The Holling Model

Since the 1980s, ecologists have been questioning the idea that biological communities pass through a well-ordered, one-directional sequence of stages in their evolution towards a climax whose characteristics are determined by climatic and edaphic conditions. Research on different types of ecosystems has revealed that: there is a significant degree of chance involved as to which species colonize an ecosystem after a disturbance or in the course of succession; pioneer species and species that characterize mature stages can both remain present throughout the course of succession; disturbances like fire, wind and herbivores are major drivers of the inner dynamics of systems and often lie at the origin of succession cycles; different disturbances may propel ecosystems towards different ranges of stability; i.e. there is more than one possible climax.

The notion of climax is altogether useful, but it yields an overly static and incomplete view of the phenomenon. Holling (1986) therefore proposed a model that identifies four main periods in the cycle of terrestrial ecosystems. This view of succession turns upon an adaptive cycle consisting of two long periods of slow accumulation and transformation of resources (a phase of exploitation, corresponding to the rapid colonization of recently disturbed areas, and a phase of conservation, with the gradual accumulation and storage of energy and matter), alternating with two shorter periods that create opportunities for innovation (a phase of release of the accumulated biomass and nutrients by fires, epidemics, etc., followed by a phase of reorganization of the ecosystem). The phase of conservation, which corresponds to a period during which the system becomes more stable and accumulates biomass, may be likened to the concept of climax, but it is embedded in a more dynamic view of ecosystems.

## 11. The Dynamic Equilibrium of Ecosystems and the Role of Disturbances

For a long time, for both practical and conceptual reasons, ecologists studied homogeneous ecosystems that were more or less independent of one another. Reality tells a different story; natural environments are heterogeneous, often fragmented, and they change over time. Ecologists

Long-term studies of ecosystems show that their state at any given time depends upon a combination of their history and the current dynamics of their environment. Over longer periods of time, they tend to oscillate around a median state with varying regularity and amplitude. Rather than remain in a so-called steady-state, an ecosystem is actually an interactive system: a change in the environment triggers a dynamic response throughout

the whole system, including numerous positive or negative feedbacks. On the other hand, the ecosystem may also have influence upon its environment, implying a reciprocal relationship; the former is not entirely subordinate to the latter.

## 12. The dynamic equilibrium of ecosystems

### 12.1. What is a disturbance?

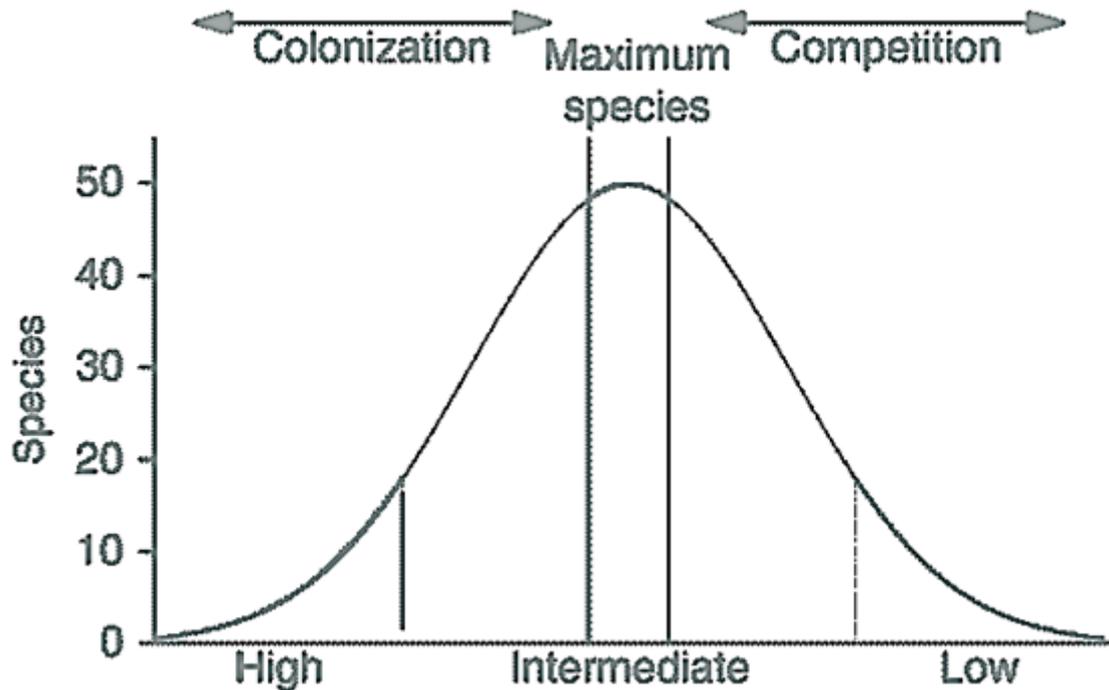
The important role that disturbances play in the dynamics of communities and ecosystems is one of the most interesting factors to shed new light on ecological paradigms in the last twenty years. A general definition of disturbance was advanced by Pickett and White (1985) and modified by Resh et al. (1988): 'any relatively discrete event in time that is characterized by a frequency, intensity and severity outside a predictable range, and that disrupts ecosystems, community or population structure, and changes resources, availability of substratum, or the physical environment'. For Townsend (1989), a perturbation is 'any relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species.' As for Sousa (1984), he holds a disturbance to be 'a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established'.

Predation is not, strictly speaking, a form of disturbance, because it is intrinsic to the life of the prey species that must adapt to it. Nevertheless, voluntary introduction of new predator species into an ecosystem can be considered a perturbation of that ecosystem, because new predators and their prey have obviously not had the time to coevolve.

Disturbances can be qualified by different descriptive characteristics: type (physical, biological, etc.), pattern of occurrence (spatial distribution, frequency, intensity, duration, etc.) and regional context. Depending upon their nature and intensity, certain disturbances elicit no response from the ecosystem, while others, for example destroying a habitat and its settlement, may qualify as catastrophes. More generally, a disturbance usually leads to a general restructuring of the ecosystem. In this sense, it can be seen as a rejuvenating process within the phenomenon of ecological succession.

### 12.2. The intermediate disturbance hypothesis

Hutchinson began as an ardent supporter of theories of competition, but several years later, he observed that the model did not apply to phytoplankton communities in lakes. In a famous paper (Hutchinson, 1961), he describes what he calls the plankton paradox: many more species of phytoplankton have been observed to coexist in a relatively simple environment than are accounted for by the theory of competition and the limitation of resources. He therefore reverses the logic of the question: could the great species richness observed not be the consequence of fluctuations in the environment that prevent it from attaining a state of equilibrium over time? If this were so, then coexistence would be the result of non-equilibrium phenomena, rather than characteristic of a state of equilibrium. In a context where equilibrium theories are the predominant paradigm, such novel ideas have been slow to receive the attention they deserve. But they point the way towards future discoveries about the impact of perturbations upon the specific richness of ecosystems.



**Figure 5.** The relationship of disturbance and diversity (species richness) is described by a unimodal hump-shaped curve.

Already, many ecological investigations have reached the conclusion that disturbances might actually work in favour of biological diversity by lowering the pressure of dominant species upon other species and allowing the latter to develop. Proposed by Cornell (1978) ‘the intermediate disturbance hypothesis predicts that species richness will be greater in communities with moderate levels of perturbation than in communities without any disturbances whatsoever or communities that are subject to overly large and/or frequent disturbances’. The initial objective of this hypothesis was to explain the high specific richness of tropical forests and coral reefs. Where disturbances are infrequent, interspecific competition limits the number of species likely to become established, and the most competitive species (resident species) occupy the available space.

### 12.3. Uprooted trees: a factor in the maintenance of forest biodiversity

In forest milieus, natural regeneration frequently succeeds the disturbance created by the accidental uprooting of a tree: a hollow forms in the place where it formerly stood and the local exposure of undergrowth to sunlight is increased. The fall may be the result of violent winds or dying tree roots. Such events occur in a chance distribution over space and time. They favour the establishment of ‘new’ species and contribute to the maintenance of biological diversity. The recolonization of these spaces is accomplished (i) by the assemblage of seeds that arrived at the spot before the disturbance occurred and were dormant in the soil, pending the arrival of favourable light conditions;

(ii) by seeds coming from external sources after formation of the hollow; and (iii) by offshoots of the trees.

### 12.4. Buffering and recuperative capacities of ecosystems

The buffering capacity of an ecosystem resides in its ability to activate internal mechanisms that dampen the impact of a disturbance. But what about ecosystems’ capacity to recuperate after disturbances? Although there has been great emphasis on evaluating the impacts of different disturbances upon the structure or functioning of ecosystems, little research has been done on long-term processes of recovery of disrupted ecosystems.

The capacity of ecosystems to recover from severe disturbances depends upon the biological characteristics of their constitutive populations: rate of generation, fecundity, capacity for dispersal, etc. (cf. box on Demographic Strategies). But there are other factors that are independent of the nature of the organisms involved, such as modifications in habitats, residual toxicity, the duration and period of the impact in relation to the reproductive

cycle, the existence and distance of refuge zones, etc. Certainly, an ecosystem's recovery capacity also depends upon the existence of refuge zones for flora and fauna, providing the reservoirs for recolonization after the disturbance.

## 12.5. Spatial Heterogeneity and Temporal Variability

Spatial heterogeneity and temporal variability are major characteristics of ecological systems. However, for a long time, ecologists underestimated their importance. Until quite recently, they did not have the conceptual and methodological tools to integrate heterogeneity into their research in any practicable way.

## 12.6. Fragmented communities

In an environment characterized by spatial heterogeneity and/or fragmentation of ecosystems, populations of the same species tend to be fragmented and more or less isolated from one another. Since the 1980s, the theory of insular biogeography has prepared the way for the theory of metapopulations, which has been the basis for many theoretical and empirical studies on the effects of habitat fragmentation upon populations.

A metapopulation is a group of geographically more or less isolated subpopulations interconnected by individual exchanges that contribute toward maintaining the gene flow between the different subpopulations. A relatively simple instance is that of populations inhabiting oceanic or continental islands with continuous or occasional exchanges among them. In a metapopulation, certain subpopulations where births outnumber deaths act as 'sources' from which individuals disperse towards other areas. Conversely, certain subpopulations live in harsh environments where mortalities exceed births. Such environments constitute 'sinks.' A metapopulation is thus a dynamic system characterized by migration flows and processes of extinction between and within the subgroups of a fragmented habitat. The concept of metapopulation can be extended to multispecific communities, a metacommunity being defined as a group of ecological units sharing certain biotic components and among which exchanges are possible.

## 12.7. The dynamics of non-equilibrium

Proceeding from the intermediate disturbance hypothesis, Huston (1979) proposed a model of 'dynamic equilibrium'. It is applicable to species belonging to the same functional group and in competition with one another within a given habitat. The model is based on the relative roles of two opposing forces that both influence species diversity:

(i) competition leading to exclusion in situations characterized by high population growth rates and a mild degree of disturbances; (ii) severe or frequent perturbations, causing mortalities and limiting the reproduction of populations with slow growth rates, to the point where such species have no time to re-establish themselves. In the real world, many systems are disrupted frequently enough (fires, tornados, droughts, etc.) to put the recovery of their communities at recurrent risk.

The model does not predict a constant level of biological diversity for a certain combination of parameters, but rather a pattern of fluctuations within limits established by the model of dynamic equilibrium. This model is analogous to that of the theory of insular biogeography (where the opposing forces are immigration and extinction) but is applicable on a smaller spatial and temporal scale.

To date, the dynamics of non-equilibrium provide the best explanation for the spatial and temporal heterogeneity observed in most ecological systems. Disturbances and heterogeneity are the interdependent factors that create opportunities for recolonization and control the structure of communities. Within the context of a perpetually changing environment, competition, predation and interspecific relationships generally appear to have little influence upon the structure of communities, except under certain circumstances and in limited periods of relative stability.

## 12.8. Patch dynamics

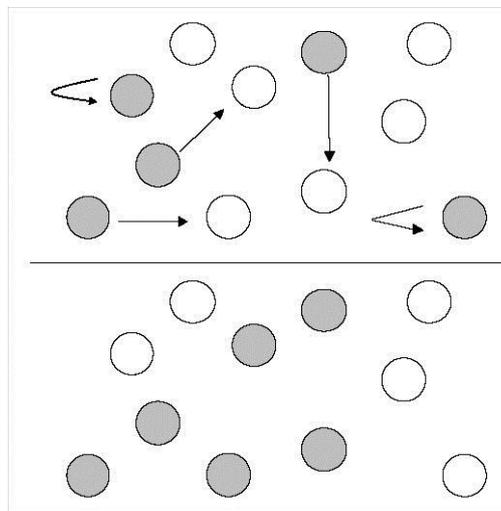
Landscape ecology provides ecologists with a simplified view of heterogeneity by defining space as a mosaic of 'patches' (spatially delimited structures at a given time) arranged over an ecologically neutral matrix. This spatial model grows progressively more complex when the varying characteristics of different patches and their temporal dynamics are taken into account.

The patch dynamics concept provides the link between the mosaic distribution of communities (metacommunities) and the spatial/temporal dynamics of the patches. Patches may either disappear or grow over time, as a function of fluctuations in environmental factors. Depending upon the prevailing tendency, associated communities can be either senescent, or pioneers or correspond to a stage in a succession cycle. Moreover, each patch of the matrix and its communities may have completely different dynamics from the others. The seasonal inundations and flood recession of river beds are a good illustration of patch dynamics in that variations in water level create and/or modify the spatial heterogeneity of the river channel.

According to Townsend (1989), the concept of patch dynamics is a major unifying principle in the ecology of running waters, where ecological characteristics such as current speed, substrates and availability of resources tend to manifest considerable spatial heterogeneity.

Patch dynamics imply the following principles.

Natural or man-made disturbances act upon ecosystems to modify the distribution of habitats over time and space. To give a simple example, river floods create new aquatic habitats as well as modify ecological conditions in already flooded habitats: current speed, depth, etc. The reverse applies equally when the waters recede.



**Figure 6.** Classical metapopulation model.

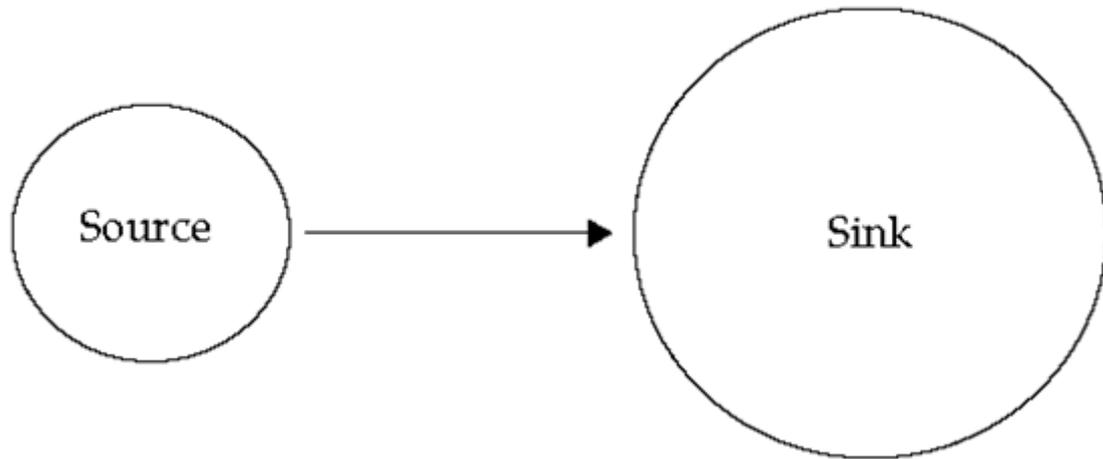
In a heterogeneous system, pioneer populations take hold as soon as habitats become available and usually evolve towards a more mature state. Thus, different patches will find themselves at different stages of ecological succession at the same time, as a function of the chronology of inundations.

Because they are dynamic over space and time, the assemblages are able to maintain a much greater biological diversity than systems evolving towards a climax in a monotonous way. Such dynamics may allow the co-existence of several species, with different ecological needs, in different patches, that are at different stages of evolution.

Thus, spatial heterogeneity and temporal variability are actually key elements in ecosystem functioning and the structuring of communities, and not just a simple ‘background noise’ that disturbs population dynamics.

## 12.9. From the continental to the local level

Phenomena occurring on large spatial and temporal scales provide a partial explanation for the composition of local communities. The example of river basins (the continental equivalents of islands in the sea) provides a good illustration for scales of interaction and the long-term consequences of certain events. The qualitative and quantitative composition of the fish communities inhabiting river basins is actually the result of numerous past events interacting with contemporary ecological factors. Tonn (1990) proposed a theoretical framework based on the principle that the local composition of species is the result of a series of filters acting on different scales of time and space. Species must have passed successfully through these successive filters to be present in the basin under consideration.



**Figure 7.** Simple sink-source model.

Historic events are sometimes expressed on a global scale. For example, the continental filter corresponds to the separation of Gondwana, since the present fish fauna on each of the continents are the result of processes of speciation and extinction that occurred subsequently.

The number of fish species in a watershed is thus the result of an equilibrium among: processes of colonization and extinction, depending in part upon the past history (climatic, geological, etc.) of the basin; processes of speciation, resulting from the evolutionary potential of the families present and the duration of their isolation; and competitive phenomena and/or epidemics. The model proposed by Tonn is actually an extension of the concept of patch dynamics on the global level and over very long periods of time.

The effect of continental richness upon the specific richness of rivers has been demonstrated. For example, given comparable environmental characteristics (surface area, discharge, regional productivity), South American rivers are richer than African rivers. This is probably the result of historical factors that favoured a greater diversification of species in South America after this continent separated from Africa.

## **12.10. Are Ecological Communities Governed by Niche-assembly or Dispersal-assembly Rules?**

There are two conflicting hypotheses on the nature of ecological communities (Hubbell, 2001). One of them is the view that communities are groups of interacting species whose presence or absence and even relative abundance can be deduced from 'assembly rules', based on the ecological niches or functional roles of each species. According to this view, the stability of the community and its resistance to disturbance derive from the adaptive equilibrium of member species, each of which has evolved to become the best competitor in its own ecological niche. Niche-assembled communities are limited-membership assemblages in which interspecific competition for limited resources and other biotic interactions determine which species are present or absent from the community.

The theory of island biogeography asserts that island communities are dispersal-assembled, not niche-assembled. If communities are largely opportunistic collections of species whose biogeographic ranges happen to overlap for historical and individualistic reasons, then it follows that species in communities are not highly coadapted or codependent. This view does not deny the obvious existence of niche differentiation. However, it breaks away from the conventional neo-Darwinian view of ecological communities as coadapted assemblages of niche-differentiated species residing at or near adaptive and demographic equilibrium. This is replaced by a new world view in which ecological communities are seen to be in perpetual taxonomic nonequilibrium, undergoing continual endogenous change and species turnover through repeated immigrations and local extinctions. It also ascribes much less importance to niches in regulating the relative abundance and diversity of species in the community. MacArthur and Wilson's theory raises the possibility that history and chance could play an equal if not larger role in structuring ecological communities than do niche-based assembly rules.

Actual ecological communities are governed by both niche-assembly and dispersal-assembly rules, but the important question is: what is their relative quantitative importance? Applied ecology and conservation biology

and policy critically depends on which perspective is closer to the truth, a fact that is not as widely appreciated as it should be.

## 13. List of animation, audio files and movies

video How Ecosystems Work.flv

## 14. Questions

- Which factors are influencing biodiversity?- What is the importance of an ecological niche?- What is the essence of niche-assembly rules? - Explain the basics of or dispersal-assembly rules?eCh05-Biogeography-v09.docx

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# 6. fejezet - Chapter 5 Island Biogeography

## 1. Classical theory of island biogeography

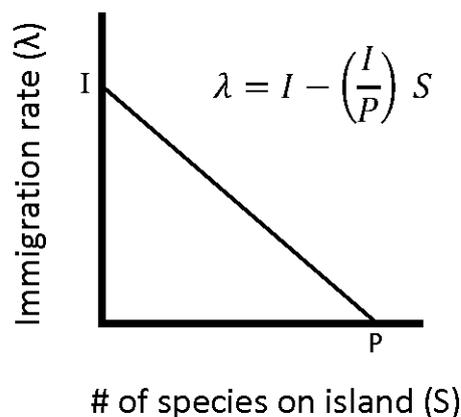
Much of our current understanding of how many species occupy a community comes from the study of island communities. Islands can be thought of as representative of many communities as they are a clearly defined collection of populations in space and time. It is thought that an understanding of community ecology on islands should apply to mainland communities as well.

MacArthur and Wilson's Equilibrium Theory (MacArthur and Wilson 1967) developed a simple framework to predict and explain the number of species found on an island. Their theory predicts that the number of species found on an island reflects a balance between ongoing immigration of new species to the island and continuous extinction of species already occupying the island. Simply

$$\text{Equilibrium} = IP / (I + E)$$

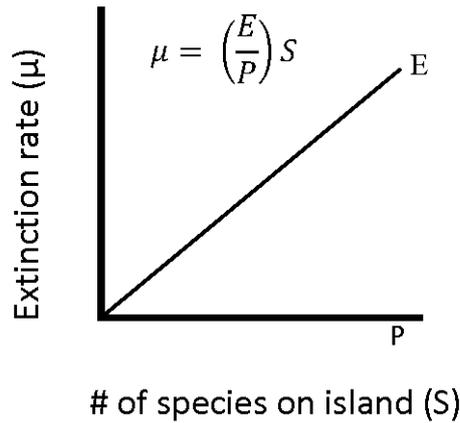
Where Equilibrium is the number of species on the island reflecting the balance of I, the maximum immigration rate of new species to the island, P is the maximum number of species that can immigrate to the island, or the number of species available in a nearby pool, typically referred to as the 'mainland', and E is the maximum rate of extinction. It is the rate of extinction when the number of species on the island, S, is equal to the number of species in the nearby pool.

We can derive this equation graphically by examining the relationship between the rate of immigration and the rate of extinction on an island with respect to the number of species on the island. First examine immigration rate:



**Figure 1.** The relationship between the rate of immigration and the rate of extinction on an island.

Immigration rate is highest when there are no species on the island (I) because all species that arrive are new to the island. As colonization of the island proceeds, many of the species arriving to the island are not new, members of these species have already colonized the island and progressively fewer and fewer uniquely new species arrive to colonize the island. Finally, the immigration rate must be zero when the the number of species on the island is equal to the number of species from the source pool (P) from which species are immigrating.

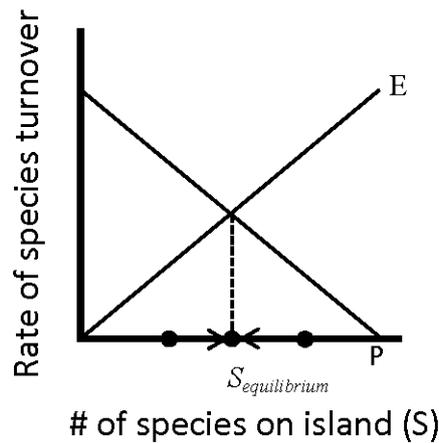


**Figure 2.** Relationship of species on island (S) and extinction rate.

Extinction rate ( $\mu$ ) shows the opposite pattern as immigration rate. Extinction rate is zero when there are no species on the island (logically). But extinction rate increases with increasing species on the island. Extinction rate is highest (E) when the number of species on the island is maximized, that is, when it equals the number of species found on the mainland. An equilibrium point occurs when the extinction rate equals the immigration rate so that:

$$I - (I/P) S = (E/P) S$$

Solving the above equation for S it yields the initial equation we started with.

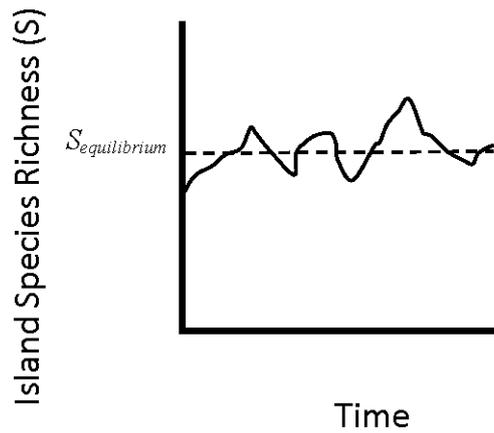


**Figure 3.** Number of species on island as resulted in by the balance of immigration and extinction.

S equilibrium is a stable equilibrium point. When the number of species on the islands becomes greater than Sequilibrium, extinction exceeds immigration and S declines to Sequilibrium. When the number of species declines below Sequilibrium, immigration rate exceeds extinction and S increases back to Sequilibrium.

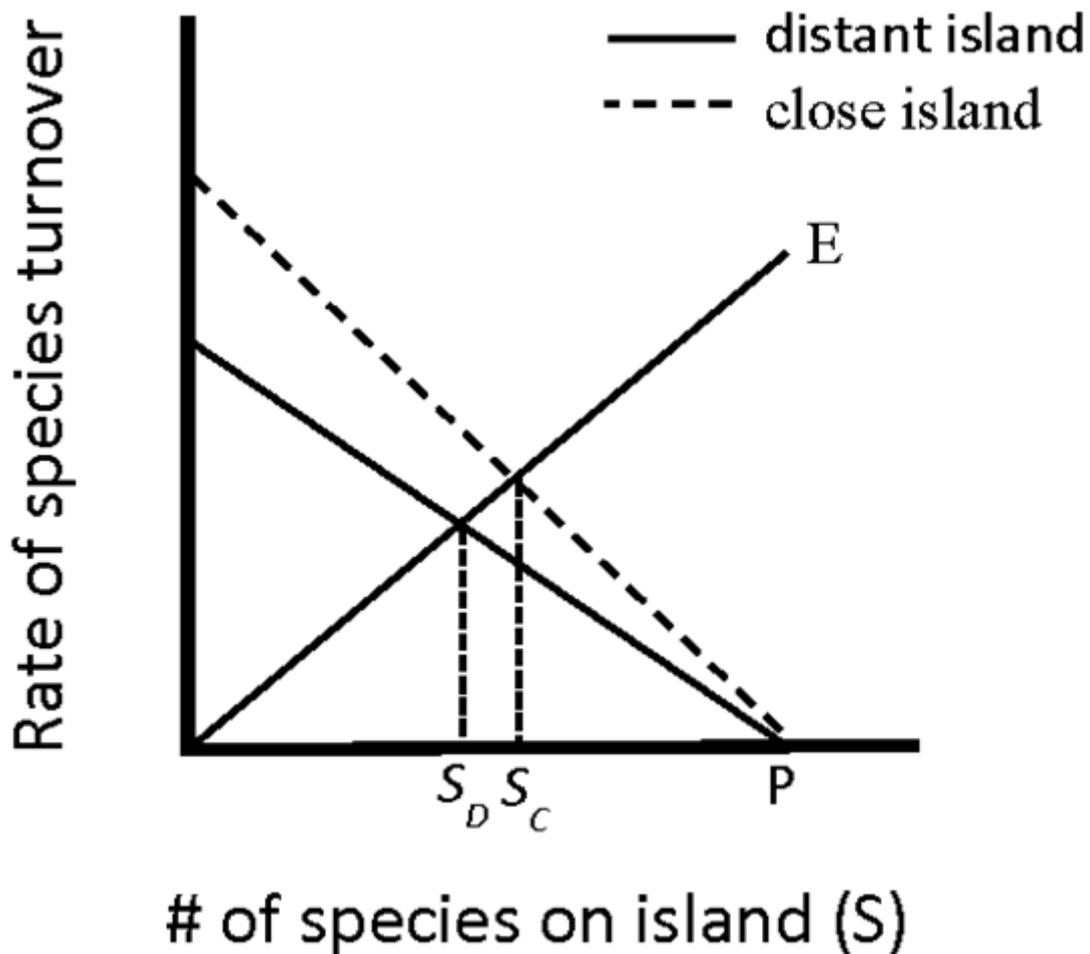
The Equilibrium Theory of Island Biogeography makes several predictions.

1. Species Richness on an island is increased with larger species pool on the mainland and high immigration rates and decreased with higher extinction rates.
2. Turnover of species on the island is not zero, because immigration rates and extinction rates are greater than zero. Species composition on islands are constantly changing although total species remains relatively constant.



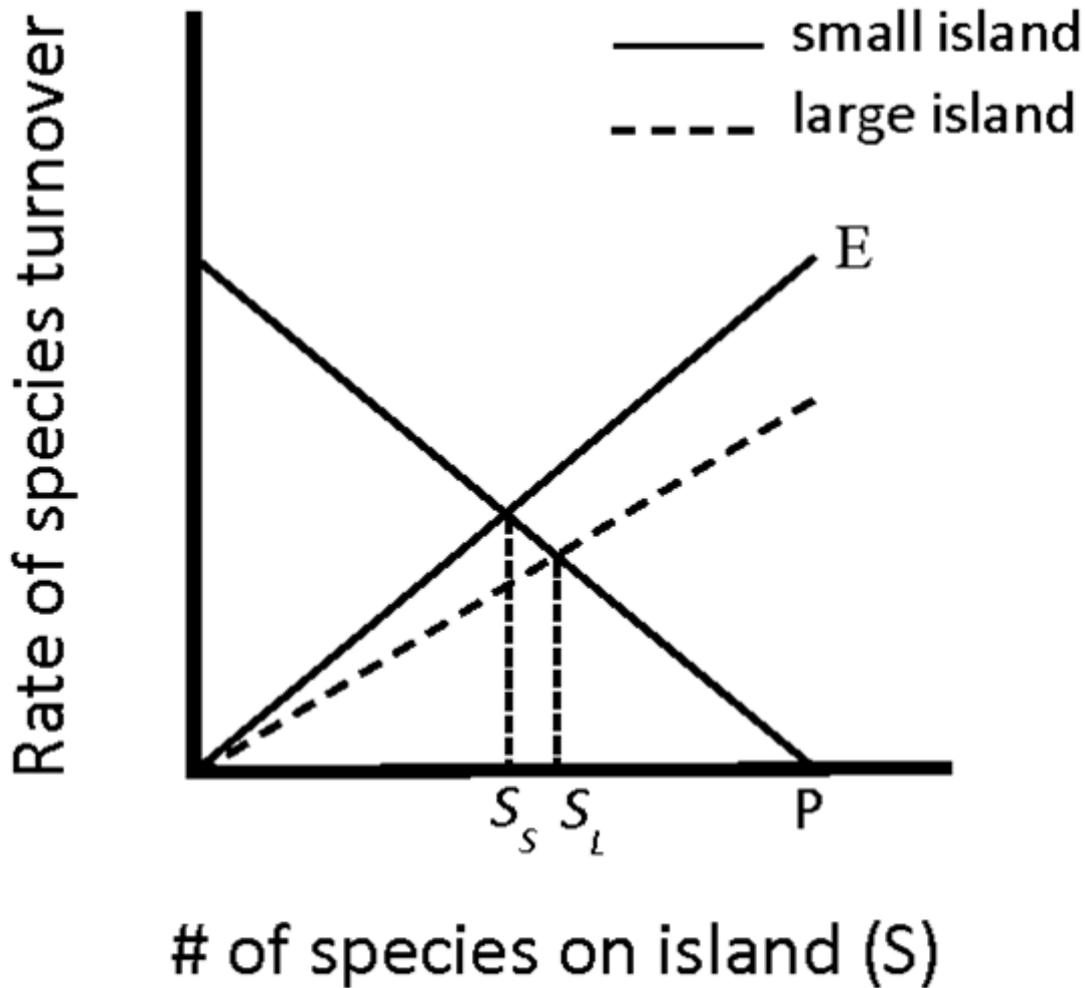
**Figure 4.** Fluctuation of the species richness on and island.

3. Islands closer to the mainland or species pool have higher species richness than distant islands because of higher immigration rates because species will find nearby islands sooner and more frequently than distant islands.



**Figure 5.** The effect of the distance from the mainland on the equilibrium number of species.

4. Larger islands have higher species richness than smaller islands because of lower extinction rates.



**Figure 6.** The effect of the of size of island to the equilibrium number of species.

This last prediction that larger islands should hold more species comes from the assumptions that (1), population density is probably the same on islands of different size and (2) probability of extinction declines with larger population size. Under these assumptions larger islands will hold more individuals of a given species population and stochastic models of population growth shows us that that larger populations are less likely to go extinct. An important assumption of these models is that immigration and extinction on the island is not affected by the existing species composition. We know of many cases where the existence of one species on an island or in an ecosystems is likely to effect the immigration or extinction of others, for example, strong competitors.

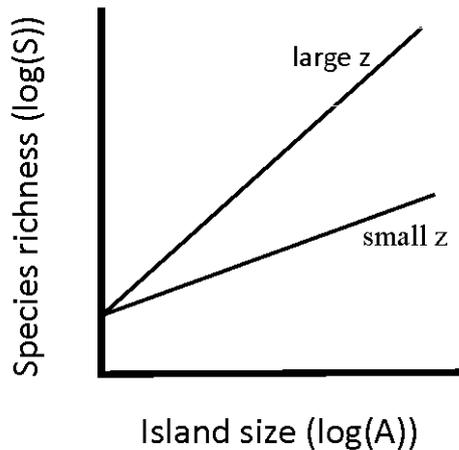
### 1.1. Further notes on Equilibrium Theory of island Biogeography

*The Target Effect* : The basic model assumes that island size only affects extinction and not immigration. However, larger islands represent larger targets that are easier for colonizing species to locate. The target effect describes this tendency.

*The Rescue Effect* : The basic model assumes that island distance from a species pool affects immigration and not extinction. However, isolated islands are more likely to experience extinction because isolated populations are less likely to be supplemented by immigrants from the species pool. The Rescue effect refers to the tendency for populations on less isolated islands to be regularly supplemented or rescued by new immigrants.

### 1.2. Species-Area Curves and Islands

One of the key results of MacArthur and Wilson's Equilibrium theory is that large islands should have more species than small islands. There is clearly a positive relationship between species richness and island area.



**Figure 7.** The effect of island's size to the species richness

The species area curve is usually defined as:

$$S = cAz,$$

where  $S$  is species richness,  $A$  is the area of the island, and  $c$  and  $z$  are constants. In this equation, it is easy to see that as area increases so does species richness. Considerable focus has been placed on estimating the proper value for  $z$ , as this determines how rapidly species are added with growing island size. To see the effects of  $z$  more clearly, we can restructure the initial equation by taking the log of both sides:

$$\log(S) = \log(c) + z \log(A).$$

This is structured as the classic formula for a straight line ( $Y = \text{intercept} + \text{slope}(x)$ ) where  $z$  defines the slope of the line relating island area to species richness.

Simberloff (1976) measured species richness on 4 islands of mangrove forest. He then took a chainsaw to three of the islands and reduced their size, but each island retained the same level of habitat diversity. As predicted by the species-area curve, species declined on the islands that were reduced in size while the control island actually saw an increase in species diversity.

## 2. Island biogeography and Ecology

As MacArthur and Wilson note in their revolutionary book *The Theory of Island Biogeography*, Charles Darwin was among the first to call attention to islands as a crucial subject for scientific study. As he was departing the Galapagos Islands in 1835, Darwin wrote when I see these Islands in sight of each other, and possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure and filling the same place in Nature. Of course Darwin's main interest was in evolution; we know now that islands can contribute enormously to our understanding of ecology as well. There are at least seven reasons why this should be so:

1. Islands are 'simple', with relatively few species and habitats. Thus, the often complex web of ecological relationships is observable in a more easily understood state.
2. Islands are 'discrete' and often small, providing a well-defined, manageable spatial unit for study.
3. Islands are 'isolated', so that they are relatively immune from outside fluxes, much as a laboratory tank or greenhouse.
4. Islands are 'natural', so unlike those human-constructed containers have biotas adjusted in at least the moderately long term to a confined state.

5. Islands are 'combinatorial', so that species occur in various combinations, often with absences and presences of key species varying as if in experimental removals or introductions, allowing comparative inference of those species' effects.

6. Islands are 'replicated' with a given set of species or environmental conditions, allowing statistical analysis and experimentation.

7. Islands are 'ubiquitous', not being limited to areas of land surrounded by bodies of water but generalizing to any patch of one type of habitat surrounded by another: mountaintops, river systems, hosts for parasites. Indeed, as MacArthur and Wilson also pointed out, natural habitat is becoming increasingly fragmented, that is, insularized by human activities so that many areas of conservation interest are effectively archipelagal.

### 3. The MacArthur-Wilson Equilibrium Theory

What was the revolution that MacArthur and Wilson effected in their 1967 book? The essence is that each island is in a state of species equilibrium, in which the number of new species immigrating per unit time is balanced by the number of species becoming extinct per unit time. To see how this could be very different from previous theoretical constructs, we can examine the effect of an island's distance on its species count. Extensive collection of information on species distributions and compilation of faunal lists shows that number of species on far islands is less than the number on otherwise similar near islands. One possible explanation is that the far islands, so removed from the source, simply did not have time to acquire the number of species near islands possess but eventually would. An entirely different explanation was advanced by MacArthur and Wilson, who argued that far islands have fewer species because their low immigration rate is balanced at equilibrium by a low extinction rate; the fewer species on far islands means fewer to go extinct per time, thus achieving a balance at a smaller equilibrium number.

#### 3.1. Tests of Species Equilibrium

A major claim of the MacArthur-Wilson theory was that a substantial portion of the world's islands are in fact at equilibrium, whereby the number of species colonizing balances the number becoming extinct. The evidence for a species equilibrium ranges from highly supportive to contradictory; we review the major cases in decreasing order of support.

1. Birds of Krakatau. In 1883 a tremendous volcanic eruption destroyed two-thirds of the Indonesian island of Krakatau and left its remnants and two neighboring islands under 30-60 m of ash, with no observable plants or animals surviving. As major confirmation of their theory, MacArthur and Wilson argued that equilibrium for land birds was re-attained only 25-36 years after the eruption. However, subsequent studies showed that the conclusion was premature: equilibrium has perhaps not yet been quite reached even after 100 years after the eruption. Much smaller gross extinction rates are now known to occur as compared to those predicted by MacArthur and Wilson (0.25-0.42% vs. 1-6% species per year).

2. Birds of the Channel Islands. The first systematic survey of birds on nine California Channel islands was accomplished in 1917. Since that time several surveys showed that the number of species over 50 years has not changed much. The degree to which the islands showed turnover was controversial and will be discussed in the next section.

3. Arthropods of Red Mangrove Islets. The red mangrove *Rhizophora mangle* grows as an emergent shrub or tree from small floating dispersal structures that root on shallow marine banks; islands so created can range from moderately large down to extremely small. Investigators took advantage of the plethora of such islands to study experimentally the recolonization by arthropods that would occur after a devastating extinction event. A pest-extermination company was hired to cover each mangrove islet with plastic sheeting and spray insecticide within; this eliminated most of the arthropods, so that when the sheeting was removed, artificially 'defaunated' islands resulted. Numbers of species rapidly increased, slightly overshooting the old equilibrium values before settling near it 1-2 years after inception of recolonization.

4. Marine epifaunal invertebrates on rocks. To simulate colonization of rocks in the intertidal, artificial panels were set out in the Massachusetts (USA) subtidal. This experiment produced an oscillating equilibrium, not unexpected in this highly seasonal environment. Thus the species equilibrium may manifest itself as a rather predictable oscillation, rather than necessarily having a constant value.

5. Plants on Krakatau. Plants showed a much slower rate of recovery after volcanic eruption than did birds. In MacArthur and Wilson's original analysis, there was no real tendency for the colonization curve for plants even to begin leveling off. The most recent censuses (c. 100 years since the eruption) show that equilibrium has been nearly attained for seed plants and ferns. However, like birds, the gross extinction and immigration curves are not monotonically related to number of species present as assumed by MacArthur and Wilson; rather apparently ecological succession causes several changes in direction, especially for immigration. For example, water- and wind-dispersal plants were the first to colonize, whereas animal-dispersed species did not colonize until a certain amount of successional change had taken place.

6. Birds on islands off Australia and New Zealand. Records for 15 islands taken over periods ranging from 50 to 124 years showed that the number of passerine bird species increased on 14 islands, up to 900% of the original values. While humans have had effects on these islands, including habitat diversification in some cases (which would allow more species), those effects did not seem to be sufficient to account for such huge increases; perhaps climatic warming for these rather high-latitude islands was involved. The investigators characterized this variation as 'nonequilibrium'; certainly it stands in contrast to Channel Island bird, as change was quite unidirectional.

7. Birds on Skokholm Island. Data on numbers of bird species for this rather northerly island off the British mainland (taken 1928-39 and then 1946-67) showed that number of species fluctuated between 5 and 13, with substantial temporal autocorrelation. These are large percent changes (over 200% by one measure), so is this evidence against equilibrium? Certainly it is evidence against species constancy; however, MacArthur and Wilson's algebraic theory (as opposed to the graphical one presented above) was a stochastic model with per-unit-time probabilities of immigration and extinction rather than fixed rates. Indeed, if we calculate for the Skokholm data the temporal variance and the mean number of species, the ratio is about 2/3, well within the possible range from the MacArthur-Wilson stochastic model, although higher than expected for equal (absolute) slopes of the gross extinction and immigration curves; an especially high extinction rate is consistent with the high ratio, unsurprising for such a small island.

8. Spiders and lizards on islands decimated by hurricanes. In 1997, certain Bahamas islands were completely inundated by the nearly 5 m storm surge of a major hurricane. As for Krakatau, no spider nor lizard individual survived; recolonization data a year later found spider species counts about where they were before the hurricane, whereas few islands to this day have been recolonized by lizards. In this case, the rapidly dispersing arthropods would be expected to reestablish equilibrium more quickly than large, terrestrial vertebrates such as lizards. Were hurricanes sufficiently frequent, certain taxa such as lizards might never reach a species equilibrium before the next disaster wiped them out again.

9. Arthropods in soybean fields. Soybean fields are an example of a highly temporary habitat that is frequently 'defaunated', here by scheduled human activities combined with climatic seasonality. The arthropods inhabiting such communities do not have time to reach equilibrium before being 'zeroed' again; hence they must constitute permanently nonequilibrium communities.

In summary, the value of the equilibrium concept varies from very useful for undisturbed islands to not so great for those that are frequently disturbed. The theory, however, does contain nonequilibrium dynamics, so that it is descriptively useful even for pre-equilibrium stages.

### 3.2. Tests of Turnover

Species turnover at equilibrium is the height of the intersection of the gross rates. That substantial turnover should exist is perhaps the most controversial part of the MacArthur-Wilson theory. What is the evidence for turnover?

1. Arthropods of red mangrove islets. Returning to the defaunation experiment, abundant turnover was demonstrated. Not only were there numerous extinctions and immigrations leading up to equilibrium, but once equilibrium had been achieved, species lists for particular islands were quite different from those before defaunation.

2. Birds of the Channel Islands. Returning to this example, Lynch and Johnson challenged the turnover data for two census times 51 years apart; among other problems they believed that species were missed in one or the other census, resulting in an inflated estimate of the degree of turnover. However, subsequent censuses by Jones and Diamond showed that turnover was in fact probably quite substantial over that period because of missed entire sequences of immigration and extinction for particular species in the intervening half-century when

surveys were not conducted. Their year-by-year data for a subsequent period in fact show turnover as 0.5-4.9% per year, whereas the two censuses in the original study gave 0.3-1.2%. Hence if the original two censuses missed species, this were more than compensated for by unobserved ins and outs during the long interval. Diamond and May presented an elegant stochastic theory predicting how 'apparent' turnover would decline with increasing time between censuses; the model successfully replicated annual breeding-bird data from the Farne Islands (another northerly group off the British mainland) and gave the result that for census intervals of decades, turnover is underestimated by about an order of magnitude.

Thus although Diamond's original conclusion for the Channel Islands was vindicated, apparently certain islands exist for which turnover is very slight. Two tropical representatives are at the extreme: Cocos Island had no turnover in 72 years, and the Tres Marias Islands had only two immigrations; perhaps tropical birds are more sedentary, thereby causing a regional difference between tropical islands and the temperate California or New Zealand islands.

3. Birds on islands radically altered in area by human activity. Various hydrological activities by humans created new islands while shrinking others in Lago Guri, Venezuela. Investigators found that a new equilibrium was achieved on the smaller remnants in just 7 years, while large islands are still declining. Similar phenomenology occurred in relation to the massive changes effected when the Panama Canal was constructed. Here as in Lago Guri, turnover was lower, the larger the island; it was also lower for far than near islands. Thus in these examples turnover is large even for tropical islands, albeit rather small, recently disturbed ones.

4. Spiders on Bahamian Islands. As assumed in the MacArthur-Wilson Model, there is a strong relation of population size to extinction rates in a variety of species. Investigators calculated the percentage of individuals for all species and islands combined belonging to populations becoming extinct over particular intervals, ranging from 1 to 5 years. Using 1 year intervals, 2.8% belonged to populations becoming extinct. Using 5 year intervals, still only 4.8% did so. It seems that turnover, while quite large in terms of species number (about 35% per year), does not involve the most abundant species, those that should often be the major players and in any event are of most interest to ecosystem as opposed to biodiversity ecologists. In this system, mostly the same species go in and out, much as portrayed in Hanski's core-satellite concept (see Metapopulation Models). To illustrate, we can construct population-persistence curves, which give the fraction of species populations remaining  $n$  years after a particular census: note that the combined-species curve levels off quite sharply, but that particular component species vary in the degree to which this is true.

In conclusion, species turnover is a salient feature of islands. There is, however, substantial variation, not only with island size, distance and region of the world as reviewed above, but also with generation time. As turnover involves rarer species it is of importance from a conservation view, yet perhaps equally unimportant from an ecosystem view.

### **3.3. Effect of Area**

The species-area relation, whereby the number of species in a spatial unit increases with that unit's area, well predates the MacArthur and Wilson theory of island biogeography, having been documented for about 150 years. Two general kinds of models for this relation have been proposed. The first has number of species predicted from an assumed species-abundance distribution and the total number of individuals of all species combined, and assumed to be proportional to area. The second develops species-area relations from MacArthur and Wilson's species-equilibrium approach. May's paper coalesces the literature for the first sort of model. Two species-abundance distributions are of particular importance. The first, a log-series distribution, has been used to describe light-trap data and other collections. Various more or less plausible ways to arrive at a log-series distribution from hypothetical biological processes have been given, perhaps the most common of which is not a biological mechanism but rather a property of the sampling procedure: species-area data in which samples of different areas are taken randomly from some homogeneous large area should have a semilog-linear plot for sample areas sufficiently large.

The second species-abundances distribution, the lognormal, is expected when individual population growth rates vary randomly over some substantial period of time or the relative abundances of each species is governed by many factors acting on the individual growth rate. Both follow from the Central Limit Theorem of statistics. Preston argues that what is constant is the number of individuals in the rarest species and the density of all individuals combined. It is fairly plausible that total number of individuals increases linearly with area for some well-defined taxon, although evidence bearing on this is not entirely supportive. While one study found that total density of birds increased with total species diversity, other results are more in accord with the assumption.

For the two-parameter distribution, some other feature also varies. However, the power of the species-area relation is fairly insensitive through the range of reasonable biological variation in the distribution.

### 3.4. Effect of Distance

While the species-area effect is documented for nearly all quantitative studies of islands, a similar effect of distance is more rarely demonstrated. This is probably true for two reasons: first, the lack of variation in distance from an outside source for islands within single archipelagos, and second, even where a variety of distances are available, the necessity of taking into account the usually very strong effect of area before a distance effect can be detected. An example is given although more examples exist from islands, so-called habitat islands, including the founding study on arthropods inhabiting thistle heads.

### 3.5. Effect of Elevation

Perhaps the most obvious potential effect of island elevation (altitude) on species occurrences is simple refuge from high water. Little documentation of such an effect has existed, but we now have a precise example. In 1999, a hurricane swept over small islands of the Great Abaco (Bahamas) region, completely inundating the lower ones with its storm surge. The islands were inhabited by a common lizard species, *Anolis sagrei*. Before the hurricane, island area was a better predictor of the occurrence of this species than was altitude. Immediately after, altitude was the better predictor. Apparently all lizards on islands lower than about 3 m maximum elevation had perished. After circa 1 year, area again became the better predictor: recovery occurred via overwater colonization and propagation from eggs that survived inundation, mechanisms that were enhanced by a larger island area. While rapid recovery often follows catastrophic disturbance, as in this example and those given above, such is not always the case. Ricklefs and Bermingham postulated that a major change in the mean age of the Lesser Antilles avifauna occurred about 0.5 million years ago, perhaps caused by a catastrophic disturbance such as a tsunami; little postcatastrophic recovery was evident.

The most commonly discussed effect of altitude on species diversity is more indirect than simple protection from high water: the greater the altitude, the more kinds of habitats, and the greater the number of habitat kinds, the more species can occur. Examples exist for the plants of the Galapagos and, to a lesser extent, the birds of the East Indies. This argument is a special case of the argument for the importance of habitat, and we turn to that topic now.

### 3.6. Effect of Habitat

We have so far reviewed two kinds of explanations for the species-area effect: (1) relation to a species-abundance distribution and (2) via the MacArthur-Wilson mechanism, extinction rate being assumed a function of population size. A third sort of explanation was advanced by Williams, who argued that area is just a proxy for habitat diversity, and it is the latter that directly drives the number of species on islands. By this interpretation, each species has its associated habitat type, and as area increases, the amount of each habitat type also increases, exceeding the thresholds for each species' occurrence one-by-one. A classic example is the avifauna of the Aegean Islands. Number of species shows a very precise relation to habitat diversity, equaling or surpassing many of the highly regular species-area relations exhibited by other groups. Multiple regression showed habitat diversity a more important prediction than area, just as was shown for elevation with respect to Galapagos plants. Similar results have been obtained for species counts in pieces of larger, mainland areas, for example, forest birds of eastern North America.

In addition to the species-area effect, a correlation with habitat diversity has also been postulated as accounting for the distance effect: Lack argued that far islands had fewer species than near because their habitats were less varied. A definitive test of the Lack vs. MacArthur-Wilson explanation of the distance effect was performed for birds and lizards of the Bahamas. Measuring the occurrences of various habitat types directly, investigators found using partial correlation that both isolation and habitat poverty contributed to a tendency for fewer species to occur on more distant islands.

### 3.7. Extinction and Conservation

It is a universal property of the extinction process, including populations on islands, that the smaller the population, the more likely extinction is to happen. This is a fundamental assumption underlying the area prediction of the MacArthur-Wilson equilibrium model. We can better understand the reasons for this relation if we examine the key processes responsible for extinction. First, demographic stochasticity, the chance

occurrence of a series of deaths before any member of a population can give birth, acts at low population sizes and can cause the population randomly to go to zero. Second, environmental stochasticity, represented as variation in species traits generated by extrinsic environmental factors that themselves are varying, is important at moderate-to-large population sizes. The environmental variation can be chronic, occurring more-or-less continuously over time, or catastrophic, occurring very infrequently but being much more severe. Finally, population ceilings are important: no population has the capacity to increase indefinitely, but rather negative feedback (densitydependence) will set in as it expands, eventually forcing the population to hover at or near some ceiling in numbers. With lower and lower values of the ceiling, a population would be correspondingly more and more vulnerable to demographic-stochastic extinction.

Many models of population extinction exist that can be applied to islands, but rarely has a single model encompassed both kinds of stochasticity as well as population ceilings. An international collaboration recently attempted to apply such a model to data for spider populations on 77 islands, censused annually over a continuous 20 year period. Two species were contrasted, one with larger populations sometimes crashing quickly to extinction and having a much weaker relation of extinction likelihood to population size than the other species. A simple model ignoring life cycles and a more complex model with detailed life-cycle characteristics estimated from the field were constructed; both models did well for large population sizes, but the complex model was necessary to fit data from small population sizes, as the life cycles interact with the various forms of stochasticity. In particular, the prediction that extinction probabilities are very sensitive to juvenile survivorship emerged from the analysis. This is in contrast to a similar approach for a noninsular species, Bonelli's eagle (*Hieraetus fasciatus*), which predicted sensitivity to adult survivorship. Conclusions such as these are in fact detailed expectations about extinction likelihood, in turn guiding conservation efforts in preserving species.

## 4. List of animation, audio files and movies

animation Green roofs explained.mp4animation Island-Biogeography.flvvoice Island Biogeography.mp3video An Indonesia Picture Show.flvvideo Biodiversity World Map.mp4

## 5. Questions

- What factors determine the number of species an island will hold?
- Demonstrate the extinction rate graphically.
- What is the exact relationship between Species Richness and island size?
- Is the species-area relationship being driven by island size alone or are there other factors that are driving this pattern, such as the tendency for larger islands to have more diversity in habitat types?
- Is the relationship between area and richness the same for different types of organisms?
- Is the relationship on the mainland the same as found on islands?
- How can contribute islands to the understanding of ecology of communities.
- How important is turnover, in terms of the population sizes of species undergoing it?

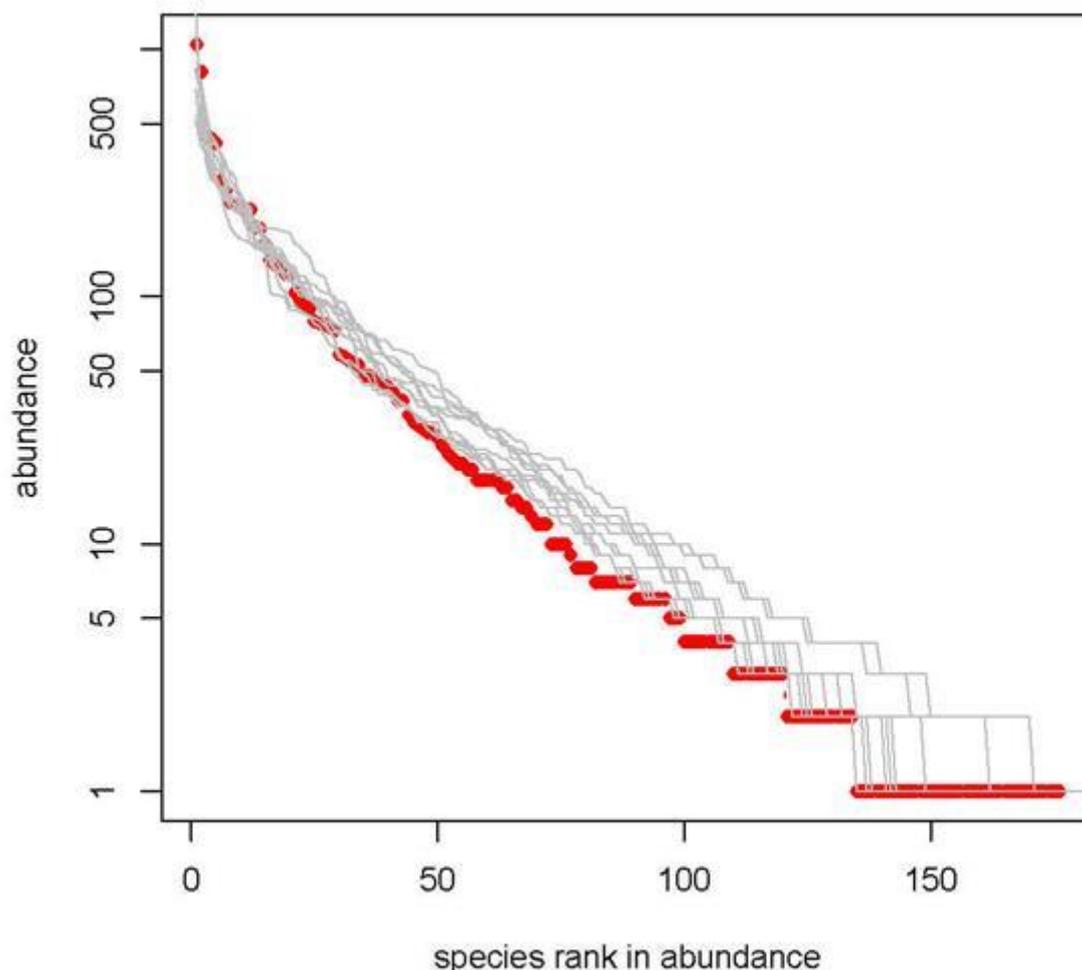
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# 7. fejezet - Chapter 6 Universal Neutral Theory of Island Biogeography

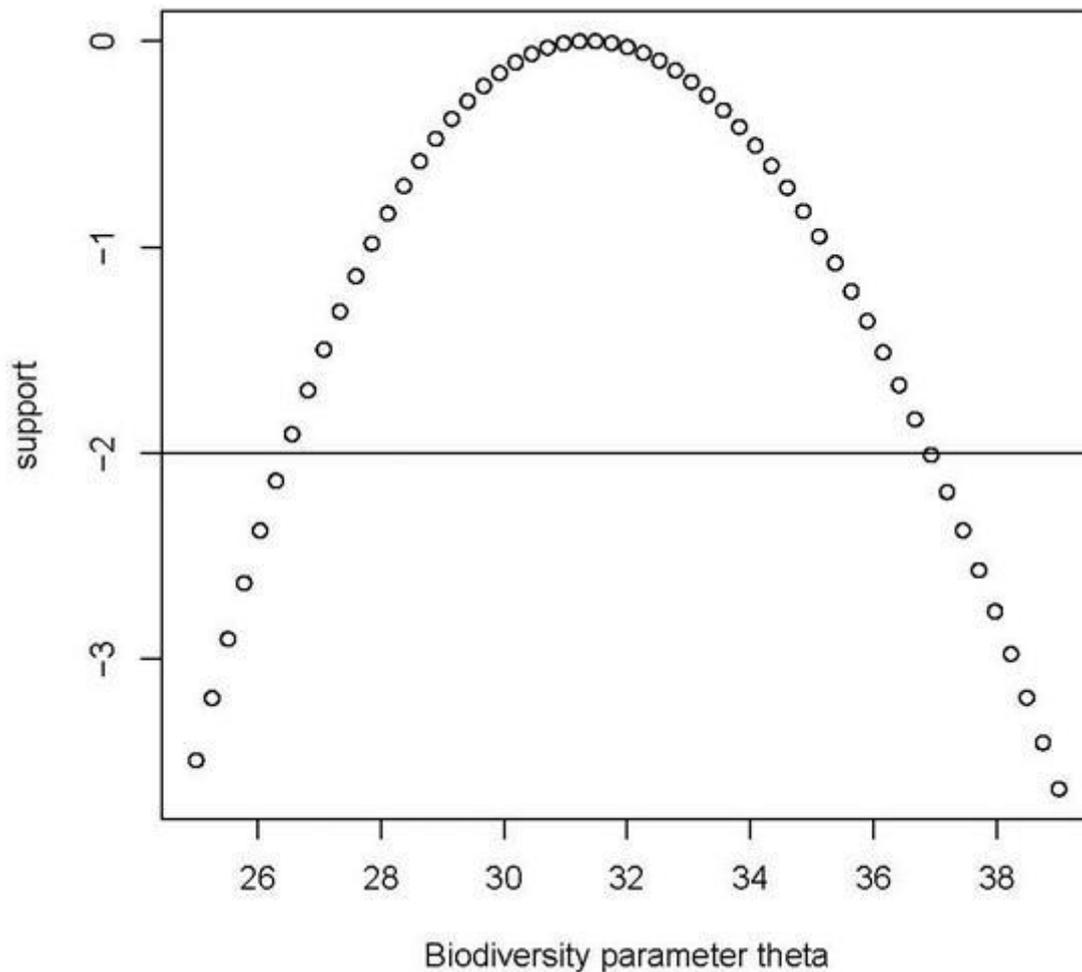
## 1. Neutral Theory of Species Diversity

Theories of island biogeography and of relative species abundance are of central importance in biogeography and community ecology. However, these two theories have been largely unconnected. Incorporating speciation into the theory of island biogeography unexpectedly results in unification of these two theories. The unified theory predicts the existence of a fundamental biodiversity number ( $\theta$ ) that controls not only species richness, but also relative species abundance in the source area metacommunity at equilibrium between speciation and extinction. With additional parameters for island size and migration rate, the theory also predicts relative species abundance on islands or local regions of continuous landscapes. Application of the theory to the biogeography and biodiversity of communities of tropical trees and reefbuilding corals are discussed. One important result is that only relatively modest migration rates are sufficient to dynamically couple the regional metacommunity and stabilize community structure on large spatiotemporal scales. Thus, regional, long-term compositional stasis in tropical rainforests and coral reefs can arise just as easily from the stabilizing effect of large numbers as from nicheassembly rules that limit species membership in communities.



**Figure 1.** The ranked abundance curve of the Saunders dataset showing real data (red) and 10 simulated ranked abundance curves, generated randomly using `rand.neutral()` using the maximum likelihood estimate for  $\theta$ .

Biogeographers and community ecologists typically work on very different spatial and temporal scales, and therefore it is hardly surprising that their theories for how biotas and ecological communities are assembled should differ. Ecologists tend to focus on small-scale processes shaping the interactions of individuals and populations. They tend to be impressed by the strength and importance of species interactions and of niche differences in stabilizing species assemblages in particular locations. Biogeographers, on the other hand, focus on much larger scale processes and ask questions about migration and range and speciation and extinction in space and time. One might label these two perspectives of the organization of ecological communities as the *niche assembly* and *dispersal assembly* views, although these terms do not adequately capture the large differences in viewpoint that exist within each perspective. For example, theories in vicariance biogeography tend to downplay the role of dispersal in assembling regional biotas compared to theories in panbiogeography.



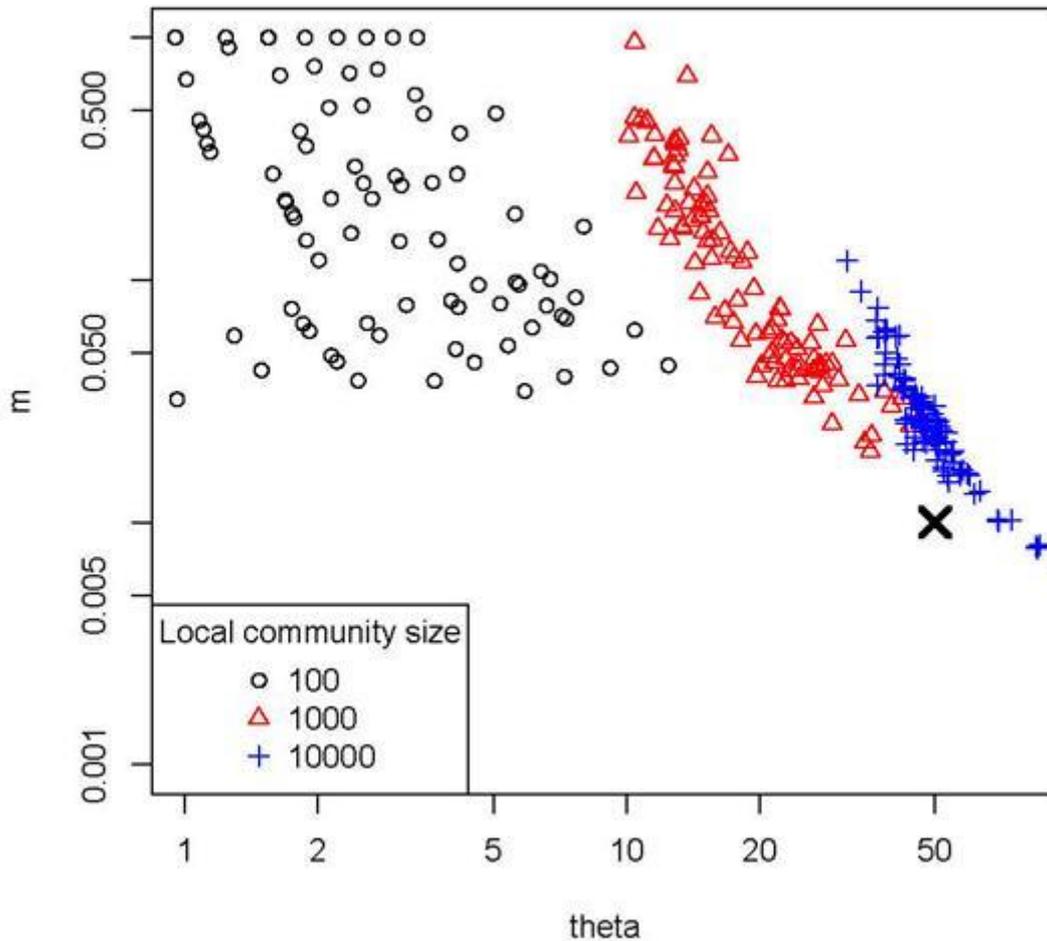
**Figure 2.** The support curve for the Saunders dataset as a function of the Fundamental Biodiversity Parameter theta.

The equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) attempted to link these two very different scales and perspectives. MacArthur and Wilson proposed that biotas inhabiting islands or insular habitats are in diversity equilibrium but not in taxonomic equilibrium. They suggested that local communities experience a continual turnover of species through immigration and local extinction of species drawn from a large source area or metacommunity. The equilibrium diversity on isolated islands was expected to be lower than on a similar-sized piece of the continuous mainland primarily because of a reduction in immigration rates due to isolation and increased extinction rates due to smaller island population sizes. Various embellishments were later added to the theory. For example, Brown and Brown (1977) suggested that immigration would interact with extinction to produce a “rescue effect”, further reducing local extinction rates in continuous landscapes.

The theory of island biogeography departs fundamentally from classical niche-assembly theory. Gone are niche differences among species. Species in the theory are treated as identical, subject to the same birth and death

processes and the same probabilities of immigration and extinction. If species are not identical, then the theory's simplification of the dynamics of island communities to enumerating species irrespective of taxa logically does not work. Thus, the theory is far closer to theories of pure dispersal assembly than to the niche assembly theories of classical ecology, which ironically, MacArthur also championed as the leading ecological theorist of his day (MacArthur 1972). Apart from whether one accepts the radical assumption of identical species, the theory of island biogeography is also conceptually incomplete in a number of important regards. From a biogeographer's perspective, it is incomplete because it embodies no mechanism of speciation. Although species can appear and disappear from islands or habitats in the theory, this is a migration and local extinction-driven phenomenon; no new species are allowed to originate in islands or in the source area.

### Maximum likelihood estimates of $m$ and $\theta$



**Figure 3.** Ensemble of 100 maximum likelihood estimates of  $m$  and  $\theta$ .

May (1975) examined the consequences of relative species abundance for species-area relationships, assuming that relative abundances were log-normally distributed (Preston 1948, 1962). However, this was a static sampling analysis, not a dynamical theory based on fundamental birth, death, and migration processes. Indeed, most of the existing models of relative species abundance are empirical statistical fits to observed distributions of abundance (Motomura 1932; Fisher et al. 1943; Preston 1948, 1962), or are based on static niche-assembly hypotheses (MacArthur 1957, 1960; Sugihara 1980) and are not grounded in a dynamical theory that can be related directly to the dynamical theory of island biogeography. The exceptions to this generalization are the theories of Casewell (1976), who proposed neutral models of community organization based on analogs in population genetics, Chesson and Warner (1981), who proposed that species abundances were determined by stochastic, frequency-dependent recruitment fluctuations, and Hughes (1984), a benthic ecologist who proposed a model similar to my own stochastic forest dynamics model (Hubbell 1979), which was a less general version of the theory discussed here.

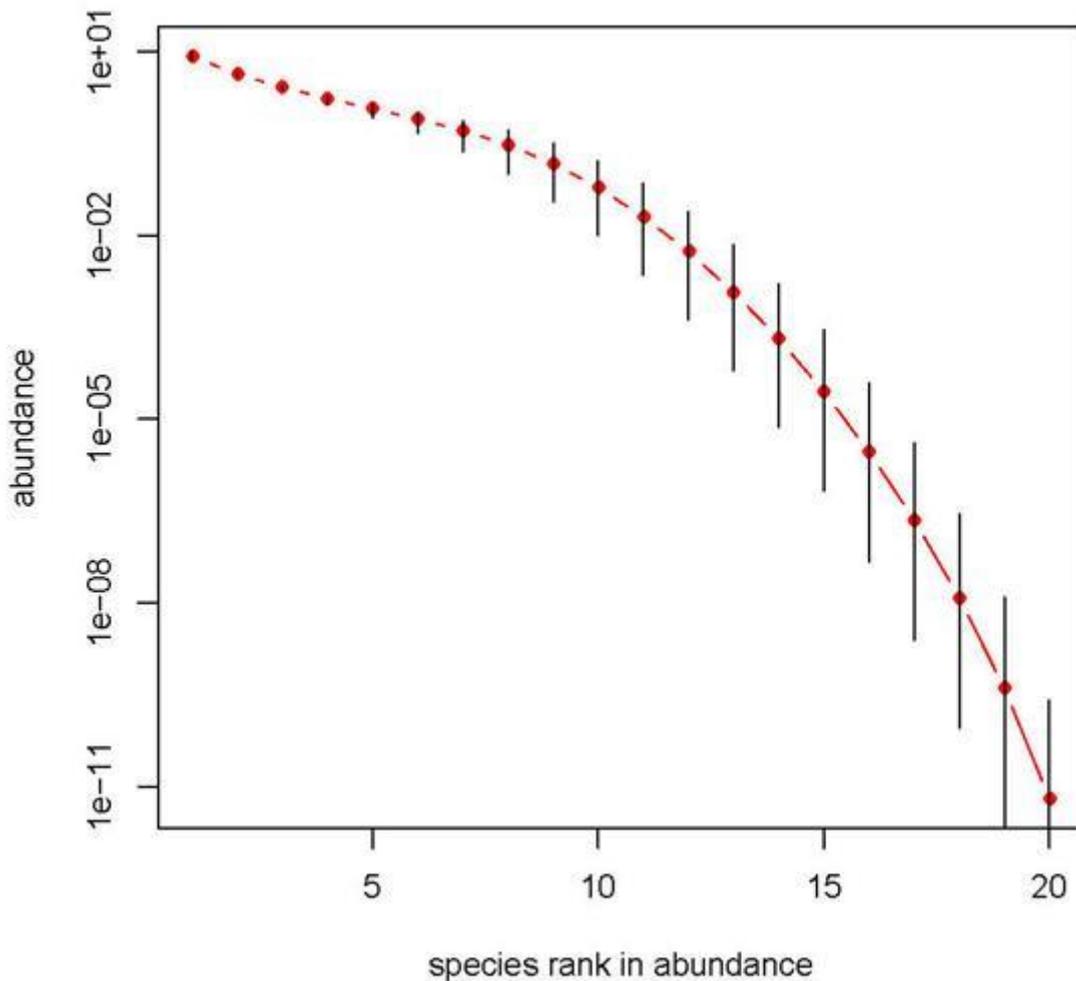


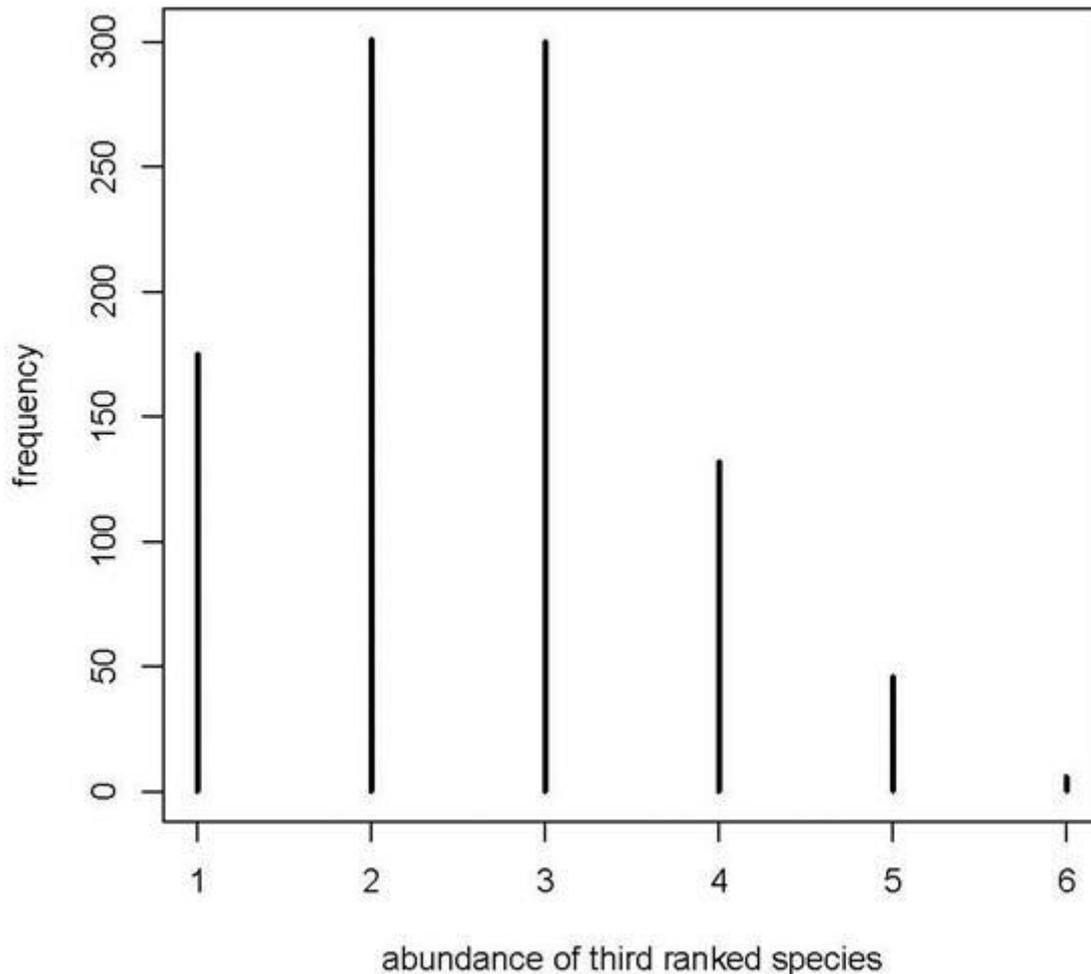
Figure 4. The expected abundances for the  $i$ th ranked species with  $JM=20$  and  $\theta=3$  for  $1 < i < 20$ .

## 2. Relative species abundance

UNTB is a direct generalization of the equilibrium theory of island biogeography. It rests on a key first principle, namely that the interspecific dynamics of ecological communities are a stochastic zero-sum game. This assumption is reasonable and appropriate for all communities of trophically similar, competing species in which individuals saturate all limiting resources. This includes space-limited communities such as closed-canopy forests, rocky intertidal communities, or communities of reef-building corals. It is also appropriate for communities limited by other resources, with the proviso that all limiting resources are utilized to saturation. By *saturated*, I mean that no births or immigrants in a community are allowed until deaths create vacancies. The theory explicitly and analytically describes the stochastic birth, death, and migration of competing species obeying this zero-sum game. The theory can then be applied to any arbitrary biogeographic situation, from the classical island-mainland problem of the theory of island biogeography, to a metacommunity fragmented over an archipelago of islands, and finally to the continuous landscape case of fully contiguous local communities (Hubbell 1995, 1997).

The theory further generalizes island biogeography theory by explicitly including a process of speciation. Given the lack of any generally accepted, quantitative genetical or ecological theory of speciation, I have chosen to model speciation in the theory by the simplest possible mechanism. New species arise in the theory like rare point mutations, and they may spread and become more abundant or, more likely, die out quickly. New species can arise anywhere: on the mainland, on islands, or in an archipelago of islands or habitats. Corals and rain forest trees almost certainly have more complicated, sometimes reticulate evolution (Veron 1995). Many species probably arise through the vicariant allopatric subdivision of ancestral species and never pass through a period

of absolute rarity at origination. It turns out that allopatric speciation does not alter the fundamental theory, but it does affect equilibrium metacommunity biodiversity (Hubbell 1997).



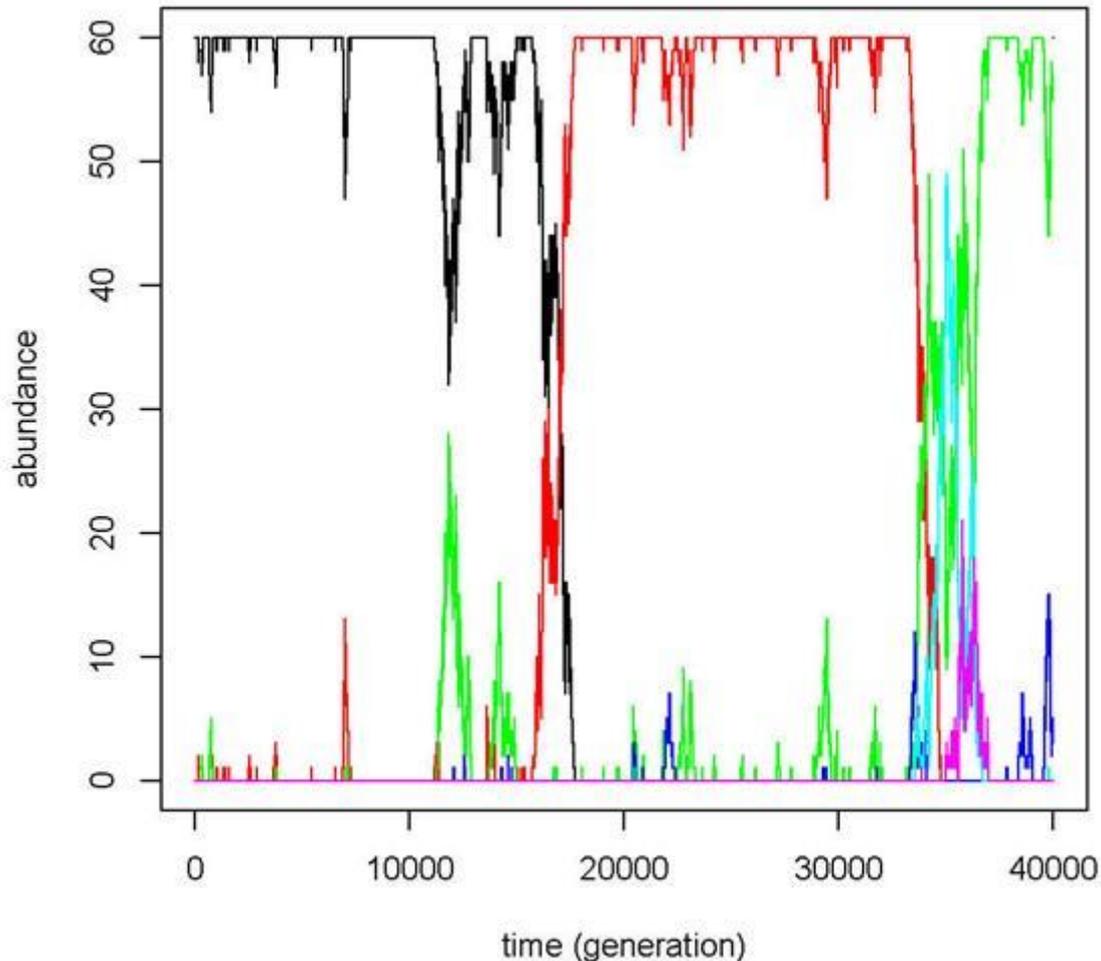
**Figure 5.** Abundance of third ranked species of an ecosystem of  $JM=20$  individuals and a biodiversity parameter  $\theta=2$ .

The unified theory of island biogeography and relative species abundance is a conceptual advance over either theory taken separately. In current theories of relative species abundance, the number of species in the community is a free parameter that cannot be derived from first principles (MacArthur 1957; 1960; Fisher et al. 1943; Preston 1948, 1962; Cohen 1968; Sugihara 1980). In the unified theory, the equilibrium number of species is a prediction as in the theory of island biogeography, but so also is relative species abundance. MacArthur and Wilson devoted a large section of their 1967 monograph to discussing the relationship between island population size and risk of extinction. Without a theory of speciation and relative species abundance, however, they were unable to make headway on many other issues of central importance to community ecology and conservation biology, including expected abundances of species on islands and in the metacommunity and their variances, species incidence functions and times to extinction and recolonization, patterns of island and metacommunity dominance and diversity, and species-individual and species-area relationships. Much progress has been made on theory for a number of these problems individually (May 1975; Casewell 1976; Coleman 1981; Quinn and Hastings 1987; Casewell and Cohen 1991; Hanski and Gilpin 1997; Durrett and Levin 1996). Now all of these problems are analytically tractable in the unified theory (Hubbell 1997).

### 3. A synopsis of the theory

There are two scales in the theory: local community dynamics and regional metacommunity dynamics. First consider a local or island community saturated with individuals of all competing species, such that all space or other limiting resource is utilized, and the dynamics are a zero-sum game. Define the scale of the local

community as the maximum patch size on which dispersal limitation can be ignored. Now kill an individual at random in the community, and replace it with another individual. Let the replacement individual be drawn from the local community at random with probability  $1-m$ , and be an immigrant from the metacommunity with probability  $m$ . Scale time so that one death occurs per unit time. Let parameter  $J$  be the size of the local community, i.e. total number of individuals of all species. Let  $N_i$  be the abundance of the  $i$ th species. Let  $P_i$  be the relative abundance of the  $i$ th species in the source area or metacommunity.



**Figure 6.** Synthetic dataset generated using neutral dynamics. Lines show the abundance of each species in time; different colours correspond to different species.

As in island biogeography theory, a species can immigrate or become extinct on an island or in a local community. The probability that the  $i$ th species will be at any abundance from 0 (extinct) to  $J$  (monodominant) in the local community (Hubbell 1997). The expected local abundance of the  $i$ th species depends only on local community size  $J$  and the source area relative abundance of the  $i$ th species  $P_i$ :  $EMN_i = JP_i$ , but the variance also depends on the immigration rate  $m$ . When the species is very abundant in the source area, it is also expected to be very abundant in the local community, and vice versa. The behavior of the eigenvector is more complex when the immigration rate  $m$  is varied. When the migration rate is large, the abundance of the  $i$ th species is strongly unimodal about its mean  $JP_i$ . When the immigration rate is small, however, the probability density function becomes U-shaped. Then the  $i$ th species spends most of its time either locally extinct or monodominant, and the proportion of time extinct or monodominant is dictated by its source area abundance  $P_i$ . The importance of this result will become more apparent when the dynamical coupling of local communities to the metacommunity by dispersal is discussed.

In the original theory of island biogeography the metacommunity was treated as a permanent pool of potential immigrant species to islands. In reality, all species ultimately become extinct in the source area, though usually at slower rates than on islands because of larger source area population sizes. In the source metacommunity speciation is analogous to immigration on islands. A steady-state species richness and relative species abundance will arise in the source metacommunity at equilibrium between speciation and extinction.

To solve for the equilibrium in the source metacommunity, we can take advantage of an analytical strategy developed by Ewens (1972) and Karlin and MacGregor (1972) for an analogous problem in population genetics. Let  $JM$  be the size of the source metacommunity (total number of individuals of all species) and  $l$  be the speciation rate. The strategy is to calculate the unconditional equilibrium probability of every possible configuration of relative species abundance in a sample of  $J$  individuals drawn randomly from the metacommunity (Ewens 1972; Hubbell 1997). With no loss in generality, rank order species in each configuration from commonest to rarest. Then the expected abundance  $r_i$  of the  $i$ th ranked species in the equilibrium rank-ordered relative abundance distribution for a random sample of size  $J$  individuals from the metacommunity. Analytical details are given in Hubbell (1997). The dynamics of the much larger source metacommunity are negligibly slow relative to the dynamics of the local or island community, so we can treat metacommunity relative species abundances as a fixed marginal distribution; and  $P_i=r_i$  of the source area distribution. Thus, we can henceforth conveniently dispense with the only species-specific parameter in the theory,  $P_i$  (Hubbell 1997). The theory then simplifies to just three parameters: the number  $h$ , island or local community size  $J$ , and migration rate  $m$ . The parameters of metacommunity size  $JM$  and speciation rate  $l$ , always appear combined into the single composite parameter  $\theta$ .

## 4. A fundamental biodiversity number

In the unified theory,  $\theta$  is a fundamental dimensionless number that controls both the steady-state species richness and the distribution of relative species abundance in the source metacommunity. When  $\theta$  is small (e.g. 0.1) the expected dominance-diversity curve is steep and geometric-like, with high dominance. However, as  $h$  becomes larger the expected dominance-diversity distributions become more  $S$ -shaped, as is observed in many species-rich communities. Eventually, the dominance-diversity curve becomes a perfectly horizontal line (infinite diversity), such that every individual sampled represents a new and different species, regardless of how large a sample is taken. At the other extreme, when  $\theta=0$ , the distribution collapses to a single monodominant species everywhere in the metacommunity. The distribution of metacommunity relative species abundances is the log-series (Watterson 1974; Hubbell 1997) and the fundamental biodiversity number  $\theta$  turns out to be identical to Fisher's alpha, which is a parameter of the log-series. Fisher's alpha is a widely used measure of biodiversity introduced by Fisher et al. (1943) more than 50 years ago.

The expected relative abundance distribution for a local community is not the log-series and therefore not the same as a random sample of size  $J$  from the metacommunity. The local distribution deviates from the log-series especially for rare species. Nor is the local distribution precisely log-normal; it is a new distribution that might be aptly named the *zero-sum multinomial* distribution. This new distribution arises because of an interaction between dispersal limitation and local extinction. This needs some explanation.

Preston (1948, 1962) criticized Fisher's log-series because it predicts that the rarest species will be the most frequent, whereas Preston's data on relative species abundance indicated that species of intermediate abundance are the most frequent. The unified theory demonstrates that Fisher and Preston were both correct, but on different spatiotemporal scales. Preston had no theoretical explanation for the interior mode of the relative abundance distribution. The unified theory's explanation is that rare species in local communities or islands are more extinction-prone (Hubbell 1997). Frequent local extinction of rare species reduces their local steady-state frequency and abundance below their random-sample expectations from the metacommunity log-series. On islands rare species are too rare and common species are too common.

At infinite dispersal ( $m=1$ ), the local community is not isolated from the metacommunity. In this limiting case, the local relative abundance distribution is a random sample of the metacommunity log-series, and singleton species will be the most frequent. However, as  $m$  becomes smaller, the island or local community becomes progressively more isolated, and the shape of the relative abundance distribution changes. Rare species become ever rarer and common species become ever more common. The unified theory thus predicts that the shape of the relative abundance distribution will be a function of  $m$ . These changes in shape enable one to estimate parameter  $m$  and thereby quantify the average dispersal limitation and degree of isolation affecting a given local community or island. The estimated value of  $m$  for the BCI plot is 0.10, or that 90% of the trees in the plot are estimated to have been locally germinated (births), and 10% were immigrants. This is a reasonable number for  $m$  given that 10% of the area of the plot lies within 17m of the outer perimeter. Once dispersal limitation is factored in, the expected equilibrium relative abundance distributions fit the observed distributions almost exactly.

The unified theory also asserts that the reduction of species richness on islands predicted by island biogeography theory will always be accompanied by an increase in the variance of relative species abundance, and therefore

by an increase in apparent dominance. This effect is predicted by the fundamental biodiversity number  $\theta$  in combination with restricted immigration. As equilibrium species richness declines, the mean and variance in abundance of the remaining species both increase relative to the metacommunity. Preston postulated a FIXED ratio of the total number of individuals in the community  $J$  to the abundance of the rarest species, which he called his canonical hypothesis (Preston 1962; MacArthur and Wilson 1967). The unified theory predicts an eventual breakdown of the apparent canonical relationship as sample size increases because of the long tail of very rare species in the metacommunity log-series (Hubbell 1995, 1996b). If the distribution were canonical, then in principle one should be able to increase sample sizes sufficiently until the last added and rarest species has abundance 1. However, in practice this never happens in real samples; the abundance of the rarest species observed almost invariably stays “locked” at 1, irrespective of sample size. The rarest species become ever rarer relative to common species in a seemingly endless regression as sample size increases. Therefore, no fixed ratio of  $J$  to the abundance of the rarest species exists.

## 5. Local species-area relationships

MacArthur and Wilson (1967) noted in their monograph that large landscapes are essentially always biotically saturated with individuals of a specified metacommunity or taxon. The unified theory of biogeography and relative species abundance asserts that on macroecological scales, to a first approximation, one need only specify the area of the biogeographic region, the density of organisms, and the speciation rate, to predict the equilibrium species richness and relative species abundances in the metacommunity or taxon. Note that this equation also relates biodiversity to landscape productivity insofar as the density of organisms per unit area  $\rho$  measures productivity.

The relationship between  $\theta$  and area implies that a function of  $\theta$  exists which specifies the species-area relationship. If dispersal is infinite ( $m=1$ ), then the unified theory makes a simple prediction for the cumulative species-individuals curve. This expectation was derived by Ewens (1972) for the problem of sampling selectively neutral alleles in the infinite allele case, and is identical to the case for zero-sum community dynamics. This is perfectly all right because an infinite number of species can be counted among an infinite number of individuals. In the real world,  $J$  is finite (but very large), so there can only be a finite number of possible species. Once parameter  $\theta$  has been fitted, the total number of species expected in a metacommunity of known size  $J$  can be calculated.

In general the equation will seldom fit observed species-individuals curves well because it assumes a completely random sample of individuals from the metacommunity, which is never possible, or a sample from a local community which is not isolated from the metacommunity, which is never encountered. All real organisms in real communities are dispersal-limited on some spatial scale. In most cases, observed species-individuals curves rise more slowly than the metacommunity species-individuals curve predicts. Fortunately, however, the dispersal-limited, real-world species-individuals curve and species-area curve can still be found analytically, but there is no longer a simple and direct formula. This is because, as we have seen, when there is dispersal limitation,  $\theta$  no longer completely determines local community species richness and relative abundance. The dispersal parameter  $m$  now becomes important, as well as local community size  $J$ .

## 6. Dispersal limitation and metacommunity organization

The potential for dynamic coupling of local communities to the metacommunity has an important bearing on the niche-assembly versus dispersal assembly debate about the organization of ecological communities, and in particular coral reefs and rain forests. For example, recent studies of a chronosequence of uplifted fossil reef terraces in Papua New Guinea found relative constancy in taxonomic composition and in species richness extending back for 95 000 y through repeated sea-level and surfacetemperature changes (Pandolfi 1996). Pandolfi (1996) concluded that this constancy was strong evidence for limited-membership coral communities, which by inference must be niche assembled. In a recent rain-forest example, Terborgh et al. (1996) reported similar dominance rankings among the 20 most abundant tree species in several 2 ha plots of terra Firme forest 40 km apart along the Manu River in Amazonian Peru. Terborgh et al. (1996) also argued that this falsified the dispersal assembly hypothesis.

These conclusions are premature according to the unified theory, for several reasons. First, common metacommunity species are likely to be very resistant to extinction and to persist for geologically significant lengths of time. Second, even moderate rates of dispersal will ensure that these species are nearly everywhere

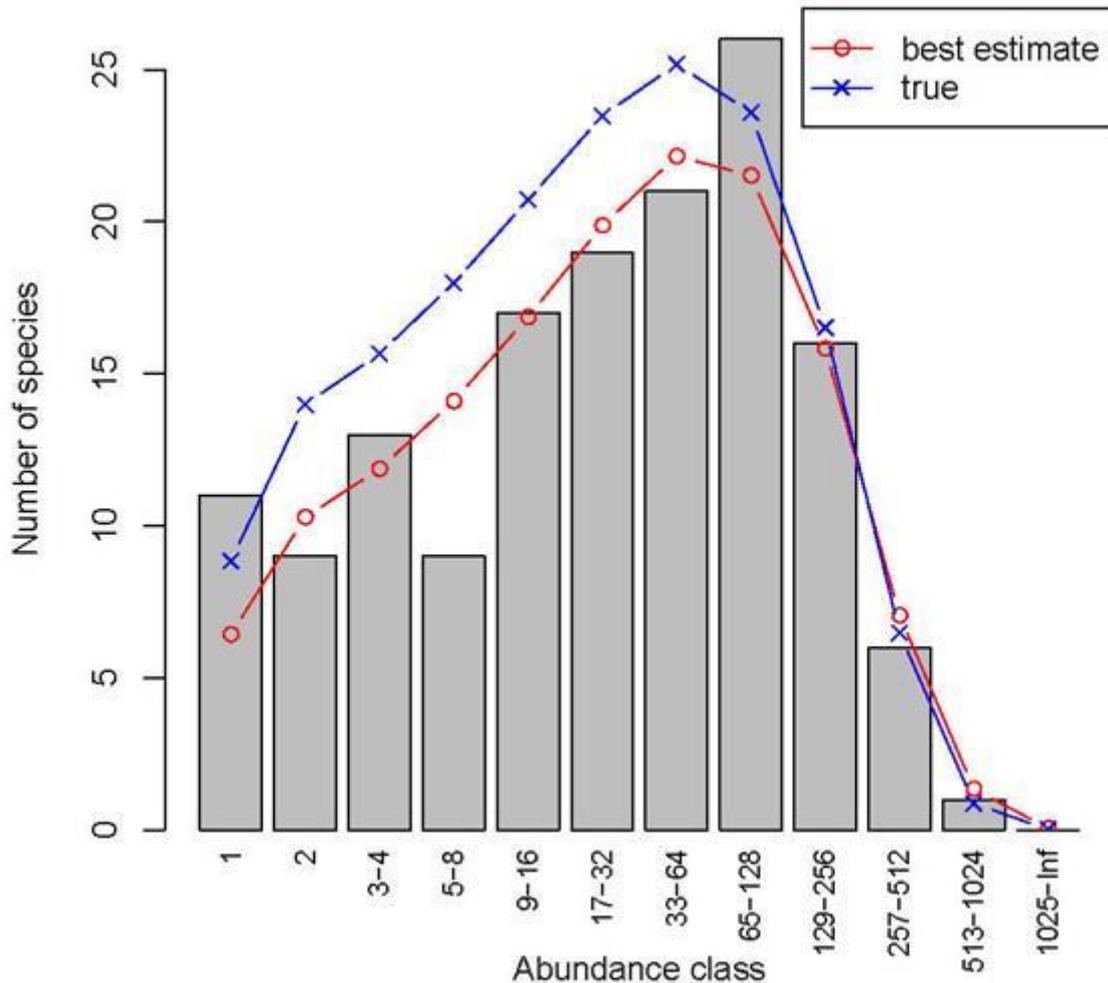
nearly all the time. Third, increasing the rate of dispersal will increase the proportion of metacommunity diversity present locally. Attempting to test the dispersal assembly hypothesis using only common species is particularly problematic. First, there is a well known correlation between local abundance and regional abundance of species (Brown 1984, 1995), so choosing to restrict attention to common species (for whatever reason) is also to choose, in general, those species that are least likely to be dispersal limited and most likely to be persistent in space and time, biasing the conclusion toward constancy of community composition. An important result of the unified theory is that the time to complete extinction of a widespread and common species under zero-sum dynamics is extremely long (Hubbell and Foster 1986; Hubbell 1996b). The time (i.e., the number of deaths in the metacommunity) for a metapopulation of a given species to become extinct is a very large number for even moderately common species. From theta we know that  $JM$  is an enormous number, on the order of the inverse of the speciation rate, which is a very small number. But  $q(N_i)$  is an even bigger number, on the order of the metapopulation size of the given species  $N_i$ , times the metacommunity size  $JM$ , times the log of metacommunity size  $\ln(JM)$ . The immensity of this number is important because it means that common species will be very persistent members of the metacommunity, often for geologically significant time periods. Another importance of this result is that it means that the ecological dynamics of metacommunities are temporally commensurate with the evolutionary dynamics of speciation and extinction. Indeed, this must be so because a theorem can be proven on the existence of an equilibrium diversity in the metacommunity uniquely determined by parameter  $h$  (Hubbell 1997). This persistence means that these common metacommunity species have ample time to disperse nearly everywhere throughout the metacommunity. Evidence that widespread species are more resistant to extinction events has been provided by Jablonski (1995) and Jackson (1995).

Without data on mean dispersal rates and metacommunity species abundances, it is difficult to quantify and test these predictions for either rain forests or coral reef communities. However, one can model the dynamic coupling of local community and metacommunity in a manner that generates patterns similar to those found by Pandolfi (1996) and Terborgh et al. (1996). Under high dispersal ( $m=0.5$ ) community similarity declines only gradually with distance; whereas under low dispersal ( $m=0.005$ ) community similarity declines very rapidly. In this numerical example, migration was possible in one time step only from neighboring communities. If, as in coral reefs, propagules can and often do disperse from communities very far away, then community similarities may remain very high over very long distances. Under complete mixis, the Bray-Curtis similarity index may barely drop below unity over long distances.

## 6.1. Neutral and niche

Niche differences are the classical explanation that ecologists have used since Darwin to explain the amazing diversity of life on Earth. A species' niche encompasses all of the factors it requires for growth and reproduction and how a species impacts its environment. For example, plants require water and nutrients at some minimum amounts, and by growing, plants decrease the availability of those resources, which negatively affects the growth of competitors. Many factors limit organisms, and no organism is best adapted for all conditions, species have tradeoffs, which allow them to perform better in some environments, but necessarily worse in others. Niche differences are a mechanism that can maintain biodiversity by allowing species to coexist.

Building on foundational ideas described in island biogeography and the neutral theory of molecular evolution, the neutral theory of species diversity makes the provocative assumption that all individuals are ecologically identical, and that niche differences are not needed to explain biodiversity patterns. Individuals of certain species may all share characteristics that make them look or function different from other species, but those differences do not influence diversity. An individual in a community interacts with and experiences its neighbors as though they were exactly the same, regardless of species. This assumption of equivalence is the essential feature of neutrality, which differs from typical niche-based assumptions that an individual's fitness depends on who its neighbors are. Neutral theory predicts that species have perfectly overlapping niches. At the other extreme would be species with unique, non-overlapping niches. Real communities, likely represent neither of these extremes but are somewhere in the middle. What neutral theory forces us to ask is how ecologically different are species, and how important are those differences for determining biodiversity?



**Figure 7.** Preston plot of a synthetic dataset of  $J=10000$  individuals, partially isolated from the metacommunity and allowed to simulate for  $10^4$  deaths per individual.

## 6.2. How Neutral Theory Works

Under the neutral theory, highly diverse communities of equivalent species arise because chance extinctions are balanced by speciation. Specifically, the assumption of fitness equivalence combined with stochastic or random processes that include death, immigration from a regional pool of species, and speciation can lead to species-rich communities. As an example, imagine a field, which will be the local community, made up of many species of plants. Plants in the surroundings landscape represent the regional species pool. The field is thus part of a larger collection of plant communities called a meta-community. Individuals in the local community die at random and create openings for seeds to grow. Individuals from the meta-community, and from the local community, randomly disperse their seeds into the field. If there are more individuals of some species than others they will contribute more seeds than will rare species, but each individual seed has an equal chance of establishing. Individuals are in that sense competing for open sites. If dispersal from the meta-community is strong, the local community look like a small version of the region. When dispersal from outside is weak, random deaths and extinctions combined with random mutations and speciation will cause the local community to drift and differ more and more from other communities over time, but in an unpredictable way. This random change in species abundance over time is termed ecological drift. There can be a limit to the number of individuals in the local community: if the community is full, a new individual can only establish if another one dies and makes space. This is known as a zero sum assumption.

## 6.3. Modeling a neutral process: What Neutral Theory Is?

Random death, dispersal and speciation are all important features of the neutral theory of biodiversity. But its essential feature is the assumption of identical individuals. Species may have differences, but those differences do not matter because all individuals have the same fitness and experience each other identically. The other features are assumptions about the processes that determine community assembly, or how species are added to and lost from communities, and how communities change over time. Another aspect of neutral theory is that it only applies to groups of similarly functioning species: trees in a forest or corals in a reef, and not to species of different size or trophic position, like microbes and elephants, or plants and herbivores. Also, there is no single neutral theory model, and different neutral models make different assumptions about these other processes. A local community could remain partly empty, or alternatively the numbers of individuals might be allowed to increase in a model continuously. Stochastic processes are important in neutral models for communities to change over time, but some parameters might be random while others might be non-random. Annual plants always die at the end of the year. Niche models, where individuals of different species do differ from each other and those differences matter for their fitness, can also be stochastic, and some purely deterministic or truly non-random processes can also be unpredictable and only apparently random. Stochasticity or randomness is often just a simplification we make when we can't predict exactly the outcome of an event: assuming something is random allows us to conveniently describe a process in terms of probability or chance.

Although dispersal, stochasticity and speciation are not unique to the neutral theory, neutral models are more interesting and useful when we add in things like dispersal and stochasticity. For this reason, neutral theory is often described as a “dispersal-assembly” theory or a “stochastic” theory, even though neither dispersal nor stochasticity is a feature uniquely or necessarily neutral. Dispersal and reproductive traits are in fact another way that species can differ in their fitness, and how organisms move through space can be an important component of a species' niche. Consider the enormous variety shown by flowering plants in their fruits and the diverse ways plants can disperse by wind, water or animals, as well as their different mating strategies, germination and pollination mechanisms. Dispersal may often be highly unpredictable, but it is not necessarily neutral.

Dispersal and speciation processes in neutral models can lead to highly diverse communities. But the coexistence of species in neutral communities is unstable. There are no mechanisms that cause one species to remain dominant or prevent rare species from going extinct. Because neutral processes are driven by random events, and because all individuals are competitively identical. Their abundances either increase or decrease purely by chance. In a closed system, stable coexistence, or long-term persisting species, can only occur when there are niche differences that cause individuals to compete most strongly with individuals of their own species compared to those of other species. Niche-based stabilizing mechanisms limit the growth of species when they become very abundant, while at the same time stabilizing mechanisms allow rare species to increase because they enjoy higher fitness when surrounded by neighbors of different species with whom they compete less strongly.

## **6.4. Pattern versus Process: Species abundance patterns**

Neutral models can predict realistic species diversity patterns from just a few parameters. One parameter is the Fundamental Biodiversity Number (usually denoted by  $\theta$ ), which is larger with greater numbers of individuals in the meta-community and with greater speciation rates. With the fundamental biodiversity number and estimates of dispersal, neutral models can predict the number of species and their relative abundance patterns in different systems. For example, when we plot the rank of a species against its abundance in a community, we usually find just a few super-abundant species (high rank) along with many very rare species (low rank). These species abundance distributions are one type of pattern that neutral models have been very good at predicting. But it turns out that many types of alternative niche models do so just as well, which makes these pattern-matching approaches a fairly weak test: showing a pattern doesn't necessarily tell you the process responsible. Where neutral models have consistently failed is in stronger tests, such as predicting which species or traits of species should be abundant, or under what environmental conditions some species increase while others decrease.



**Figure 8.** Simulated ecosystems of size  $JM=100$  for varying parameters, with each organism represented by a dot, the colours representing different species; spatial locations are functionally identical.

## 6.5. The Utility of Neutral Theory

Neutral theory is still a powerful and useful concept for several reasons. Stephen Hubbell's 2001 monograph, *The Unified Neutral Theory of Biodiversity and Biogeography*, has sparked vigorous debate among ecologists, and has led to more rigorous, and much needed, tests of niche mechanisms and explanations of biodiversity. Ironically, neutral theory has reinvigorated niche theory. As with all models, the neutral model is a simplification of processes we think important in the natural world. Thus, the strength of the neutral model is that it provides us with a logical place to start: an elegant and simple null model, with clear and testable

assumptions and predictions. We can then ask if other mechanisms, and their added complexity, are necessary to explain what we observe.

The neutral theory of species diversity starts with the key assumption that all individuals in a community of trophically similar species are ecologically identical. Neutral models that additionally include random death, speciation, extinction, and dispersal from the meta-community can lead to highly diverse communities that have similar species abundance patterns to what we observe in real communities. The abundances of species in neutral models fluctuate randomly over time leading to ecological drift, where diversity is due to unstable coexistence and the balance between extinction and speciation, in contrast to niche models that assume the importance of species' niche differences and stabilizing mechanisms. Neutral theory provides a null model, or a starting point, from which we can test niche-based hypotheses for how species' evolutionary adaptations and niches maintain biodiversity.

## **7. List of animation, audio files and movies**

animation Loss of Biodiversity.flv

## **8. Questions**

- What is the basic assumption of UNTB?
- How to interpret the theta parameter of UNTB?
- What is the relationship between UNTB and the classical theory of biogeography?
- What is the Fundamental Biodiversity Number?
- What neutrality means in UNTB ?

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# 8. fejezet - Chapter 7 Number of Species and Simple Measures of Diversity

## 1. Measuring Biological Diversity

Quantifying biodiversity is of practical importance. Different methodologies are adopted for measuring biodiversity. None of them is universally accepted, and the choice of methods and scales tends to depend on the objective pursued. From a theoretical standpoint, the correct procedure would be to evaluate all aspects of biodiversity in a given system. Estimates of diversity based on a number of indicators, including genetics, species or populations, the structures of habitats, or any combination that provides a relevant, albeit relative, evaluation of biological diversity.

The most common unit of measurement is the species richness determined for all the taxa, or subsets of taxa, identified in a given environment. However, confusion should be avoided between biodiversity and species richness: the former includes the latter but is not restricted to it. A high number of species in a given environment is likely to be a good indicator for a larger genetic, phylogenetic, morphological, biological and ecological diversity. In groups with well-known taxonomies, the list of species is relatively easy to establish.

The relative diversity (also known as evenness) has also been used to compare different communities or ecosystems. The most frequently used indices are based on the estimated relative abundance of the species found in the samplings. However, these indices assign an equal functional weight to all species, for which there is no clear justification. Other indices have therefore been developed, taking into consideration such factors as taxonomic position, trophic state, or body size of the species. Generally speaking, the usefulness of such indices is limited, because they do not provide much information that is relevant on a practical level. Attempts have been made to enhance them with genetic and ecological input. Analogous indices are used in genetics, in economics, statistical physics, and heterozygosity, which associates the number of alleles with their relative frequency. Another approach involves identifying the diversity of ecosystems in a landscape, or habitats within an ecosystem. It is possible to proceed as in taxonomy by identifying, naming and classifying entities, comparing different situations, and then attempting to generalize one's observations. This typological approach has established several categories of classification based on floral or faunal characteristics, on assemblages of species, or on landscape features.

## 2. Number of Species

The simplest measure of diversity of a system is just the total number of different species found in that system. This is often referred to as species richness. Species richness is widely used in ecology as a measure of species diversity. One example is the long-standing and recently revitalized diversity-stability debate: the question whether more diverse ecosystems are more stable and productive than less diverse systems (Odum 1953, MacArthur 1955, Elton 1958, May 1974, Lehman and Tilman 2000, McCann 2000, Loreau 2001). Another example are the so-called species-area relationships, which are important for the present conservation debate because they are virtually the only tool to estimate the number of species that go extinct due to large-scale habitat destruction (MacArthur and Wilson 1967, Whitmore and Sayer 1992, May et al. 1995, Rosenzweig 1995, Kinzig and Harte 1997, Gaston 2000).

However, one might argue that not all species should contribute equally to a measure of species diversity. Two different strands have evolved in the literature both of which develop measures of diversity where different species are given different weight. The first strand, which has evolved mainly in ecology, weighs different species according to their relative abundance in the system. This is vindicated by the observation that the functional role of the species varies in proportion to the abundance of that species in the system. The other strand, which has been contributed to the discussion of biodiversity mainly by functional ecologists and/or economists, stresses that different species should be given different weight in the diversity measure due to the attributes they possess.

### 3. Diversity indices based on the number of species and abundances

Ecologists have tackled the problem of incorporating the functional role of species in a measure of species diversity by formulating diversity indices in which the contribution of each species is weighted by its relative abundance in the ecosystem. Intuitively, rare species should contribute less than common species to what one might think of as the effective number of species in an ecosystem. However, there are virtually infinitely many different ways in which information about the heterogeneity, or unevenness, of the distribution of relative abundances can be used to calculate an index of effective species number. Generally, that index should have the property that it is smaller than pure species richness, and that it decreases as heterogeneity of relative abundances increases. In that sense, dominance of a few species, or, more generally, a heterogeneous distribution of relative abundances, should bring down the index of effective species number from its maximal value. Only for maximal homogeneity of the distribution of relative abundances, when abundances are evenly distributed over different species, such that all species are equally common, should the index assume its maximal value.

### 4. Species and biodiversity

The living world is organized into phenomenological species. It is a common biological wisdom that phenomenological species richness captures a crucial dimension of biodiversity. There are many routes through which one population can become demographically isolated from populations that were once sources and sinks of its own genes. But the fact of isolation and evolutionary independence is of immense importance to the fate of local adaptation in such populations. So the phenomenological species richness of a region is a catalogue both of phenotypic variety and of the potential evolutionary resources available in that region. There is an important difference between a single widespread and phenotypically variable species and a set of closely related species. The available phenotypes, population sizes, and ecological roles might be exactly the same. But one set of phenotypes will be entrenched by speciation mechanisms, and hence will survive minor ecological changes that increase migration rates across the landscape; the other set is much more fragile in the face of relatively minor ecological change. So it does not just matter what phenotypes are present; how they are bundled into species is also important. In effect, we have defended a version of an evolutionary species concept, and we accept that the collection of independently evolving lineages in a region is a key component, perhaps the key component, of that region's biological diversity. The identification of phenomenological species with metapopulations in partial stasis holds good only for some chunks of the tree of life. It may not fit plants. It clearly does not fit microbes. Even if we set that aside, phenomenological species do not represent equal amounts of evolutionary information and evolutionary potential. In different lineages, there are enormous differences in species richness and morphological diversity. In the next two chapters, the focus changes to the relationship between species richness and morphological diversity. If species richness is only one albeit crucial component of biodiversity, what do we need to add, and for what explanatory, predictive, and practical projects?

For analyses of how biodiversity contributes to ecosystem functioning, how it enhances human well-being, and how these services are currently being lost, a quantitative measurement of biodiversity is crucial. Ecologists, for that sake, have traditionally employed different concepts such as species richness, Shannon entropy, or Simpson's index (e.g. Begon et al. 1998, Magurran 1988, Pielou 1975, Ricklefs and Miller 2000). Recently, economists have added to that list measures of diversity that are based on pairwise dissimilarity between species (Gans and Hill 1997, Solow et al. 1993, Weikard 1998, 2002, Weitzmann 1992, 1993, 1998) or, more generally, weighted attributes of species (Nehring and Puppe 2002a, b). The full information about the diversity of species in an ecological community is only available in the full description of the system in terms of the number of different species, their abundances and attributes. Such a full description comes in different and complex statistical distributions. For the purpose of comparing two systems, or describing the system's evolution over time, both of which is essential for policy guidance, it seems therefore necessary to condense all this information into a small number of easy-to-calculate and easy-to-interpret numbers, although that certainly means a loss of information. Most often all the relevant information about the diversity of a system is condensed into a single real number, commonly called a measure of diversity or diversity index. As there are virtually infinitely many ways of calculating such a diversity index from the complex and multifarious information about the system under study, it is crucial to be aware of which aspects of information are being stressed in calculating the index and which aspects are being downplayed, or even neglected altogether. Not surprisingly then, the purpose for which the index is calculated and used is crucial for understanding how a particular index is prepared.

## 5. Margalef Index

Ramon Margalef Lopez proposed a species diversity index during the 1950s. Diversity indices can be broadly divided into two types: those that assess species richness (how many types are there) and those that assess species evenness or dominance (how individual organisms are distributed among species). Margalef's diversity index is a species richness index. Many species richness measures suffer from the problem that they are strongly dependent on sampling effort. The greater the sampling effort, potentially the higher the index value. Thus comparing metrics from samples collected with differing levels of sampling effort can be difficult and possibly misleading. Margalef index was one of the first attempts to compensate for the effects of sample size by dividing the number of species in a sample by the natural log of the number of organisms collected. The index is thus

$$S - 1 / \ln N$$

where  $S$  is the number of species in a sample and  $N$  is the number of organisms in the sample. The use of the index rests on the assumption that there is a relationship between the number of species and the number of organisms in a sample. If this is not the case then the index still sensitive to the number of organisms collected, that is, it increases as the number of organisms sampled increases. Margalef index increases in much the same way as the number of species increases. The Menhinick index is a similar index except that rather than dividing  $S$  by the natural log of the number of organisms you divide by the square root of the number of organisms.

There are now several more efficient techniques for removing the effect of sampling effort from diversity estimates such as rarefaction. The approach involves randomly drawing a set number of individuals from the samples and calculating species richness, so that in effect samples have the same number of organisms and can then be compared directly. Although the index suffers from a sensitivity to sampling effort, it continues to be used as a measure of species richness in ecological studies of freshwater, marine, and terrestrial systems as well as in other areas of science as diverse as genetics and sociology. It is an available option in several software packages that calculate diversity measures such as Primer. Certainly one of the key advantages of the index is that it is simple to use and easy to understand. If it is used with an awareness that it is sensitive to the number of organisms collected, then it will continue to be a useful tool in the ecologists' arsenal of diversity indices.

## 6. Species and ecosystems

Biological diversity can be considered on different hierarchical levels of life: gene, population, species, genus, family, order, phylum, ecosystem, etc. (Groombridge 1992). In this article, I shall only be concerned with the level of species, as this is the level of organisation which is currently being given most attention in the discussion of biodiversity conservation policies. That is, biodiversity is here considered in the sense of species diversity. Before discussing different indices for the measurement of species diversity, let me introduce a formal and abstract description of the ecosystem of which its species diversity is then a certain property.

Let  $S = \{s_1, \dots, s_n\}$  be the set of the different species which are potentially present in the ecological system under study. Each  $s_i$  (with  $i = 1, \dots, n$ ) represents one distinct species. For example,  $S$  could be a list of animal and plant species found in an ecosystem. For short, call  $S$  the species list henceforth. The number  $n$ , which measures the total number of different species potentially available in the system, defines at the same time the dimensionality of the so-called species space  $X$  in  $R^n$ . The species space contains as elements vectors  $a = (a_1, \dots, a_n)$  that describe viable ecosystem states in terms of the abundance  $a_i$  of individuals of species  $i$  for all  $i = 1, \dots, n$ . If the system under study contains only species of the same or a very similar kind, e.g. the warbler community of a woodland, the abundance of a species in an ecosystem may be measured by simply counting the number of individuals of that species. For example, if  $S = \{\text{deer, trout, owl}\}$  is a (simplified) description of an ecosystem and abundances are measured by counting individuals, a particular ecosystem state can be described by  $a_1 = (40, 40, 4)$ , where in  $a_1$  there are the following species: 40 is the number of deer, 40 is the number of trout and, 4 is the number of owl in that ecosystem. Another viable state of the same ecosystem could, for example, be given by  $a_2 = (10, 40, 4)$ . However, if the system comprises all animal species of the woodland it makes little sense to use the same sort of quantification for very different animals, such as deer, birds, woodlice or protozoa (Begon et al. 1986: 594). Their enormous disparity in size would make a simple count of individuals very misleading. In that case, the abundance of a species may be measured by the total biomass stored in all individuals of that species. Ceballos and Ehrlich (2002) have recently warned that the extinction crisis is even more pressing at the population level rather than at the species level.

Sometimes, it is useful not to consider the absolute abundance  $a_i$  of species  $i$  in an ecosystem, but its relative abundances which may be defined as  $p_i = n_i/N$ . By definition,  $p_i$  in  $[0, 1]$  where  $p_i=0$  means that species  $i$  is effectively absent from the system and  $p_i=1$  means that species  $i$  is effectively the only species in the system. If species abundances are measured by counting individuals of that species, the relative abundance  $p_i$  indicates the probability of obtaining an individual of species  $i$  in a random draw from all individuals of all species in the system. When abundances are measured in biomass, the relative abundance  $p_i$  indicates the relative share of the ecosystem's biomass stored in individuals of species  $i$ . Without loss of generality, assume that  $p_1 > p_2 > \dots > p_{n-1} > p_n$ , i.e. species are numbered in the sequence of decreasing relative abundance, such that  $i=1$  denotes the most common species in the system whereas  $i=n$  denotes the rarest species.

Species attributes are another property besides abundance in describing the state of the system. Let  $F=\{f_1, \dots, f_m\}$  be the list of relevant species attributes which serve to distinguish one species from another. Each  $f_j$  (with  $j=1, \dots, m$ ) represents one distinct attribute. For example, possible attributes could include the following: (i) being a mammal/bird/fish, (ii) being a herbivore/carnivore/omnivore, (iii) unit biomass consumption/production, (iv) being a 'cute little animal'.

The number  $m$ , which measures the total number of different species attributes, defines at the same time the dimensionality of the so-called attribute space.  $x_{ij}$  is then the description of species  $i$  ( $i = 1, \dots, n$ ) in terms of attribute  $j$  ( $j = 1, \dots, m$ ). Altogether, the various relevant properties of the ecosystem and the different species that make up the system are:  $n, S, m, F, \{a_i\}_{i=1, \dots, n}$  and  $\{x_{ij}\}_{i=1, \dots, n; j=1, \dots, m}$ . The formal description of a concrete realisation of an ecosystem is thus given by the vector  $= (n, S, m, F, \{a_i\}_{i=1, \dots, n}, \{x_{ij}\}_{i=1, \dots, n; j=1, \dots, m})$ . In general, a measure of diversity  $D$  of the ecosystem will be a function of all these elements. Formally:

$$D() = D(n, S, m, F, \{a_i\}_{i=1, \dots, n}, \{x_{ij}\}_{i=1, \dots, n; j=1, \dots, m})$$

## 7. Effective number of species

Diversity indices like the Shannon entropy and the Gini-Simpson index are not themselves diversities. They are just indices of diversity, in the same way that the diameter of a sphere is an index of its volume but is not itself the volume. Using the diameter in place of the volume in engineering equations would give dangerously misleading results. Things would be even worse if some engineers liked to use surface area, and if others liked to use circumference in place of volume. Imagine the chaos if they called all of these things by the same word and used them interchangeably in engineering equations that required volume. This is what biologists are doing with diversity indices.

Diversity indices have a wide variety of ranges and behaviors; if applied to a system of  $S$  equally common species, some give  $S$ , some give  $\log S$ , some give  $1/S$ , some give  $1-1/S$ , etc. Some have unlimited ranges while others are always less than unity. By calling all of these indices "diversities" and treating them as if they were interchangeable in formulas or analyses requiring diversities, we will often generate misleading results.

## 8. So what is a true diversity? What units should it be measured in?

It is possible to arrive at a natural and intuitive definition. In virtually any biological context, it is reasonable to say that a community with sixteen equally-common species is twice as diverse as a community with eight equally-common species. This is so obvious that it seems odd to have to write it. But it is important to realize what this simple statement implies. Most diversity indices do not double as we go from eight species to sixteen species. Some biologists have noticed this and concluded that all diversity indices other than species richness are therefore not to be trusted. We will see below that this is an incorrect conclusion. Species richness is the least informative and most imprecise diversity index, in the sense that it is more subject to random variation than any other index. Frequency-based diversity indices tell us something important, but they are not themselves diversities.

Going back to the obvious, it seems completely natural to say that a community with eight equally-common species has a diversity of eight species, or a community with  $S$  equally-common species has a diversity of  $S$  species. This definition behaves as we expect of a diversity; the diversity of a community of sixteen equally-common species is double that of a community with eight equally-common species. Diversity is an unambiguous concept when we are dealing with communities of equally-common species.

What happens when the species aren't equally common? This is where the choice of diversity index comes into play. If we choose a particular index as our index of diversity, then any two communities that give the same value of the index must have the same diversity. Any two communities with a Shannon index of 4.5 have the same diversity, according to this index. We don't know what that diversity is yet, but we do know that all communities with a Shannon index of 4.5 have the same diversity according to this index. Now if one of those communities consisted of  $S$  equally-common species, we would know that its true diversity is  $S$  by our above definition, and then we would know that all other communities with a Shannon index of 4.5 must also have diversity  $S$ , even if their species were not equally common. The number of equally-common species required to give a particular value of an index is called the *effective number of species*. This is the true diversity of the community in question. For example, the true diversity associated with a Shannon index of 4.5 is  $\exp(4.5) = 90$  effective species.

Converting indices to true diversities (effective numbers of species) gives them a set of common behaviors and properties. After conversion, diversity is always measured in units of number of species, no matter what index we use. This lets us compare and interpret them easily, and it lets us develop formulas and techniques that don't depend on a specific index. It also lets us avoid the serious misinterpretations spawned by the nonlinearity of most diversity indices. As an example of the practical importance of this, suppose you are comparing the diversity of aquatic microorganisms before and after an oil spill. You wouldn't want to measure that diversity by species richness because even a massive toxic event is sure to leave a few vagrant individuals of each pre-spill species, and species richness doesn't distinguish between one individual of Species X or a million; the pre-and post-spill species counts might not be very different, even if the pre-and post-spill species frequencies are very different. So if you are a good traditional biologist you might use the popular Gini-Simpson diversity index, which is  $1 - (\text{Sum of the squares of species frequencies})$ . Suppose that the pre-spill Gini-Simpson index is .99 and the post-spill index is .97. If you are a good traditional biologist you would figure out that this drop is statistically significant, but you would conclude that the magnitude of the drop is small. You might even say (very wrongly) that the diversity has dropped by 2%, which sounds like a small drop, nothing to worry about. The error which virtually all biologists make is that the Gini-Simpson index is not itself a diversity, and is highly nonlinear. The pre-spill community with a Gini-Simpson index of 0.99 has the same diversity as a community of 100 equally-common species. The post-spill community with a Gini-Simpson index of 0.97 has the same diversity as a community of 33 equally-common species. The difference between the pre-and post-spill diversities is in fact enormous. The drop in diversity is 66%, not 2%. This is not just a matter of different definitions of diversity, as some people would like to say. Rather, it is a matter of the indices being nonlinear with respect to our intuitive concept of diversity. The Shannon index is also highly nonlinear. A Shannon entropy of 6.0 corresponds to 403 equally-common species while a Shannon entropy of 5.5 corresponds to 244 equally-common species. The former is twice as diverse as the latter even though the difference in the values of the indices is only 8%.

When we convert to true diversities (effective number of species) we create a powerful and intuitive tool for comparing diversities of different communities. If one community has a true diversity of 5 effective species based on some diversity index, and another has a true diversity of 15 effective species based on the same diversity index, we can truly say that the second community is three times as diverse as the first according to that index. We couldn't draw this conclusion from the raw index itself, because it uses a nonlinear scale. Other sciences have long ago recognized the importance of the true diversity of a diversity index, though the concept goes by different names in different fields. The use of the exponential of Shannon entropy,  $\exp(\text{Shannon})$ , in thermodynamics dates from the dawn of the modern atomic theory of matter over a hundred years ago; in that field it gives the number of equally-likely states needed to produce the given entropy. Economists have also long made this fundamental distinction; the term "numbers equivalent" for the effective number of elements of a diversity index is used in that field (Patil and Taillie 1982). The distinction between Shannon entropy and its numbers equivalent or true diversity can be visualized by imagining a dichotomous key to the species of a community. Shannon entropy is proportional to the mean depth of the maximally-efficient dichotomous key to the species of the community (the average number of yes-or-no questions that must be asked to identify a species), but the true diversity is the effective number of terminal branches in the key, and that number increases exponentially with the depth of the key. Several biologists, notably MacArthur (1965), Hill (1973), and Peet (1974), correctly identified diversity with  $\exp(\text{Shannon})$ , the effective number of species, but authors of influential standard texts such as Magurran (2004) did not recognize the significance of this, and the concept is seldom used. Yet the results presented here show that this concept clears up most of the many problems in diversity analysis in biology, just as it does in physics and economics.

## 9. List of animation, audio files and movies

animation Biodiversity Richness Evenness and Importance.flv

## **10. Questions**

- What is the most common unit of measurement ?
- How to use relative diversity indices to quantify diversity ?
- How to overcome of the sampling problem estimating species richness?
- What is the advantage of effective number of species from the point of view of ecological interpretation?
- What is the advantage of Margalef's measure of species richness?

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# 9. fejezet - Chapter 8 Classical diversity statistics

## 1. Diversity and biodiversity

Following Hurlbert (1971), many ecologists adopted the practice of restricting the term diversity to heterogeneity measures, that is those that combine richness and evenness. This convention appears to have weakened in the last decade, as popular interest in biological diversity, which is often treated as synonymous with species richness, has heightened.

Diversity indices, sometimes referred to as heterogeneity measures, distil the information contained in a species abundance distribution into a single statistic. Heterogeneity measures fall into two categories: parametric indices, such as log series  $a$ , that are based on a parameter of a species abundance model, and nonparametric indices, such as the Simpson index, that make no assumptions about the underlying distribution of species abundances. Nonparametric measures can be further divided into those that emphasize the species richness component of diversity, for example the Shannon index, and those, for instance the Berger-Parker index, that focus on the dominance/evenness component. Although nonparametric measures are not linked to specific species abundance models the underlying distribution of species abundances can influence their performance. One of the most popular diversity statistics, the Shannon index, has properties that can impede the interpretation of results. On the other hand, the Simpson index performs well, both as a general purpose diversity statistic and when recast as an evenness measure. Communities may be identical in terms of richness and evenness but differ in the taxonomic diversity of their species. A new class of measures takes this aspect of biological diversity into account. One promising method, the Warwick and Clarke taxonomic distinctness measure, is an extension of the Simpson index and has the advantage of being robust against variation in sampling effort. Confidence limits can be applied to many of these measures.

## 2. An index of diversity

There are endless ways of emphasizing different aspects of the species abundance relationship, the number of candidate diversity indices is infinite (Molinari 1996). All measures emphasize one or other component of diversity (richness or evenness), no perfectly unified diversity index is possible. As the literature testifies, the challenge of devising ever better measures has been taken up by many ecologists over the years. There are a plethora of indices from which to choose and this diversity of diversity measures can make it difficult to select the best approach. The matter is complicated by the fact that the most popular indices are not necessarily the best.

Since even the most elegant methodology cannot redeem an illconceived investigation, the single most important consideration in the measurement of diversity is that the user has a clear idea of the objectives of the study. Is it intended to estimate the species richness of potential nature reserves? Is a measure of pollution stress required? Does the user need to assess the effects of disturbance? Are confidence limits on the diversity estimate essential? Once the objectives have been clearly delineated it is relatively straightforward to select a diversity measure. Sampling must also be adequate for the purposes of the study.

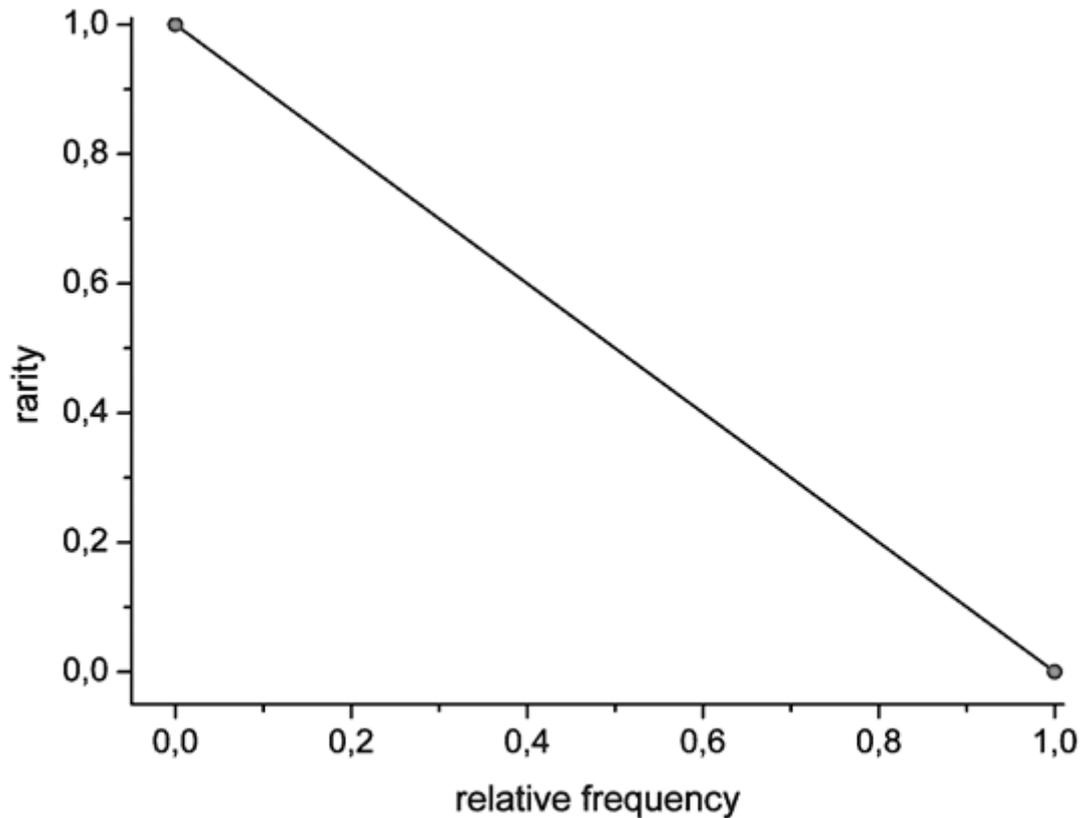


Figure 1. Rarity function (1-p) leading to the simpson diversity.

### 3. Diversity measures

Diversity statistics are conventionally classified as either **species richness** measures (McIntosh 1967) or **heterogeneity** measures (Good 1953). Heterogeneity measures are those that combine the richness and evenness components of diversity. Evenness measures were later developed by Lloyd and Ghelardi (1964) and subsequent workers. Evenness measures assess the departure of the observed pattern from the expected pattern in a hypothetical assemblage. This assemblage may either be completely uniform, i.e. all species equally abundant or represent some biologically achievable pattern of evenness, such as the broken stick distribution; see Lloyd and Ghelardi (1964).

Heterogeneity (and evenness) measures my categories into two categories: either a measure that makes no assumption about the underlying species abundance distribution (sometimes described as nonparametric diversity indices), or a parameter of a species abundance model.

This kind of terminology (parametric versus nonparametric indices) is inherited from the classical statistics. It is a rather unfortunate, misleading terminology. It would be much better to speak about distribution-free diversity statistics and diversity statistics based on abundance distributions.

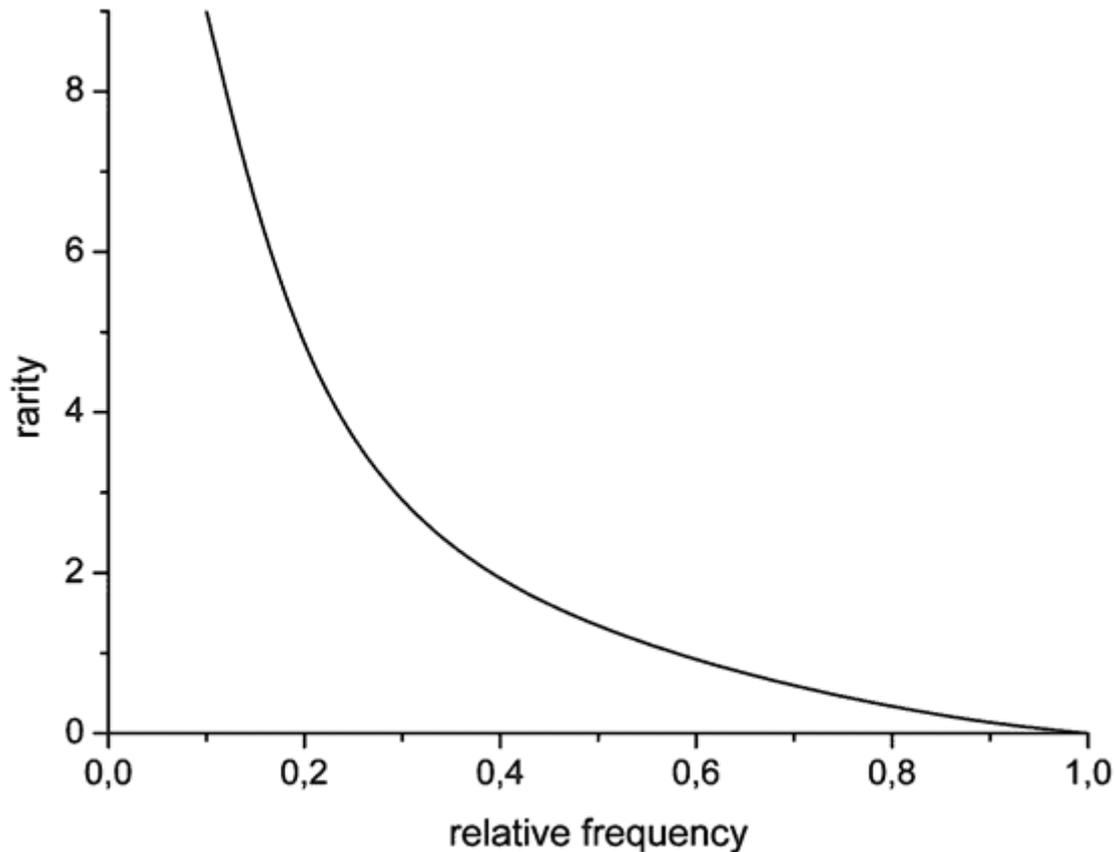


Figure 2. Rarity function (1/p) leading to the species richness.

#### 4. Distribution-free diversity statistics (“nonparametric measures”)

#### 5. Information statistics

One of the most enduring of all diversity measures is the Shannon index. Such endurance is all the more remarkable in light of the fact that most commentators who discuss the relative merits of the various methods of measuring diversity go out of their way to underline some disadvantages of the Shannon index (May 1975; Magurran 1988; Lande 1996; Southwood & Henderson 2000). Many people feel happier about adopting a measure with a long tradition of use. Its origins in information theory and its association with concepts such as entropy likely also contribute to its continuing appeal (Martin & Rey 2000).

The Shannon index is based on the rationale that the diversity, or information, in a natural system can be measured in a similar way to the information contained in a code or a message. It assumes that individuals are randomly sampled from an infinitely large community (Pielou 1975), and that all species are represented in the sample. The Shannon index is calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

The quantity  $p_i$  is the proportion of individuals found in the  $i$ th species. In a sample the true value of  $p_i$  is unknown but is estimated using its maximum likelihood estimator,  $n_i/N$  (Pielou 1969). Since the use of  $n_i/N$  to estimate  $p_i$  produces a biased result, the index should, strictly speaking, be obtained from the following series (Hutcheson 1970; Bowman *et al.* 1971):

$$H' = \sum p_i \ln p_i + (1 - \sum p_i) \ln (1 - \sum p_i)$$

In practice, however, this error is rarely significant (Peet 1974) and all the terms in the series after the second are very small indeed. A more substantial source of error arises when the sample does not include all the species in the community (Peet 1974). This error increases as the proportion of species represented in the sample declines. As the true species richness of an assemblage is usually unknown, an unbiased estimator of the Shannon index does not exist (Lande 1996).

For historical reasons  $\log_e$  is often used when calculating the Shannon diversity index. There are no pressing biological reasons why this tradition should be preserved. Indeed it is computationally simpler, and ecologically just as valid, to use natural logs ( $\log_e$ , also known as  $\ln$ ) or even  $\log_{10}$  in the equation. There is an increasing trend towards standardizing on natural logs (see, for example, Cronin & Raymo 1997) and it is essential to use these in the series. What is important is to be consistent in the choice of base when comparing diversity between samples or studies or when using the Shannon index to estimate evenness.

Pielou (1969) lists the terms used to describe the units in which the Shannon index measures diversity. These stem from information theory and depend on the type of logarithms used. "Binary digits" or "bits" apply when  $\log_2$  is adopted, "natural bels" or "nats" when it is  $\log_e$ , and "decimal digits" or "decits" for  $\log_{10}$ . These terms are rarely applied these days, a sensible trend since they do not assist in the interpretation of estimates of diversity. However, references to bits and vats do crop up from time to time in the older literature. The value of the Shannon index obtained from empirical data usually falls between 1.5 and 3.5 and rarely surpasses 4 (Margalef 1972). It is only when there are huge numbers of species in the sample that high values are produced. May (1975) notes that, given a log normal pattern of species abundance,  $10^5$  species would be needed to produce a value of  $H' > 5.0$ .

The fact that the Shannon index is so narrowly constrained in most circumstances can make interpretation difficult. The ecologist confronted by values of  $H' = 2.27$  and  $H' = 2.51$  may have little idea whether the two sites in question have similar diversities or are substantially different. A similar criticism can be directed towards the log series index. Some investigators sidestep the problem by using  $eH'$  instead of  $H'$ .  $eH'$  is an intuitively meaningful measure as it gives the number of species that would have been found in the sample had all species been equally common. Transforming the index has the useful function of spreading the values out, but it still does not shed much light on whether estimates of diversity are significantly different or not.

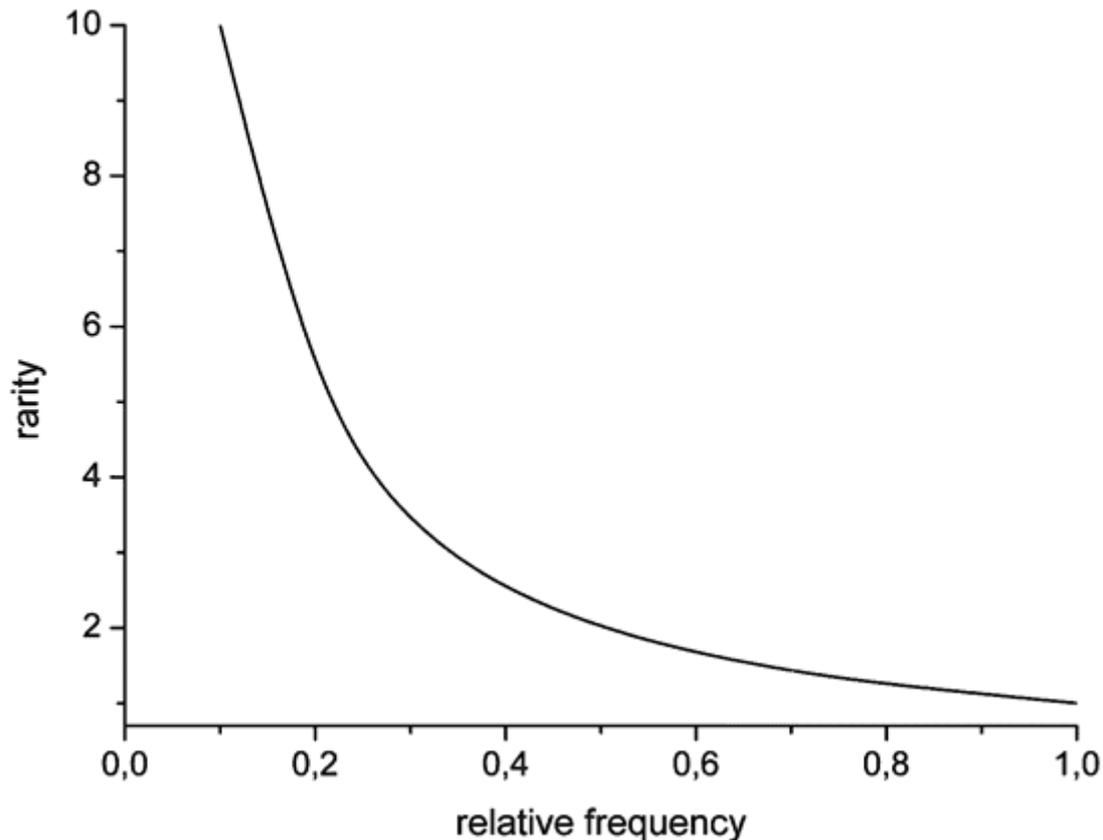


Figure 3. Rarity function –  $\log p$  leading to the Shannon diversity.

A better approach, assuming that there is an a priori hypothesis why one assemblage should be more or less diverse than another, is to employ a statistical test. In the past one of the only options was to use Hutcheson's (1970) "t" test for the Shannon index. Hutcheson (1970) sets out the method for calculating the variances of the two estimates, the value of *t* and the degrees of freedom used to assess significance. However, Taylor (1978) pointed out that when the Shannon index is calculated for a number of sites, the indices themselves will be normally distributed. This property makes it possible to use parametric statistics, including powerful analysis of variance methods (Sokal & Rohlf 1995), to compare sites for which diversity has been calculated (see, for example, Kaiser *et al.* 2000). Recently, attention has switched to resampling procedures such as bootstrap and jackknife methods (Lande 1996).

## 6. The Shannon evenness measure

As a heterogeneity measure the Shannon index takes into account the degree of evenness in species abundances. None the less, it is possible to calculate a separate evenness measure. The maximum diversity ( $H_m$ ) that could possibly occur would be found in a situation where all species had equal abundances, in other words if  $H' = H_m = \ln S$ . The ratio of observed diversity to maximum diversity can therefore be used to measure evenness (*J'*) (Pielou 1969, 1975):  $J' = H'/H_{max} = H'/\ln S$

Beisel and Moreteau (1997) provide a simple method of calculating *Hmin*, a value used in other forms of the Shannon evenness (Hurlbert 1971).

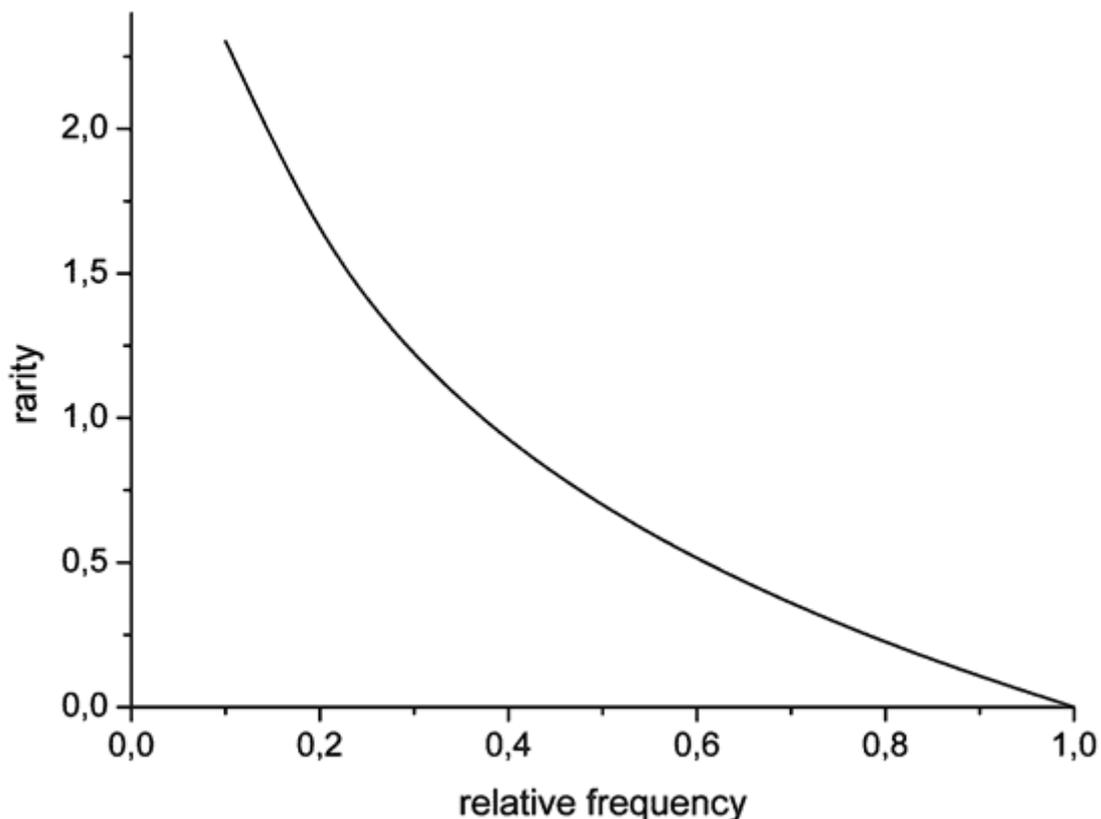


Figure 4. Standardized rarity function (1-p)/p.

## 7. Heip's index of evenness

Heip (1974) felt that evenness measures should not be dependent on species richness, and that they should have a low value in contexts where evenness is obviously low. His proposed measure was intended to meet these criteria:

$$E_{Heip} = (S - 1) / (eH - 1)$$

Although  $H'$  is less sensitive to species richness than  $p$ , it does not meet the requirement of being independent of sample size when there are fewer than about 10 species in the sample (Smith & Wilson 1996). It does, on the other hand, satisfy the expectation of attaining a low value when evenness is low. Smith and Wilson (1996) showed that the minimum value of Heip's measure is 0 and that it registers 0.006 when an extremely uneven community is used.

## 8. SHE analysis

Shannon index combines two aspects of diversity: species richness and evenness. This is often viewed as a disadvantage since it can make interpretation difficult; an increase in the index may arise either as a result of greater richness, or greater evenness, or indeed both. However, Buzas and Hayek (1996) and Hayek and Buzas (1997) realized that this characteristic of the Shannon index can actually be turned to an advantage. Their reasoning is as follows. They first note that one measure of evenness is  $E = e' / S$  (Heip 1974) and then go on to observe that the Shannon index is simply the sum of the natural log of this value ( $\ln(E)$ ) and the natural log of species richness ( $\ln(S)$ ). It follows that the index can be decomposed into its two components:

$$H' = \ln S + \ln E .$$

The most obvious advantage of this decomposition is that it allows the user to interpret changes in diversity. Thus, an ecologist can attribute a decrease in the diversity of a community following a pollution incident to a loss of richness or evenness, or a combination of these. SHE analysis can also shed light on the underlying species abundance distribution. The essence of SHE analysis is the relationship between  $S$  (species richness),  $H'$  (diversity as measured by the Shannon index), and  $E$  (evenness). The manner in which this relationship changes as a function of sample size can be remarkably informative. Like the estimation of species richness, this approach makes use of accumulated samples. Hayek and Buzas (1997) point out that when a sample of large and small  $N$  are compared, five scenarios are possible.

Arita and Figueroa (1999) used SHE to examine geographic patterns of body mass diversity in Mexican mammals. They substituted the number of body mass categories for  $S$  and calculated  $p$  as the proportion of species per category rather than the usual proportion of individuals per species. The authors concluded that evenness (of the distribution of body mass values) was high at intermediate spatial scales but low at the regional one. This is a novel application of the SHE approach, but since no other evenness measures were considered it is unclear whether it is more informative than the alternatives. Buzas and Hayek (1998) describe how SHE can be used to identify communities (of Foraminifera in their example) along a gradient.

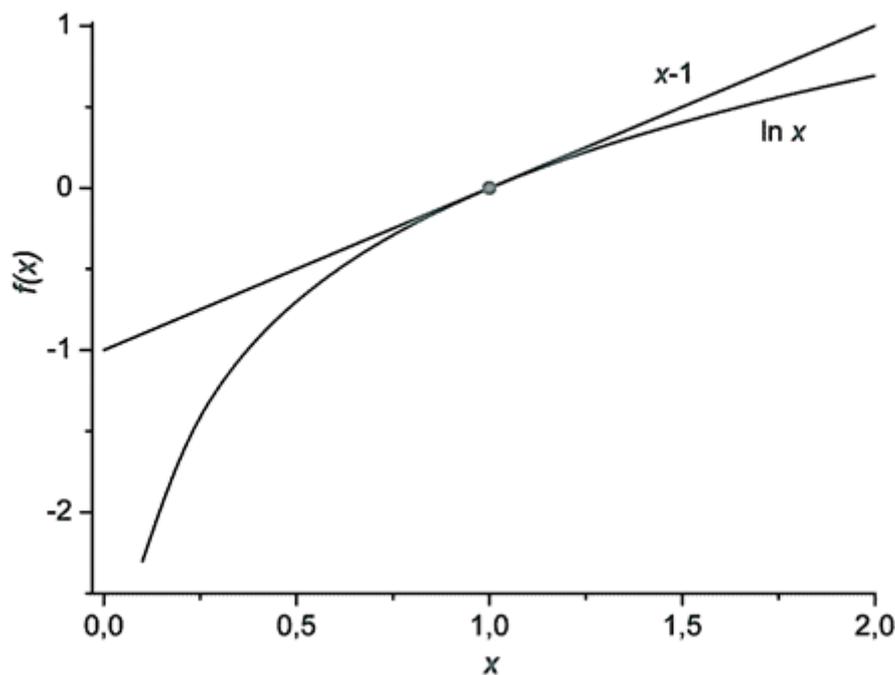


Figure 5. A demonstration of the Shannon and Simpson diversity.

## 9. The Brillouin index

When the randomness of a sample cannot be guaranteed, for example during light trapping where different species of insect are differentially attracted to the stimulus (Southwood & Henderson 2000), or if the community is completely censused and every individual accounted for, the Brillouin index (HB) is the appropriate form of the information index (Pielou 1969, 1975). It is calculated as follows:

$$HB = \ln N! - \sum Y \ln n_i! / N$$

Both the Shannon and Brillouin indices give similar and often correlated estimates of diversity. However, when the two indices are used to measure the diversity of a particular data set, the Brillouin index will always produce the lower value. This is because the Brillouin index describes a known collection about which there is no uncertainty. The Shannon index estimate the diversity of the unsampled as well as the sampled portion of the community. *Evenness (E)* for the Brillouin diversity index is obtained from:  $E = HB/Hb_{max}$

An important difference between the two measures of diversity is that the Shannon index always provide the same answer so long as the number of species, and their proportional abundances, are held constant. Thus, if one site has 10 species each with five individuals and another site has 10 species each with 10 individuals, the Shannon index would return a value of 2.30 in both cases. The value of the Brillouin index, by contrast, would be 2.01 in the site with 50 individuals and 2.13 in the site with 100 individuals.

Since the Brillouin index measures the diversity of a collection, as opposed to a sample, each value of HB be different from every other. This means that the index has no variance and that no statistical tests are needed to demonstrate significant differences. Evidently, it is possible to use the jackknife or bootstrap procedure to generate a mean estimate along with an associated variance but whether such figures have any real meaning is open to debate. Laxton (1978) concludes that the Brillouin index is the superior of the two information measures of diversity. Pielou (1969, 1975) strongly advocates its use in all circumstances where a collection is made, or samples are nonrandom, or where the full composition of the community is known. In practice, however, few ecologists take this advice as the Brillouin index is more time consuming to calculate, and less familiar, than the Shannon index. Its dependence on sample size can also sometimes lead to unexpected results, though admittedly only when there is a highly unusual species abundance distribution or when number of individuals is low. The index cannot be used when abundance is measured as biomass or productivity (Legendre & Legendre 1983; Krebs 1999). The Brillouin index seems to suffer from many of the disadvantages of information statistics and offer few of the benefits. Notwithstanding this, it continues to be used often (Lo et al. 1998; Dans et al. 1999; Ito & Imai 2000), but not invariably (Andres & Witman 1995; Bartsch et al. 1998), to describe parasite assemblages.

## 10. The Q statistics

The Q statistic, proposed by Kempton and Taylor (1976, 1978) is an interesting and innovative approach to diversity measurement. This measure is based on the distribution of species abundances but does not require the user to fit a model to the empirical data. Instead, a cumulative species abundance curve of the empirical data is constructed and the interquartile slope of this curve is used to measure diversity. In theory, as in an earlier index suggested by Whittaker (1972), the whole curve could be used to describe diversity, but the practice of restricting the measure to the interquartile region means that neither very abundant, nor very rare, species bias the outcome.

The following equation is estimated from empirical data:  $Q = \ln(R_2/R_1)$  where  $n_s$  = the total number of species with abundance  $R$ ;  $R_1$  and  $R_2$  = the 25 % and 75 % quartiles;  $n_{R1}$  = the number of species in the class where  $R_1$  falls; and  $n_{R2}$  = the number of species in the class where  $R_2$  falls. Kempton and Wedderburn (1978) point out that Q, expressed in terms of the log series model, is analogous to  $a$ . For the log normal model  $Q = 0.371 S^*/a$ .

Although Q maybe biased in small samples, this bias is low if >50% of the species in the community have been censused (Kempton & Taylor 1978). Despite its simplicity and ease of interpretation the Q statistic has not been widely adopted by ecologists. Pettersson (1996), however, used it when comparing the diversity of spiders in lichen-rich, natural spruce *Picea abies* forests in northern Sweden with selectively logged, lichen-poor forests. Spider diversity was found to be higher in the unlogged forests. Interestingly, rarefaction plots also used by Pettersson (1996) indicated no differences between the sites apart from a lower abundance of spiders on

branches in lichen-poor forests. Ghazoul (2002) also adopted the measure to track shifts in butterfly diversity in relation to disturbance level in a tropical dry forest in Thailand. An evenness measure, conceptually similar to the Q statistic, has been proposed by Nee *et al.* (1992).

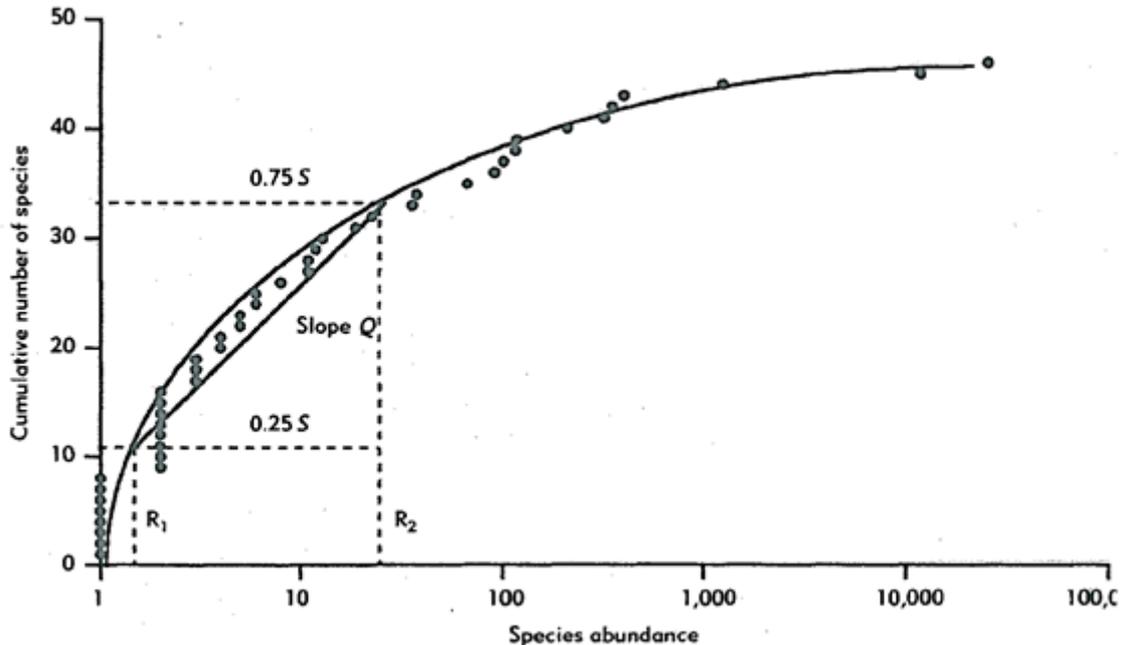


Figure 6. Graphical demonstration of the calculation of Q-statistics.

## 11. Dominance and evenness measures

The information statistics described above tend to emphasize the species richness component of diversity. Another group of diversity indices are weighted by abundances of the commonest species and are usually referred to as either dominance or evenness measures. One of the best known dominance measures is the Simpson index. It is occasionally called the Yule index since it resembles the measure G. U. Yule devised to characterize the vocabulary used by different authors (Southwood & Henderson 2000).

## 12. Simpson's index (D)

Simpson (1949) gave the probability of any two individuals drawn at random from an infinitely large community belonging to the same species as:

$$D = \sum p_i^2$$

where  $p_i$  = the proportion of individuals in the  $i$ th species. There is a form of the index appropriate for a finite community. As  $D$  increases, diversity decreases. Simpson's index is therefore usually expressed as  $1-D$  or  $1/D$ . Simpson's index is heavily weighted towards the most abundant species in the sample, while being less sensitive to species richness. May (1975) has shown that once the number of species exceeds 10, the underlying species abundance distribution is important in determining whether the index has a high or low value. Confidence limits can be applied by jackknifing.

The Simpson index is one of the most meaningful and robust diversity measures available. In essence it captures the variance of the species abundance distribution. Thus, when expressed as the complement ( $1-D$ ) or reciprocal ( $1/D$ ) of  $D$ , the value of the measure will rise as the assemblage becomes more even. Although the reciprocal ( $1/D$ ) is the most widely used form of the Simpson index, Rosenzweig (1995) notes that it can have severe variance problems, and recommends instead  $-\ln(D)$ , a transformation introduced by Pielou (1975) following the advice of C.D. Kemp. Rosenzweig (1995) advises that Kemp's transformation is easily interpretable, that it will reflect underlying diversity, and that it is independent of sample size. Lande (1996) observes that the overall diversity of a set of communities, measured as  $1/D$ , may be less than the average diversity of those communities, a conceptually intriguing notion, and recommends  $1-D$ .

Lande *et al.* (2000) find the Simpson index more effective than species accumulation curves in ranking communities. May (1975) approves of the measure because it is intuitively meaningful. Its utility has been illustrated in a range of contexts: for example, Ito (1997), Azuma *et al.* (1997), and Gimaret-Carpentier *et al.* (1998). Clarke and Warwick's (1998) index of taxonomic distinctness is a natural extension of Simpson's index. Lande (1996) demonstrates how the index can be partitioned to give a measure of diversity among, as well as within, assemblages, and describes how analysis of variance can be used to accurately estimate the total diversity in a region. Simpson's index is inexplicably less popular than the Shannon index.

### 13. Simpson's measure of evenness

Simpson's diversity measure emphasizes the dominance component of diversity. A separate measure of evenness can, however, be calculated by dividing the reciprocal form of the Simpson index by the number of species in the sample (Smith & Wilson 1996; Krebs 1999):

$$(1/D) E_1 = D - S .$$

The measure ranges from 0 to 1 and is not sensitive to species richness. It is usually termed  $E_1 I_D$  to denote the use of the reciprocal form of the index. Smith and Wilson (1996) note that  $E_1 I_D$  is formally related to its parent index:

$$(1/D) = E_1 I_D S$$

Bulla (1994) asserted that any good evenness index becomes a heterogeneity measure if multiplied by  $S$ . Molinari (1996) criticised this comment. The Simpson evenness index is relatively unusual in that this multiplication restores the standard measure of Simpson diversity (Smith & Wilson 1996). The Shannon index can also be decomposed in the same way and it was this property that Buzas and Hayek (1996) and Hayek and Buzas (1997) exploited in their SHE analysis.

### 14. McIntosh's measure of diversity

McIntosh (1967) proposed that a community can be envisaged as a point in an  $S$ -dimensional hypervolume and that the Euclidean distance of the assemblage from its origin could be used as a measure of diversity. The distance is known as  $U$  and is calculated as:

$$U = N - \sum p_i .$$

The McIntosh  $U$  index is not formally a dominance index. However, a measure of diversity ( $D$ ) or dominance that is independent of  $N$  can also be calculated, and a further evenness measure can be obtained from the formula (Pielou 1975).

### 15. The Berger-Parker diversity index

The Berger-Parker index,  $d$ , is an intuitively simple dominance measure (Berger & Parker 1970; May 1975). It also has the virtue of being extremely easy to calculate. The Berger-Parker index expresses the proportional abundance of the most abundant species:

$$d = N_{\max} / N$$

where  $N_{\max}$  = the number of individuals in the most abundant species. Conceptually  $d$  can be regarded as equivalent to geometric series  $k$  since both measures describe the relative importance of the most dominant species in the assemblage. As with the Simpson index, the reciprocal form of the Berger-Parker index may be adopted so that an increase in the value of the index accompanies an increase in diversity and a reduction in dominance. The simplicity and biological significance of the index leads May (1975) to conclude that it is one of the most satisfactory diversity measures available. In large assemblages ( $S > 100$ ),  $d$  is independent of  $S$ , but in smaller ones its value will tend to decline with increasing species richness.

### 16. Nee, Harvey, and Cotgreave's evenness measure

Nee *et al.* (1992) proposed the slope ( $b$ ) of a rank/abundance plot (in which the abundances had been log transformed) as an evenness measure; see also Wilson (1991). The resulting measure falls between infinite and 0, where 0 is perfect evenness. This range of values makes the measure difficult to interpret. This measure is more properly a measure of diversity than of evenness and rather similar to Kempton and Taylor's (1976)  $Q$  statistic (Smith & Wilson 1996). Smith and Wilson (1996) therefore proposed a new form of the measure:

$$E_Q = -2/n \cdot \arctan(b')$$

In this measure the ranks are scaled before the regression is fitted. This is achieved by dividing all ranks by the maximum rank so that the most abundant species takes a rank of 1.0 and the least abundant a rank of  $1/S$ . The transformation  $(-2/n \arctan)$  places the measure in the 0 (no evenness) to 1 (perfect evenness) range.

## 17. Carmargo's evenness index

Carmargo (1993) also introduced an evenness measure. Although the index is simple to calculate and relatively unaffected by rare species (Krebs 1989), Mouillot and Lepetre (1999) found it to be biased, especially in comparison with the Simpson index.

## 18. Smith and Wilson's evenness index

Smith and Wilson (1996) proposed a new index designed to provide an intuitive measure of evenness. This index measures the variance in species abundances, and divides this variance over log abundance to give proportional differences and to make the index independent of the units of measurement. The conversion by  $-2/\arctan$  insures that the resulting measure falls between 0 (minimum evenness) and 1 (maximum evenness).

## 19. Smith and Wilson's consumer's guide to evenness measures

It can be difficult to know which evenness index is best in which context. Smith and Wilson (1996) conducted an extensive set of evaluations of available measures using a range of criteria. These included four **requirements** and 10 desirable **features** of measures. Their requirements were as follow:

- 1 The measure is independent of species richness.
- 2 The measure decrease if the abundance of the least abundant species is reduced.
- 3 The measure decrease if a very rare species is added to the community.
- 4 The measure is unaffected by the units used to measure it.

The additional features were as follow:

- 1 The maximum value of the index is achieved when abundances are equal.
- 2 The maximum value is 1.0.
- 3 The minimum value is achieved when abundances are as unequal as possible.
- 4 The index shows a value close to its minimum when evenness is as low as is likely to occur in a natural community.
- 5 The minimum value is 0.
- 6 The minimum is attainable with any number of species.
- 7 The index returns an intermediate value for communities that would be intuitively considered of intermediate evenness.
- 8 The measure should respond in an intuitive way to changes in evenness.

9 The measure is symmetric with regard to rare and common species, that is as much weight is given to minor species as to very abundant ones.

10 A skewed distribution of abundances should result in a lower value of the index.

Smith and Wilson found that different indices often produced strikingly different results. For example, when asked to assess the evenness of a community in which the species abundances were 1,000, 1,000, 1,000, 1,000, 1,000, and 1 the measures produced values ranging from 0.046 to 0.999 (on a 0 to 1 scale). However, some measures did emerge as being significantly better than their competitors. Independence from species richness was Smith and Wilson's (1996) primary criterion. This was satisfied by the Simpson evenness measure, a measure that also responded in an intuitive way to changes in evenness (feature 8 above, named by Smith and Wilson (1996) as the Molinari test after Molinari (1989)). Carmargo's index,  $E_c$  (Smith & Wilson 1996), the new index  $E_w$ , and their modification of Nee *et al.*'s (1992) index,  $E_o$ , also met the species richness criterion and demonstrated other desirable properties. Smith and Wilson (1996) concluded with the following recommendations. When symmetry between rare and abundant species (feature 9 above) is required, that is, where rare and abundant species should be weighted equally with regard to their influence on the evenness measure select:

- (a)  $E_{i/D}$  if minimum evenness should be 0, or a good response to an intuitive gradient in evenness is essential; or
- (b)  $E_c$  if intermediate values for intermediate levels of evenness are sought.

When symmetry between rare and abundant species is not required, that is, where common species receive a higher weighting than rare ones, select:

- (a)  $E_o$  if a good response to the intuitive evenness gradient is not required; or
- (b)  $E_{var}$  if it is.

Overall, Smith and Wilson (1996) rate  $E_{var}$  as the most satisfactory evenness measure. It will be interesting to see if it is widely adopted in the future. On the other hand the sound performance of Simpson's  $E_{i/D}$  and its unambiguous relationship with its parent heterogeneity index—which is itself an excellent measure of diversity—are important recommendations.

## 20. Taxonomic diversity

If two assemblages have identical numbers of species and equivalent patterns of species abundance, but differ in the diversity of taxa to which the species belong, it seems intuitively appropriate that the most taxonomically varied assemblage is the more diverse. Moreover, measures of taxonomic diversity can be used in conjunction with species richness and rarity scores in the context of conservation (Virolainen *et al.* (1998) provide an example. The quest for measures that incorporate phylogenetic information can be traced back to Pielou (1975), who pointed out that diversity will be higher in a community in which species are divided amongst many genera as opposed to one where the majority of species belong to the same genus. The approach has gained impetus in the last decade as a consequence of their perceived role in setting conservation priorities (Vane-Wright *et al.* 1991; Williams *et al.* 1991; Vane-Wright 1996; Williams 1996).

As long as the phylogeny of the assemblage of interest is reasonably well resolved, measures of taxonomic diversity are, in principle, possible. Pielou (1975) adapted the Shannon index to include familial, generic, and species diversity and showed how the idea could be extended to the Brillouin index. Izsak and Papp (2000) and Ricotta (2002) describe how a taxonomic weighting factor can be incorporated into various diversity measures. May (1990b), Vane-Wright *et al.* (1991), and Williams *et al.* (1991, 1994) used a different approach and devised methods based on the topology of a phylogenetic tree. Information on taxonomic diversity can also be gleaned by summing the branch lengths within a taxonomic tree, as in Faith's (1992, 1994) measure of phylogenetic diversity (PD).

Measures of taxonomic diversity are not spared the conceptual or practical problems of their species diversity counterparts. Both sets of measures give a predetermined weighting to the richness and evenness components of diversity. Sometimes this weighting can lead to a loss of information. For example, because Faith's PD measure reflects the cumulative branch length of the whole tree, it emphasizes the taxonomic richness of a set of organisms at the expense of its evenness (Clarke & Warwick 1998). This could hinder the identification of vulnerable assemblages. Another consideration is sensitivity to sampling effort, a problem that species, and

taxonomic, richness measures are particularly vulnerable to. Two recent developments, a taxonomic distinctness measure (Clarke & Warwick 1998; Warwick & Clarke 1998) and a functional diversity measure (Petchey & Gaston 2002a, 2002b) merit further consideration.

## 21. Clarke and Warwick's taxonomic distinctness index

A very promising recruit to this suite of methods is Clarke and Warwick's taxonomic distinctness measure (Warwick & Clarke 1995, 1998, 2001; Clarke & Warwick 1998, 1999). Webb (2000) has independently derived a very similar index for rain forest trees. A particular virtue of this measure, which is a natural extension of Simpson's index, is its robustness in the face of variable or uncontrolled sampling effort. Taxonomic evenness of an assemblage is also accounted for. Warwick and Clarke (2001) highlight the distinction between their **taxonomic distinctness** measure, which summarizes the pattern of relatedness in a sample, and **taxonomic distinctiveness**, which is used primarily to identify species of particular conservation importance.

The Clarke and Warwick measure has two forms. This measure describes the average taxonomic distance is simply the path length between two randomly chosen organisms through the phylogeny of all the species in an assemblage. The first form or "taxonomic diversity" (appropriate for species abundance data), takes account of species abundances as well as taxonomic relatedness. It measures the average path length between two randomly chosen individuals (which may belong to the same species). The second form or "taxonomic distinctness", represents the special case where each individual is drawn from a different species. A pure measure of taxonomic relatedness, is equivalent to dividing the first form by the value it would take if all species belonged to the same genus, that is in the absence of a taxonomic hierarchy. When presence/absence data are used both measures reduce to the same statistic, which is the average taxonomic distance between two randomly selected species. It is calculated as follows:

An important consideration is the weighting ("v") assigned to each of the levels in the taxonomic hierarchy. The simplest approach, as used by Warwick and Clarke (1995, 1998) and Clarke and Warwick (1998) is to set the value of v as 1. Each step up through the hierarchy in search of a shared taxonomic level increments the value of v by 1. For instance, the path length for two species in the same genus is v=1. As pairs of species become more distantly related the scores increase. If the species belong to the same family (but not genus) v=2; if they share no more affinity than being members of the same class, v=6.

As Clarke and Warwick (1999) recognize, there are cases where it may be inappropriate to treat v as a constant. This will arise if some taxonomic groupings convey little or no additional information. To resolve this problem, Clarke and Warwick (1999) suggest defining the weight of a step as proportional to the percentage of taxon richness accounted for by the step. Such scaling of richness weighting insures that the inclusion of a redundant taxonomic subdivision in the analysis cannot alter the value of the taxonomic distinctiveness.

Rogers *et al.* (1999) contrasted the default weighting and the weighting based on taxon richness in their analysis of fish communities in the northeast Atlantic and found that they produced highly correlated values. Clarke and Warwick (1999) also analyzed different weightings and concluded that their measure of taxonomic distinctness is robust as long as the distinction between taxonomic levels is preserved. Thus, although it may appear logical to adjust the weighting of v in line with the distribution of phylogenetic diversity, unless the circumstances are exceptional the advantages of these extra calculations seem rather slight. Furthermore, because the weighting is based on the richness of a particular assemblage, comparisons across assemblages are problematic (Clarke & Warwick 1999).

One of the difficulties that frequently besets diversity measurement is sensitivity to sample size. Changes in sampling effort often have a dramatic impact on the value of the measure and the investigator is faced with the dilemma of trying to standardize sampling across sites or to sample each site exhaustively. A particular virtue of the taxonomic distinctness index is its lack of dependence on sampling effort (Price *et al.* 1999).

A further advantage is that a significance test can be carried out. The test examines the departure of the distinctness measure for a set of m species, from the value calculated for the global species list, and has potential application in identifying impacted areas or localities of exceptional taxonomic richness. Clarke and Warwick (1998) derived the method and explain it in detail. Their starting assumption is that there is a reasonably complete inventory of species for a region -and, of course, that at least a Linnean taxonomy exists for these species. This condition is likely to be met for well-studied taxa, such as birds and mammals, in most parts of the world, and for less engaging organisms in the parts of the world well populated by taxonomists. The null

hypothesis that the taxonomic distinctness of a locality is not significantly different from the global list is tested by repeatedly subsampling species lists of size  $m$  at random from the global list and constructing a histogram of the resulting estimates. The observed index value can be compared with the simulated values. To reject the null

Since the simulation must be repeated for each locality with a different number of species ( $m$ ) the procedure can be computationally demanding. However, a faster method is also available. This is based on the variance of the subsample estimate which is then used to construct an approximate 95% confidence interval ( $\text{mean} \pm 2 \text{ s.d.}$ ) across the full range of  $m$  values.

Variation in taxonomic distinctness (Clarke & Warwick 2001b; Warwick & Clarke 2001) measures the evenness with which the taxa are distributed across the hierarchical taxonomic tree. Taxonomic distinctness is largely independent of sample size and (as with  $A^+$ ) can be tested against an expectation based on the species list for the region. It is also possible to construct a two-dimensional envelope plot. This combination provides a statistically robust summary of the taxonomic diversity of the assemblage. The PRIMER package is recommended for all these analyses.

As Clarke and Warwick (1998) note, these tests, in contrast to virtually all other diversity statistics, can be used in situations where sampling is uncontrolled and where the data are in the form of species presence/absence. Indeed, they argue that the method is relatively robust against sampling inconsistencies, so long as these do not bias the estimates in any systematic way. For example, recorders in different localities might vary in expertise but this will not matter if misidentifications occur at random across the species pool. Of course, certain groups are more taxonomically challenging and it is important that the user is vigilant for any potential biases. In addition, some sampling techniques, such as notoriously different types of light trap (Southwood & Henderson 2000), can favor the collection of some taxa and prejudice the recording of others.

## **22. Diversity measures of based on fitting abundance distributions**

### **23. Log series $a$**

The diversity index  $a$  is a parameter of the log series model. Its calculation is a necessary prelude to fitting the distribution. A series of studies (Kempton & Taylor 1974, 1976; Taylor 1978) investigating the properties of  $a$  have come out strongly in favor of its use, even when the log series distribution is not the best descriptor of the underlying species abundance pattern. It is an absolutely biased view of ecologist educated in English culture. Hayek and Buzas (1997) criticised Fisher's  $a$ . In fact it is almost always  $>0.9$ , and often close to 1. Recall that the first term of the log series, which predicts the number of species, is  $ax$ . Thus,  $a$  is approximately equal to the number of species represented by a single individual. Moreover, it is possible to attach confidence limits to  $a$ .  $a$  is relatively unaffected by variation in sample size, and completely independent of it if  $N > 1,000$  (Taylor 1978).

### **24. Log normal $A$**

It might be expected that the standard deviation of a log normal distribution would be a good measure of diversity. Although it can be used as an evenness measure it is a poor index for discriminating amongst samples and cannot be estimated accurately when sample size is small (Kempton & Taylor 1974). Nor is  $S^*$  a good predictor of total species richness. Unexpectedly, however, the ratio of these parameters ( $S^*/(Y)$ ) turns out to be an effective diversity measure (Taylor 1978). Its ranking of sites, from high to low diversity tends to accord well with Fisher's  $a$ .

## **25. List of animation, audio files and movies**

animation BioDiversity.flv animation Biodiversity-cube.flv animation Using Excel to Calculate Biodiversity.mp4

## **26. Questions**

- What is the difference between the parametric and nonparametric measure of diversity?
- Which is the the most frequently used diversity statistics?

## Chapter 8 Classical diversity statistics

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- Why Fisher's  $\alpha$  is especially important for the ecologist?
- Enumerate the advantages of taxonomic distinctiveness over the classical diversity statistics.
- What are the two components of diversity statistics?
- What are the advantages of the Brillouin index over the Shannon index.

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# 10. fejezet - Chapter 9. Scalable diversity statistics

Nowadays the loss of biological diversity is considered to be a major problem. This is shown by the fact that many organisations both public and private are busy studying the topic. These include the UN, the WWF, most governments. Two central questions in the biodiversity debate are: 'How to stop the declining of biodiversity?' and 'What to preserve?' Because we are facing problems of choice in welfare, economists tend to have an interest in the subject. Because biodiversity is about species, preserving ecosystems and life in general, ecologists also have an interest in the subject.

Ecologists have developed indices and other ways of measuring biodiversity so we can compare different areas. Traditional (ecological) diversity measures like the index and Simpson index have a weakness: their ordering of the same areas is not always equal (Tóthmérész, 1993). Recognising this Tóthmérész (1993) proposes to use families of parametric indices. To calculate them he also wrote a computer program: 'Divord'. From 1990 several authors have come up with the concept of measuring biodiversity by looking at distances between species, be it genetic, taxonomic or other. Solow et al. (1993) have done some pioneering work, in their article 'On the measurement of Biological Diversity.' Another article worth mentioning comes from Vane-Wright (1991) 'What to Protect? Systematics and the Agony of Choice.' In 1992 Weitzman wrote an extensive article in which he develops a workable measure of diversity with the distance between species as a base. In a number of follow up articles in 1993 and 1998 the concept is extended.

One of the best indices of the ones included in Tóthmérész's programme is Rényi's index. This index is an extension of Shannon's index for entropy and collapses for certain points to the Shannon index, the logarithm of the number of species and the logarithm of the Simpson's index. It can be shown that under theoretical constraints Weitzman's algorithm and Rényi's index can be equal. Weitzman (1992) has also shown that his algorithm is equal to the index divided by two for certain cases. And since Rényi's index equals the index at the correct parameter value, too, there's another proof the two are closely related. However if no constraints are imposed the two are not equal and they can provide different ordering for the same case. They move in the same direction but are not equal. When we look at the results with the constraints and at the orderings that came out of the case study, Weitzman's algorithm proves to be closely related to the first part of the line the Rényi's index.

## 1. The problem of biodiversity

In the last decades people have been more and more concerned with the problem of extinction of species and whole ecosystems. This loss of biological diversity often called 'biodiversity' led together with other environmental problems to the UN Conference on Environment and Development (also known as the Earth Summit) in . The UN stated in their Conference on Biodiversity (part of the Earth Summit) in the preamble: "The Contracting Parties, Conscious of the intrinsic value of biological diversity and of the ecological, genetic, social, economic, scientific, educational, cultural, recreational and aesthetic values of biological diversity and its components. Concerned that biological diversity is being significantly reduced by certain human activities. Noting that it is vital to anticipate, prevent and attack the causes of significant reduction or loss of biological diversity at source. Determined to conserve and sustainably use biological diversity for the benefit of present and future generations."

Two major points about biodiversity can be concluded from this phrase from the preamble: firstly: we are concerned about biodiversity and secondly: biodiversity has utility to us. In environmental economics the value of environmental goods (such as biodiversity, species, landscapes, ecosystems or nature reserves) is divided into several sub-values. According to Pearce & Morran (1994) the value of biodiversity falls apart into the use value and the non-use value. The use value is further divided in the direct use value, the indirect use value and the option value. The direct use value is the value we put on direct outputs of biodiversity such as timber. Indirect use values are functions of biodiversity from which we benefit indirectly such as watershed protection. Option value is the value we derive from the fact that we may use biodiversity in the future.

The non-use value falls apart into the bequest value and the existence value. The bequest value is the value we derive from the fact that we know that someone in the far future may benefit from the biodiversity. Existence value is the value that is derived from the simple fact that a species is known to exist and has a value from itself (Pearce & Morran, 1994). Apart from these values Fromm (2000) argues that there is something like the

contributory value: the value a species has in the sense that it increases diversity in general and by existing, preventing ecosystems collapses and safeguarding ecological processes. This diversity in general is correlated with ecosystem stability, although the relation is not yet quite clear (McCann, 2000). This is what one might call some sort of insurance value, and should therefore be incorporated in the direct use values.

The total value of the global ecosystem including its biodiversity has been estimated as an average of (1994US) \$ 33 trillion per year (Costanza et al., 1998). Although this estimate has been thoroughly disputed (Nunes & van den Bergh, 2001; Müller, 2000) it made one point quite well: biodiversity has a high value. The conservation budget however is restricted.

In order to provide ways to conserve as much biodiversity as possible within the available budget, economists and ecologists have searched for an adequate way to measure biodiversity that covers all aspects of this concept. Several indices, indicators and ways of measuring have been proposed. The most well known indices among ecologists are probably the Simpson-index (first described by Simpson in 1949) and the Shannon index (first described by in 1948). These indices take the number of species as well as their abundance into account (Begon et al, 1996). Tóthmérész (1993) shows that these indices are inconsistent for certain communities of species. To overcome this problem he proposes to use parametric families of diversity indices. The diversity values of these indices are plotted graphically against a scale parameter. Biodiversity is thus not reduced to a single number but a series of numbers. Tóthmérész also wrote a computer program, DivOrd, to implement these families. One of the families he uses collapse at certain values of the scale parameter to the Simpson-index or the index, as he shows. The families he uses thus include both indices (Tóthmérész, 1993).

Weitzman approaches biodiversity from an economic perspective. Weitzman argues that biodiversity should be conserved for future human use, and that future human use is based upon species attributes and these again are based on its genes. Thus, he states, what we conserve should cover as many genes as possible and the protection of these genes should be very firm (Weitzman, 1993).

Weitzman further argues that species have a direct value to the present generation. Taking into account each species distinctiveness (i.e. how much it differs genetically from its closest relative) and its direct value a he creates a ranking criterion for the problem of biodiversity conservation (Weitzman, 1998).

The problem of how to measure biodiversity is thus considered from the ecological side differently then from the economic side. It is interesting to see whether these different ways (the parametric families of diversity indices and the genetic diversity) are related and whether the results they state for a project are the same.

## **2. Measuring biodiversity**

The main objective is to provide insight in the working and the relation between the framework for measuring biodiversity by Weitzman and the parametric families of diversity indices by Tóthmérész.

The research questions are:

- Is there a mathematical relationship between the Weitzman-index and the families of Tóthmérész?
- Is the Weitzman-index part of the parametric families of diversity?
- Can the parametric families of Tóthmérész be considered as a special case of the Weitzman index?
- Does the Weitzman-index provide the same answers concerning biodiversity, as do the families of Tóthmérész?
- Can the indices be combined to one index for biodiversity?

In the review the available literature on biodiversity measurement will be reviewed, an overview will be given of the history and mathematical background of biodiversity-indices with special attention to the Weitzman-index and the parametric families of diversity indices as described by Tóthmérész. In the theoretical approach the maths of both indices will be thoroughly explored. I will then try to link both indices. I will look into the connections between both indices and look for similarities between both indices.

In the case study I will apply both indices to the vegetation data of several plots and calculate both indices. The purpose is to see whether both indices provide the same (kind of) answers and ranking among plots or whether

there are differences and how these differences can be explained. This should provide an illustration of the theory.

### 3. Biodiversity in general

Thomas Lovejoy first introduced the concept of biological diversity in 1980. The term biodiversity itself was introduced by E. O. Wilson in a report for the first American Forum on biological diversity organised by the National Research Council (WordIQ, 2004). The concept has been widely in use ever since, and is used by a lot of people from every walk of life. Typing the word in Google™ results in approximately 3,3 million hits including pages from the UN, the WWF, libraries, museums and universities (Google™, 3 June 2004).

The UN being concerned about biodiversity organised their Earth Summit in which they proclaimed that they were “Determined to conserve and sustainably use biological diversity for the benefit of present and future generations.”

The WWF stated in their mission that they want to “stop the degradation of the planet's natural environment and to build a future in which humans live in harmony with nature, by:

- conserving the world's biological diversity”

The definitions of biodiversity are as wide spread as its number of hits on Google™. As Hurlbert states in his article in 1971 (about species diversity): “since diversity (everyone agrees on the word!) has never had a single unequivocal definition (...) We can therefore muddle along with a plethora of indices, each one supported by at least one person’s intuition and some recommended by fashion”.

In general biodiversity is regarded from three different levels: genetic, species and ecosystems. These different levels all have their own indices to measure biodiversity.

Genetic biodiversity focuses on the diversity of genes within and between species. Genetic researchers are most of the time concerned whether a population is viable, and have defined minimum standards of diversity to prevent inbreeding (Pearce & Morran, 1994).

Species biodiversity focuses on the number of species and their abundance. At the moment we do not know the current number of species on earth or their extinction rates. Estimations of species numbers on earth run from 3 million to 30 million (May, 1990) from which approximately 1,8 million are described (Begon et al., 1996). These species are not evenly distributed among the earth.

There are several ‘hot-spots’ among the world (see figure 1) where a lot of endemic species live. The total number of species in these hot-spots is also higher than the number of species anywhere else is. The hot-spot classification was made on the base of the plant species distribution among the world. Rich flora however, can reasonably be supposed to be leading to evolutionary to a rich invertebrate fauna (Myers, 1990). Hot-spots together are 0.5 % of the Earth’s land surface and they cover 20% of the Earth’s plant species. The hot-spots are especially important because many of them are under high pressure from growing and (often) poor populations which are more interested in developing than nature conservation (Myers, 1990).

Ecosystem biodiversity is diversity among habitats, communities and processes. Because ecosystems are very complex interactions between species, their communities and the environment, no simple relations between diversity and one of these exists. Ecosystem diversity is therefore very hard to measure (Pearce & Morran, 1994).

### 4. Biodiversity: The ecological view

Ecologists have mainly focused on the species diversity level. Some of the oldest indices (Simpson (1949) and Shannon (1948)) are on species level; of course the term biodiversity wasn’t used at the time. Most indicators of biodiversity used in the EU are still based on species richness, and its relation to biodiversity (EU, 2002).

Species richness is often combined with species abundance, because if one considers a community with five species where these species are equally abundant, this is considered to be more diverse than a community with five species with one species being 80% of the total and the other four each 5%.

## Chapter 9. Scalable diversity statistics

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The Simpson index is probably the most well known index. Simpson introduced this index in his article 'Measurement of diversity'. Its mathematical description for a community of S species is:

$$D = 1 / \sum_{i=1}^S p_i^2$$

With  $p_i$  being the proportion of biomass (or number) of the  $i$ -th species in the total of the community S.

The index is another well-known index. first introduced this index in an article about the mathematical aspects of communication: 'A mathematical theory of communication'. It was later on implemented by ecologists to measure diversity. Its mathematical description for a community of S species is:

$$H = - \sum_{i=1}^S p_i \ln p_i$$

With  $p_i$  being again the proportion of biomass of the  $i$ -th species in the total of the community S. The original index used a logarithm with a base of 10 but in ecological literature the natural logarithm is common.

The problem with these kinds of indices is that one tries to catch two different dimensions in one number. This results sometimes in both indices giving a different ranking order for the same communities of species (Hurlbert, 1971).

For example if we have a community A of five species (33, 29, 28, 5, 5) and a community B of six species (42, 30, 10, 8, 5, 5) then  $D(A) = 3,6 > D(B) = 3,5$  but  $H(A) = 1,4 < H(B) = 1,5$ . The origin of this problem lies in the fact that the different indices have different sensitivity. 's index is more sensitive to rare species while the Simpson index is just the opposite (i.e. sensitive to dominant species) (Tóthmérész, 1993)

Recognising this problem Tóthmérész (1995) proposed to use not just one index but a parametric family of indices. He plots an index against a scale parameter  $a$  and then compares the graphs. He describes this family as follows:

Let A be a community of S species and  $p_i$  be the relative abundance of the  $i$ -th species within community A. The distribution of  $p$  is

$$G := \{(p_1, p_2, \dots, p_S) : p_i \geq 0, \sum_{i=1}^S p_i = 1 \text{ for } i = 1 \text{ to } S\}$$

Diversity is a real function defined on G

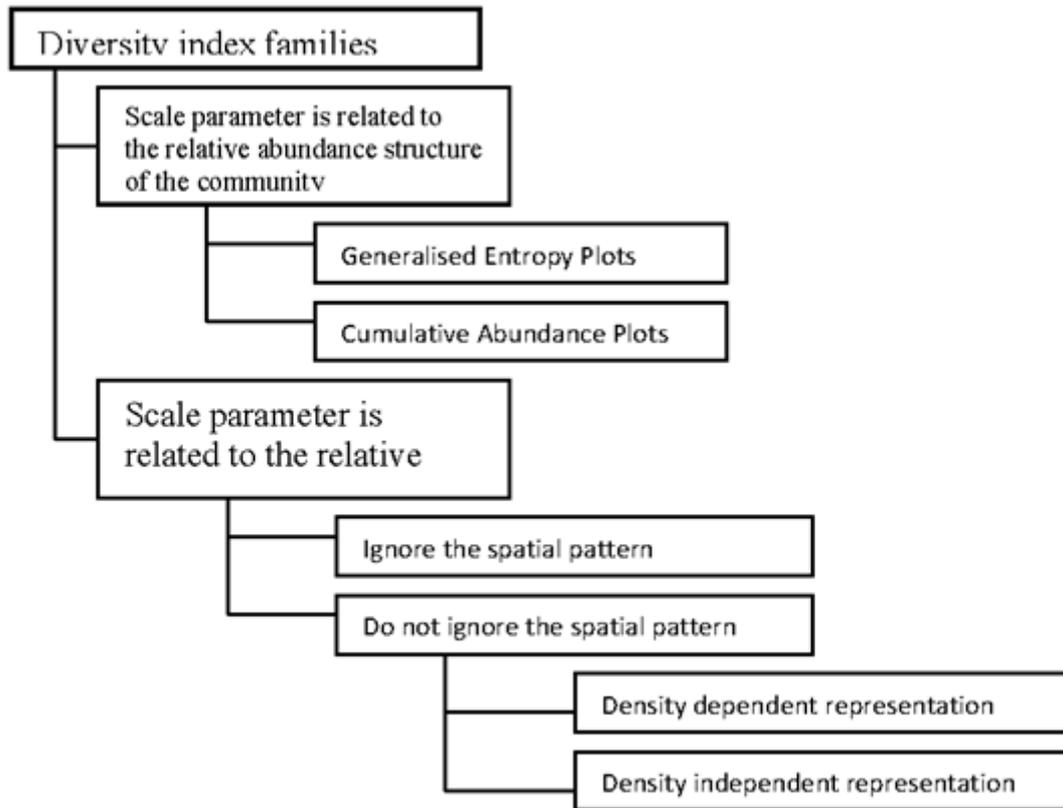
$$D: G \rightarrow \hat{A}$$

where  $\hat{A}$  is the set of real numbers. Furthermore we define community diversity as the average species diversity. Depending on which rarity function is used the function of diversity differs.

Now we note the rarity of species  $i$  from the set (S,p) by  $R(i;p)$ . In other words the rarity of each species is a numerical value associated with that particular species. The diversity function then becomes:

$$D: G \rightarrow \hat{A}, D(p) = \sum_{i=1}^S p_i R(i; p)$$

In general there are two kind of families in diversity ordering. In the first group the scale parameter  $a$  is linked to the dominance structure of the community, in the second group it's related to sample sizes (Figure 1).



**Figure 1.** Methods of diversity ordering (Tóthmérész, 1993).

After this general model we turn to some specific families mentioned to be very useful by Tóthmérész. First of all: the Rényi's index family (first described by Rényi in an article about information and entropy). This family is an extension of the previously mentioned Shannon-index.

$$H_a = 1/(1-a) \log \sum p_i^a \text{ with } a \in [0, 1]$$

In this equation  $a$  is a scale parameter for the order of diversity. This equation collapses to Shannon's index at the value of the scale parameter  $a \rightarrow 1$  (using the l'Hospital rule), to the log of the Simpson index for  $a = 2$  and to the simple (log of) number of species for  $a = 0$  (Hill, 1973).

Some other useful indices mentioned by Tóthmérész are the exponential Rényi's index (first described by Hill in 1973)

$$N_a = \left( \sum p_i^a \right)^{1/(1-a)}$$

This index is particularly useful for species-poor communities because it produces clear figures, the figures are less clear when the number of species increases (Tóthmérész, 1995). It is closely related to Rényi's index ( $H_a = \log N_a$ ).

Another index for species-poor communities is the right-tail sum diversity (first described by Patil & Taillie, 1979):

$$T_i(p) = p_{(i+1)} + \dots + p_s = \sum_{j=i+1}^s p_j \text{ for } j = i+1 \text{ to } S \text{ with the } p \text{ arranged in descending order.}$$

The last family that Tóthmérész (1995) mentioned as being useful is the logarithmic dominance plot method:

$$P_i = (\log i, \sum_{j=i+1}^s p_j) \text{ for } j = i+1 \text{ to } S$$

This method plots the logarithmic species rank against the right-tail sum diversity.

To implement this family and others and use them for diversity ordering Tóthmérész wrote a computer program DivOrd in 1993. This program can calculate and plot the Rényi index, the exponential Rényi index, the right-tail sum diversity, the logarithmic dominance plot and some other parametric indices.

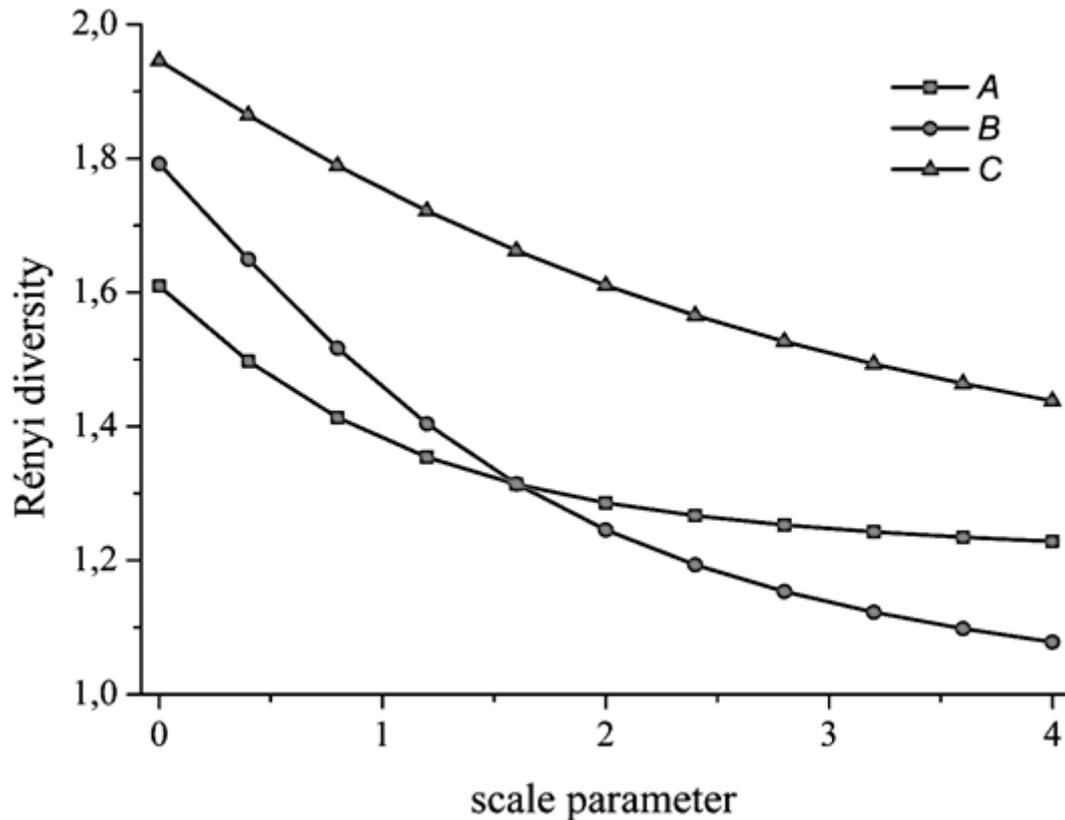


Figure 2. Rényi's index for communities A, B and C.

As we can see community C is always the more diverse while A and B cross at a scale parameter of approximately 1.7. This was to be expected from the different values of the and Simpson index, which are values of the Rényi's index for the scale parameter  $a=1$  and  $a=2$ , respectively.

For ecological conservation the abundance is often neither very well known nor very relevant, for many people it is enough to know that the species is simply there (Izsák & Papp, 2000). Recognising this Ricotta (2004) following the earlier work of Vane-Wright et al. (1991) developed from one of the parametric indices an index combining taxonomic distances between species and expected diversity.

This index is the index of Hurlbert (1971) combined with a weight factor for taxonomic distinctiveness. The Hurlbert index takes the following form:

$$\sum_{i=1}^S (1-p_i)^a \quad \text{for } i \text{ is } 1 \text{ to } S$$

Ricotta then combines this index with a weight factor  $w_i$  calculated for each species. Here  $w_i$  is calculated from the pairwise distance  $d(i,j)$  following Solow & Polasky (1994). This  $d(i,j)$  is the taxonomic distance between species  $i$  and  $j$ . A matrix is created for all species showing the  $d(i,j)$  for each species. These  $d(i,j)$  are then summed up per species and divided through the number of species  $S$  minus one to calculate  $w_i$ . Ricotta's index then becomes:

$$T(a) = \frac{\sum_{i=1}^S w_i (1 - (1 - p_i)^a)}{\sum_{i=1}^S (1 - (1 - p_i)^a)} \quad \text{for } i \text{ is } 1 \text{ to } S \text{ and } a \geq 1$$

This index has several drawbacks however: the (ecological) axiom about diversity-indices that an even community has the greatest diversity is violated. It also violates the permutation axiom by Pielou (1975) that the diversity value corresponding to the set  $(p_1, p_2, \dots, p_s)$  is the same as the diversity of the permuted set  $(p'_1, p'_2, \dots, p'_s)$  Ricotta therefore calls this index a 'weak indices' (Ricotta, 2004).

## 5. The parametric indices

The indices Tóthmérész (1995) described as the best indices were the Rényi's index and the logarithmic dominance index. Both indices were calculated with Divord 1.70, the program written by Tóthmérész to calculate these indices. Other indices were calculated as well but their results were less clear. The exp (Rényi), Daróczy, Patil & Taillie and Right-tail-sum diversity all pressed the curves more toward each other so the intersections were hard to distinguish. The species-individual and species-area curves produced clear results for sample-community relations but diversity ordering was not retrieved from it (both as described by Tóthmérész, 1995).

## 6. The comparison

Because Rényi doesn't have one ordering but a series of orderings I considered the ordering of Rényi's index at intervals. The closest match was for  $a = [0, 0.5]$  and the years separated. This is the result as shown in Table 3. As soon as the years are combined the picture becomes more complicated and the results are not exactly the same anymore. A Spearman rank correlation test is still easily passed, though.

In the follow up tables we see the ordering of the Rényi index change further as the scale parameter increases and the results start to differ more and more from Weitzman's index. As the scale parameter increases a Spearman rank correlation test is less and less easily passed.

The orderings provided in table 4 are more or less the same, but the differences that are there, are quite large (as can be seen in the graphs). H05 1986 is by far the most diverse in Weitzman's graph while in Rényi's graph H05 2000 is clearly the most diverse.

The difference is not that large however that correlation can be denied. A Spearman rank correlation test is easily passed at  $a = 0.005$  significance level (not to be mixed up with scale parameter  $a$ ). There definitely is a correlation between the two at this stage of Rényi's index but what about later stages?

The orderings, which are provided by table 8, even fail a Spearman rank correlation test at a 0.05 significance level. Only for values  $>0.05$  than this it's not failed, but this would be a rather high significance level.

So for this case study Weitzman's algorithm and Rényi's index are correlated for the parameter values of  $a = [0, 2]$ . At higher values correlation is only proven for higher significance levels. Especially at the level of  $a = [2, 4]$  the correlation becomes doubtful.

This is rather logical: as the scale parameter increases the index becomes more sensitive to abundance patterns and this is completely ignored by Weitzman's index. At the beginning of the index Rényi's index is more sensitive to species numbers, and these are not ignored by Weitzman's algorithm.

Interesting point is furthermore that most communities are not comparable according to the parametric indices, there are many intersections between the communities. Apparently the stands were quite the same.

This research started with the problem of biodiversity and the indices that are available to measure biodiversity. There are many indicators and indices of biodiversity. In the EU alone an inventory of biodiversity indicators reached the number of 665 indicators (EU, 2002).

Of course indicators is not the same as indices and there are probably fewer indices than indicators (after all indicators are used in general to use simpler things than indices) but the fact that there are whole books written about the subject of diversity indices and there are conferences on the subject does indicate the importance that science confers to the topic.

Because there are so many indices, it is important to know which indices are the same and whether we use more or less the same measures.

The relations between indices are also important because they are often developed from different views on (bio)diversity. If there are relations between indices or they prove to be the same then perhaps we can capture more aspects of biodiversity with one index.

The purpose of this research was neither to make an inventory of all biodiversity indices nor to show all the relations between them. Rather it makes a small contribution to the world of indices and tries to show the relations between two indices that spring forth from rather different viewpoints on biodiversity.

One of the major differences between these viewpoints is the different goals of the diversity indices have. The ecological indices are designed to compare areas at the level of which one has the highest diversity. This is not necessarily true for economic indices, since economy does not focus on diversity per se but on utility, or to be exact on the utility of diversity. A high diversity does not automatically imply a high utility.

This is the reason that Weitzman (1993, 1998) in his follow up articles includes discounting and the utility of separate species, to make his algorithm more economically viable. These modifications however, separate this algorithm further from the ecological indices.

Another consequence of the difference in viewpoints between ecologists and economists is that Weitzman's algorithm violates an ecological axiom about diversity indices. This is the axiom that the maximum diversity is reached in a community in which all species of that community are equally abundant. This is true for the Rényi, Simpson and Shannon index, but not necessarily for the Weitzman index since it completely ignores abundance patterns.

The literature review of this research merely touches upon the vast number of indices there are to measure biodiversity in this world. Nonetheless it tries to show the origin of some of the oldest indices on diversity and the origin and some of the viewpoints of the developers of the indices that are compared in this research.

Besides the history of indices in the literature review, it also tries to touch upon the current state of affairs of biodiversity indices. Although indices become more complicated as time goes by, we have modern computers to help us with the calculations nowadays.

The theoretical framework is a piece of maths in which is shown that under very strict constraints Weitzman's algorithm equals Rényi's index. Unfortunately when these constraints are released this is no longer true. The ordering can still be the same nonetheless, as both indices keep on increasing as the number of species increases, but the amount is not the same.

Perhaps there are other possibilities to link Weitzman's algorithm to the index of Rényi that I didn't find. The subject is interesting enough to look into a bit further.

The case study then finally illustrates the aspects that partially came out of the theoretical framework. It also adds the Spearman rank correlation test to the result, which adds a point to the fact that both indices produce more or less the same results, or that their results are at least correlated.

As the scale parameter  $a$  increases the ordering of Rényi starts to differ more and more from the ordering of Weitzman. The Spearman rank correlation test fails as soon as the value of the scale parameter became larger than 2, unless the significance level is increased (larger than 0.005).

The correlation is most clear in the beginning, but this is logical for Rényi's index is close to species count there and Weitzman's algorithm heavily relies on species numbers (and under constraints is equal to the number of species). Weitzman's algorithm is under constraints also related to the index, which is also in the beginning of the Rényi index ( $a@1$ ).

One has to keep in mind that all data for the case study were taken from the same forest. Although the circles were different it might be interesting to see how both indices work out on larger and different scales, for example when comparing for example a meadow with a forest.

## **7. Conclusions**

The research questions of this research were:

- Is there a mathematical relationship between the Weitzman-index and the families of scalable diversity ordering?
- Is the Weitzman-index part of the parametric families of diversity?
- Can the parametric families of Tóthmérész be considered as a special case of the Weitzman index?

- Does the Weitzman-index provide the same answers concerning biodiversity, as do the families of Tóthmérész?
- Can the indices be combined to one index for biodiversity?

In answer to the first question: Yes there is a relationship between Rényi's index and Weitzman. This does not mean that there is a relation between Weitzman and all the families described by Tóthmérész but that there is at least a relation between one of the families and Weitzman. Weitzman and Rényi are, under very strict constraints, the same.

In answer to question two: Again yes but only under very strict constraints (see theoretical framework)

In answer to question three: This question was only raised in case question two would be answered with a no. Since the two are equal for some special cases, both are the same. So yes but only under strict constraints.

In answer to question four: The answers provided by Weitzman and the families of Tóthmérész are more or less the same. On some parts they differ but the difference is not enough to fail a Spearman Rank Correlation test for this particular example.

In answer to question five: Under strict constraints both indices are the same and can thus be combined. If this is not enough one can combine Weitzman with a family as Ricotta (2004) does. One has to keep in mind though that as soon as Weitzman's algorithm is introduced that the ecological axiom about abundance patterns is violated.

## **8. A field study: Management of non-native spruce plantation**

Sampling area is located at the North Hungarian Mountain Range at the Aggtelek National Park. In this region the typical, native forest type is oak-hornbeam forest (*Quercus-Carpinetum*). Carabid assemblages of a managed Norway spruce plantation and a native oak-hornbeam forest were compared.

The managed Norway spruce plantation was planted after clear-cutting of an oak-hornbeam forest stand. The spruce was dominant in the canopy layer with 70% cover in the tree layer, but oak and hornbeam were also represented. The presence of native species in the canopy was due to thinning of the spruce which resulted in a re-invasion of native trees, herbs and shrubs, and produced relatively thick leaf litter patches spreading over the 75% of the soil surface.

The native oak-hornbeam forest was used as a control area. The shrub and herbaceous layer were moderate and the leaf litter layer was thick. Both of the studied forest stands were larger than 2 ha and they were approximately in the same age. The managed plantation's distance from the native forest was 2 km. In each studied habitat 18 pitfall traps were used during the sampling procedure. Unbaited pitfall traps (diameter 100 mm, volume 500 ml) containing ethylene-glycol as a killing-preserving solution were used, which is a standard studying ground beetles. Trapped individuals were collected monthly from April to October which was the main activity period of the species. All ground beetles taken in pitfall traps were identified to species using standard keys (Freude et al. 1976).

### **8.1. The effect of the management**

There were no differences between the traps of the managed plantation and the native forest by the MDS based on the Bray-Curtis dissimilarity index (Magura et al. 1997, 2002). This is an important message of the research. Even a simple management practice may increase the diversity of the ground beetles remarkably. On the other hand the species richness is still different; the ground beetle assemblage of the native forest is more species rich than the managed spruce plantation.

The similarity in the diversity and composition between the native deciduous forest and the managed spruce plantation revealed the usefulness of this kind of nature management practice. It encourages the recolonization of herbs, shrubs and trees of the native vegetation by thinning the spruce and especially by creating gaps in the spruce stand. Advantageous effects of the nature management practice were also manifested in the ground beetle assemblages of the managed plantation. The mixed tree composition of the managed plantation resulted in abundant leaf litter. Leaf litter covered a much larger area than the needles; its cover was approximately 75% or

more. In earlier papers, in a litter manipulation experiment, we demonstrated that the cover of the leaf litter significantly contributed to the maintenance of ground beetle diversity (Magura et al. 2002, 2004). It was reported that leaf litter increased diversity of ground beetles through producing favourable microsites (Niemelä et al. 1992; Niemelä & Spence 1994). In the managed plantation the cover of trees, and of the herbs were similar to the native deciduous forest. The species composition of the herbs, the structure and thickness of the leaf litter were also similar to the native forest. All of these factors contribute to the heterogeneity of these habitats and the diversity of ground beetle assemblages were influenced by habitat heterogeneity (Butterfield 1997; Niemelä et al. 1996).

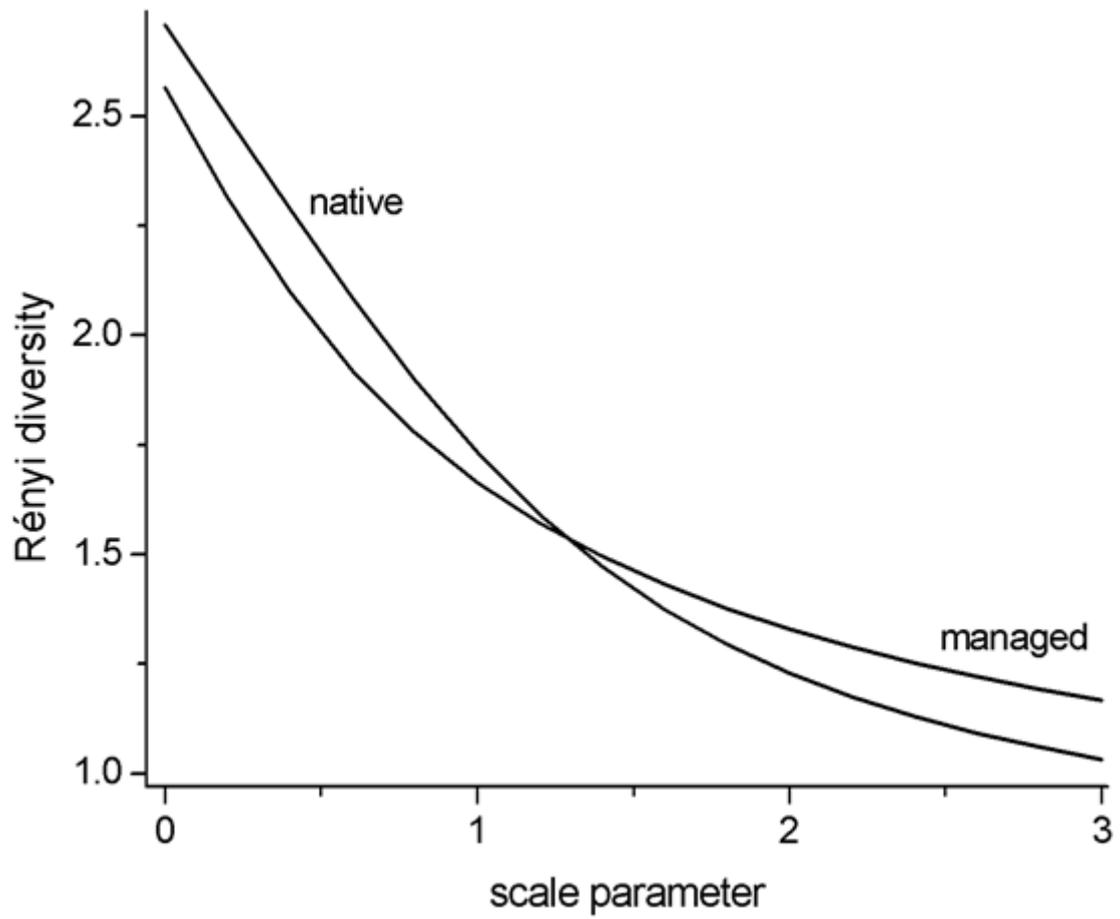
**Table 2.** A few statistics for the assemblages of the native oak-hornbeam forest and the pine plantations; diversity statistics are in the form of effective number of species.

	<i>native forest</i>		<i>pine plantations</i>
Number of species	19	>	17
Number of individuals	1199	>	826
Shannon diversity	5.74	>	5.58
Quadratic diversity	3.62	<	3.99
Berger-Parker index	2.52	<	2.44

## 8.2. Diversity of the native forest and managed pine plantation

There were 20 ground beetle species captured altogether in the two habitats. There were 17 versus 19 species in the native oak-hornbeam forest and in the managed spruce plantation. There was also a remarkable difference in the number of captured individuals between the managed spruce plantation and the native forest (Table 2). Using traditional diversity statistics the native forest was more species rich and more diverse for the Shannon diversity, while the managed stand of the pine plantation was more diverse using the quadratic or Simpson diversity and the Berger-Parker index of dominance (Table 2). The solution of this ambiguity is shown by Figure 5. Using the Rényi diversity profiles of the carabid assemblages of the oak-hornbeam forest and the pine plantation it is evident, that the profiles cross each other and the native forest is more diverse in the rare species, while the plantation is more diverse regarding the dominant species. Using the RTS-diversity profile we can locate the change in the diversity order; the RTS-diversity profiles cross each other between the 3-rd and 4-th species (Figure 3).

The  $ES(m)$ -diversity profiles are shown in Figure 4.



**Figure 3.** Diversity profiles of the assemblages by the one-parametric Rényi diversity index family.

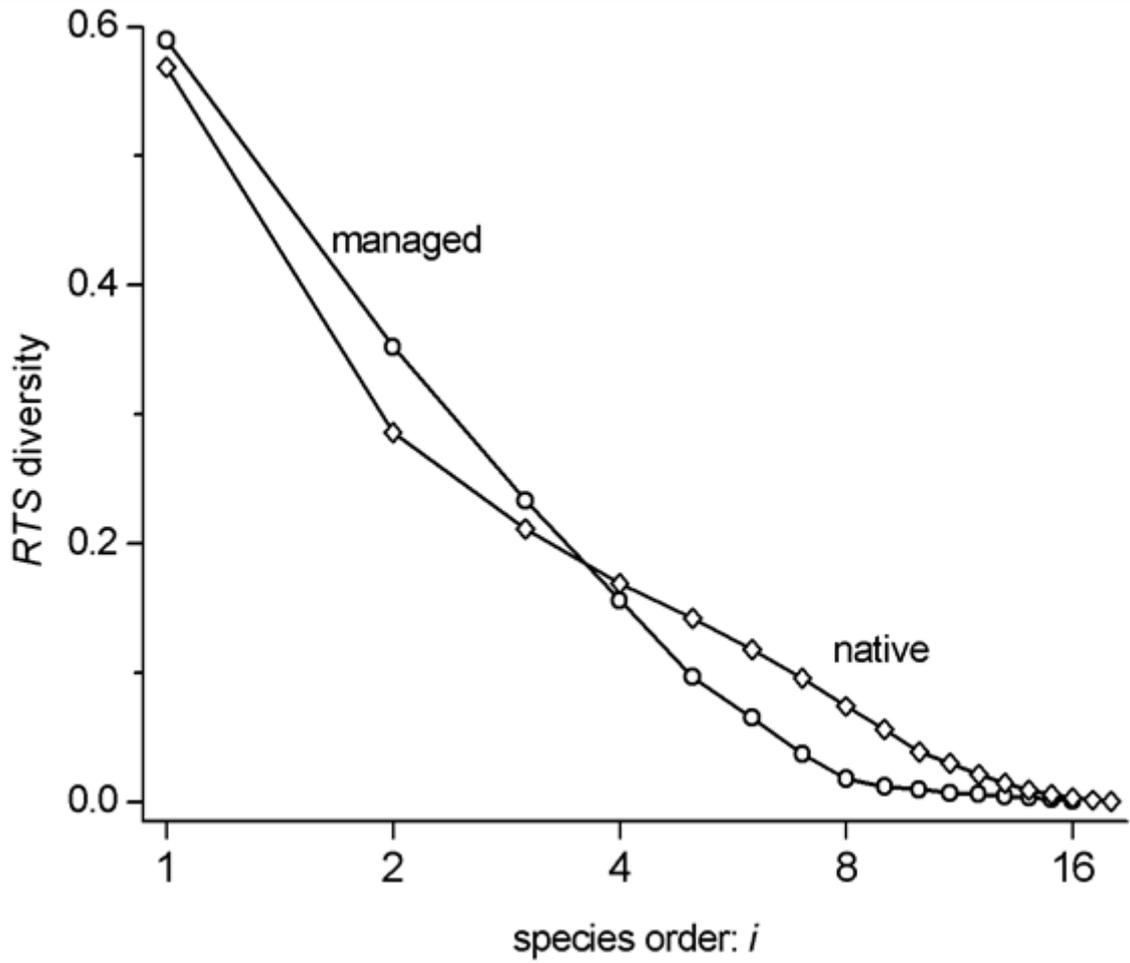
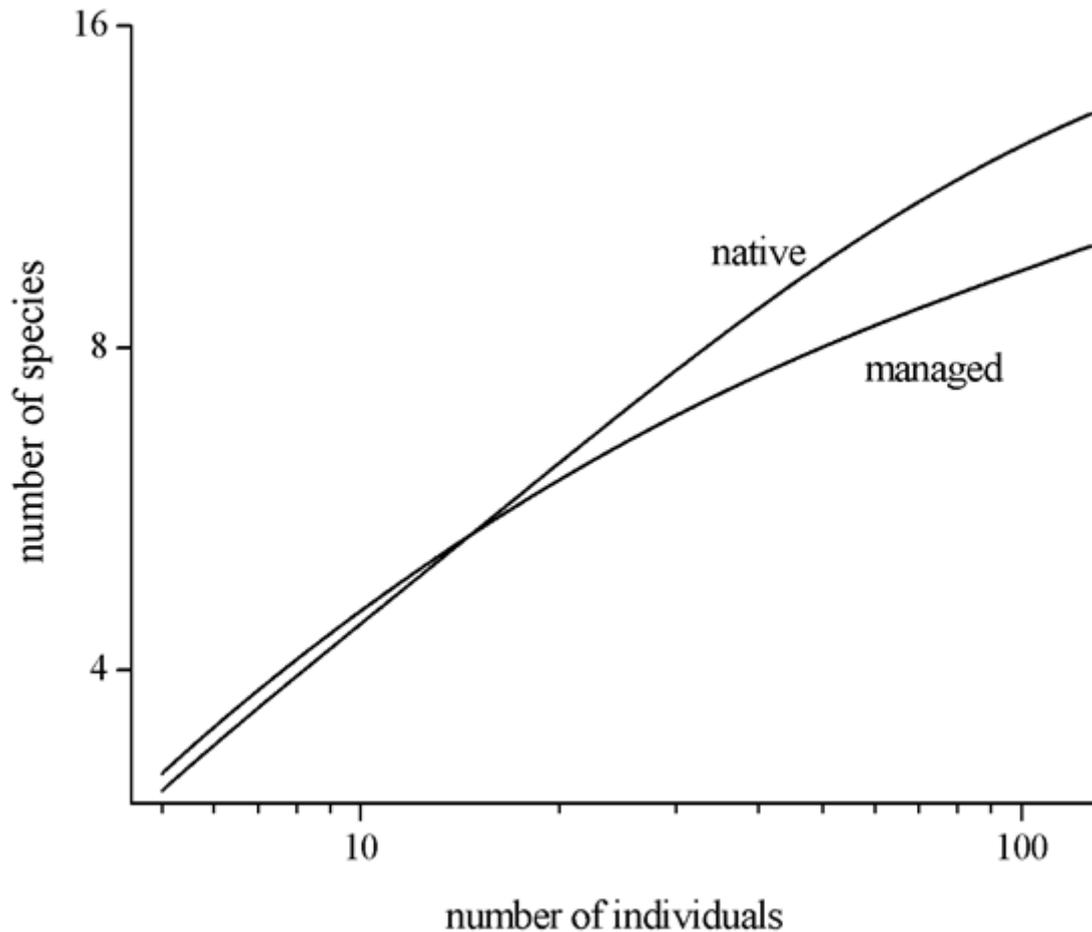
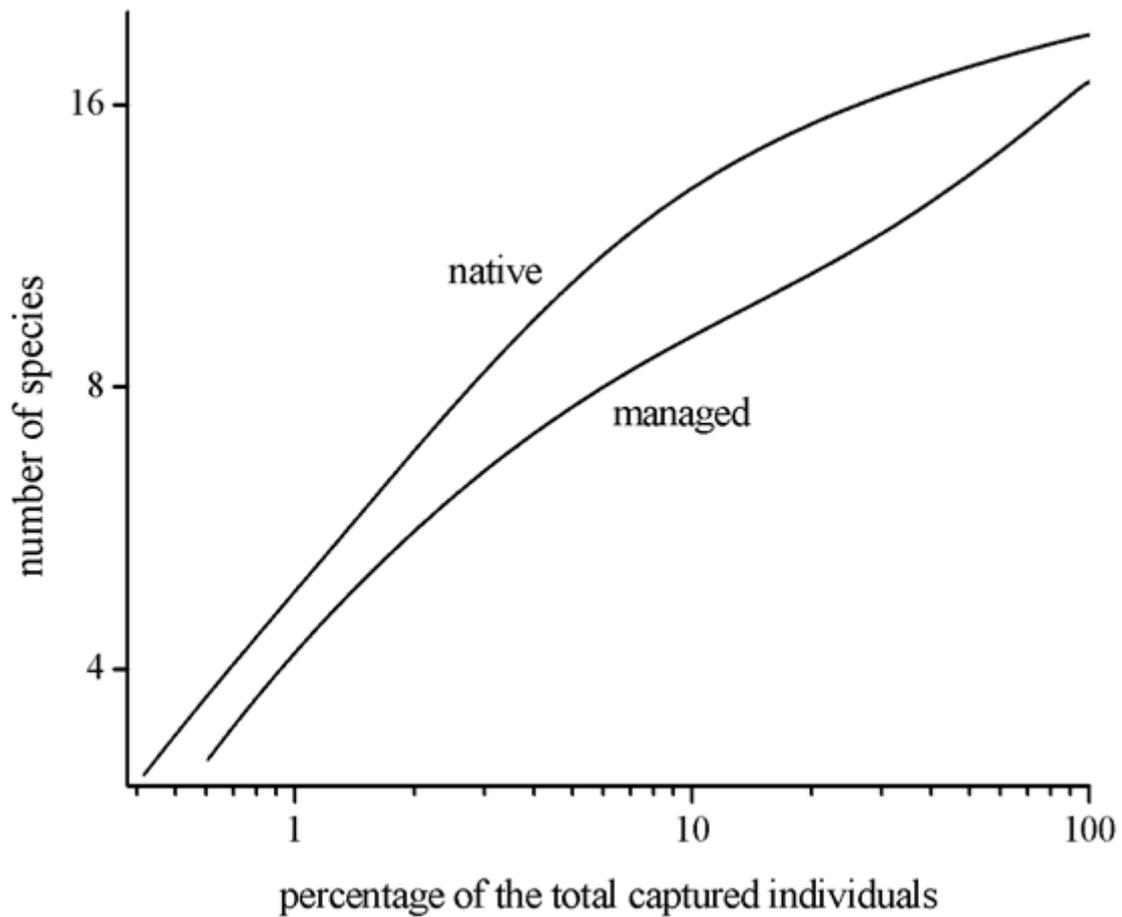


Figure 4. Diversity profiles of the assemblages by the one-parametric *RTS* diversity index family.



**Figure 5.** Expected number of species or  $ES(m)$ -diversity profiles (species accumulation plots).

It is evidently known even from the classical literature of ecology (Gleason 1922), that the number of species depends on the number of individuals. It may be especially important in the case of different densities. The total number of captured individuals was larger by one-third of the number of individuals than in the case of native forest than in the case of spruce plantation. Using a density independent representation of the diversity relationships of the native and managed stands by the  $ES(m)$  diversity profiles we receive the diversity profiles shown by the Figure 8. Each of the diversity profiles produced by the previous methods (Figure 4 – Figure 7) was based on density independent representations. An important difference in the case of the management example between the result regarding the diversity ordering by density dependent and density independent representations that the density dependent representation of the diversity profiles of the managed and non-managed stand do not cross each other. Therefore, they can be ordered according to their diversity, and the native forest is more diverse than the managed plantation.



**Figure 6.** Density dependent representation of the expected number of species diversity profiles.

## 9. List of animation, audio files and movies

animation Biogeography Evidence for Evolution.mp4

voice Identifying Priority Sites for Biodiversity Conservation.mp3

## 10. Questions

- Define Rényi diversity?
- What is the solution of diversity measuring paradigm.
- What does “intrinsically more diverse” means?
- Why is important the RTS-diversity in ecology?

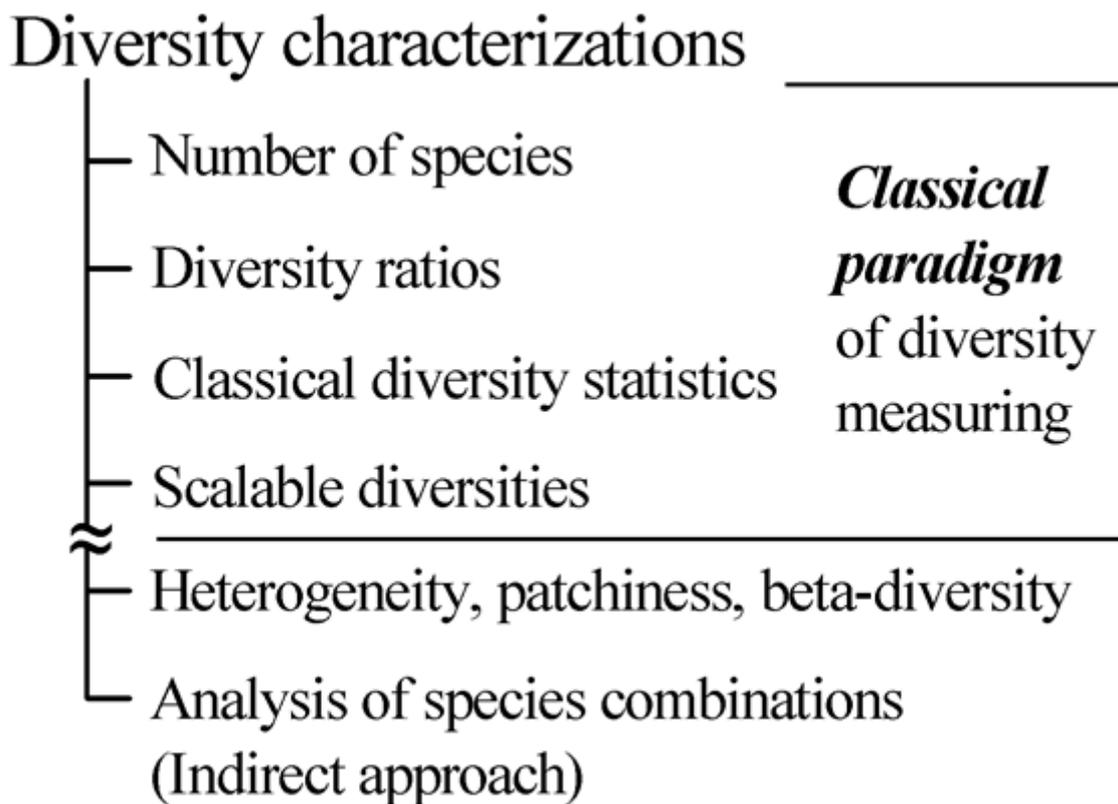
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# 11. fejezet - Chapter 10 Classical paradigm of Measuring Diversity

## 1. Introduction

The *number of species* is certainly the oldest, and still one of the best measure of diversity. It depends, however, on the number of individuals in the sample and/or the area to be sampled. This is the basic motivation of the standardizations, when the number of species is divided by the number of individuals or the area to be sampled (e.g. plot size). The number of species do not increase linearly by the number of individuals. The standardization is more correct, when the number of species is divided by the logarithm of the number of individuals, because the number of species increases linearly or almost linearly with the logarithm of the number of individuals. These simple, richness-type measures of diversity are quite useful in many situation, although they may be criticized. A species, which is represented by just 1 individual, has the same contribution to the number of species of the community than a species which has more than 1000 individuals.



**Figure 1.** Evolutionary tree of the methods to characterize diversity.

Comparing the communities represented in Figure 1, we certainly do not feel, that they are equally diverse, instead of that they have the same number of species and the same number of individuals. The first community is very strongly dominated by the species represented by the "+" sign on the "map". In the case of the other community the dominance of the most frequent species is not as strong as that. It is also evident from the abundance vectors of the communities F1 and F2.

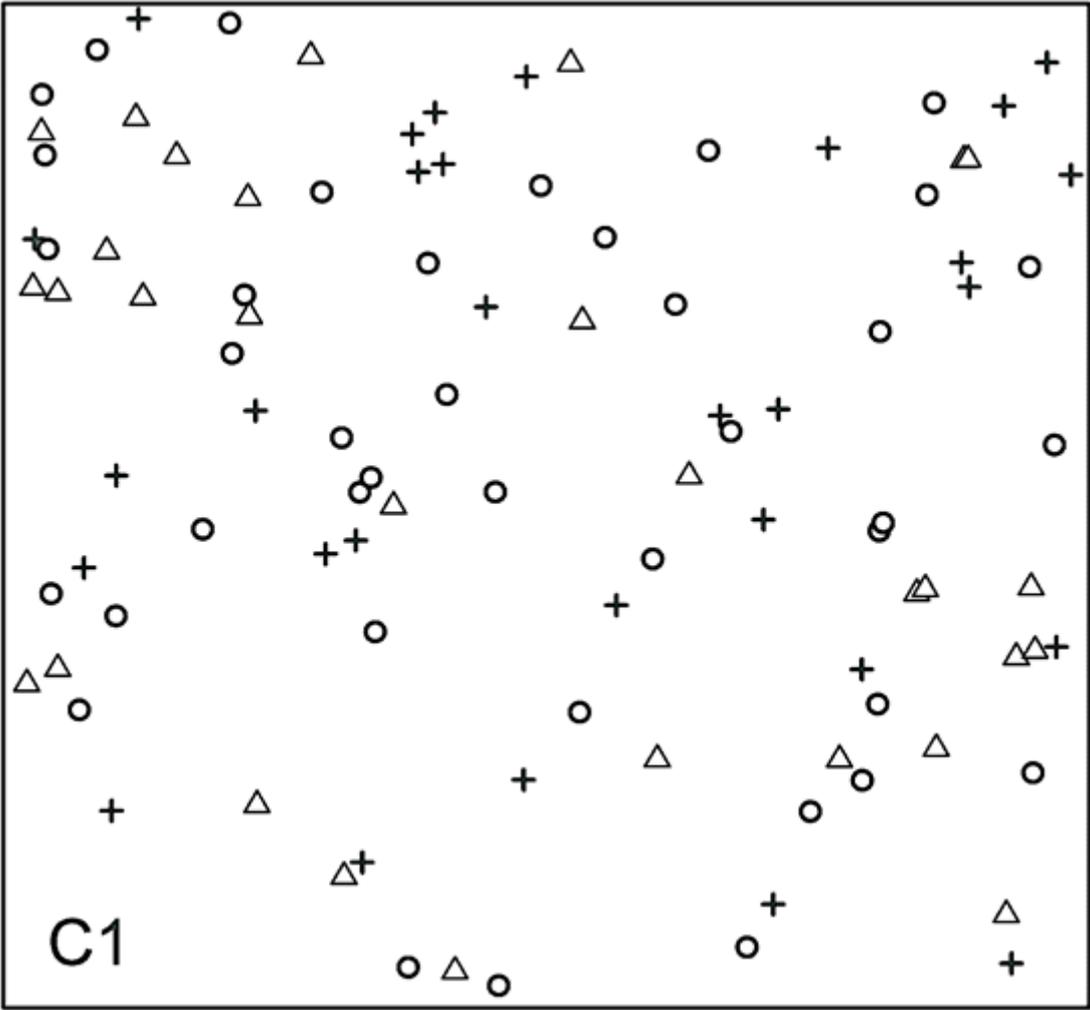
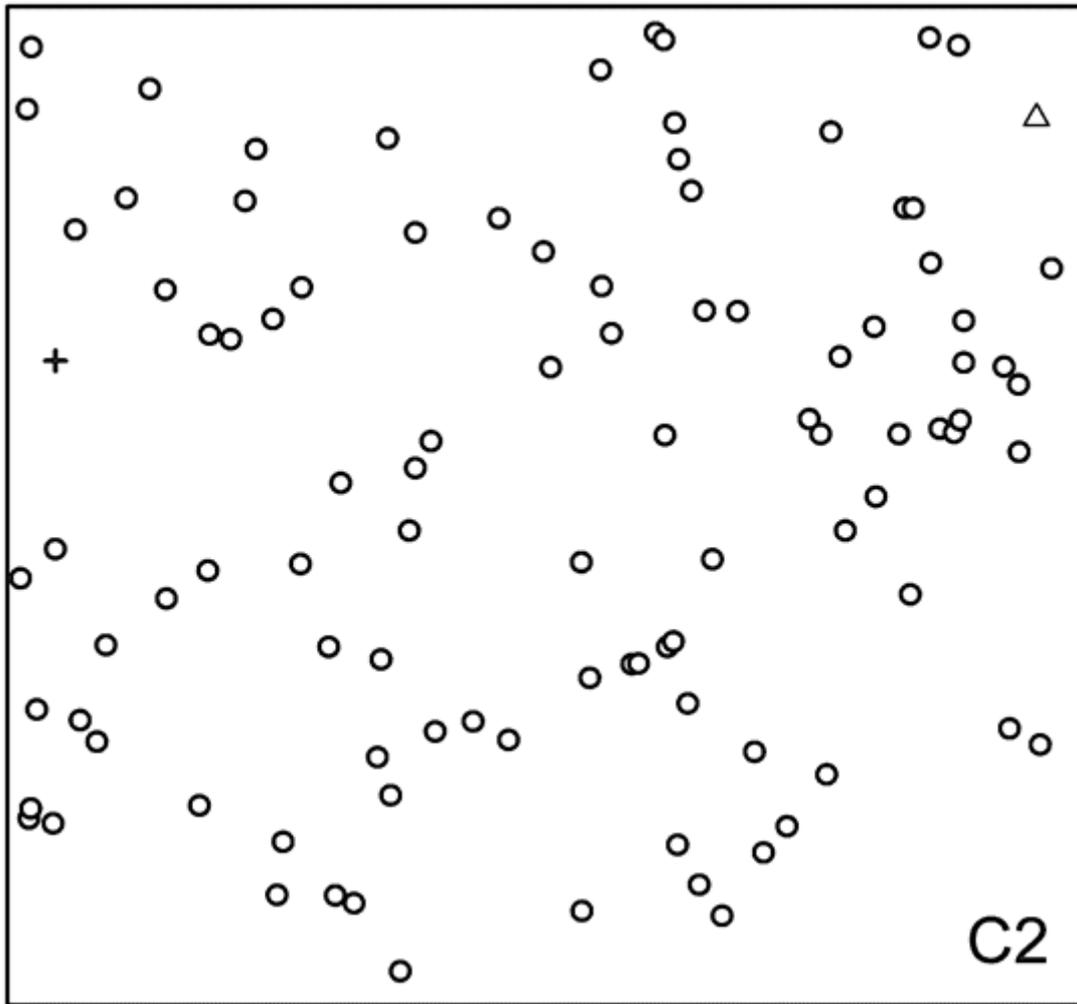


Figure 2. Point map of the community F1.



**Figure 3.** Point map of the community F2.

This problem is easily overcome by *traditional diversity statistics*, like *Shannon diversity* or *quadratic diversity*. These methods utilize the information about the *relative frequencies* of the species in the communities (ecologists sometimes prefer to say dominances).

## 2. Some Notations

To keep on, we have to get acquainted with some formalism. We are frequently speaking about the number of individuals of a species. Let say, about the number of individuals of *Aphanolejeunea capensis*. Discussing the details of the calculations, however, it would be rather long to write, that "number of individuals of *Aphanolejeunea capensis*". It may be "abbreviated" as " $n(\textit{Aphanolejeunea capensis S.Arnell})$ ", which is still "too long" as a symbolic notation. We prefer to identify each species with a positive integer; i.e. we use a numerical character instead of the latin name of the species. In this way, the first species in the species list is denoted by "1", the second one by "2", etc. Therefore, the number of individuals of the "first" species is denoted by  $n(1)$  or even more simply by  $n_1$ . These notations,  $n(1)$  and  $n_1$  are used interchangeably depending on the "readability" of the numerical formulas. Generally, the number of individuals of the  $i$ -th species is denoted by  $n_i$ . If we sum up all the individuals, we receive the total number of individuals of the community, which is denoted by  $N$ . The number of species of the community usually denoted by  $ST$  in a general case. So, the total number of individuals is:

$$N = n_1 + n_2 + \dots + n_i + \dots + n_{ST} = \sum_{i=1}^{ST} n_i.$$

Studying more than one community, we have to make differences between them by the formalism. We denote "the name of the communities" by capital letters, like  $A$ ,  $B$ ,  $C$ , etc. Particularly, the number of individuals of the community  $A$  is denoted by  $N(A)$  or  $N_A$ . Similarly the number of species is denoted by  $S(A)$ . Sometimes, when we would like to stress that we are speaking about the total number of species in a pooled samples, we denote it by  $ST$  (as an acronym of Species Total).

Summarizing the notations, a *community*  $A$  may be described by the abundance vector of the community:  $n(A)=(n_1, n_2, \dots, n_{S(A)})$ , where  $S(A)$  is the number of species that are present, and  $n_i$  is the abundance of the  $i$ -th species of the community. For our purposes it is frequently enough to know the relative abundances of species:  $p(A)=(p_1, p_2, \dots, p_{S(A)})$ , where  $p(A)$  is the *relative abundance vector*  $p_i=n_i/N$  is the *relative abundance* of the  $i$ -th species. If we are speaking generally about communities, we frequently write simply  $p=(p_1, p_2, \dots, p_{ST})$ .

Frequently we would like to know which one is the most frequent species, or the second most frequent, etc. In this case, when the species are arranged in descending order, we use the following notation:

$$p^{\downarrow}=(p_{[1]}, p_{[2]}, \dots, p_{[i]}, \dots, p_{[ST]}) ,$$

where  $p_{[1]}$  is the relative frequency of the most frequent species,  $p_{[2]}$  is the relative frequency of the second most frequent,  $\dots$ , and  $p_{[ST]}$  is the relative frequency of the rarest species. The sign " $[ ]$ " in the subscript means that the elements of the vector is arranged in descending order. Therefore:

$$p_{[1]} > p_{[2]} > \dots > p_{[i]} > \dots > p_{[ST]} .$$

I use a simple example to demonstrate how to apply these notations. There were 6 species on a leaf in the C3 sample site, and they were represented by the following number of individuals: Aphanolejeunea exigua Evs. (27 individuals), Cololejeunea leloutrei (E.W.Jones) Schust. (4 individuals), C. lemuriana Tixier (4 individuals), C. tanzaniae Pócs (13 individuals), Drepanolejeunea cultrella (Mitt.) Steph. (95 individuals), and Leptolejeunea maculata (Mitt.) Schiffn. (8 individuals). More formally,  $S=6$  and the abundance vector of the stand is as follows

$$n = (27, 5, 3, 13, 95, 8) .$$

The total number of individuals is:  $N=\sum n_i=27+5+3+13+95+8=151$ . The relative abundances of the species is calculated in the following way:  $p_1=n_1/N=27/151=0.179$ ,  $p_2=n_2/N=5/151=0.033$ ,  $\dots$ . It can be written as a relative abundance vector:

$$p = (0.179, 0.020, 0.033, 0.086, 0.629, 0.053) .$$

Evidently:  $0.179 + 0.02 + 0.033 + 0.086 + 0.629 + 0.053 = 1.0$ , and

$$p^{\downarrow} = (0.629, 0.179, 0.086, 0.053, 0.033, 0.02) .$$

### 3. Two classical diversity statistics

These methods can overcome the difficulties, which were introduced by comparing communities in Figure 2 and Figure 3. Both of them had the same number of species and the same number of individuals. The abundance-dominance structure of the communities, however, was different. We denoted the communities by  $F1$  and  $F2$ . Using the notations of the previous section, the abundance vectors  $\mathbf{n}(F1)$  and  $\mathbf{n}(F2)$  are as follows:

$$n(F1)=(90,5,5) \quad \text{and} \quad n(F2)=(50,30,20) .$$

The relative abundance vectors can be calculated very simply, because  $N(F1)=N(F2)=100$ ; therefore  $p(F1)=(0.9,0.05,0.05)$  and  $p(F2)=(0.5,0.3,0.2)$ . Applying the above introduced notations, *Shannon diversity* is defined as follows:

$$HS(p) = - \sum_{i=1}^{ST} p_i \log p_i .$$

Natural logarithm is used the most frequently; sometimes logarithm of base 2 and 10 is also used.

Another frequently used classical diversity statistics is the quadratic diversity:

$$DQ(p) = 1 - \sum_{i=1}^{ST} p_i^2 .$$

It is frequently mentioned as Simpson diversity. It was invented and re-invented by so many people, that Good (1982) proposed to name it after the way it is calculated. We accept his very reasonable proposal. Calculations are demonstrated below for communities F1 and F2 .

$$HS(F1) = -(0.9 \ln 0.9 + 0.05 \ln 0.05 + 0.05 \ln 0.05) = -0.0948 + 0.1498 + 0.1498 = 0.3944.$$

$$HS(F2) = -(0.5 \ln 0.5 + 0.3 \ln 0.3 + 0.2 \ln 0.2) = 0.3466 + 0.3612 + 0.3219 = 1.0297.$$

$$DQ(F1) = 1 - (0.92 + 0.052 + 0.052) = 1 - (0.81 + 0.0025 + 0.0025) = 1 - 0.815 = 0.185.$$

$$DQ(F2) = 1 - (0.52 + 0.32 + 0.22) = 1 - (0.25 + 0.09 + 0.04) = 1 - 0.38 = 0.62.$$

These diversity statistics clearly show that community F1 is less diverse than community F2, which could not be seen from the number of species and/or individuals. Sometimes Shannon diversity is calculated in the following way, which avoids the tiresome calculation of the relative frequencies:

$$HS = \log N - 1/N \left( \sum_{i=1}^{ST} n_i \log n_i \right) .$$

Derivation of this formula is not presented here, but it can be received by simple algebraic manipulations from the Shannon formula. By this formula:

$$HS(F1) = (\ln 100 - 90 \ln 90 + 5 \ln 5 + 5 \ln 5) * 100 = 0.3944.$$

## 4. Effective number of species

Diversity statistics introduced in the previous section are clearly showing the influence of dominance structure on the diversity. Evidently

$$HS(F1) = 0.3944 < HS(F2) = 1.0297 .$$

At first sight, however, there is not much biological meaning of these numerical figures. We would like to have a diversity characterization which has a straightforward biological meaning. This is provided by the *effective number of species*. It is defined as the number of species, having the same number of individuals for each species, produced the same diversity as the studied one; i.e. it is the number of species that would be found in a hypothetical community of perfect evenness having the same diversity as the community whose diversity is to be measured.

For the Shannon diversity the effective number of species is defined as  $SHS = \exp HS$ , where  $\exp$  is the exponential function. Shannon diversity receives its maximum, when all the species are present with the same number of individuals. In this case the diversity is  $\max \{ HS \} = \log ST$  . Therefore, the effective number of species is exactly  $ST$  for that community; it is less than  $ST$  for any other communities.

Quadratic diversity looks slightly different from Shannon diversity. It is based on  $\sum p_i^2$  , and then a "converse" of it is created by subtracting it from one; i.e.

$$DQ = 1 - \sum_{i=1}^{ST} p_i^2$$

is devised. Actually,  $\sum p_i^2$  is a measure of *concentration* and, in this particular case, diversity is defined as its *opposite*. There are, however, other ways to create a *converse* and/or *opposite*, like  $SDQ = 1 / \sum_{i=1}^{ST} p_i^2$ , or  $HR(2) = -\log \sum_{i=1}^{ST} p_i^2$  .  $DQ$  and  $SDQ$  are trivial.  $HR(2)$  is based on the properties of the logarithmic function.  $SDQ$  can be used for measuring effective number of species related to the quadratic diversity.  $SDQ$  is closely related to  $HR(2)$  , because  $SDQ = \exp \{ HR(2) \}$  .  $SHS$  and  $SDQ$  are also strongly related, although it is not evident from the first sight. It will be evident later on, after the introduction of diversity profiles, and especially the one-parametric diversity index family of Rényi. It is also evident from their relationships, that  $SHS \geq SDQ$ , and the equality is valid just in the case of perfectly even community (all the species have the same number of individuals).

For the communities F1 and F2 :

$$SHS(F1) = e^{0.3944} = 1.5, SHS(F2) = e^{1.0297} = 2.8, DQ(F1) = 1/0.815 = 1.2, DQ(F2) = 1/0.38 = 2.6.$$

The interpretation of these values are more straightforward. An effective number of species like 1.2 means, that the community was dominated by one species and all the other species has not much share from the total abundance. A value like 2.6 means, that all of the three species really contributed to the total number of species, although the effective number of species do not reach the total number of species of the community, which is 3.

## 5. A simple question: Which community is more diverse?

Table 1. The trichotomy of diversity for the assemblages C1 and C2.

	C1		C2
Number of species	3	<	4
Shannon diversity	1.0889	=	1.0889
Quadratic diversity	0.66	>	0.58

## 6. Resolution: diversity profiles

### 6.1. Historical notes

The problem of *index choice* is well known in the classical diversity literature (Hurlbert 1971, Peet 1974). Peet (1974) discusses the need for a theory of index response to help the choice of diversity indices: one may wish the index to be sensitive to the composition of the dominant species but relatively indifferent to that of the rare ones, etc.

Unfortunately, the solution is not as well known as the problem. It was proposed by Patil and Taillie (1979) and it is based on the use of one-parametric diversity index families, where the diversity of a community is characterized by a (scale-dependent) diversity profile instead of a numerical value. The first of these techniques, a *generalized entropy*, was published by Rényi (1961). As a special case, Rényi diversity includes the number of species, Shannon diversity, quadratic diversity, and Berger-Parker diversity. Nowadays, there is a quite large family of the methods, which can be used for scale-dependent diversity characterization; a review of them is provided by Tóthmérész (1995).

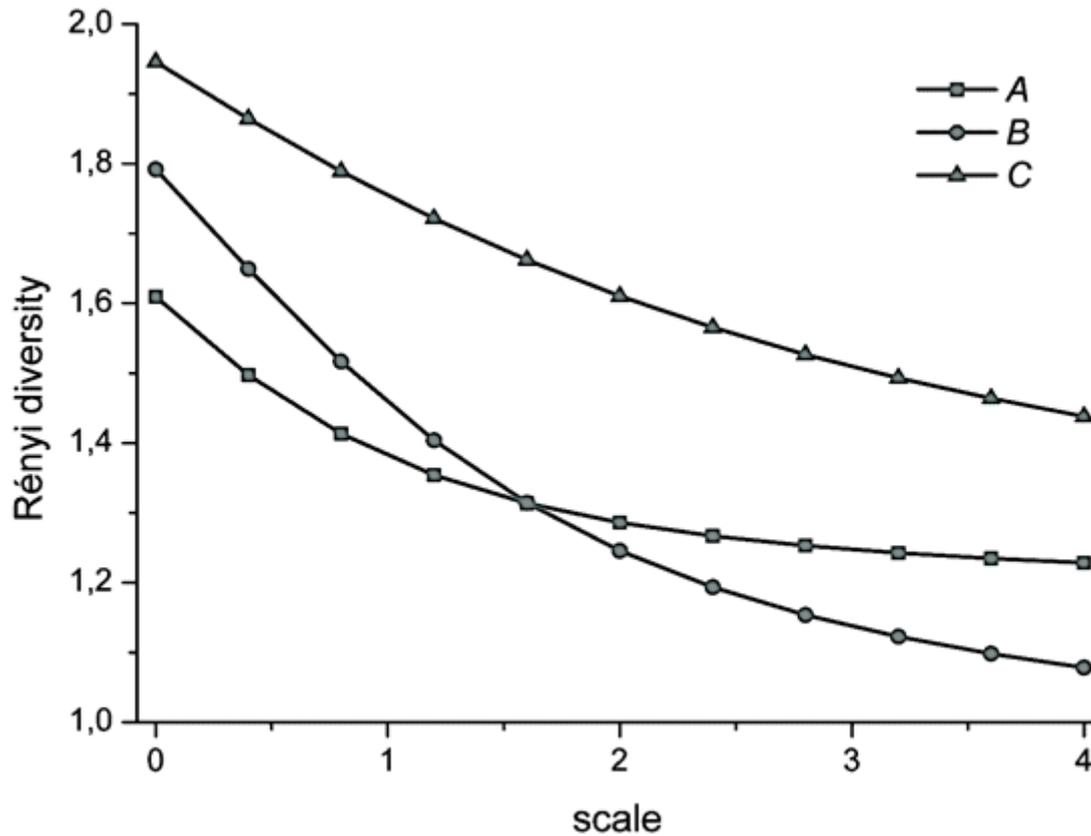


Figure 4. Diversity profiles of the communities.

## 7. Rényi diversity and diversity profiles

Figure 4 shows the diversity profiles of three communities based on Rényi diversity. The solution of the above mentioned "contradiction" is clear.

When the value of the scale parameter is 0, then the value of Rényi diversity is the logarithm of the *number of species* of the community:  $HR(0) = \log ST$ . In this case the method is extremely sensitive to the contribution of the rare species to the diversity.

When the value of the scale parameter is 1, then the Rényi diversity is identical with the Shannon index of diversity:

$$HR(\alpha \rightarrow 0) = HS(p) = - \sum_{i=1}^{ST} p_i \log p_i .$$

In this case the diversity is sensitive to the rare species, although the sensitivity is not as high as it is when the value of the scale parameter is 0. Now, the diversities of the compared communities are identical.

When the value of the scale parameter is 2, then the Rényi diversity is related to the *quadratic diversity*:  $HR(2) = - \log \sum_{i=1}^{ST} p_i^2$ .

In this case the method is more sensitive to the frequent species than to the rare ones; and now, community B is more diverse than community A.

When  $\alpha \rightarrow \infty$ , then  $HR(\alpha \rightarrow \infty)$  is identical with the logarithm of the Berger-Parker diversity.

$$HR(\alpha \rightarrow \infty) = \log \frac{1}{p_{[1]}} = \log \frac{N}{n_{[1]}} .$$

Now, the problem has been solved. What is even more important, we have a useful method for scale-dependent characterization of diversity. Therefore, community A is more diverse for the rare species, while community B is more diverse for the frequent ones; therefore, in the provided example the communities cannot

be ordered by diversity. It can be used in a graphical form to visualize the diversity relations of communities as it is demonstrated by Figure 3. When we are using a one-parametric diversity index family  $\{D(\alpha); \alpha \in R\}$  of diversity indices, then the family may be portrayed graphically by plotting diversities  $D(\alpha)$  against the (scale) parameter  $\alpha$ . This curve, the graph of the  $\{D(\alpha); \alpha \in R\}$  family, frequently mentioned as the *diversity profile of the community*. Basically,  $\alpha$  serves as a *scale parameter*, and members of the  $D(\alpha)$  family have varying sensitivities to the rare and abundant species as  $\alpha$  changes.

Using diversity profiles we can define the diversity ordering of communities in the following way: Community A is more diverse than community B (written  $A > B$ ) when the diversity profile of A is above or equal to the diversity profile of B on the whole range of the scale parameter. It can be shown that diversity ordering is a partial order. When  $A > B$  and  $B > C$ , then  $A > C$ . However, it is not true that for every communities A, and B, either  $A > B$  or  $B > A$ ; i.e. curves of two diversity profiles may intersect. This situation may reflect important ecological processes which can be interpreted clearly. The name is referred to that in mathematics a relation is an ordering (partial ordering, quasi-ordering) when it is reflexive, anti-symmetric, and transitive. The "more diverse" relation fulfills these three properties, therefore it can be mentioned as diversity ordering. It is important to know some special cases of diversity index families to interpret the result of diversity orderings. For Rényi diversity ordering the following relations are valid.

## 8. A short overview of diversity index families

Rényi (1961) has extended the concept of Shannon entropy by defining the *entropy of order*  $\alpha$  or Rényi diversity ( $\alpha \geq 0, \alpha \neq 1$ ):

$$H_R(\alpha) = 1 / (1 - \alpha) \log \sum_{i=1}^{ST} p_i^\alpha, .$$

It was the first published family of diversity indices. In the original definition the base number of the logarithm was 2; in ecological applications natural logarithm is the most frequently used.

For a generalized entropy, like Rényi diversity, the most tedious work is to calculate  $PSum$ :

$$PSum = \sum_{i=1}^{ST} p_i^\alpha .$$

Rényi diversity can be derived easily from that:

$$H_R(\alpha) = 1 / (1 - \alpha) \log PSum .$$

Calculations are displayed for community F2, when  $\alpha = 0.5$ :

$$PSum = 0.5^{0.5} + 0.3^{0.5} + 0.2^{0.5} = 0.7071 + 0.5477 + 0.4472 = 1.702 \quad . \quad H_R(0.5) = \ln(1.702) / (1 - 0.5) = 2 \cdot \ln(1.702) = 2 \cdot 0.532 = 1.064 \quad .$$

Nowadays a lot of one-parametric diversity index families are known. Their family-tree is presented by Figure 3; Tóthmérész 1993b, 1995. Rényi diversity is a typical member of *generalized entropies*. RTS diversity (Right-Tail-Sum diversity) plays also a central role in scale-dependent diversity characterizations; Patil and Taillie 1979, Solomon 1979. RTS diversity is a typical member of the cumulative relative abundance plots, and it is defined as follows:

$$RTS(i) = p_{[i+1]} + \dots + p_{[ST]},$$

where  $p_{[1]}, \dots, p_{[S]}$  are the relative abundances of the species of a community arranged in *descending order*. Tóthmérész (1995) has demonstrated that Rényi diversity can be used very effectively in ecological studies. RTS diversity is more important from theoretical than from practical point of view; it can be used very effectively to prove mathematical theorems of vital importance; Patil and Taillie 1982, Solomon 1979. It may be the reason that Patil and Taillie proposed to say a community is intrinsically more diverse, when its RTS diversity is larger for all values of the scale parameter than that of the other community. In the form of a logarithmic dominance plot is advised to use as a diversity profile (Tóthmérész 1993b, 1995).

For the community C3, the ordered relative abundance vector is

$$p^{\downarrow} = (0.629, 0.179, 0.086, 0.053, 0.033, 0.02) .$$

Therefore,

$$RTS(1) = 0.179+0.086+0.053+0.033+0.02=0.371 .$$

It is easier to receive this result using that

$$0.629+0.179+0.086+0.053+0.033+0.02=1.0 .$$

This way

$$RTS(1)=1-p_{\{1\}}=1-0.629=0.371 .$$

Similarly,

$$RTS(2)=1-p_{\{1\}}-p_{\{2\}}=RTS(1) - p_{\{2\}}=0.371-0.179=0.192 .$$

In the case of generalized entropies and cumulative relative abundance plots, the scale parameter is related to the abundance-dominance structure of the community. Therefore, these methods scale along the abundance-dominance. *Species-accumulation plots* are slightly different from that point of view. One of them is the so-called *ES(m) diversity* (Hurlbert 1971):

$$ES(m) = ST - \sum_{i=1}^{ST} (1-p_i)^m .$$

It produces the expected number of species present when  $m$  individuals are drawn at random from the population. Conceptually  $m$  is an integer, but real values make mathematical sense.  $ES(m)$  also used to be mentioned as *expected species-individual diversity*. The minimum variance unbiased estimator for  $ES(m)$  was devised by Smith and Grassle (1977).

The expected number of individuals on an area is proportional to the size of the area. Therefore, we can calculate the *expected species-area curve* using the following relationship

$$m=N / \text{plot size} * \text{total area} ,$$

where  $N$  is the total number of individuals on the area.

Species-accumulation plots are extremely important because they can be used producing *density dependent* and *density independent representations* of the diversity profiles (Tóthmérész 1994b). These methods are also related to *spatial series analysis* through pattern dependent representations (Tóthmérész 1994a). All these diversity profiles are provided by the DivOrd and the NuCoSA program packages on PC's (Tóthmérész 1993a, 1993b, 1994b).

## 9. Classical diversity statistics

The process which lead to the scale-dependent diversity *scale-dependent diversity* through one-parametric diversity functions and their graphical representation, has also modified the view and interpretation of classical diversity statistics. The *average rarity interpretation* proposed by Patil and Taillie (1979) looks especially useful. We would like to present the classical diversity statistics from this viewpoint.

Diversity can be defined to be the *average species rarity* of the individuals of a community. Denote the rarity of species  $i$  of the studied community by  $R(i;p)$ ; i.e. a numerical measure of rarity is to be associated with each species. Therefore, the diversity measure of a community is defined as its average rarity:

$$D(p)=1/N \sum_{k=1}^N R(i;p)= \sum_{i=1}^{ST} n_i/N R(i;p) = \sum_{i=1}^{ST} p_i R(i;p).$$

We require that a *rarity function* assign greater rarity to physically rarer species:

$$R(i;p) < R(j;p), \quad \text{if } p_i < p_j .$$

Depending on the rarity function, great many diversity functions can be defined. There are two types of rarity functions: *rank-type rarity measures* and *dichotomous-type rarity measures*. In the case of ranking the rarity of species depends only on its descending rank. For dichotomy, the rarity of the species  $i$  depends only on the numerical value of  $p_i$ . The above mentioned criteria for rarity functions is sufficient for rank-type rarities; for dichotomous rarities this is not the case, although we do not present more strict criteria because it would involve

more mathematics. Generally, it is related to some *monotonicity* requirement or more biologically to the forward transfer of abundance (see e.g. Patil and Taillie 1982).

This is a fairly general definition of diversity, which induced an important development of diversity measurements, also producing the utilization of one-parametric diversity index families in ecology. By nowadays, even this definition looks a bit obsolete and a more general definition is inevitable based on the notion of *Schur-concavity* or the idea of majorization and *weak majorization* (Tóthmérész and Katona 1996).

We recite it as a demonstration without comments: Diversity diversity is a real-valued non-negative function defined on  $R^{\{ST\}_+}$ , which preserves in backwards the order of *majorization* or weak majorization. When the order of weak majorization is preserved we speak about density dependent representation of diversity while the other case is mentioned as density independent. Rarity functions *rarity function* can be created on the basis of biological and/or statistical ideas. The relative frequency,  $p_i$ , is high for a frequent species. Therefore it is reasonable to characterize the rarity of a species by  $R(i;p)=(1-p_i)$ . Then we receive the *quadratic diversity*,  $DQ$ :

$$DQ = \sum_{i=1}^{\{ST\}} p_i(1-p_i) = 1 - \sum_{i=1}^{\{ST\}} p_i^2 .$$

When the rarity of a species is characterized by  $R(i;p) = -\log p_i$ , the *Shannon diversity* is received:

$$HS = \sum_{i=1}^{\{ST\}} p_i (-\log p_i) = -\sum_{i=1}^{\{ST\}} p_i \log p_i .$$

It is natural to standardize  $(1-p_i)$  by  $p_i$ . Then the rarity is measured by  $(1-p_i)/p_i$ , and the diversity function is

$$DS_n = \sum_{i=1}^{\{ST\}} p_i (1-p_i)/p_i = ST - 1 .$$

This is exactly the *species richness* of the community. We prefer to say, that  $ST$  is the *number of species*, while  $ST-1$  is the *species richness*. This is partly motivated by the "axiomatic" treatment of diversity concept, which is not discussed here; see e.g. Aczél and Daróczy's monography (1975) of the axiomatic treatment of entropy. There are many other ways to choose rarity functions. Further diversity functions produced that way, is not discussed here.

## 10. Significance of significance

During the previous sections, diversity was used merely as a descriptive statistics. Referees of "highly polished" journals frequently addressing the question whether a difference in diversity is significant or not, irrespectively whether this question is significant or not. Testing statistical hypotheses is certainly important. Still, there is no reason to mistify them (Perry 1986).

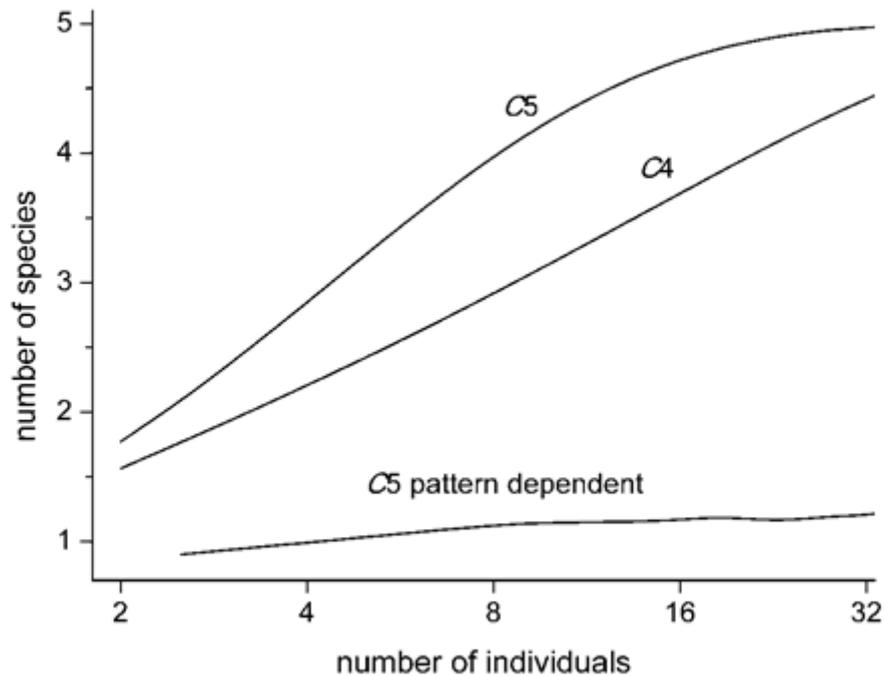


Figure 5. Density independent representation of the diversity profiles.

## 11. Density dependent and density independent representations

It is evident from the previous sections, that an  $ES(m)$  curve plotted against  $m$  can be regarded as a diversity profile. Therefore, it can be used for diversity ordering of communities. Diversity profiles of the studied communities are displayed by Figure 4. The result is generally the same as with the Rényi diversity index family with the technical exception, that this method is sensitive to the dominant species when the value of the scale parameter is low and it is sensitive to the dominants for large scale parameter values.

We can argue, however, that the number of species is plotted against the same number of individuals for each sample. The number of individuals, however, is different on the leaves in the communities. Therefore, we can argue that we should have taken into account this difference of the densities. To plot the number of species that way, the result is significantly different: community  $Cm3$  is more diverse than  $Cm4$  for the whole range of the scale parameter; Figure 5. We prefer to mention the first plot (Figure 4) as a density independent representation, because we ignored the differences in the densities of the communities. The second one will be mentioned as a density dependent representation. This is a crucial point of measuring and especially comparing diversities.

## 12. Numerical example

An important property of  $ES(m)$  diversity (as well as the species-individual diversity plot) that the scale parameter has a direct biological interpretation. It is the number of individuals in a sub-sample. When  $m$  is small, just the frequent species can be found in the sub-sample, therefore  $ES(m)$  is small. Increasing the sub-sample size, the expected number of species also increases. Plotting  $ES(m)$  against  $m$ , a diversity profile is received. In fact, this is a species-area curve. It is well-known that the number of species in the sample depends on the number of individuals. This relationship, however, is not linear.

Let see a numerical example. Compare the number of species of three plant communities. Suppose that the number of individuals is 10 for the total study area, which is the same for each studied community. The first community is denoted by E, the second one by F, and the third one by G. The relative abundance structure of the

## Chapter 10 Classical paradigm of Measuring Diversity

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community G is totally identical with that of E. The only difference is that the density of the community G is less than the density of community E. The ratio is

$$\text{density}(E) : \text{density}(G) = 2.5 : 1 .$$

The abundance vectors are as follows:

$$n(E) = (1000, 500, 250, 250, 150, 100, 100, 75, 50, 25),$$

$$n(F) = (1100, 625, 263, 175, 125, 75, 50, 37, 27, 23),$$

$$n(G) = (400, 200, 100, 100, 60, 40, 40, 30, 20, 10).$$

We use a plot size that a plot contains 25 individuals for the communities E and F . The density of community G is less than the density of E or F . Therefore, the number of individuals for the same plot size is just 10, because

$$N(E) : N(G) = 25 : 10 .$$

We can calculate the number of species for that plot size for each community using  $ES(m)$  diversity:

$$ES_{\{E\}}(25) = 10 - \{(1-0.4)^{25} + (1-0.2)^{25} + \dots\} = 7.071 \approx 7,$$

$$ES_{\{F\}}(25) = 10 - \{(1-0.44)^{25} + (1-0.25)^{25} + \dots\} = 6.185 \approx 6,$$

$$ES_{\{G\}}(10) = 10 - \{(1-0.4)^{10} + (1-0.2)^{10} + \dots\} = 4.862 \approx 5.$$

So, the communities can be ordered according to their species richness in the following way:

$$ES(E) = 7 > ES(F) = 6 > ES(G) = 5 .$$

When we compare the species richness by  $ES(m)$  for the same number of individuals, then

$$ES_{\{G\}}(25) = 10 - \{(1-0.4)^{25} + (1-0.2)^{25} + \dots\} = 7.071 \approx 7.$$

Now, the order is quite different:

$$ES(E) = ES(G) = 7 > ES(F) = 6 .$$

Even this simple example illustrates clearly that the density dependent and density independent representations may produce very different conclusions. The interpretation of the results is certainly not simple. Sometimes a density independent comparison is justified and sometimes certainly not. I would like to mention an example for each interpretation.

We are comparing two communities, where the individuals are distributed randomly and independently of each other, and the relative abundance vectors of the communities are identical. The only difference is that the density of the second community is the double. Using the same plot size, we find that the community with the higher density is more diverse. In this particular case this looks not entirely true, because the relative abundance vectors (i.e., the ratio of the species) and the spatial structures of the communities are identical. The only difference is the density. We may say, that in this case the comparison based on the same number of individuals is more advised. (I'd like to mention a simple, non-biological example. We have a detailed street-map of a big city - just like a vegetation map. We have random plots on the map, and the "number of species" is the number of streets in the plot. Using a xerox machine, we can make a copy of the map using 1:0.5 zoom. Then, using the same plot size we compare the number of streets in the plots of the original size, and the conclusion is that the diminished map is more "species/street rich". Is it? Or, just we have compared them on a wrong scale?)

Another example is, when we are comparing animal communities of water bodies; e.g. ponds. The number of individuals supported by the pond is characteristic to the trophic status of the pond. Therefore, in this case we may argue that there is no reason to "eliminate" this information from the data set. The density dependent interpretation fits better to the ecological goals of the study.

Specialists of different sub-disciplines of ecology are using traditionally different representations. In botany always entirely density dependent representation is applied, because plots of the same size is used for the

comparison. In algology frequently 100 or 1000 individuals are counted and the number of species is determined in that way. In soil zoology also a similar technique is used to determine species richness. This is a density independent representation of the number of species.

## 13. Effect of spatial and/or temporal pattern

In the case of the previously analysed data sets, the abundances characterizing communities C3 and C4 were based on pooled samples of the stands. It frequently happens in ecological studies. There are many reasons of pooling. The separate samples are too "small" or we would like to characterize the flora of an area, therefore we pool the samples of a region or a time period, etc. All of the presented calculations were based on pooled samples. Frequently it is worth to look into the details of the separate samples.

Tóthmérész (1996) has produced the following, rather surprising example. He has compared two communities based on pooled samples of 10 plots. Community A was more species diverse than community B (20 vs. 11 species). His conclusion was that, in some respect, it is an artifact because neither of the plots of the community A is richer than the plots of B. The average number of species was 4.7 for the plots of community A and 9.4 for the plots of community B. The much higher number of species was resulted in just by the rather high variability of species composition from plot-to-plot. Sometimes it is mentioned as beta-diversity, while the diversity of a plot is mentioned as alpha-diversity or just simple as diversity. In the case of the epiphyllous liverworts, a very similar situation arises. The diversity of a moss stand on a leaf may be mentioned as alpha-diversity, while the stand-to-stand variability of the community as a beta-diversity. The total diversity of the community is composed of by the alpha- and beta-diversity. There are a few difficulties, however, with the measuring beta-diversity. The simplest one is that there is no standard, generally accepted measure of beta-diversity. The more sophisticated one is that all of the measures of beta-diversity looks to be related to the study problem and to the rather general problem of community organisation. Therefore, it is not possible to measure "automatically" the beta-diversity of a community as in the case of alpha-diversity. It always involves some "modelling" even if we "do not know that we do it".

As a vital conclusion, it should be emphasized that the pooling of samples may be dangerous in the presence of definite temporal and/or spatial pattern, because it mask the variability and may produce artificially high diversity. Naturally there is no such danger, when we would like to know just the total species pool, etc.

## 14. How to measure beta-diversity?

Whittaker (1960) proposed a simple measure of beta-diversity:

$$\text{beta}_w = \frac{ST}{\text{aver}(ST)} - 1 ,$$

where  $ST$  is the total number of species, and  $\text{aver}(ST)$  is the average number of species in the samples. In the case of the mentioned problem (Tóthmérész 1996) it was  $20/4.7-1=3.26$  and  $11/9.4-1=0.13$ , respectively. These values are suggesting the strong difference in beta-diversity for community A and B, and also explaining the rather high number of species for community A in the case of pooled samples.

It is worth mentioning that the measure of beta-diversity proposed by Routledge (1977) does not reflect the high variability in species composition for the community A. It is defined in the following way:

$$\text{beta}_R = \frac{ST^2}{2 * I2 + ST} - 1 ,$$

where  $ST$  is the total number of species, and  $I2$  is the number of species pairs whose occurs in the same sample at least once. This method is based on the "second order" interactions, while Whittaker's measure may be regarded as a measure related to "first order" interactions.

beta-diversity may be characterized by more sophisticated methods; some details can be found in Pócs and Tóthmérész 1995, 1996, Tóthmérész 1996. The way of characterization, however, heavily depends on the model of the community, and the deepness of the characterization. Technical details are presented very briefly in the following paragraph. If we have a community where each stand has identical species composition, it is clear that the variability of the species composition, or the beta-diversity of the community is zero. When just a very few species are changing from stand to stand, then beta-diversity is low. In the case of high variability, the beta-diversity is high. It is relatively easy to characterize the species composition of two stands using some of the traditional similarity functions. It is easuring, however, the similarity of two stands. The number of possible

plot-pairs are rather high even in the case of small number of stands. For 15 stands there are  $15 * 14/2 = 105$  pairs. Generally, in the case of  $n$  stands there are  $n(n-1)/2$  possible stand-pairs. It is too high figure to capture the rules by eye. To create an average also may be dangerous. An ideal representation may be based on the nonparametric estimation of the distribution of stand-to-stand similarities; it was proposed to display the beta-diversity of a community by Tóthmérész (1996). For community C3 and C4 it is shown by Figure 6 using *kernel smoothing* it is evident from the Figure that beta-diversity is much higher for community C4.

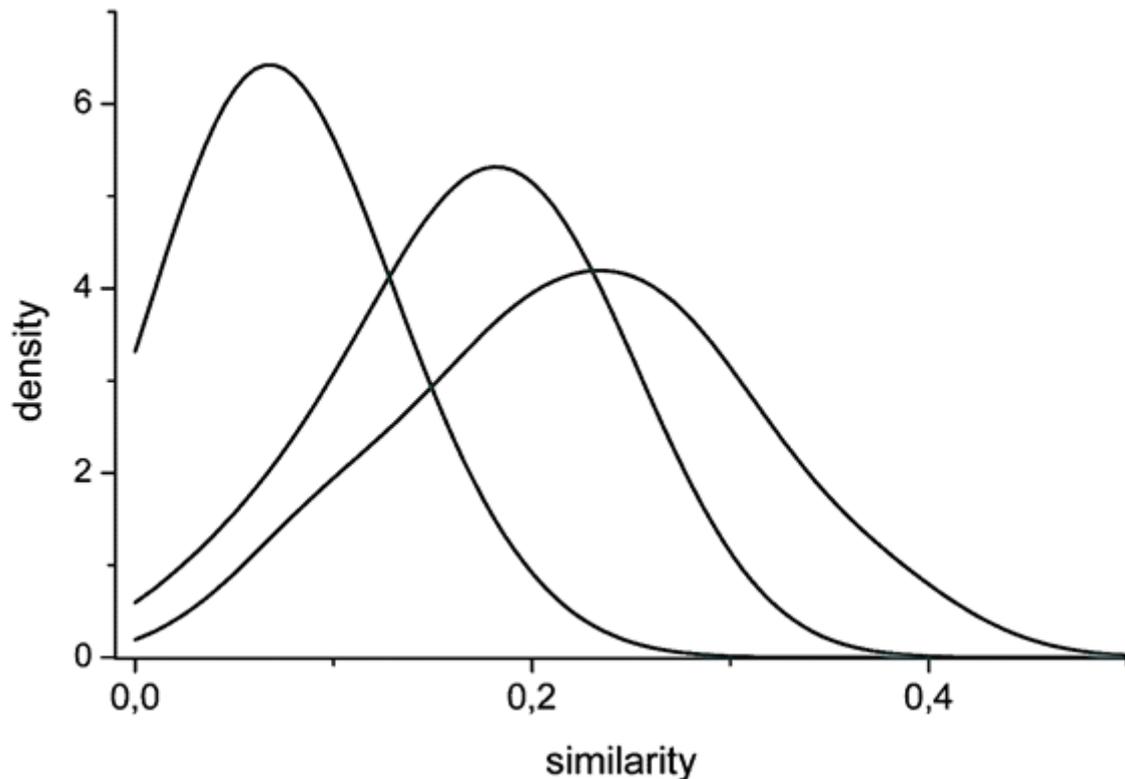


Figure 6. Histograms of the plot-to-plot dissimilarities by kernel smoothing.

### 14.1. A Field example

For the purpose of analysis 50-60 ovate-lanceolate, coriaceous leaves well covered by epiphyllous liverworts, within the same size range (of 10-100cm<sup>2</sup> leaf area) with smooth surface were collected from each habitat within an approximately 1000m<sup>2</sup> area. On 15 randomly selected leaves from the above sample the coverage of foliicolous algae, lichens and bryophyta were estimated. All bryophyta (mostly liverwort) species were identified. The number of specimens of each species per each leaf was then counted and in most cases the percentage of coverage estimated.

We found that the number of species of the most diverse communities was 8-9 species per leaf. In a degraded habitat it may decrease until 3-4 species per leaf. The total number of species was 25 for the richest community, summing up the species of 15 leaves. The total number of species was 14 for the least diverse community. Average number of individuals of the leaves was approximately 100; it ranged from 48-204.

It is a rather difficult task to answer which community is more diverse? It is especially difficult in the studied situation, because the foliicolous communities are living in a really coarse-grained environment. The community is composed of from individual stands living on separate leaves. The number of species, which is supported by the leaves limited surface, is certainly less than the species pool of the community. These two species numbers may be very different, as it is in the studied situation; see more details in Pócs and Tóthmérész (1996) and Pócs (1996).

The total number of species was the highest for the community 2 ( $S=25$ ). It also was high for the community 4 ( $S=24$ ). For communities 1 and 5 the number of species was 20 and 19, which is definitely less than the number of species for the communities 2 and 4. The number of species was the least for the community 3 ( $S=14$ ); it is still relatively high.

The average or "typical" number of species of the stands gives remarkably different results, although the main tendencies are similar. The least species rich are the stands of community 3 with 4 species on the leaves. Stands of the community 5 also has rather few species. Community 3 was also the least rich for the total species pool, but the pooriness is even more pronounced for the stands. The case is even more difficult for the community 5. The total species pool of that community was almost as high as for the community 1. In spite of that, the stands of the community 5 are very species poor while the number of species of the stands for community 1 is the highest. Stands of the community 2 are also relatively species rich. Stands of the community 4 are still species rich, although they are certainly less species rich than the communities 1 and 2.

These differences are suggesting that the number of species are regulated differently on the level of stands and on the level of the total community. Therefore, it is an especially difficult situation how to characterize the diversity in such situations. There is a primary level of diversity/richness which is supported by the leaves. Surplus, the species composition changes from leaf to leaf. Depending on that stand to stand variation the total number of species of the community may be very different. This stand-to-stand variation is reflected very accurately by beta-diversities.

## 14.2. Comments and conclusions

Pócs and Tóthmérész (1996) found that Whittaker's beta-diversity looks more dependant on the geographical position. According to the few samples, all originating from submontane-montane rainforests, comparable to each other, the highest beta-diversity was represented by a Mauritius sample, the second and third by the Seychelles samples and the last are the Tanzanian samples from continental Africa. This order probably reflects among others the richness of island floras in endemics and in Asian species not reaching the continent. The "insularity" is also expressed in the fact, that until species on mainland are restricted to a certain niche, on islands occupy more unsaturated niches and an altitudinal and latitudinal stratification is much less developed in the vegetation.

The rate of degradation of the concerned host rain forest community is not expressed directly in the total diversity of the community, but much more by the average number of species per leaf and by the average number of individuals per leaf. Both properties are easily detectable and may be used, as markers of degradation. Both of these characteristics are sensitive indicator of the degradation of a community in this case. Total number of species of the community is not relevant as a measure of degradation because the community is composed of stands which are living on completely separated leaves. The number of species living on a leaf is less than the species pool of the community and the increased stand to stand variation disguise the effect of degradation on the level of community. In the case of small and medium degradation the increased beta-diversity of the leaves may balance the loss of species of the individual leaves. Therefore, the species pool of the total community does not, or just slightly, change.

In the studied situation the increased beta-diversity was also a definite sign of degradation. This is another important piece of information pointing out, how dangerous is the "automatic" use of diversity as the indicator of the well-being of communities. The interpretation of a statistics, like diversity, always should be closely related to the particular ecological situation.

The scale of the study has vital influence to the result and it is rather easy to produce a spurious result with the ignorance of it. Using diversity profiles we have demonstrated that depending on the choice of the scale parameter we can receive a conclusion that the community 2 is the most diverse and community 3 is the less diverse. Choosing another value of scale parameter the result suggest just the opposite: community 3 is the most diverse and community 2 is the less diverse; see Pócs and Tóthmérész 1996. The number of individuals seems to be in negative correlation with increasing degradation, probably due to the worsening conditions for reproduction with decreasing number of juvenile specimens.

## 15. List of animation, audio files and movies

animation Biodiversity and Conservation.flv  
animation Climate change energy action.flv

## 16. Questions

- What is the relationship between diversity and pattern?
- What is the connection of the pattern of a community and the processes of community dynamics?

## Chapter 10 Classical paradigm of Measuring Diversity

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- Why the idea of „intrinsically more diverse” is based on RTS-diversity ?
- Define the dichotomous-type rarity measure.
- Mention a rank-type rarity measure.

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# 12. fejezet - Chapter 11 Beta Diversity

## 1. Diversity in space (and time)

Whittaker (1960) proposed the distinction between alpha and beta diversity. Alpha diversity is the property of a defined spatial unit, while beta diversity reflects biotic change or species replacement. In essence then, beta diversity is a measure of the extent to which the diversity of two or more spatial units differs. Whittaker (1960) originally conceived beta diversity as a measure of the change in diversity between samples along transects or across environmental gradients but there is no reason why the concept cannot be applied to different spatial configurations of sampling units. Indeed, the same approach can be used to examine changes in diversity over time. Temporal changes in diversity are usually referred to as turnover. The term usually also applied to spatial changes.

The relationship between alpha and beta diversity is scale dependent. An increase in the size of the sampling unit relative to the boundaries of the study area typically result in an increase in a diversity. Estimates of beta diversity can also vary with scale, even when measures apparently independent of species richness are used. Whittaker (1972) recognized this difficulty and devised terms to accommodate the hierarchy of scales across which diversity can be described. **Inventory diversity**, in other words the diversity of defined geographic units, can be measured at different levels of resolution. Under this scheme **point diversity** is the diversity of a single sample, whereas alpha diversity is the diversity of a set of samples (or within-habitat diversity). Gamma diversity represents the diversity of a landscape and epsilon diversity the diversity of a biogeographic region. These levels of inventory diversity are matched by corresponding categories of **differentiation diversity**. Pattern diversity describes the variation in the diversity of samples (point diversity) taken within a relatively homogenous habitat (or area of beta diversity). Beta diversity is a measure of between-habitat diversity, while delta (delta) diversity is defined as the change in species composition that occurs between units of beta diversity within an area of epsilon diversity.

There is also disagreement about the extent to which the scales of diversity should embrace ecologically coherent entities. Pielou (1976) and Loreau (2000) envisage a diversity as the property of a community. Substituting the term assemblage helps set the taxonomic, if not the geographic, limits. Delineating a habitat is not necessarily straightforward either, but at least habitats are generally identifiable on the basis of their physical characteristics and usually have recognizable boundaries. Other investigators have made no assumptions about ecological coherence and have measured the a diversity of predefined spatial units. Grid squares of varying sizes are a common approach (Harrison et al. 1992; Lennon et al. 2001). Although it is recognized that gamma diversity occurs at a larger scale than alpha diversity, and is more heterogenous, there is no consensus about just how large a landscape or region is involved. Whittaker's final category, epsilon diversity, is rarely used.

This confusion prompted Gray (2000) to propose a unifying terminology. He advocates the recognition of four scales of species richness: **point** species richness, **sample** species richness, **large area** species richness, and **biogeographic province** species richness. These are distinguished **from habitat** species richness and **assemblage** species richness since neither habitats nor assemblages fit neatly into a logical progression of increasing scale. Although Gray describes these scales in the context of species richness, other heterogeneity diversity measures are acceptable. Furthermore, since beta diversity is not a scale of diversity, Gray recommends, following Clarke and Lidgard (2000), that the term turnover diversity be substituted. Other authors have also used the word turnover instead of beta diversity. As noted above, one potential source of confusion is that turnover is often assumed to refer to temporal variation in species composition and diversity, whereas beta diversity is almost invariably applied to spatial patterns.

The advantage of Gray's approach is that it forces the user to think clearly about, and report, the scales of the investigation. It should also foster comparability within disciplines with standard sampling techniques. However, the terms alpha, beta, and gamma diversity are well entrenched in the ecological literature and will probably persist for the foreseeable future. This will not necessarily impede progress, for, as Loreau (2000) has noted, scales of diversity are not discrete entities but rather intergrade along a continuum. Indeed, it can be illuminating to examine the relationship between alpha and beta diversity at different scales. This conclusion follows from Lande's (1996) observation that inventory and differentiation diversity can be partitioned:

$$D_r = D_a + D_o$$

When species richness is used to measure alpha and gamma diversity, beta diversity may be estimated as follows:

$$D_R = S_T - S_j$$

where  $S_T$  = species richness of the landscape (gamma diversity);  $S_i$  = the richness of assemblage  $j$ . The method can also be adapted for the Shannon and Simpson diversity measures; Lande (1996) explains how this is done.

Lande's (1996) approach, in which the average value of a diversity is added to the beta diversity to produce gamma diversity, contrasts with Whittaker's (1972) method (see below) where alpha diversity and beta diversity are multiplied. One advantage of Lande's additive partition is that it can be applied across different scales. The relative contributions of alpha and beta diversity to landscape diversity are also clearly identified. Many small sampling units will result in low alpha and high beta diversity, while the converse will hold if there are fewer but larger samples. Both sampling strategies, all other things being equal, lead to the same inferences about gamma diversity. Moreover, if identical sampling protocols are applied to different landscapes, insights into the relative contribution of alpha and beta diversity to gamma diversity are possible. Beta diversity will increase in heterogeneous landscapes, in which few species are shared by sampling units, and decline in homogeneous ones where the species' composition of sampling units is identical.

## 2. Measuring beta diversity

There are a variety of methods of measuring beta diversity. These fall roughly into three categories. The first set of measures examine the extent of the difference between two or more areas of a diversity relative to gamma diversity, where gamma diversity is usually measured as total species richness. Whittaker's original measure, beta<sub>w</sub>, is part of this group, as is Lande's partition method, described above. These measures were often explicitly proposed as measures of beta diversity. The second set focus on the differences in species composition amongst areas of a diversity and were formulated as measures of complementarity or similarity/dissimilarity. They include the Jaccard and Bray-Curtis coefficients and evaluate the biotic distinctness of assemblages. Such analysis need not be restricted to species identities; some beta diversity measures, like the new generation of alpha diversity measures, take phylogenetic information into account (Izsak & Price 2001). Indeed the difference between assemblages in taxonomic distinctness  $A$  and/or variation in taxonomic distinctness  $A+$  (Clarke & Warwick 2001b; Warwick & Clarke 2001) could be treated as a measure of beta diversity. The final group of measures exploit the species-area relationship and measure turnover related to species accumulation with area (Harte et al. 1999b; Lennon et al. 2001; Ricotta et al. 2002). As Lennon et al. (2001) observe, the slope  $z$  in the relationship between  $\log(S)$  and  $\log(A)$ , or the slope  $m$  in the relationship between  $S$  and  $\log(A)$ , can reasonably be considered as a measure of turnover if areas are nested subsets.

## 3. Indices of beta diversity

### 3.1. Whittaker's measure $P_n$ ,

One of the simplest, and most effective, measures of beta diversity was devised by Whittaker (1960):  $R_w = S/d$ , where  $S$  = the total number of species recorded in the system (i.e., gamma diversity); and  $a$  = the average sample diversity, where each sample is a standard size and diversity is measured as species richness. When Whittaker's measure is used to compute beta<sub>w</sub> between pairs of samples or adjacent quadrats along a transect, values of the measure will range from 1 (complete similarity) to 2 (no overlap in species composition). The maximum possible value is the same as the number of samples used to calculate mean alpha diversity. Subtracting 1 from the answer has the effect of putting the result on the 0 (minimum beta diversity) to 1 (maximum beta diversity) intuitively meaningful scale that many other measures of beta diversity use.

Harrison *et al.* (1992) introduced a modification of Whittaker's measure. This allows the user to compare two transects (or samples) of different size:

$$RH1 = \{[(S/a) - 1]/(N - 1)\} * 100,$$

where  $S$  = the total number of species recorded;  $a$  = mean alpha diversity; and  $N$  = the number of sites (or grid squares) along a transect. The measure ranges from 0 (no turnover) to 100 (every sample has a unique set of species) and can be used to examine pairwise differentiation between sites. Since this measure (like Whittaker's

original measure) does not distinguish between true species turnover along a transect or across a landscape, nor does it identify situations where species are lost without new species being added, Harrison *et al.* (1992) suggested a second modification which is insensitive to species richness trends:

$$RH2 = \{[(S/\alpha_{max}) - 1]J(N - 1)\} * 100 .$$

Here  $\alpha_{max}$  is the maximum within-taxon richness per sample.

### 3.2. Cody's measure

Cody (1975) was interested in the change in composition of bird communities along habitat gradients. His index, which is easy to calculate and is a good measure of species turnover, simply adds the number of new species encountered along a gradient to the number of species that are lost:

$$PC = g(H) + l(H)$$

where  $g(H)$  = the number of species gained; and  $l(H)$  = the number of species lost.

### 3.3. Routledge's measures betaR, betaI, and betaE

Routledge (1977) was concerned with how diversity measures can be partitioned into alpha and beta components. The following three measures are derived from his work. His first index, betaR, takes overall species richness and the degree of species overlap into consideration.

$$\text{betaR} = S^2 / (2r + S) - 1$$

where  $S$  = the total number of species in all samples; and  $r$  = the number of species pairs with overlapping distributions.

*betaI*, the second index, stems from information theory, and has been simplified for presence/absence data and equal sample size by Wilson and Shmida (1984):

$$\text{betaI} = \log T - [(1/T) \sum_j e_j \log e_j] - [(1/T) \sum_i S_i \log S_i]$$

where  $e_i$  = the number of samples in the transect in which species  $i$  is present;  $S_i$  = the species richness of sample  $j$ ; and  $T = \sum e_i = \sum S_i$ . The third index, PE, is simply the exponential form of betaI.

### 3.4. Wilson and Shmida's index betaT

Wilson and Shmida (1984) proposed a new measure of beta diversity. This index has the same elements of species loss ( $l$ ) and gain ( $g$ ) that are present in Cody's measure, and the standardization by average sample richness present in Whittaker's measure.

Wilson and Shmida chose four criteria to evaluate these six measures of beta diversity. These criteria were: number of community (assemblage) changes; additivity; independence from a diversity; and independence from excessive sampling. The degree to which each index measured community turnover was tested by calculating the beta diversity of two hypothetical gradients, one of which was homogenous, that is the same species were present throughout its length, and one of which consisted of distinct communities with no overlap. Whittaker's index  $\beta_w$  accurately reflected these extremes of community turnover.  $\beta_T$  was more limited in that it only adequately represented turnover in conditions where the alpha diversity at both ends of the gradient was equal to average alpha diversity.

Their second criterion was additivity, that is the ability of a measure to give the same value of beta diversity whether it is calculated using the two ends of a gradient or from the sum of beta diversities obtained within the gradient. For instance, given three sampling points (a, b, and c),  $\beta(a,c)$  should equal  $\beta(a,b) + \beta(b,c)$ . Only one index,  $\beta_C$ , was completely additive.

Independence from a diversity, the third property, was examined using two hypothetical gradients that were identical except that one had twice as many species as the other.  $\beta_C$  alone failed this test. Without this independence it is difficult to compare beta diversity in species-rich and species-poor assemblages.

The final criterion, independence from sample size, was tested by increasing the number of (identical samples) taken at each site. All measures apart from those derived from information theory were found to be unaffected by this.

Out of the six measures tested by Wilson and Shmida, betaW emerged as fulfilling most criteria with fewest restrictions, showing that the oldest techniques are sometimes the best. Wilson and Shmida's own index, betaT, came a close second. A more recent evaluation (Gray 2000) came to a similar conclusion. Because the Harrison et al. (1992) methods are an improvement on Whittaker's formulation.

### 3.5. Indices of complementarity and similarity

The term complementarity, which was introduced by Vane-Wright *et al.* (1991), describes the difference between sites in terms of the species they support. The concept is primarily directed towards conservation planning. Complementarity algorithms are used to select a suite of reserves that together preserve the maximum number of species (Pimm & Lawton 1998; van Jaarsveld *et al.* 1998). There are a number of potential difficulties with the application of beta diversity measures (Prendergast *et al.* 1999), but a new generation of methods, that take account of turnover in time as well as in space, look promising (Rodriguez *et al.* 2000).

Complementarity is beta diversity by another name. The more complementary two sites are, the higher their beta diversity. Measures typically combine three variables: a, the total number of species present in both quadrats or samples; b, the number of species present only in quadrat 1; and c, the number of species present only in quadrat 2. This terminology follows Pielou (1984).

One of the easiest, and most intuitive, methods of describing the beta diversity of pairs of sites is to use a similarity/dissimilarity coefficient. Given their utility in ordination and phylogenetic reconstruction, a vast number of such measures exist (Legendre & Legendre 1983; Pielou 1984; Southwood & Henderson 2000). However, for the purposes of measuring beta diversity some of the oldest coefficients are also the most useful. Following Pielou (1984), Colwell and Coddington (1994) recommend the Marczewski-Steinhaus (MS) distance as a measure of complementarity. This measure is in fact the complement of the familiar Jaccard (1908) similarity index. As suggested by Pielou (also Colwell & Coddington 1994), the statistic can also be adapted to give a single measure of complementarity across a set of samples or along a transect.

The Marczewski-Steinhaus dissimilarity measure (and thus the complement of the Jaccard similarity measure) is what is known as a metric measure. This means that it satisfies certain geometric requirements. The important consequence from the user's perspective is that it can, therefore, be treated as a distance measure and can be used in ordination (Pielou 1984).

Another popular similarity measure was devised by Sorensen (1948). Sorensen's measure is regarded as one of the most effective presence/absence similarity measures (Southwood & Henderson 2000). It is identical to the Bray-Curtis presence/absence coefficient.

Lennon *et al.* (2001) note that if samples differ markedly in terms of species richness the Sorensen measure will always be large. They introduce a new turnover measure that focuses more precisely on differences in composition. This is related to a measure derived by Simpson (1943). Any difference in species richness inflates either b or c. The consequence of using the smallest of these values in the denominator is thus to reduce the impact of any imbalance in species richness. Lennon *et al.* (2001) find that this measure-performs well.

$$C_s = 2a / (2a + b + c)$$

One of the great advantages of these measures is their simplicity they are easy to calculate and interpret. However, this virtue is also a disadvantage in the sense that the coefficients take no account of the relative abundance of species. As with richness measures of a diversity, a species that dominates an assemblage carries no more weight in a presence/absence beta diversity measure than one represented by a singleton. This consideration has led to the development of similarity/dissimilarity measures based on quantitative data. Bray and Curtis (1957) introduced a modified version of the Sorensen index. This is sometimes called the Sorensen quantitative index (Magurran 1988).

The Bray-Curtis index is widely used (see, for example, Thrush *et al.* 2001; Burd 2002; Ellingsen & Gray 2002). Clarke and Warwick (2001a) conclude that the measure is a particularly suitable one. They tested the index using six criteria: (i) the value should be 1 (or 100) when two samples are identical; (ii) the value should be 0 when samples have no species in common; (iii) a change of measurement unit does not affect the value of

the index; (iv) the value is unchanged by the inclusion or exclusion of a species that occurs in neither sample; (v) the inclusion of a third sample makes no difference to the similarity of the initial pair of samples; and (vi) the index reflects differences in total abundance (and not just relative abundance). Although most coefficients satisfy the first three criteria the Bray-Curtis index is one of the few to meet them all (Clarke & Warwick 2001a). Faith *et al.* (1987) also conclude that this is a particularly satisfactory measure.

Wolda (1981) investigated a range of quantitative similarity indices and found that all but one, the Morisita-Horn index were strongly influenced by species richness and sample size. A disadvantage of the Morisita-Horn index (MH) is that it is highly sensitive to the abundance of the most abundant species. Nevertheless, Wolda (1983) successfully used a modified version of the index to measure beta diversity in tropical cockroach assemblages.

The Morisita-Horn measure is widely used (e.g., Green 1999; Arnold *et al.* 2001; Williams-Linera 2002). Southwood and Henderson (2000) provide a version of Morisita's original index that is suitable for easy computation. A further simple measure is percentage similarity (Southwood & Henderson 2000; after Whittaker 1952).

Smith (1986) carried out an extensive evaluation of similarity measures using data from the Rothamsted Insect Survey (Taylor 1986). Qualitative and quantitative techniques were included. Smith concluded that the presence/absence (qualitative) indices were generally unsatisfactory. Of those tested, the best proved to be the Sorensen index. The large number of quantitative similarity measures made selection difficult and Smith advised that the choice of index for any particular study would depend on the aims of the investigation and the form of the data. However, she did conclude (like Wolda 1981) that versions of the Morisita-Horn index are among the most satisfactory available. Many other similarity measures are discussed by Legendre and Legendre (1998).

Clarke and Warwick (2001a) note that quantitative measures can be unduly influenced by the abundance of the most dominant species. Their solution is to transform the raw data. They recommend either the root transform, or where a more severe correction is required, the double root transform. An alternative method, similar in effect is  $\log(x + 1)$ . Of course the ultimate transform is to allocate every species an abundance of 1, which has the result of changing a quantitative measure into a presence/absence one.

### **3.6. Estimating the true number of shared species**

Colwell and Coddington (1994) note that, for statistical reasons, complementarity is more likely to be overestimated between rich samples than between species-poor ones unless sampling effort is sufficiently large throughout, or has been proportionally increased for the rich sites. Fortunately Anne Chao and her colleagues (Chao *et al.* 2000) are developing new techniques to estimate the number of species that two communities have in common. Their approach is based on the coverage estimator ACE. The shared species estimator,  $V$ , requires abundance data. Like ACE,  $V$  assumes that rare species (those with  $< 10$  individuals) contain the most information about the true similarity in the composition of two assemblages. Accordingly, the number of rare shared species is used to estimate the number of unobserved shared species (Chao *et al.* 2000). The number of abundant shared species is then added to this. Confidence limits may be attached. Simulations reveal that the true number of shared species may be severely underestimated in samples (Chao *et al.* 2000). Empirical studies confirm this conclusion. Chao *et al.* (2000) examined bird assemblages in two Taiwanese estuaries: Ke-Yar estuary had 155 species and Chung-Kang estuary had 140 species. Some 111 bird species were recorded in both areas. The estimate of the number of shared species was 134. This was derived from 90 abundant shared species. Those observed more than 10 times in one or both areas, plus a correction factor of 44. In other words it appeared that the survey had failed to discover a further 23 shared species.

#### **Diversity and scale: practical implications**

Most measures of beta diversity are sensitive to scale. Comparisons between investigations that examine turnover on different scales can be difficult. However, as Lennon *et al.* (2001) point out, the mean number of species gained and lost between assemblages is independent of scale. As they explain, this is a consequence of the species-area relationship. The semilogarithmic species-area relationship ( $S$  versus  $\log(A)$ ) assumes that the difference in species richness between larger and smaller quadrats is constant. Moreover, Lennon *et al.* (2001) note that, in their investigation of British birds, local richness gradients have a major impact on estimates of  $\beta$  diversity. For example, greater turnover is observed in localities with low species richness. Lennon *et al.*'s (2001) result may be because depauperate assemblages are more likely to be random mixtures of species than rich assemblages are. The negative relationship that they detected between richness and turnover is likely to

diminish or vanish altogether at regional scales since the ranges of many species will be contained within a single sample. A further consideration is that undersampling diverse habitats -for example by selecting a constant number of individuals in sites with different richness -can miss rare species and underestimate turnover (Colwell & Coddington 1994). Since most practitioners measure beta diversity at local scales it is important to be aware of the inherent biases involved. Reserve selection algorithms also need to take account of these factors.

### **3.7. Comparing communities**

Assuming that the correct number of shared species has been enumerated or estimated, and that scaling issues and richness gradients have been dealt with, how might an investigator make comparisons amongst communities in terms of the level of beta diversity? Several graphic and statistical options are presented below.

Cluster analysis is a very simple, and intuitively meaningful, method of representing differences amongst samples and communities. Similarity or distance measures are used to measure the distance (based on species composition) between all pairs of sites. Either presence/absence or quantitative data can be used. The two most similar sites are combined to form a single cluster. The analysis proceeds by successively clustering similar sites until a single dendrogram is constructed. There are a variety of techniques for deciding how sites should be joined into clusters and how clusters should be combined with each other. For an introduction to the subject see Pielou (1984), Southwood & Henderson (2000). Many packages (including Species Diversity and Richness and PRIMER) can be employed for this purpose. Sites or samples that cluster together are revealed as being more similar to one another. Depending on the method used, the distance between nodes on the dendrogram may represent 0 diversity. Bootstrap values may also be attached to dendrograms. They indicate the robustness of the analysis, that is the percentage of times a tree reconstructed using a resampling algorithm would exhibit the same branching pattern. Alternatively, ordination can be used to describe the relationship between a set of samples or localities based on their attributes (the presence and relative abundance of species found there). Principal components analysis is one of the most widely used methods but there are a large range of other techniques available (Southwood & Henderson 2000). Clarke and Warwick (2001 a) recommend nonmetric multidimensional scaling (MDS) for its conceptual simplicity and its flexibility.

A second approach is to complete an analysis of similarities (ANOSIM) (Clarke & Green 1988). ANOSIM is a nonparametric test applied to the rank similarity matrix. It uses a permutation procedure following Mantel (1967) and tests the null hypothesis that there is no difference in community composition amongst sites. Significance levels are generated using a randomization approach. The test can be performed in a one-way design, where comparisons are made amongst  $x$  localities each with  $y$  replicates (Clarke & Green 1988). Clarke and Warwick (2001a) point out that it is essential that pseudoreplication is avoided. Alternatively, a two-way design, where sites have been allocated to treatments or categories on the basis of some a priori criterion such as pollution level or habitat structure, can be used (for examples of this method see Clarke 1993; Clarke & Warwick 1994). PRIMER includes these procedures.

Third, an investigator may contrast the observed pattern of beta diversity with some null expectation. Clarke and Lidgard (2000) examined the alpha, beta, and gamma diversity of bryozoans in the North Atlantic. Data were pooled into bins of latitude. Interestingly, the study revealed higher beta diversity at lower latitudes, though the paucity of marine studies and the pitfalls of comparisons with terrestrial systems make interpretation of these results complex. In an attempt to further explore beta diversity in this system, Clarke and Lidgard (2000) constructed two null models. The first model drew a set number of species at random from a regional assemblage of 100 species. Jaccard coefficients were calculated between all pairs of samples. The second model imposed a log normal distribution on the regional species pool. Individuals were then sampled (without replacement) until a predetermined number of species had been recorded. In this log normal scenario the likelihood of a species appearing in a given sample was a product of its abundance in the overall distribution. Once again, pairwise Jaccard coefficients were produced. Although this study did not formally compare the observed and expected frequency distributions of coefficients (it was not one of the authors' goals to do this), it is easy to see how such an approach could represent a powerful test of empirical patterns of beta diversity. Clarke and Lidgard (2000) did, however, conclude that the species richness of assemblages had important consequences for beta diversity and that while the species abundance distribution also has a strong influence on the results obtained, the log normal distribution may not be the most appropriate model for bryozoans.

### **3.8. Turnover in time**

Turnover, defined as "the number of species eliminated and replaced per unit time" is the concept that lies at the heart of MacArthur and Wilson's (1967) theory of island biogeography. Like turnover in space it can be

measured in a variety of ways. Indeed, many of the methods presented above can be used to describe the change in species composition over time. Percentage similarity between successive time periods is one common approach. The proportion of species not present in the previous year is another (Nichols et al. 1998; Lekve et al. 2002). Brown and KodricBrown (1977) defined turnover as:

$$b+c$$

where b =the number of species present only in the first census; c = the number of species present only in the second census.

Diamond and May (1977) observed that turnover rates will be influenced by the length of time between censuses. In a similar vein, Preston (1960) pointed out that species-time curves can be constructed in the same manner as species-area curves. The slope of this relationship might therefore reasonably be assumed to reflect turnover.

Mean turnover values can be computed and compared amongst localities (see, for example, Lekve *et al.* 2002) or turnover rates can be plotted in relation to time (Russell *et al.* 1995). Of course temporal turnover is just as vulnerable to biases related to sample size, species richness, and incomplete inventories as spatial turnover is. The same comment might equally be applied to investigations of alpha and beta diversity (spatial turnover) and, the temporal status of species in an assemblage has implications for the shape of the species abundance distribution.

Sepkoski (1988) completed an interesting analysis of alpha and beta diversity during the Palaeozoic. a diversity was estimated as the mean generic diversity of marine macrofossils in a range of soft-bottom communities (for example the peritidal and deep-water zones). The beta diversity of these zones was estimated using the Jaccard index. Global taxonomic diversity increased by a factor of four during the Ordovician radiations (between the Cambrian and the later Palaeozoic). Some of this could be attributed to a rise in a diversity. However, Sepkoski also concluded that, as a result of increasing habitat specialization by taxa, beta diversity increased by about 50% during the same period. Thus a and beta diversity jointly contribute to changes in diversity over evolutionary time. Indeed, Sepkoski concludes that "hidden" sources of beta diversity, such as the expansion of new community types including bryozoan thickets and crinoid gardens, are a major component of the rise in global taxonomic richness. The interplay of a and beta diversity over ecological, and evolutionary, time is a topic that surely warrants much more consideration.

Beta diversity (or turnover) is a measure of the extent to which the diversity of two or more spatial units differ in terms of their species composition. Complementarity, a concept widely applied in conservation planning to help select reserves that together preserve the maximum number of species, is a form of beta diversity. Beta diversity can be measured in a variety of ways. These include tailored measures such as Whittaker's index, measures of similarity/dissimilarity and complementarity, and the slope of species-area relationship. beta diversity is the diversity (usually measured as species richness) of a landscape or other large area. Following Lande, gamma diversity can be treated as mean a diversity plus beta diversity. Thus, the larger the areas of a diversity relative to y diversity, the smaller the contribution of beta diversity to overall diversity.

## 4. Questions

- Who proposed the idea of alpha, beta, gamma, and epsilon diversity?
- Define the Whittaker's beta diversity.
- What is the relationship between beta diversity and species turnover?
- What complementarity means?

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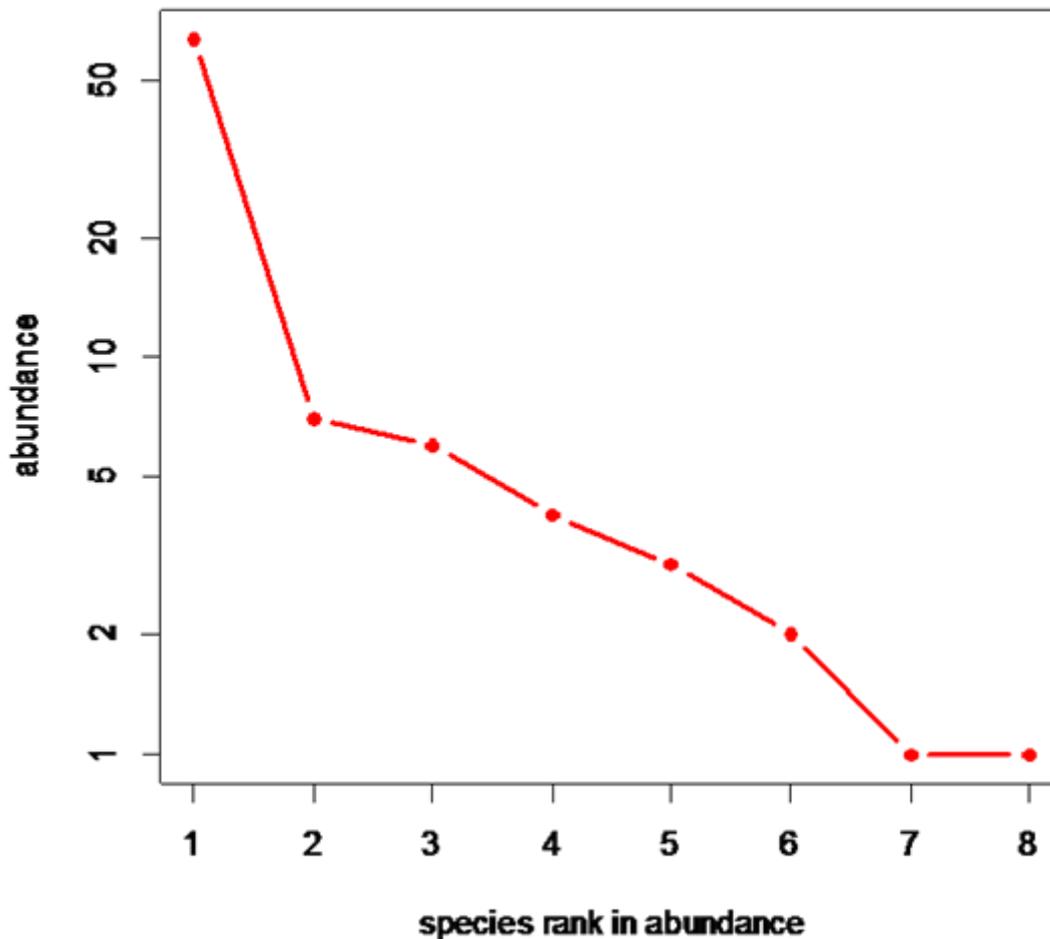
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# 13. fejezet - Chapter 12 Species Abundance Distributions

The species abundance relations (SAR), the relations between abundance and the number of species are clearly of fundamental interest in the study of ecological communities. Different types of such species abundance relations have been proposed on theoretical grounds, and are observed in real situations. What these relations mean, and how they are best characterized, has been the subject of considerable discussion, much of it focused on one or another particular aspect of a specific species-abundance relation. The species-abundance relations also provides the basis for a consideration of species-area relations, the relation between the area of real or virtual islands, and the number of species on the island, and for some rough suggestions relating to practical problems of sampling all the species in a community.

## 1. What is an SAD?

Often, the SAD is presented visually in a rank-abundance diagram (RAD), where log-abundance is plotted on the y-axis vs. rank on the x-axis (Figure 1). This plot contains exactly as much information as the vector of abundances. In contrast, histograms involve binning and thus a loss of information (Figure 2). The term 'community' is slightly vague (Fauth et al. 1996), but the choice becomes important when we study the role of scale and sample size in SADs. The two most salient features of the SAD are the fact that the species are not 'labelled' by having a species identity attached to the abundance and that zero abundances are omitted. This loss of labels allows for comparison of communities that have no species in common, for example, a freshwater diatom community and a tropical tree community. At the same time, SADs enable nuanced questions and comparisons such as asking which community has a higher proportion of rare species



**Figure 1.** Rank-abundance plot of a Fisher distribution.

A species abundance distribution (SAD) is a description of the abundance, usually number of individuals, for each different species encountered within a community. As such, it is one of the most basic descriptions of an ecological community. When plotted as a histogram of number (or percent) of species on the y-axis vs. abundance on an arithmetic x-axis, the classic hyperbolic, 'lazy J-curve' or 'hollow curve' is produced, indicating a few very abundant species and many rare species. In this form, the law appears to be universal; we know of no multispecies community, ranging from the marine benthos to the Amazonian rainforest, that violates it. When plotted in other fashions, such as log-transforming the abundances, more variability in shape occurs, giving rise to considerable debate about the exact nature of SADs. Nevertheless, the hollow-curve SAD on an arithmetic scale is one of ecology's true universal laws.

## 2. Why are SADs important?

Not only is the hollow-curve SAD universal, but it is a surprising, counterintuitive and therefore informative law. A null expectation is for abundances to be more or less evenly distributed with some minor variation because of body size, life history. In fact SADs are so uneven that this null expectation is not even useful in studying SADs. If we can explain this high degree of unevenness, then we likely will be in a position to make strong statements about which mechanisms structure communities, be they species interactions, random chance or some other factor. Thus understanding SADs is a major stepping stone to understanding the rules governing the communities in general.

The raw data underlying an SAD is among the most commonly collected data in ecology. The overall availability of data combined with the intermediate complexity of SADs, their potential for comparison among disparate communities, and their visual nature have made SADs very popular in ecological research. SADs are commonly taught in undergraduate ecology classes. The SAD is also pivotal in conservation, described as the 'science of scarcity' (Soule 1986); the relative terms 'common' and 'rare' are given a clear definition in the context of an SAD. In short, the SAD has played and is likely to continue to play a central role in ecology.

### 3. History

The existence of a few very common species and many very rare species was an obvious fact even to casual observation. Darwin (1859) noted „Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?“ The first formally published quantitative analysis of an SAD is published by Raunkiaer (1909), although technically he measured occupancy rather than abundance. By the 1940s the use of histograms had become well-established (Fisher et al. 1943; Preston 1948) and the use of a log-transformed abundance (Preston 1948) was introduced. The RAD plot was probably introduced by MacArthur (1957). Note that the empirical cumulative distribution (ECDF) is not often used, but is mathematically equivalent to the RAD involving only a swapping and rescaling of the axes. Two reviews on SADs were written in the 1960s and 1970s that implied we had worked out the basic patterns and processes of SADs (Whittaker 1965; May 1975). But later reviews (Gray 1987; Marquet et al. 2003) express a belief that there has been a disappointing lack of progress in the study of SADs.

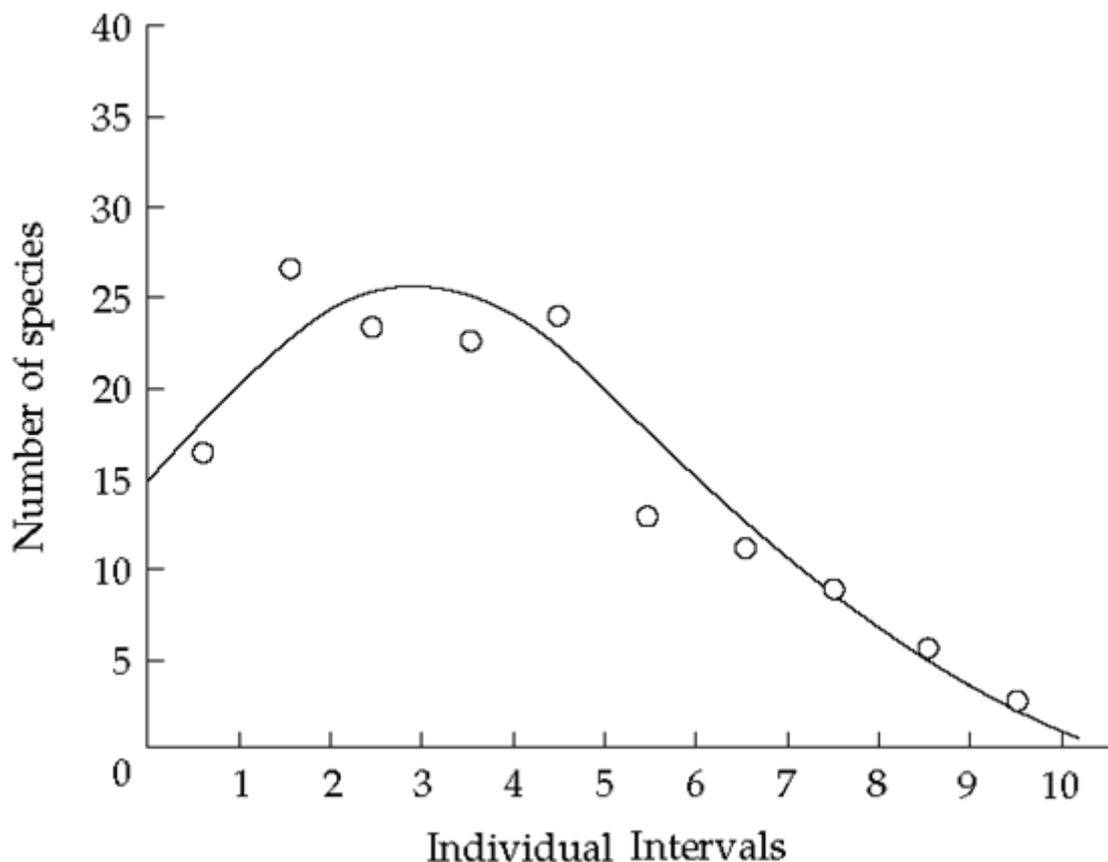


Figure 2. Histogram of a lognormal distribution.

MacArthur's (1957, 1960) broken-stick distribution may be derived in various ways; it is specified by one parameter, namely  $ST$ . It is discussed most fully by Webb (1973). Similar remarks pertain to the other distributions. expected whenever an ecologically homogeneous group of species apportion randomly among themselves a fixed amount of some governing resource. For appropriately small and homogeneous taxa, field observations seem to fit this distribution. Two other interesting distributions are the simple geometric series and the logseries. If the community ecology is dominated by some single factor, and if division of this niche volume proceeds in strongly hierarchical fashion with the most successful species tending to preempt a fraction  $k$ , and the next a fraction  $k$  of the remainder, and so on. we arrive at a geometric series distribution (as the ideal case),

or a logseries distribution of relative abundance (as the statistically realistic expression of this underlying picture). A few natural communities, particularly simple plant communities in harsh environments, conform to these patterns. Both geometric and logseries are two-parameter distributions.

## 4. Classical theoretical developments in SADs

The first theory attempting to explain the mechanism underlying hollow-curve SADs was by Motomura (1932). He pointed out that a sequential partition of a single niche dimension by a constant fraction leads to the geometric distribution. Fisher et al. (1943) argued for the logseries distribution as the limit of a Poisson sampling process from a gamma distribution, where the gamma was chosen only because of its general nature. Kendall (1948) put the logseries on a more mechanistic footing by deriving it from birth-death-immigration models. Preston (1948) argued for a modified lognormal on the basis of the central limit theorem. MacArthur (1957) built on Motomura's idea of partitioning a one-dimensional niche but used a random stick-breaking process. This would seem to have set the stage for a clear test with empirical data. Each theory made distinct predictions: the geometric model predicts extremely uneven abundances, broken stick predicts an unduly even abundances, while lognormal and logseries are intermediate with distinct predictions about the proportions of extremely rare species. The proportions of extremely rare species is high in logseries, low in lognormal. With the possible exception of the broken stick, none of the four classical hypotheses have been eliminated. Instead, we have seen literally dozens of new hypotheses added without elimination of older hypotheses.

## 5. Diversity of the models

Starting in the 1970s mechanistic models and alternative interpretations and extensions of prior theories have proliferated (May 1975; Gray 1987; Tokeshi 1993; Marquet et al. 2003). A classification of these models are as follows:

- (1) **Purely statistical:** purely statistical theories take some combination of the continuous gamma and lognormal distributions with the discrete binomial, negative binomial, and Poisson distributions. The lognormal has many versions; we recommend using either the simple, untruncated continuous lognormal because of the extreme ease with which it isor the Poisson lognormal because of its technical merits (Bulmer 1974; Etienne & Olf 2005).
- (2) **Branching processes:** when dealing with biological processes, individuals are always derived from ancestor individuals. This suggests a random-branching process as a model.
- (3) **Population dynamics:** a variety of population dynamic models arrayed along a spectrum from purely deterministic to purely stochastic can also produce realistic SADs.
- (4) **Niche partitioning:** another group of models is based on dividing up a one-dimensional niche space. The oldest SAD model is of this type (Motomura 1932).
- (5) **Spatial distribution:** one can build spatial models of SADs if one conceives of the SAD as counting all the individuals falling within a particular region of space and if one knows (or can model statistically): (i) the spatial distribution of individuals within a species and

Evidently, these models are not independent. Several of these families overlap. For example, neutral models (Caswell 1976; Bell 2000; Hubbell 2001) are stochastic population dynamic models but also branching process models (Etienne & Olf 2004b), and the lognormal can be the limit of population dynamics (Engen & Lande 1996b) or niche partitioning (Bulmer 1974; Sugihara 1980).

Given the proliferation of theories there has been considerable debate (e.g. Alonso et al. 2006; Nekola & Brown 2007) over whether some of the several dozen models are 'better' types of models a priori than other models (independent of how well they fit the data). This is of course a normative statement, which depends heavily on one's criteria for judging models. And there are many possible criteria. Some of the non-empirical criteria for favouring one theory over another that have been invoked in the context of SADs include:

- (1) Many favour more mechanistic theories (usually the statistical models are considered non-mechanistic), but there is debate about what constitutes a mechanism. Some consider neutral models that are derived from basic principles of population dynamics more mechanistic while others consider the niche partitioning models that are a bit more abstract and static, yet based on more 'realistic' biological assumptions to be more mechanistic.

- (2) In a purely predictive paradigm (Peters 1991), predictive success takes priority over mechanism.
- (3) Others prefer parsimony (Ockham 1495) and related issues of elegance and having few parameters.
- (4) Some models develop or use extensive mathematical machinery that allow for many different predictions to be derived (such as the neutral models and the spatial distribution models).
- (5) Some models have parameters that can be easily estimated independent of the SAD data one is trying to fit. In principle neutral theory can do this, but in practice this has not been performed successfully for neutral theory (Enquist et al. 2002; Ricklefs 2003; McGill et al. 2006b) or any other SAD model to our knowledge.
- (6) The models also invoke varying degrees of symmetry among the species. Many consider requirements of symmetry undesirable because of obvious differences among species. The most extreme such assumption is the 'neutrality' assumption of neutral theory (Hubbell 2001). This symmetry has also been controversial in the derivation of the lognormal using the central limit theorem (Central Limit Theory, May 1975, Pielou 1977, Ugland & Gray 1982, McGill 2003a, Williamson & Gaston 2005). But, in fact, all SAD models constructed so far necessarily make some assumption of symmetry or exchangeability between species. For example, the niche partitioning models treat all species as identical except for a single factor leading to pre-emption; often suggested to be order of arrival which is stochastic and independent of any species property. The resolution of this may lie in recognizing that there are ecological asymmetries but that species started from symmetric initial conditions and later evolved asymmetries (distinct life histories, physiology, and population dynamics) in evolutionary time (Hubbell 2006; Marks & Lechowicz 2006).

Ultimately, which model approach is 'best' depends on the question at hand. Predicting the rate of shifts in rarity over time would likely require a mechanistic model, perhaps based on population dynamics, while just predicting the proportion of rare species might be better served by a simple, easy to estimate statistical model.

## **6. Causes of the proliferation**

The main cause of the extensive proliferation of SAD models is a failure to successfully test and reject theories with data. Successful branches of science use strong inference (Platt 1964), theories face off against each other and the data pick a winner. The loser disappears to science's dustbin while the winning theory may then be refined through additional iterations. The ever increasing supply of new SAD theories without the rejection of any old theories is the diametric opposite of what Platt (1964) suggested and must be counted as a collective scientific failure. The central problem has been that while most theories make one and only one prediction, that SADs will be a hollow-curve, predicting a hollow curve alone cannot possibly be the basis of a decisive test between competing theories because all the theories make this prediction. In precise mathematical terms, SADs are 'necessary' but not 'sufficient' for testing mechanistic theories. Any theory that produces an SAD which is not a realistic hollow curve SAD must surely be rejected (e.g. Etienne et al. 2007b), but having a theory that produces a realistic hollow curve is not sufficient to strongly support the theory. Further discussion on why SADs have failed to lead to strong inference can be found in McGill (2003a) and Magurran (2005).

Historically, ecologists hoped that predicting subtle variations in the hollow curve would produce a decisive test. But this has not worked well. Robert H. Whittaker (1975) noted that 'the study of (SADs) has not produced the single mathematical choice ... that the early work suggested might be possible' which was echoed by Gray (1987). This is in part because most attempts to evaluate SAD models have not been sufficiently rigorous. Specifically rigorous tests must compare multiple models using multiple measures of goodness of fit on multiple data sets.

## **7. Integrating SADs with other patterns – towards a unified theory?**

One positive theoretical development in the study of SADs is the demonstration that SADs are intimately linked in a mathematical sense with a wide variety of other well-known and novel macroecological patterns. This begins to approach the rather grandiose goal of 'unified theories' (Hanski & Gyllenberg 1997; Hubbell 2001; McGill 2003a; Harte et al. 2005). These linkages can go in one of two directions:

- (a) One can start with only a hollow-curve SAD and then derive other macroecological patterns from it, or.

(b) One can start with some set of assumptions and then derive many macroecological patterns (including SADs) from these assumptions.

Type (a) approaches are essentially elaborations of the consequences of sampling from an uneven, hollow curve SAD. Although many find this biologically uninteresting, it is important to identify just how much is explained by sampling from the hollow curve of the SAD alone. For example, few people realize that Preston (1960) showed that most of the species area relationship was well explained by sampling from the logseries up to fairly large spatial scales. From a testing point of view, it is also important to realize that testing a prediction based on sampling from an SAD is not really an independent prediction from the hollow curve SAD prediction.

## **8. Classical empirical work**

The bulk of the empirical work (and again the work put into textbooks) has established two facts: (i) SADs follow a hollow curve (on arithmetic scale) in every system studied and (ii) Within this broad constraint, there is a great deal of variation in the details, especially as highlighted on a log-scale. We cannot possibly list every empirical measurement of SADs as this is one of the most common types of data collected in ecology. And in all likelihood, the majority of such data sets have never even been published (e.g. collected for management or monitoring purposes). Hughes (1986) gives a compilation of 222 different SADs and Dewdney (2000) gives a compilation of 100. To our knowledge no SAD ever measured violates the basic hollow-curve shape on an arithmetic scale, justifying the claim that it is a universal law. As with any pattern, it is possible that more work will uncover an exception. For example, our knowledge of the shape of SADs amongst taxa such as bacteria or mycorrhizae is poor. But there is no debating that the hollow-curve SAD is unusually general in nature.

At the same time enormous debate has gone into the nature of the left side of SADs when plotted on a log-abundance scale (Preston 1948, Hughes 1986, Southwood 1996, Hubbell 2001, McGill 2003b). Ecologists have observed patterns ranging from a histogram that increases to a mode in the middle through to data that is largely flat until the middle abundances then on to data that has its mode at the lowest abundance of  $N = 1$  and decreases continuously from there. This goes back to the earliest days, with Fisher suggesting that a lognormal was impossible as his insect data showed the mode at the lowest abundance. Preston explained this with the concept of a veil line (Preston 1948). Preston's veil line suggests that small samples do not capture the truly rare species which causes the left side of the SAD to be truncated behind a veil resulting in a mode at  $N = 1$ . The veil line gradually disappears with increased sampling (Marquet et al. 2003). But later authors have argued that the mode remains at  $N = 1$  no matter the extent of the sampling (Hughes 1986; Southwood 1996). Whittaker (1965) attempted to resolve this debate by suggesting that no one curve fit all data; the geometric model applied to species poor communities while the lognormal applied to more species rich communities, only being fully unveiled in large samples. As already discussed, this classical empirical work has not proven sufficient to differentiate among various mechanistic models, even with variation in the left tail on a log scale. This is in part because the patterns are inconsistent in this regard (perhaps because the role of sampling effects have not been well worked out to distinguish between empirical pattern vs. sampling), and in part because the difference is just too subtle to give a decisive test. In the rest of this section we identify eight alternative, less well-known empirical patterns which might lead to decisive tests. All of these patterns need much more work to assess their generality.

## **9. Empirical pattern 1 – environmental gradient analysis**

Community ecology is regaining interest in the environmental (abiotic) context in which communities occur. In particular, gradients of changing environment provide a natural experiment or comparative basis for testing theories about communities (McGill et al. 2006a) including SADs. The 1970s saw a burst of analysis of SADs along gradients. Whittaker interpreted the results as showing that low productivity systems have extremely uneven SADs and are well fit by a geometric SAD, while high productivity systems are well fit by lognormal curves, and show the highest evenness. Later, Whittaker (1975) repeated this analysis with a similar outcome, but with the unique twist that he compared vastly different communities like birds, trees, etc. He thereby illustrated one of our aforementioned advantages of SADs: the ability to compare unrelated communities. Hubbell (1979) likewise showed a similar plot along a latitudinal productivity gradient, comparing different tree communities ranging from boreal to tropical, again with little overlap in species between communities compared. Thus a general pattern of increasing evenness with productivity was suggested. Unfortunately, this pattern seems to have had little follow-up. It is also unclear how much this pattern was driven solely by the change in species richness which has a strong effect on the shape of RADs; better analytical methods are

needed. One study that did control for species richness (Hurlbert 2004) confirmed that sites with greater productivity had more species for a given number of individuals and less dominance by the most abundant species, indicating a positive productivity-evenness relationship. Cotgreave & Harvey (1994) showed that more complex habitats (often correlated with productivity) showed SADs with higher evenness (they also showed that communities with more similar body sizes showed less evenness, suggesting a mechanism of competitive overlap affecting SADs). Although the pattern of greater evenness in high productivity environments is far from well documented, evidence to date is consistent; but we know of not even one instance where a model for SADs attempted to explain the change of SADs with productivity.

## 10. Empirical pattern 2 – successional and other temporal gradients

Instead of comparing communities across space (gradients) it is also possible to compare communities across time (Magurran 2007). Bazzaz (1975) showed a series of SADs along a successional gradient in old fields with more lognormal, more even communities occurring late in succession just as for productivity. Caswell (1976) studied changes in diversity over succession and found that his version of neutral theory failed to produce empirically observed patterns. This allowed Caswell to make a strong (Plattian) inference about an SAD theory, supporting our contention that this comparative approach holds promise. Wilson et al. (1996) demonstrated fairly complex but significant changes in which SAD fits the best over succession in several grasslands, with evenness increasing. Thibault et al. (2004) showed a significant directional change in the shape of SADs over a 25 year period in a system which was known to have experienced a strong climatic trend.

## 11. Empirical pattern 3 – deconstruction or subsetting

Rather than comparing SADs from two communities, one can compare SADs for two subsets within the same community. This approach has been coined deconstruction (Marquet et al. 2004). For example Labra et al. (2005) studied a set of invasive bird species vs. a paired set of similar native species and a random (unpaired) set of native species and found that exotics showed a clear tendency towards higher abundances, especially in the rare species (although they pooled data from many sites making it not strictly an SAD). The division of species into resident and transient also shows very distinct differences in the shape of the SAD (Magurran & Henderson 2003; Ulrich & Ollik 2004). On the theoretical modelling side, a somewhat similar idea was suggested by Etienne & Olf (2004a) who explored constraints based on body mass between body size guilds, but assumed neutrality within body size guilds. We know of few other analyses, but imagine that deconstructions comparing the SADs of species from different trophic levels (predator vs. prey), ontogenetic stages (juvenile vs. adult) or taxonomic groups (passerines vs. nonpasserines) might also prove interesting.

## 12. Empirical pattern 4 – transient species, scale and left-skew

Recent years have seen a rapid advance in understanding what drives the shape of the left tail on a log scale, and in particular the common observation that large scale data sets are left-skewed, i.e. have more rare species. Gregory (2000) showed that left skew on a log scale is common in large (country-sized) assemblages of birds, but that it disappears when species arguably not part of the community are removed. Magurran & Henderson (2003) showed that amongst fish in an estuary, the permanently resident species were lognormal (with no excess of rare species), but the transient species were logseries indicating a disproportionate number of rare species. A similar result was obtained for beetles (Ulrich & Ollik 2004). McGill (2003b) explored this same idea in the context of autocorrelation. He showed low autocorrelation (all transients) and high autocorrelation (few transients) leads to zero skew, while intermediate autocorrelation (mixture of residents and transients) leads to log-left-skew (excess rare species) in both Monte Carlo models and empirical data. Finally, neutral theory (Hubbell 2001) predicts that higher rates of migration, modelled by the parameter  $m$ , lead to more log-left skew. Although immigration rates per se are hard to measure, several authors (Hubbell 2001; Latimer et al. 2005) have used empirical data to the neutral theory and found more left-skew (i.e. higher values of  $m$ ) in cases where greater immigration was expected. These independently developed but intertwined lines of evidence point both empirically and theoretically to the idea that communities more open to immigration will have a higher proportion of rare species.

## 13. Empirical pattern 5 – multiple modes

It has occasionally been observed that SADs of large assemblages appear to be multimodal, that is have more than one peak in a histogram (Ugland & Gray 1982; Gray et al. 2005). This is in contrast to most theories which have only a single peak. Sampling noise and binning effects can produce multiple peaks, but only small ones, while peaks much larger than could be produced by these effects are claimed to be observed. Preston's method of displaying SAD histograms on a log<sub>2</sub> scale by dividing the boundaries (1, 2, 4, etc) between adjacent bars has the effect of smoothing out peaks that might actually occur at  $N=1$  or  $N=2$  thereby hiding the potential for multiple peaks (Gray et al. 2006). The existence and implications of multiple modes in the SAD has been little explored. An analysis of 100 Breeding Bird Survey routes found that all 100 routes had a peak at  $N=1$  or 2 and a second peak at higher numbers (McGill unpublished data). One can use a finite mixture of normal distributions on a log scale fit by expectation maximization (MacLachlan & Peel 2000; Martinez & Martinez 2002) combined with AIC or likelihood ratios to test for the number of peaks.

The exact number of peaks chosen will depend on one's personal preference in tradeoffs for parsimony vs. goodness of fit, or the information criteria one chooses that makes these tradeoffs for you. The fact that there is more than one peak in the data for many communities suggests there is much to be gleaned by documenting, testing, and explaining this pattern. While the existence of multiple peaks on a log scale does not reject the universal hollow curve law on an arithmetic scale, it does reject every existing SAD theory which all produce unimodal curves. One possibility is that these studies inappropriately lumped together distinct guilds. If true then deconstruction analysis might find appropriate separations (Magurran & Henderson 2003; Marquet et al. 2004).

## 14. Empirical pattern 6 – High and low diversity systems

The vast majority of SADs have been studied in systems with a moderate number of species. Recent debate over SADs has relied extensively on a single data set: the approximately 225 species, 50 ha tropical tree plot from Barro Colorado Island. Yet patterns from extremely species poor and extremely species rich systems do not necessarily match generalizations derived from systems of intermediate richness. For example, large swaths of boreal forest may contain only half a dozen tree species. It is tempting to ignore such systems as uninteresting, but they of course represent large areas of the world's surface and are of considerable economic importance. Boreal forest SADs tend to produce histograms that are quite flat (non-modal) on a log-abundance histogram (or equivalently a straight line on a RAD). These can be fit by the geometric model (Motomura 1932). Models of SADs generated by neutral theory or the lognormal actually fit such data very poorly. Moreover, it is not uncommon in few-species SADs for the two most abundant species to be very similar in abundance, which contradicts the geometric model. At the other extreme, extraordinarily speciose communities tend to produce an SAD that still looks hyperbolic on a log-abundance scale, again fitting SAD models other than the logseries quite poorly.

## 15. Empirical pattern 7 – measurement currencies other than abundance

Ecologists have a long tradition of plotting histograms of abundance, but plant ecologists sometimes use other measures (e.g. percent cover) for reasons of convenience and preference. It seems desirable to explore the implications of using different currencies to assess the importance of a species (Tokeshi 1993). Abundance is clearly an important measure, but perhaps biomass, resource use (roughly biomass; Savage et al. 2004) or percent cover is more relevant (Chiarucci et al. 1999). More importantly, perhaps one of these distributions can lead more directly to a mechanistic theory. In particular, niche partitioning models might be expected to more directly explain resource use than abundance (Tokeshi 1993; Thibault et al. 2004; Connolly et al. 2005). Ecologists studying marine systems have long used differences in biomass and abundance plotted together in curves called Abundance Biomass Comparisons (ABC curves; Warwick 1986) as a diagnostic tool. Connolly et al. (2005) showed that the effects of scale and the rate of unveiling differ substantially between abundance and biomass distributions. Thibault et al. (2004) also found that the two curves showed very distinct patterns.

### Empirical pattern 8 – Patterns based on 'labelled' SADs

SAD is 'unlabelled', but as we seek to advance our empirical understanding of the patterns related to SADs, comparing the abundance of individual species over time or space is an obvious direction to turn (Dornelas et al. 2006; Etienne 2007). For example, how often does a rare species become common or a common species become rare? Some theories (Hanski 1982) predict fairly quick exchanges, others (Hubbell 2001) predict fairly moderate rates of change, while empirical data suggest that species retain their basic status as common or rare up to one million years (McGill et al. 2005). Wootton (2005) was able to reject a particular SAD theory by experimentally removing the dominant species and showing that the abundances of the remaining species changed more than expected under neutral theory. A similar result was obtained for fragmented tropical rainforests (Gilbert et al. 2006). MacNally (2007) also shows greater difference in labelled than unlabelled studies and introduces the 'abundance spectrum' as a means of studying changes in labelled SADs. Murray et al. (1999) has shown the potential of comparing labelled SADs between sites.

A theory which not only predicts a hollow curve SAD but predicts which species (or types of species) should be abundant or rare would be extremely powerful. There has been a great deal of speculation about which species should be abundant (e.g. Rosenzweig & Lomolino 1997), but there has been comparatively little success to date in the empirical search for patterns (Murray et al. 1999, 2002). For example, more common species tend to have smaller body size (Damuth 1981, 1991; Marquet et al. 1990; White et al. 2007) but the exact nature and strength of the relationship is still debated (Russo et al. 2003; White et al. 2007). Careful control for spatial variation and phylogeny may lead to clearer results (Murray & Westoby 2000). Perhaps this is an area where theory can produce new predictions to guide empirical research. Recent work centred on traits may provide such a solution (Shipley et al. 2006).

Finally, with labelled species we can look at questions related to the phylogenetic context of the SAD (Webb et al. 2002). For example, how do the abundances of sister species compare? A study by Sugihara et al. (2003) suggests that sympatric, closely related species have reduced abundances, presumably because of competition for more similar resources than non-sister pairs.

In summary the classical empirical work on SADs clearly established that the hollow-curve SAD is very general, but that when placed on a log scale that magnifies the rarest species considerable variation occurs. The classical work has failed to strongly test and reject different mechanistic theories. We identify eight patterns involving comparison of SAD shape between communities or subsets of communities, seeming exceptions and alternative views of SADs that have promise for leading to stronger tests of mechanistic models. Note that even the seeming exceptions occur only on log-scales and do not violate the hollow-curve rule on an arithmetic scale.

## **16. Linking theory and data – statistical issues in SADs**

Data and theory are tied together through a process of measurement and quantification. In the case of SADs a variety of statistical issues arise that may substantially affect the appearance of the observed patterns and should be resolved to ensure a tie between data and theory in which we can have confidence. We identify four broad areas.

### **17. How does sampling affect the shape of SADs?**

Every SAD is a finite sample, yet we know very little about how much this affects the patterns we observe. Sampling leads to variance. Variance means that SADs have error bars around the curves that represent them. We know little about how to place error bars and do significance tests on SADs, and it is rarely performed. Neutral theory has a sampling theory built in (Etienne 2005; Etienne & Alonso 2005; Alonso et al. 2006), which is a tremendous advantage, but this needs to be extended to SADs more generally. Some basic machinery has been developed (Pielou 1977; Dewdney 1998; McGill 2003b; Green and Plotkin 2007), but much work remains. We cannot currently answer several closely related basic questions of high practical importance: what number of individuals /proportion of individuals in a community /spatial extent do we need to sample to have reasonable confidence that the SAD obtained is a good approximation of the underlying community?

### **18. How does scale affect the SAD?**

Closely related to the question of sample size is the question of scale. As one samples larger areas or for longer time periods, the sample size increases, and issues of habitat heterogeneity, beta-diversity, clumping of

individuals, and autocorrelation must be addressed. It is entirely possible that both the patterns and processes influencing the SAD will change with scale (Wiens 1989; Levin 1992) as has been found for other macroecological patterns (Rosenzweig 1995). For example, it has been suggested that the shape of an SAD changes with log left (negative) skew increasing with scale possibly due to spatial autocorrelation (McGill 2003b). Is there, then, a natural or optimal scale at which to measure SADs? This returns to our original definition of the SAD and the imprecision that is inherent in measuring a poorly defined concept like 'community'. Some of the aforementioned links between SADs and other macroecological theories may prove important.

## 19. How do we compare SADs?

Nearly all comparisons of SADs along gradients, deconstructions or time trajectories to date have been purely by visual inspection (Whittaker 1965; Hubbell 1979). Most particularly, these visual inspections have been performed on rank-abundance plots which, by using an x-axis that runs from 1 to S (species richness), seriously confounds the effects of species richness per se with other changes in the shape of the SAD. Changes in species richness are a legitimate factor that should be considered a change in shape of the SAD. However, changes in richness so strongly dominate in rank-abundance plots that no other changes are easily considered. Is there any other change in the shape of an SAD after controlling for the fact that productivity affects richness? We cannot say at the present time (but see Hurlbert 2004). It may be that the use of empirical cumulative density function (ECDF) plots can remove some of this bias. Plots that use relative abundance (percent) of individuals or percent of total species may help. Such methods represent an improvement, but are still visual. More rigorous multivariate methods are needed.

## 20. What kinds of variation are commonly found in SADs?

We know almost nothing about the main axes of variation in SADs. In morphometric analyses it is common to perform some form of principal components analysis and have a few orthogonal axes capture most of the variation. A similar result has occurred in landscape ecology where over four dozen landscape metrics were found to reduce to only six distinct axes of variation (Riitters et al. 1995) capturing 87% of the total variation. This needs to be performed for SADs. Species richness, evenness and proportion of rare species might well turn out to be distinct axes of variation, but at the same time these factors may be correlated with each other. Empirical results to date are mixed (Kempton & Taylor 1974; Weiher & Keddy 1999; Stirling & Wilsey 2001; Wilsey et al. 2005). What are the optimal indices that capture the major axes of variation in SADs? We do not know. Two recent developments are promising. The observation (Pueyo 2006) that the power distribution, logseries and lognormal are all just successive terms in a Taylor series expansion suggests that we may be able to develop a rigorous framework for how flexible an SAD is needed in a particular case (as well as giving some credence to the parameters of these distributions as possibly being more general in interpretation than currently believed). Secondly, a new model, the gamma-binomial or gambin (Ugland et al. 2007), seems to be able to fit a great many datasets well while having only a single parameter that seems to do a good job of discriminating along gradients.

## 21. Further perspectives

Like any field, the study of SADs has had successes and failures. A major success is the frequent measurement of SADs in a wide variety of taxa and geographic areas leading to the establishment of the relative universality of the hollow-curve SAD law. Another major success is uncovering a variety of tantalizing possible empirical patterns that go beyond the hollow-curve. A final success is that the SAD has inspired a great deal of theoretical development in community ecology. Against these successes must be weighed several failures. These include not firmly establishing any empirical patterns beyond the hollow curve and a failure to develop tools to differentiate how much of the patterns are due to sampling effects vs. other more ecologically based effects. Probably the biggest shortcoming to date has been the lack of strong inference where in an extreme proliferation of mechanistic models remains largely untested.

How can we bring strong inference into the field of SADs? Platt (1964) not only argues that we must bring theories into competition with each other, which has happened often enough in the study of SADs (Wilson 1991; Wilson et al. 1996; Etienne & Olf 2005), but the theories must make distinct enough predictions that we

can have a decisive test. Similarly, Lakatos (1978) suggests that it is the quality and novelty of predictions that make for a successful research program.

SADs, like most of ecology, will never find the kinds of predictions that physics makes and which Lakatos praised. Ecology does not make predictions that are accurate to five decimal places like physics does. Instead, Rosenzweig & Abramsky (1997) argues that not just SAD theory but all of ecology does and should proceed by 'dipswitch testing'. What ecology does well is to make a lot of binary predictions. A single binary prediction that is empirically confirmed is weak evidence for a theory (a priori 50 /50 odds). But if, like a dipswitch, we have enough binary predictions strung together, then it creates a strong test that is achievable in ecology. This of course assumes that the model making these multiple predictions is parsimonious and not over-parameterized.

So where does the dipswitch of multiple predictions emerge in the study of SADs? We have argued the greatest failing in the study of SADs is the development of theories that make only a single prediction – the hollow-curve shape. We advocate placing SADs into a larger ecological context, such as the abiotic environment, the trophic level in a food web, or the status as invasive species. This will lead to many predictions resulting in stronger testing and simultaneously demonstrate exactly how centrally SADs are embedded in ecology as a whole. These more integrated SADs are much more likely to increase our understanding of the mechanisms that lead to hollow-curve SADs. In a sign of the strength of these more integrated approaches, it is possible to imagine controlled, manipulative experiments (field or microcosm) that test such integrated theories; heretofore SADs have depended entirely on observational data. These ideas of integration have been the main themes identified throughout the theoretical, empirical and statistical sections of this review. We summarize them into a top dozen list of future directions for going forward in the study of SADs.

## 22. Quantitative relations

Many people have sought to go beyond the simple characterization of a community by the two numbers ST and NT, yet stop short of describing the full distribution S(N), by adding one further single number which will describe the evenness or diversity or dominance within the community. Some of these relations have been explored for particular distributions by previous authors, but a comparative anatomy is lacking, and the lognormal distribution has received essentially no attention of this kind. The statistical variance to be expected in the usual Shannon diversity index, H, is also discussed for the various distributions.

The canonical lognormal and brokenstick are one-parameter distributions. Therefore if ST is given, leading to unique relations of ST versus J for these two species-abundance distributions. The general lognormal, geometric series, and logseries are twoparameter distributions, leading in each case to a one-dimensional family of curves of ST versus J. Unique curves may be specified by assigning a value to the remaining parameter (i.e., by specifying y for the lognormal, k for the geometric series, a for the logseries). Such S versus J relations may be converted to species-area relations by adding the independent biological assumption that the number of individuals is roughly proportional to the area, A:

$$J = pA ,$$

where p is some constant. This assumption is of doubtful validity, but may serve as a reasonable estimate in island biogeographical contexts, with "island" interpreted in a broad sense (MacArthur and Wilson, 1967). Preston (1962) and MacArthur and Wilson have shown that the canonical lognormal distribution in conjunction with eq. 1.5 leads to a species-area curve that accords with much field data. This work begs the question of where the canonical lognormal came from in the first place. In Section 5 it is shown that for all reasonable lognormal distributions (the canonical lognormal being merely one special case) one gets species-area curves in rough agreement with the data. Although none of these relations are simple linear regressions of  $\ln ST$  on  $\ln A$  (they have a steeper dependence of S. on A for small A than for large A), they point to the approximate rule

$$\ln ST \approx x \ln A + (\text{constant})$$

with x in the range around 0.2 to 0.3. This agrees with the data (Table 5), and suggests that the property is a rather general consequence of the lognormal speciesabundance distribution (not just of the special canonical distribution). We also note the species-area relations predicted by eq. 1.5 in conjunction with the brokenstick distribution (significantly steeper than the lognormal curves), and with the geometric series or logseries distributions (significantly less steep than the lognormal curves).

It is noted that sampling distributions often tend to be of logseries form (e.g., Boswell and Patil, 1971). One consequence is that if the species-area curve reflects sampling properties, with  $A$  being a simple measure of sample size, the relation may be

$$ST \propto \ln A + (\text{constant}).$$

Here  $a$  is a parameter of the logseries distribution. This point is briefly discussed and applied to some field data in Section 6. Estimates of the fraction of species likely to be present in small samples from the lognormal and the broken-stick distributions are also given.

A series of appendices sets out the mathematical properties of the various distributions treated in the main text. Such properties as have been discussed by earlier authors are simply listed, whereas the new work is usually developed somewhat more fully. The appendices are not exercises in mathematical pedantry, but form the backbone of the paper. They are intended to be useful to those who seek a thorough understanding of the morphology of the various distributions. On the other hand, the main text simply quotes the results as they are required, and is designed to present the main points in a self-contained and generally intelligible way, free from mathematical clutter.

## 23. Specific Distributions

Some of the salient forms proposed for the species abundance distribution  $S(N)$  are now reviewed, both with respect to theoretical ideas which lead to the distribution, and to corroborative evidence from field data. Note that while specific biological assumptions imply a unique  $S(N)$ , the converse is not true; a variety of different circumstances can imply the same  $S(N)$ . This lack of uniqueness in making ecological deductions from observed  $S(N)$  discouraged MacArthur (1966). Even so, worthwhile distinctions can be made between properties which stem from the statistical Central Limit Theorem as opposed to broad biological features.

## 24. Log-normal Distribution

At the outset, there is a need to distinguish two qualitatively different ecological regimes, commonly referred to as those of opportunistic and of equilibrium species. In the former limit, the ever-changing hazards of a randomly fluctuating environment can be all-important in determining populations, and thus relative abundances; in the latter limit, a structure of interactions within the community may, at least in principle, control all populations around steady values. The essential point here is that populations tend to increase geometrically, rather than arithmetically, so that the natural variable is the logarithm of the population density. This central point has been particularly stressed by Williamson (1972, Chapter 1), Williams (1964), Montroll (1972), and others.

In the equilibrium regime, a lognormal distribution of relative abundance among the species is again most likely, once one deals with communities comprising a large number of species fulfilling diverse roles. In this event, Whittaker (1970, 1972) and others have observed that the distribution of relative abundance is liable to be governed by many more-or-less independent factors, compounded multiplicatively rather than additively, and again the Central Limit Theorem applied to such a product of factors suggests the lognormal distribution.

Alternatively, MacArthur (1960) and Williams (1964) have noted that a suggestion of Fisher's (1958) concerning community evolution can imply a lognormal distribution. Assuming roughly that beneficial genes are fixed at a rate proportional to population size, the relative abundances of species in a large community will be lognormally distributed. In brief, the lognormal distribution is associated with products of random variables, and factors that influence large and heterogeneous assemblies of species indeed tend to do so in this fashion. Such considerations apply quite generally to multiplicative processes where, as it were, the rich grow richer. Thus the distribution of wealth in the United States could be expected to be lognormal, and data in the Statistical Abstract (1971) show this to be so. Similarly, McNaughton and Wolf (1973) have shown that the international distribution of human populations among the nations of the world, and even the distribution of the gross national products of nations, is lognormal.

The essential point to grasp is that the general lognormal species abundance distribution requires two parameters for a unique specification. These two parameters may be chosen to be  $a$  and  $y$ , in which case other interesting properties of the distribution such as  $S_0$ , and the overall  $ST$  and  $J$  follow. Alternatively, given the quantities  $ST$  and  $J$ , which are of direct biological significance, the distribution is again uniquely described, and all other properties follow. Preston's (1962) canonical hypothesis, which will be more fully discussed below, may

conveniently be mentioned here, as it is the only reason for the orgy of notation leading up to the definition of the cumbersome parameter  $y$ .

This is now a one-parameter family of canonical lognormal distributions. Given  $ST$ , all else follows: the shape of the distribution is uniquely specified; unique values of  $J$  and of various diversity indices may be calculated; there is a unique species-area relation. The hypothesis has a purely empirical basis. In view of its predictive successes, particularly as to species-area relations, it is surprising that no theoretical justification has previously been attempted.

As remarked by MacArthur (1960), the lognormal abundance distributions in communities of opportunistic creatures reflect nothing about the structure of the community. Such patterns for opportunistic species have been documented by Patrick, Hohn, and Wallace (1954) and Patrick (1968). In steadier ("equilibrium") communities, fits to lognormal species-abundance distributions have been described for a wide variety of circumstances, including geographically diverse communities of birds, intertidal organisms, insects, and plants (Preston, 1948, 1962; Willants, 1953, 1964; Whittaker 1965, 1972; Battli, 1969). Excellent reviews have been given by Whittaker (1970, 1972), who notes: "When a large sample is taken containing a good number of species, a normal distribution is usually observed, whether the sample represents a single community species per Octave or more than one, whether distributions of the community fractions being combined are of geometric, lognormal or MacArthur form" (Whittaker, 1972, p. 221). Gauch and Chase (1975), who have just produced a useful computer algorithm for fitting normal distributions to ecological data, reexamined the data originally surveyed (and fitted by eye) by Preston (1948), and showed in one typical instance that 96% of the variance in the observed distribution could be accounted for by a lognormal.

Preston (1962) reviewed a considerable body of material and showed that in all cases the shape of the distribution corresponded roughly to the special value  $y = 1$ . This "canonical hypothesis" has been further discussed by MacArthur and Wilson (1967), and the ensuing unique  $S$  versus- $J$  relation applied to explain much species-area data. Another rough rule, first noted by Hutchinson (1953) and subsequently confirmed by a growing amount of field observation, is that  $a \sim 0.2$ . (The rule holds true even for the international distribution of human populations, or of the gross national products, referred to above.) Reviewing the current status of the lognormal distribution, Whittaker (1972, p. 221) observes "the constant  $a$  is usually around 0.2." This enigmatic rule has prompted many speculations, from Hutchinson's relatively cautious "it is likely that something very important is involved here" (Hutchinson, 1953, p. 11), to one recent ecology text that indulges in the thought that "it does seem extraordinary that the constant should have the same value no matter the size or reproductive capacity of the organism, whether we are dealing with diatoms, moths or birds. Perhaps it bears some subtle relationship to the range of variation in the earth's environment. A more prosaic explanation of these two rules will now be offered. They appear to be approximate mathematical properties of the lognormal distribution, once  $ST$  is large.

## 25. MacArthur's Broken-Stick Distribution

If attention is restricted to Communities comprising a limited number of taxonomically similar species, in competitive contact with each other in a relatively homogeneous habitat, a more structured pattern of relative abundance may be expected. As pointed out by MacArthur (1957, 1960), and lucidly reviewed by Whittaker (1972), if the underlying picture is one of intrinsically even division of some major environmental resource, the statistical outcome is the well-known "broken-stick" distribution. This is the distribution relevant, for example, to collecting plastic animals out of cornflakes boxes, assuming the various plastic animal species to have a uniform distribution at the factory. The most thorough treatment of the statistical properties of the relative abundances within a group of species, which apportion randomly among themselves a fixed amount of some governing resource, is due to Webb (1974). He not only shows that the familiar broken-stick distribution is the average outcome, but also considers the statistical fluctuations to be expected about this average. The broken-stick distribution of relative abundance is considerably more even than lognormal ones. It is characterized by a single parameter,  $ST$ . Thus once the number of species in the community is specified, diversity indices and species-area relations uniquely follow.

For appropriately restricted samples, such broken-stick relative-abundance patterns have been found, for example, by MacArthur (1960), King (1964), and Longuet-Iliggins (1971) following Trainer (1969), for birds; by Kohn (1959) for some snails; and by Goulden (1969), Deevey (1969), and Tsukada (1972) for microcrustaceans deposited in lake-bed sediments. As pointed out by Cohen (1968), and reviewed by Pielou (1969) and others, the observation of a broken-stick distribution does not validate the very specific model initially proposed by MacArthur (1957, 1960). It does indicate, however, that some major factor is being

roughly evenly apportioned among the community's constituent species (in contrast to the lognormal distribution, which suggests the interplay of many independent factors).

## 26. Geometric Series and Logseries Distributions

Let us consider again a relatively small and simple community of species, whose ecology is governed by some dominant factor; the opposite extreme to an intrinsically even (or random) division of resources is one of extreme "niche preemption." In its ideal form, this limit sees the most successful species as preempting a fraction  $k$  of the niche, the next a fraction  $k$  of the remainder, and so on, to give a geometric series distribution of relative abundance. An equivalent way of framing this hypothesis is to assume that all species are energetically related to the other species in the community, the magnitude of the relation being proportional to the species abundance; the addition of another species then requires the same proportional increase in the abundance of all other species (Odum, Cantlon, and Kornicher, 1960). It does not seem to be commonly appreciated that the ensuing species-abundance distribution discussed by these authors, and in particular their  $ST$ -versus- $J$  relation, is precisely that of the geometric series distribution. Semantically, this identity is not surprising, as their assumptions constitute a form of niche-preemption hypothesis.

If one considers statistically more realistic expressions of the ideas that in their ideal form lead to a geometric series distribution, one is commonly led to a logseries distribution of relative abundance. For example, suppose that the geometric series niche-preemption mechanism stems from the fact that the species arrive at successive uniform time intervals and proceed to preempt a fraction  $k$  of the remaining niche before the arrival of the next; randomization of the time intervals leads to a logseries distribution (Boswell and Patil, 1971). Kendall's (1948) remarks as to how an intrinsically geometric series distribution of species per genus is converted into a logseries distribution are also obliquely relevant here (Williams, 1964, and Boswell and Patil, 1971). Several other ways of arriving at a logseries distribution are comprehensively reviewed by Boswell and Patil (1971), and Pielou (1969). The distribution often arises as a sampling distribution, in which form it was first obtained by Fisher, Corbet, and Williams (1943). It has the elegant property that samples taken from a population distributed according to a logseries are themselves log series.

Whittaker (1965, 1970, 1972) has reviewed data from some plant communities, generally with but a few species and either in an early successional stage or in a harsh environment. where the species-abundance distribution approximates a geometric series. The phenomenon of strong dominance may be most expected in such circumstances. McNaughton and Wolf (1973) have also reviewed a series of examples which they interpret as geometric series: however, many of their examples would seem to be fitted better, and certainly at least as well, by lognormal distributions. As we would expect, the simple models of Markovian forest succession presented by Horn (1973) give rise to an explicitly geometric series distribution of relative abundance.

## 27. Contrast Between these Distributions

In short, the broken-stick and geometric or logseries may be viewed as distributions characteristic of relatively simple communities whose dynamics is dominated by some single factor: the broken-stick is the statistically realistic expression of an intrinsically uniform distribution; and at the opposite extreme the logseries is often the statistical expression of the uneven niche-preemption process, of which the ideal form is the geometric series distribution. Both forms reflect dynamical aspects of the community.

However, if the environment is randomly fluctuating, or alternatively as soon as several factors become significant (as they may in general, and must if  $ST > 1$ ), we expect the statistical Law of Large Numbers to take over and produce the ubiquitous lognormal distribution. This species-abundance distribution is in most respects intermediate between the broken-stick and geometric series or logseries extremes. The empirical rules  $a = 0.2$  and  $y = 1$  are probably no more than mathematical properties of the lognormal distribution for  $ST > 1$ .

## 28. Species-Area Relations

A subject of considerable interest, enjoying a growing literature, is the species-versus-area relation for communities of species isolated on real or virtual islands. The above species-abundance distributions  $S(N)$  imply predictions as to the relations between  $ST$  and  $J$ , and these can be turned into relations between  $ST$  and area  $A$  by addition of the biological assumption, the plausibility of which was discussed briefly in Section 1 (Preston, 1962; MacArthur and Wilson, 1967). As long as we are looking at islands or other isolated biota, this

procedure may be justifiable; once  $A$  represents areas of different size from a large homogeneous mainland region, the relation of  $ST$  versus  $A$  is likely to reflect sampling properties.

A unique relation of species versus area may be obtained from the general lognormal distribution by Preston's canonical hypothesis. The relation has been successfully applied, initially by Preston (1962) and in more detail by MacArthur and Wilson (1967), to describe a wide range of data. These authors approximate the canonical lognormal relation  $ST$  versus  $A$  by a simple linear regression of  $\ln ST$  on  $\ln A$ , a procedure that tends to overestimate the slope at large  $A$  and underestimate it at small  $A$ . In brief, the successes of the Preston and MacArthur-Wilson species-area theories are not pathological consequences of their special canonical lognormal distribution, but rather are robust properties of any reasonable lognormal species abundance distribution. It may be argued that such species-area discussions are likely to involve large numbers of species, and therefore that the lognormal pattern of species abundance is the only one to work with here. Even so, the species-area consequences of the opposite extremes of broken-stick and of geometric series or logseries distributions should be mentioned.

### **Sampling Problems and $S(N)$**

Up to this point, it has been assumed that we are dealing with situations in which the full values of  $S$ , and  $NT$  or  $J$  are known. All species in the community are represented in our samples. This assumption has allowed an unclouded discussion of some issues of principle. The assumption is often unrealistic, however, and in practice there will commonly be a need to work with less complete samples in which not all species are represented. To put it another way, our lognormal distributions are always (in Preston's terminology) fully unveiled; the complications introduced by distributions that are not unveiled would be distracting.

The analysis of incomplete samples from distributions  $S(N)$  constitutes a large and significant subject. The following discussion is confined to a few brief comments. As first observed by Fisher, and discussed by Williams (1964), Pielou (1969), and particularly by Boswell and Patil (1971), the logseries distribution can describe sampling distributions under a diversity of circumstances. One consequence is that, if relatively small samples are taken from some large and homogeneous area, the relation between sample area (or volume),  $A$ , and the number of species represented in the sample,  $S(A)$ , is likely to obey the logseries distribution; that is,

$$S(A) = a \ln[1 + A] .$$

If this be the case, a regression of  $S$  on  $\ln A$  will fit the data better than the  $\ln S/\ln A$ , if an attempt is made to fit a relation with a  $\ln S/\ln A$  regression, the coefficient  $x$  thus deduced will be small, and the fit poor.

## **29. List of animation, audio files and movies**

animation Diversity.flv animation Threats to Biodiversity.mp4 animation Urban Biodiversity.flv

## **30. Questions**

- What is SAR ?
- What is SAD ?
- What is the relationship of Fishers-distribution and the lognormal distribution?
- What is Preston's the canonical hypothesis?

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# 14. fejezet - Chapter 13 Spatial Pattern

## 1. Point patterns

It is vital the distinction between treating the information on the spatial arrangement of plants as dimensionless points in a plane or as a mosaic of patches filling the plane. In this chapter, we will examine a number of methods that evaluate certain properties related to spatial pattern using the positions of individual plants in a plane. Several reviews of the analysis of spatial point patterns are available (Diggle 1983; Upton & Fingleton 1985; Cressie 1991), and it is not the intention to repeat a great deal of the material covered in those books. Instead, those methods that parallel the approaches described elsewhere in this book, but using points rather than density or presence, will be emphasized. In general, the kind of data that will be used here is mapped plant positions within a defined study area or plot.

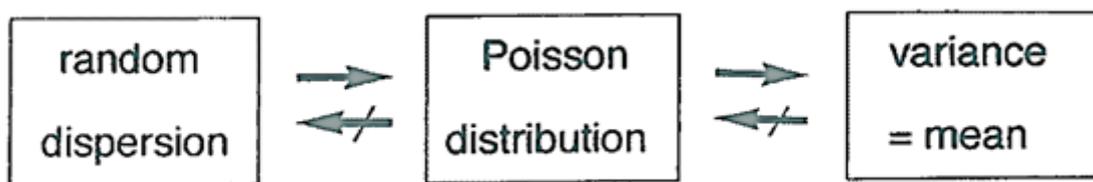
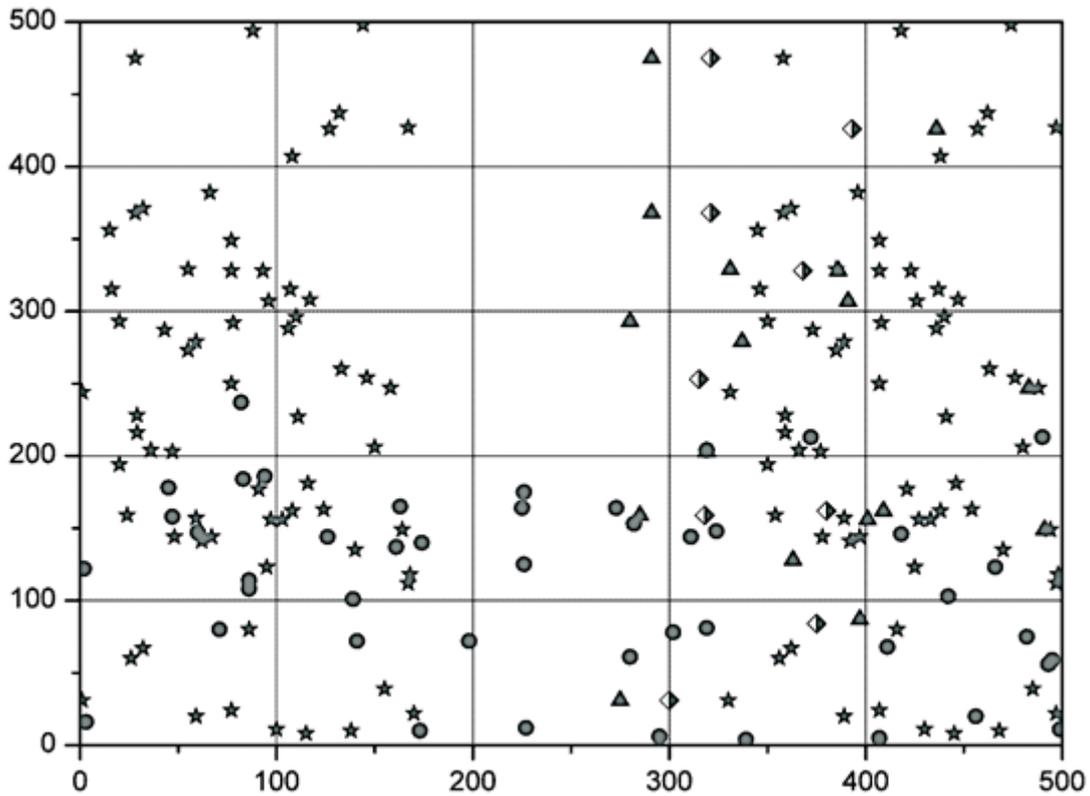


Figure 1. Randomness and some casual relationships.

## 2. The random pattern

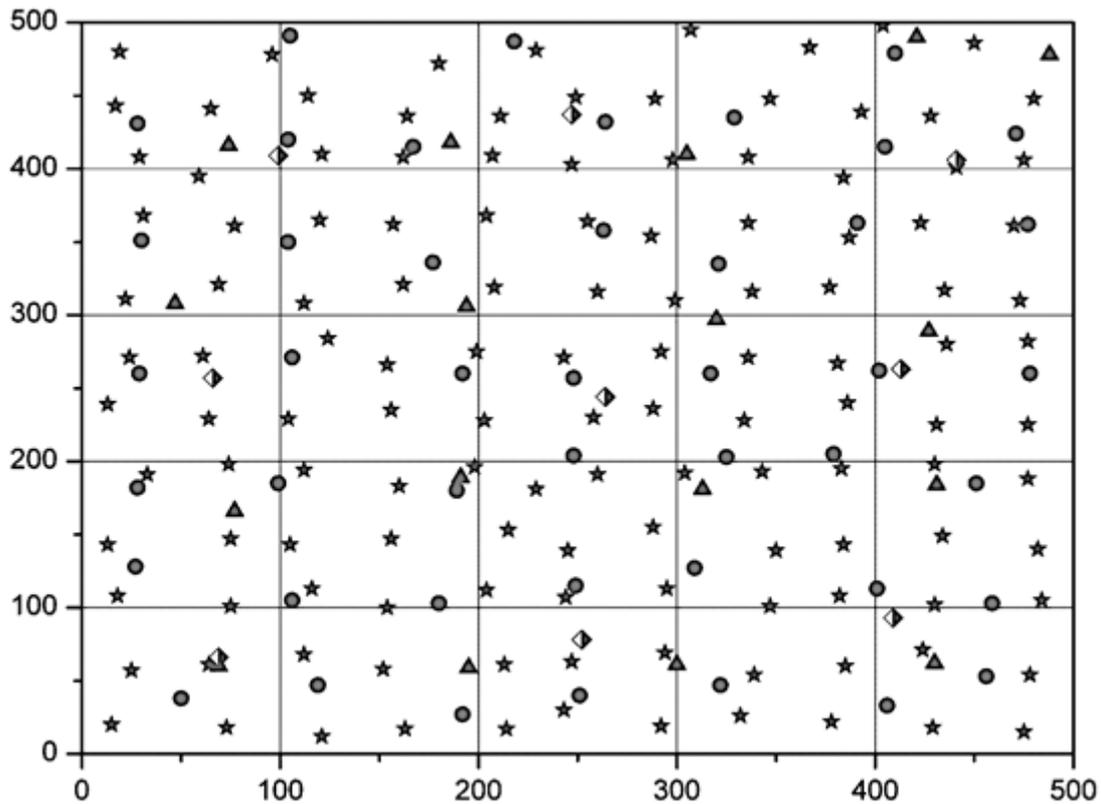
The hypothesis of complete spatial randomness (henceforth CSR) for a spatial point pattern asserts that (i) the number of events in any planar region  $A$  with area  $\#A$  follows a Poisson distribution with mean  $\#A$ ; (ii) given  $n$  events  $x_i$  in a region  $A$ , the  $x_i$  are an independent random sample from the uniform distribution on  $A$ . According to (ii), CSR also implies that there are no interactions amongst the events. For example, the independence assumption in (ii) would be violated if the existence of an event at  $x$  either encouraged or inhibited the occurrence of other events in the neighbourhood of  $x$ . In developing tests of CSR for sparsely sampled patterns the starting point will be property (i), whilst for mapped patterns the starting point will be (ii); thus inferences for mapped patterns will be made conditional on the number of events observed in  $A$ .



**Figure 2.** Realization of CSR events.

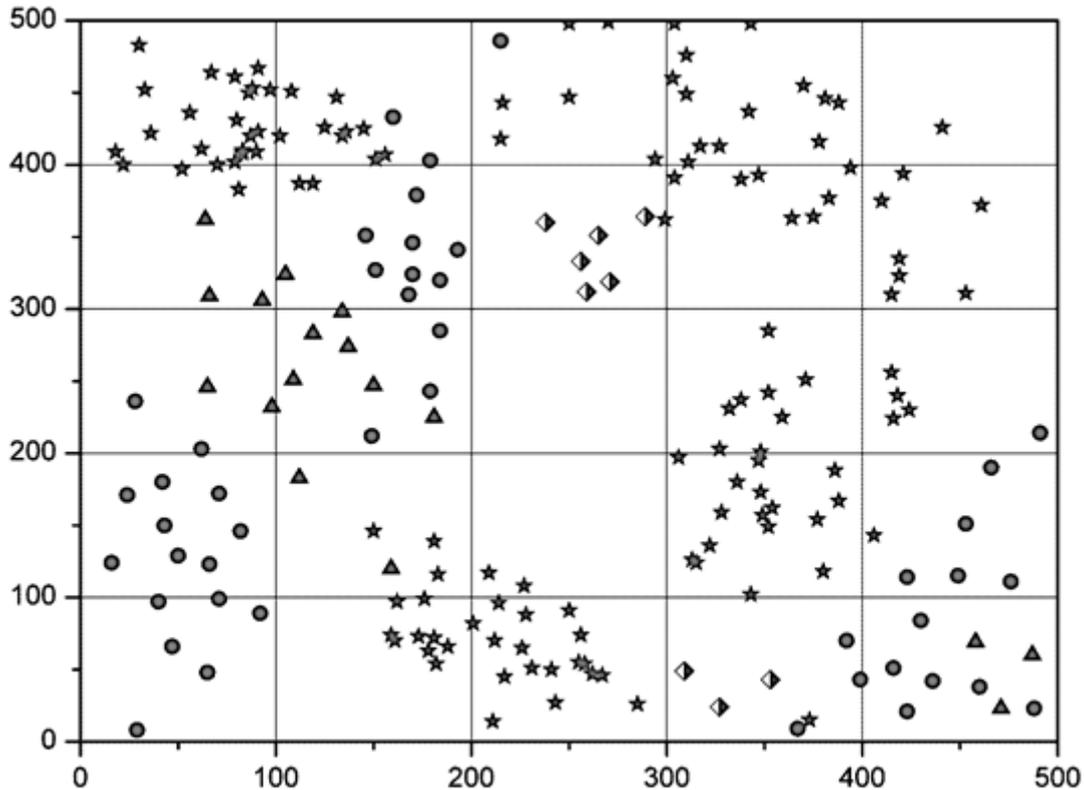
Intuitive ideas about what constitutes a random pattern can be misleading. Any visual impression of aggregation is illusory. Our interest in CSR is that it represents an idealized standard which, if strictly unattainable in practice, may nevertheless be tenable as a convenient first approximation. Most analyses begin with a test of CSR, and there are several good reasons for this. Firstly, a pattern for which CSR is not rejected scarcely merits any further formal statistical analysis. Secondly, tests are used as a means of exploring a set of data, rather than because rejection of CSR is of intrinsic interest. Greigh-Smith, in the discussion of Bartlett (1971), has emphasized that ecologists often know CSR to be untenable but nevertheless use tests of CSR as an aid to the formulation of ecologically interesting hypotheses concerning pattern and its genesis. Thirdly CSR acts as a dividing hypothesis to distinguish between patterns which are broadly classifiable as "regular" or "aggregated".

Pattern is the zero-dimensional characteristic of a set of points which describes the location of these points in terms of the relative distances of one point to another (Hudson and Fowler, 1966). The reason for the interest in a pattern of points is that, with an appropriate choice of scale, even huge objects may be best represented by a point.



**Figure 3.** Uniform distribution of events.

Suppose, for convenience, that the region that we are considering has area  $A$  (in some convenient units) and suppose also that there are a total of  $A$  points scattered at random within this region. We now imagine that the region as a whole is made up of a huge number,  $N$ , of extremely small sub-regions each having size  $A/N$ . Clearly, if we make  $N$  sufficiently large, then there will be a negligible chance of any subregion containing more than one of the points. The random pattern implies that the points could exist absolutely anywhere within the region, so that each of the  $N$  subregions must have an equal probability of actually containing a point. Since there are  $N$  subregions and  $A$  points it follows that this common probability must be  $A/N$ . We now enquire what happens as  $N$  increases towards infinity. Since the preceding argument is precisely equivalent to the argument used in deriving the Poisson distribution as a limit of the binomial distribution, it follows that the probability of observing exactly  $r$  points in a unit area. The result explains why a random distribution of points in space may be referred to as a (spatial) Poisson process: Keuls et al. (1963) describe the arrangement of points as a Poisson forest. An example of a Poisson forest is given in Figure 2.



**Figure 4.** Clustered distribution of events.

A question of immediate interest is the following : Is it reasonable to expect a pattern of real data points to display randomness? Naturally, the answer depends on what these points represent. As an example of a situation in which randomness might well be a reasonable description, consider the colonization of a newly ploughed field by plants that are propagated by airborne seeds. It is surely reasonable to suppose that these seeds land and germinate at haphazardly placed positions within the field so that the initial distribution of the newly germinated plants is entirely consistent with the hypothesis of randomness.

Two contradictory forces are liable to have an effect on the observed plant location. On the one hand, the competition between neighbouring plants is likely to result in some thinning out of close neighbours, so that the pattern becomes rather more regular in appearance. On the other hand, variations in the local ecology will result in some regions being more favourable for growth than are other regions. This will result in an apparent patchiness (or clustering) in the plant distribution. These two effects, and others such as interspecies competition, may well be sufficiently in balance that the resulting much-modified plant distribution may yet retain the appearance of randomness.

In view of the remarkable diversity of mechanisms which may lead to an apparently random pattern, it must be stressed that 'to say that a distribution is random . . . is to say that the pattern has no discernible order and that its cause is undeterminable' (Dacey, 1964): it is clear that 'a pattern is not necessarily indicative of the process which produced it' (Hudson and Fowler, 1966). However, implausible the concept of randomness of distribution may appear on intuitive grounds, the above arguments suggest that it must be the first pattern that we should contemplate as an explanation for our own particular point distribution. Some tests for randomness will be the subject of a later section; we consider first the alternatives to a random pattern.

There are several considerations to be included in our examination and evaluation of methods based on the positions of individual plants. The first is that for an investigation of spatial pattern, techniques that merely distinguish among the three possibilities of clumped, more-or-less random, and overdispersed are not really of interest for the purposes of this book. We want to get more out of the analysis; for example, if the plants are overdispersed, what is their spacing, how uniform is the spacing, is the spacing the same between plants of different kinds? If the plants are clumped, what size are the clumps, what size are the gaps between them? If there

are two or more kinds of plants, are the different kinds segregated or are they aggregated? How does the segregation or aggregation relate to the overall pattern of the plants?

### 3. Univariate point patterns

A large number of methods have been described that can be used to quantify the characteristics of spatial point patterns such as the mapped positions of plants (Diggle 1983). Many of them concentrate on determining whether the plants are clumped or overdispersed as opposed to being randomly arranged in the plane. Spatial dispersion is scale dependent: the same set of points can appear overdispersed at one scale and clumped at another. In this section, one focus will be the investigation of the scale of spatial pattern: given that the plants are clumped, we want to determine the size of the clumps and their spacing.

The size of the clumps combines with the overall density of plants to determine the local density of plants. It is the local density that is of ecological importance, since, if all else is equal, plants with the highest local density of neighbors grow more slowly and experience the highest rates of mortality (Mithen et al. 1984; Silander & Pacala 1985, 1990).

### 4. Neighbor distance methods

The literature on the analysis of point patterns includes a large number of methods based on the distance of each plant to its nearest neighbor. One of the most famous is the Clark and Evans (1954) test that distinguishes random dispersion from clumped or overdispersed based on nearest-neighbor distances. From the point of view of analyzing spatial pattern, the draw-back of many of these methods is that while they can distinguish the kind of dispersion, having found clumping, for instance, they give no information on the size or spacing of the clumps. In other words, they are related to the intensity of pattern rather than to the scale (Pielou 1977a). It is easy to see why this is so by considering that very different spatial patterns can have the same distribution of nearest neighbor distances, for example when all nearest neighbor distances are the same. For this reason, the usefulness of nearest neighbor distances for spatial pattern analysis is very limited.

If the distances from plants to their single nearest neighbor cannot be used to analyze or characterize spatial point pattern fully, an obvious extension is to look at the first and second nearest neighbors or first, second, and third nearest neighbors (Thompson 1956). Clearly, the characteristics of the pattern will be captured more fully as more neighbors are used.

### 5. Plant-to-all-plants distances

The most extreme extension of nearest neighbor analysis uses the distances between all possible pairs of plants and the method is therefore called plant-to-all-plants distance analysis (Galiano 1982b). It looks at the frequency distribution of the distances between all pairs of plants in the plot. Where  $t$  is one of a given range of distances, let  $f(t)$  be the number of pairs of plants,  $i$  and  $j$ , for which the distance between them,  $d_{ij}$ , is in the range of  $t$ .  $f(t)$  is then plotted as a function of  $t$  and the plot is interpreted: large increases in  $f(t)$  indicate overdispersion at scale  $t$  and decreases indicate clumping. For example, if the plants occur in clumps of diameter  $d$  separated by gaps also of size  $d$ , then there will be an excess of distances smaller than  $d$ , due to distances between plants within clumps. There will also be a deficit of distances of length  $d$  and greater because, for most plants, points at distance  $d$  will be outside their own clump. There will also be an excess of interplant distances just under  $3d$  due to pairs of plants in adjacent clumps (Galiano 1982b).

Based on the null hypothesis of complete spatial randomness, the expected value of  $f(t)$  increases linearly with  $t$ . Galiano (1982b) suggests converting the frequencies to 'conditioned probabilities' by calculating the number of distances within each distance class per unit area. Another modification suggested by Galiano (1982b) is that to avoid edge effects, the distances to all other plants should be calculated only for those plants in the center of the sample plot, specifically those further from the edge than the maximum distance examined. Unfortunately, if the plot is circular, and the maximum distance examined is  $2/3$  of the plot's radius, the result is that less than half the plants are fully used.

### 6. A field example

There is a long tradition of *species-accumulation plots* in ecology (Engen 1978, Fisher et al. 1943). These curves also can be used for scalable diversity characterization (Patil & Taillie 1979), and they are defined as follows:

$$ES(m) = S - \sum_{i=1}^S (1 - p_i)^m$$

This is the expected number of species present when  $m$  individuals are drawn at random from an infinitely large population.  $ES(m)$  is also referred to as *expected species-individual diversity*. An important property of  $ES(m)$  is that here the scale parameter has a direct biological interpretation: it is the number of species in a sub-sample of size  $m$ . Plotting  $ES(m)$  against  $m$  may be interpreted as a diversity profile that is essentially a species-individual curve.

The expected number of individuals in an area is proportional to the size of the area. We can calculate the *expected species-area curve* using the following relationship:

$$m = N \cdot \frac{\text{size of the area}}{\text{total area}}$$

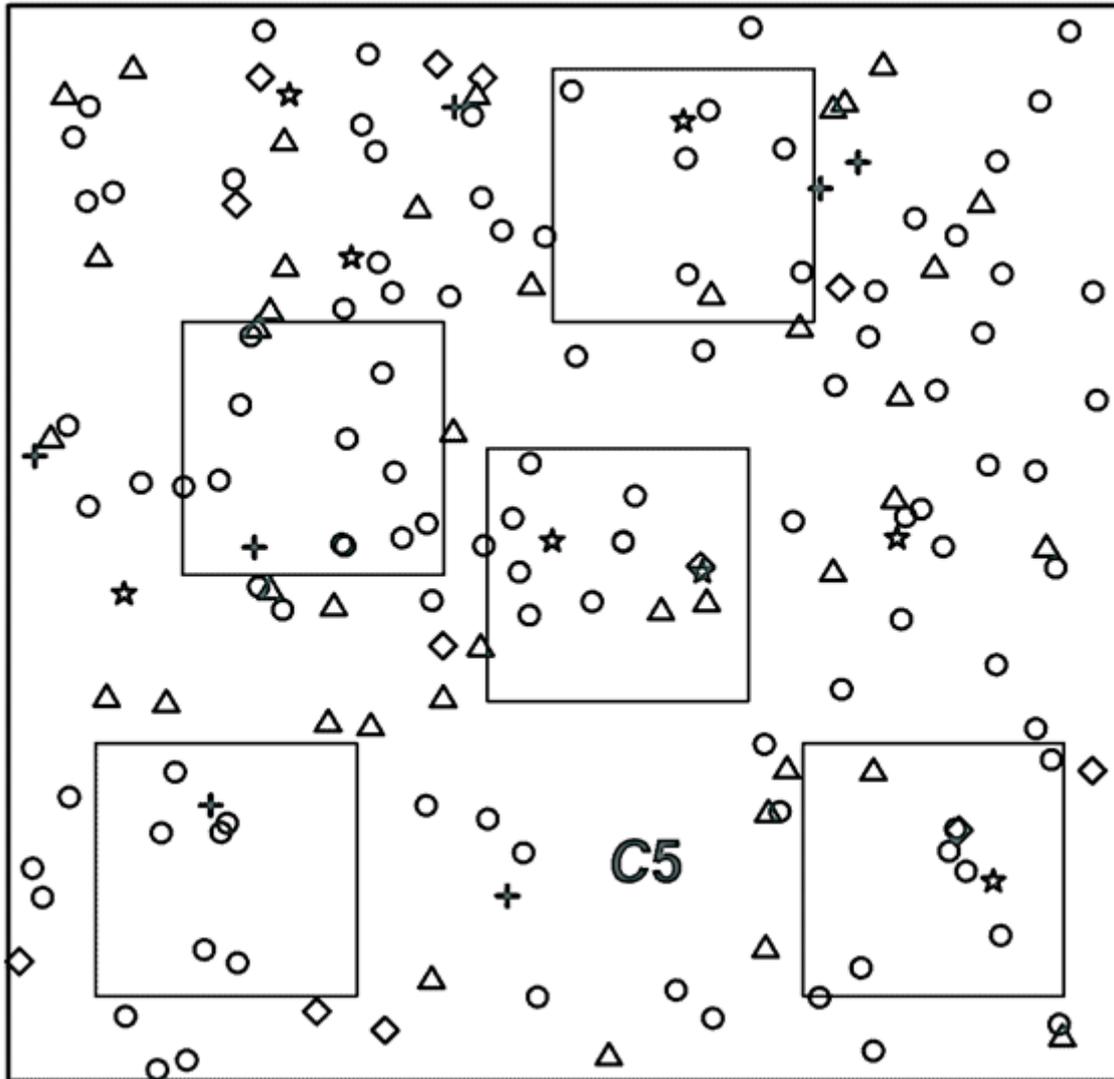
Specialists of different sub-disciplines of ecology traditionally use different representations. In samples from pitfall traps, the estimation of the species richness is based on the number of individuals in the traps. This may be mentioned as a density-dependent representation, because there are different number of individuals in the traps. In plant ecology, density dependent representation of the species richness is also used since field surveys use plots of the same size, yet they usually contain different number of individuals. In other cases, a density-independent representation of the species richness is used. In algology, species number is often determined by identifying 100 (or 400) individuals. A similar technique is frequently used to determine species richness in samples of soil invertebrates. Both of these are density independent representations of the number of species. Tóthmérész (1993, 1998) stressed the importance of these two representation of the species accumulation curves, because they may produce strikingly different ecological interpretations.

Let's look at two communities (A and B). I would like to demonstrate the consequences of a strongly nonrandom pattern using 5 plots in the case of each community. The species composition of the plots is demonstrated by Table 1. The "+" sign means that the species is present in the plot, while the "-" sign denotes that the species is missing from the plot. It is obviously that the two communities are not identical and they are different in diversity (Table 2). Community A is more species rich based on the average number of species, while the total number of species is higher for the community B. The difference is due to the highly different degree of patchiness. In the case of community A almost all species of the community occur. This community is homogeneous with respect to the species composition. Each plot is species poor in the case of community B, but the species composition varies significantly from plot to plot.

**Table 1.** Az A és B közösségekből származó 5-5 kvadrátban lévő fajok.

Plots	A					B				
	1	2	3	4	5	1	2	3	4	5
species 1	+	+	+	+	+	+	-	+	+	+
species 2	+	+	+	+	+	+	-	+	-	-
species 3	+	+	+	+	+	-	+	-	-	-
species 4	-	-	-	-	-	-	-	-	+	-
species 5	-	+	+	+	+	-	-	+	-	-
species 6	+	-	-	-	+	-	+	-	-	-
species 7	+	+	+	+	-	-	+	-	+	-
species 8	+	-	-	+	-	-	-	-	-	+
species 9	-	-	-	-	-	-	-	-	-	+
S	6	5	5	6	5	2	3	3	3	2

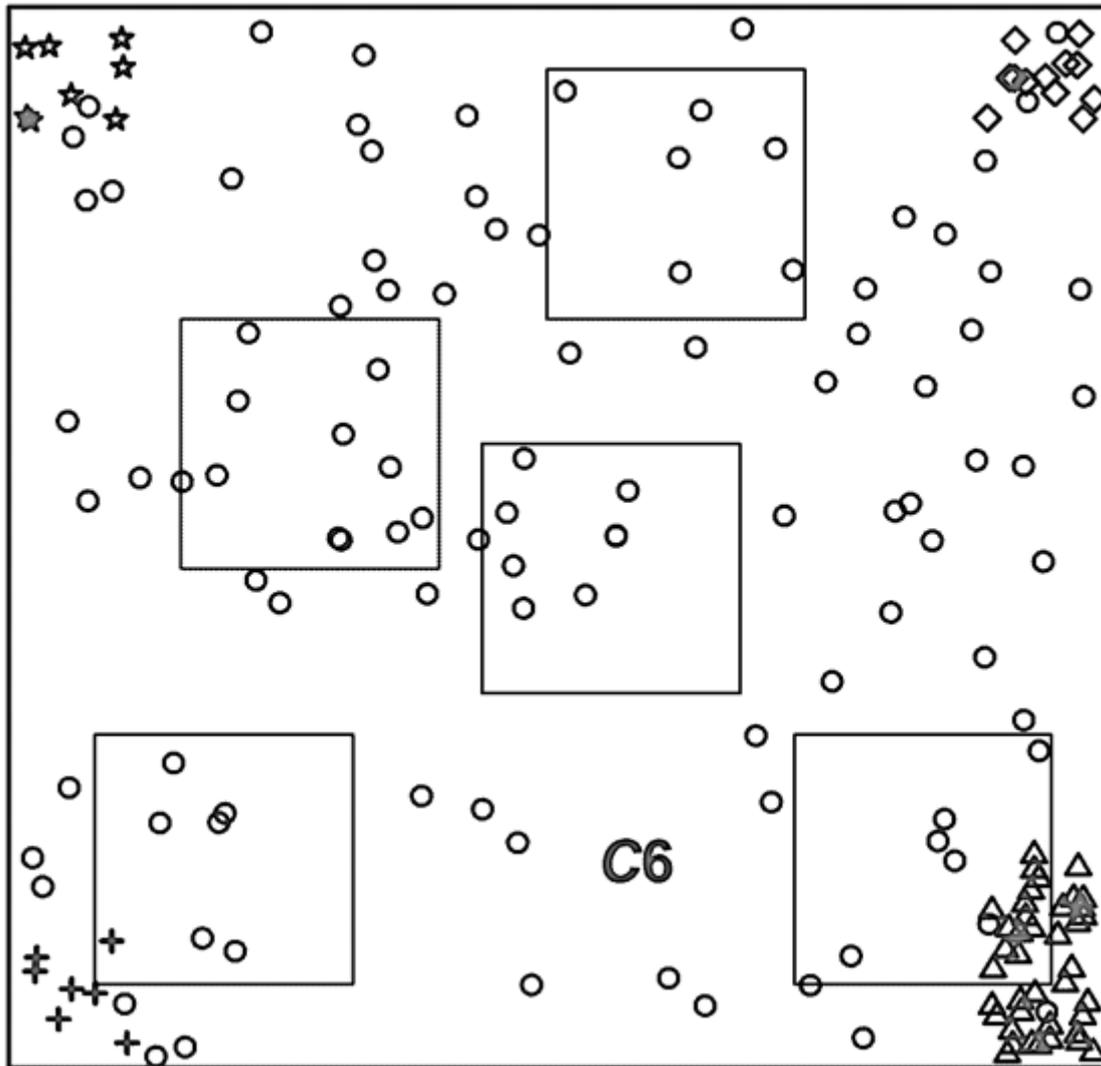
This example also demonstrates well the problem of pooling the samples (plots) which is common practice in ecology. Based on the pooled 5 samples community B is more species rich than community A. Similar problem may occur when the plot size is too large. Inspecting the plots separately this conclusion looks false. The conclusion is just the opposite comparing the average number of species or the median of the species richness of the plots (Table 2).



**Figure 5.** Point patterns of the communities C5 and the sampling plots.

Comparing the species-area curves it is obvious that  $ES(m)$  diversity can only be correctly characterized where individuals were completely randomly distributed. A similar statement is true for the other classic diversity statistics.

Let's look at an actual realization of the C5 community, shown by Figure 2. This is a completely spatially random pattern. Compare this community to the pattern of C6 community shown by Figure 2. The C6 vector of the same community, abundance of the C4 community. The same species and numbers of individuals in the community are the same. The only difference is that the most common species, except in the aggregate behavior of each species is very strong show.



**Figure 6.** Point patterns of the communities C6 and the sampling plots.

## 7. Patchiness and beta-diversity

The beta-diversity measures of the communities are based on the variability of species composition. If the community is homogeneous, ie the species composition is identical everywhere, then there is no changes in species composition. Thus, the beta-diversity of the community is zero. Greater beta-diversity of the community, the greater the variability in community species composition. It is important to stress that the beta-diversity is named as diversity, but in a technical sense it is not diversity. The scope is beyond the classical diversity paradigm.

Contrary to the terminology beta-diversity is not only about the diversity of the community, but its spatial variability as well. That is, the pattern of the community has a vital contribution to the beta-diversity. Thus, methods of beta-diversity measures are different from the classical diversity statistics. One of the simplest procedure to quantify beta-diversity, I am propose to measure it, is apparent when looking at the Table 3. The number of species of the plots is much smaller in the case of community B than the total number of species in the community. This is not really the case for the community A. That is, compare the median (or the average) number of species of the plots to the total number of species (ST). Thus, we get the typical number of species missing from the plots:

$$D_{\text{beta}} = ST - \text{median}\{S_i: i=1, \dots, n\} .$$

If all species are present in all plots, beta-diversity of the community is zero. This way the changes (variability) of the species plot is zero; this is coherent with our scientific intuition as well as with the common sense. The fewer species are present in the plots, the greater the value of Dbeta. This metric is exceptionally useful measure to quantify beta-diversity even if it is a very simple measure. Using the previous example, A and B, it performs well:

$$Dbeta(A) = 2 < 6 = Dbeta(B) .$$

The high difference in beta-diversity (patchiness) is the reason that the average number of species of the plots is higher for the community A, but the total species richness is higher for the community B. It is important to emphasize that the patchiness is an inherent, natural biological feature of the communities which can not be eliminated in a trivial way, like increasing the plot size or the number of sample plots. In some cases, it is conceivable that this method would work, but it would not make sense, since often the patchiness is the most "valuable" feature of the community which should be conserved (and measured).

The above method of measuring patchiness may be criticized, because it only takes into account the number of species missing from the plot, but it does not matter which species are missing. We can compare the species composition of the plots. Similarity of the species composition of two plots can be characterized by the number of common species. Many aspects should be standardized, ie the number of species shared a common compared with fajszámával quadrates. The literature that Jaccard's hasonlóságként wont mention. Value varies between 0 and 1, and this similarity átszámolhatjuk natural diversity in a way that the value is extracted from 1. As usual in such cases the difference in Jaccard's similarity komponenséről talk. The community of the 2nd and 4 kvadrata of the common species 5 and the number of species with two quadrate 6th Thus, the value of diversity:  $1 - 5/6 = 0.1667$ , ie, the two differ slightly quadrate vegetation of the fajösszetétel. AB community for only a single species is the 2nd and 4 quadrates. The number of species with two quadrate 5th Thus, the value of diversity  $1 - 1/5 = 0.8$ , which means that the two quadrate fajlistája 80% different. If all the cases, the quadrates calculate the similarity of species composition, it is essentially a mozaikossági rate obtained. If these values are small, ie, the difference is hardly quadrates vegetation, the vegetation is homogeneous. In the case of an individual to represent quadrates significantly different vegetation patches, then these values are great. Since the beta-diversity and mozaikosság measured in relation to the concept of change, such as beta-diversity Our Approach usually easy to suggest an incorrect interpretation. The above-described methods [0,1] between the values characteristic of the mozaikosságot. This is not to say anything about the variability of 1-2 species fajösszetétel or the order of 20-30 fajnyi the magnitude of change. If for some way to combine the similarity values fajszámokkal, you get such a characterization. Relatively lengthy számolással foreseeable future, however, that in many respects this is little or no different from the previously proposed and calculated relatively easily

$$Dbeta = ST - \text{median}\{S_i: i=1, \dots, n\}$$

A community where the average species richness S and there were N average individual in the plots the expected value in a community with CSR pattern is  $ES(N)$ . This is a kind of null-model. In the case of a structured community with definite pattern the difference between the average number of species and the expected value in a community with CSR pattern is caused by the pattern:

$$|ES(\bar{N}) - \bar{S}|$$

This is a natural and useful measure of the patchiness and/or beta-diversity of the community. This can be expressed as a ratio:

$$|ES(\bar{N}) / \bar{S}|$$

The number of species (S) evidently depends on the number of individuals in the sample and/or plot (N). Thus, it may be useful to standardize the number of species by the logarithm of the number of individuals, as usual in the case of diversity statistics (\*\*\*) ; this is motivated by the fact the the relationship of the number of species and the logarithm of the number of species is linear or close to linear .

The pattern dependent version of the

$$\bar{S} / \log \bar{N}$$

diversity statistics is

$$ES(\bar{N})/\log \bar{N}$$

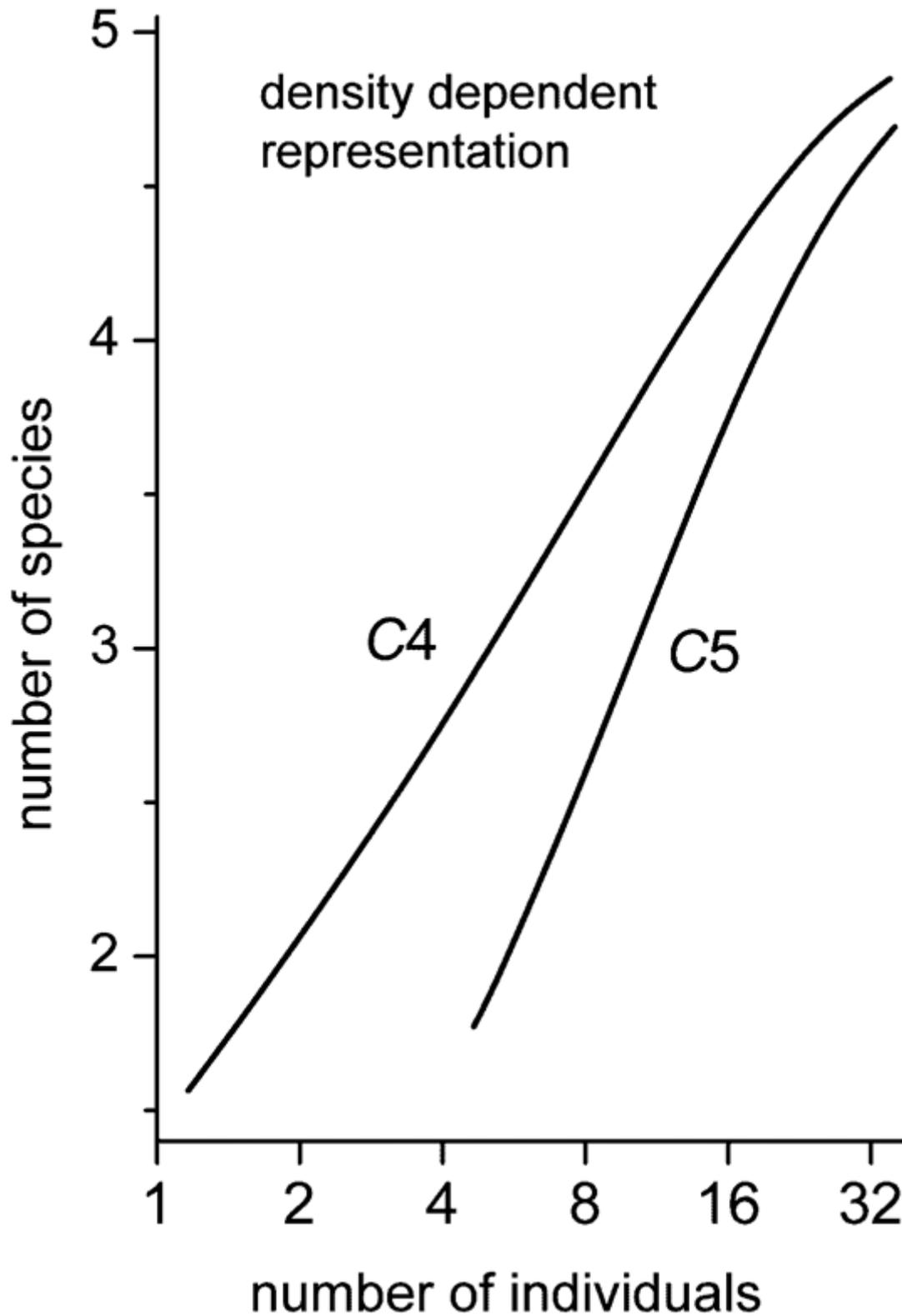
Thus, the difference between the actual pattern and the CSR community:

$$|ES(\bar{N})/\log \bar{N} - \bar{S}/\log \bar{N}| = \frac{|ES(\bar{N}) - \bar{S}|}{\log \bar{N}}$$

*Examples.* Examine the communities shown by the Figure 2 using 5 random sample plots. Both of them have identical species-abundance structure. Thus, they are identical in diversity according to the classical diversity paradigm. Anyway, it is a kind of nonsense inspecting the pattern of communities. They are very different using the spatial dependent beta-diversity measures. In the case of a CSR pattern the expected number of individuals in the plots is 10 specimens; the total area of the community is 100×100 unit; the plot size is 24×24 unit. There are 172 individuals in the total area. Thus, the expected number of individuals is 10 specimens. The expected average species richness of a plot of that size is

$$ESC5(10) = 3.16 \approx 3.2 .$$

In the case of community B the number of species in the sample plots are as follows: 2, 1, 1, 1, 2. The average species richness is  $(2 + 1 + 1 + 1 + 2) / 5 = 1.4$ . Using large number of plots and repeat the sampling for different sized plots we can plot the pattern dependent version of the species-area curve (Figure 3).



**Figure 7.** Density dependent representation of the expected number of species or  $ES(m)$ -diversity profiles.

The above calculations may be used to quantify the difference in the number of species caused by the non-random pattern in the case of a plot of  $24 \times 24$  unit:

$$|ES(\bar{N}) - \bar{S}| = |3.2 - 1.4| = 1.8.$$

Comparing this difference to the CSR pattern this difference compared to the total number of species, it is  $1.8/3.2 \cdot 100 = 56.3\%$ . It is a high value as it is evident based on Figure 3. In the case of the CSR community C5, shown by Figure 3, the number of species are as follows: 2, 3, 4, 3, 4. Thus, the average number of species is  $(2+3+4+3+4)/5 = 3.2$ . This is identical with  $ES(10)$ .

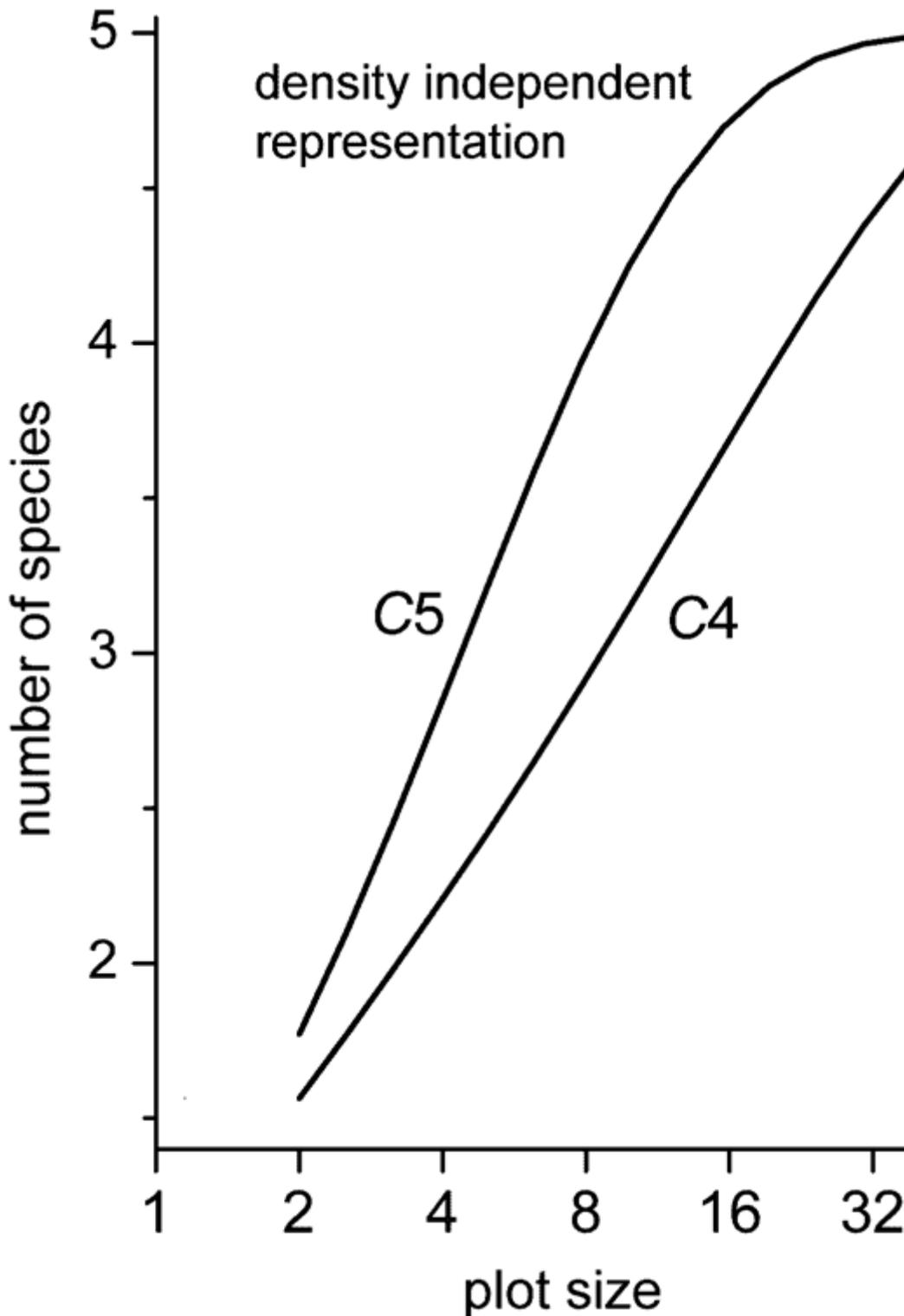


Figure 8. Density independent representation of the expected number of species or  $ES(m)$ -diversity profiles.

## 8. Direct and indirect analysis of diversity

There are preferred species combinations compared to a random, null-model. It means that there are species combinations which are more frequent than expected. Also, there are inhibited species combinations, which occur less frequently than expected under the null model or never occur. Complete spatial randomness provides the neutral or null model. This means that any individual anywhere on the site and the individual may occur independent of each other. If all these are met, then a sufficiently large area, sufficiently numerous plot after placing any plot size, all species combinations should be found. It is evident that the number of possible species combinations in an ST-species community is  $2^{ST}$ . In the case of 3 species it is only 8 species combinations. For 10 species there are 1024 species combinations. For 30 species there are 1'073'741'824 species combinations. And it's not even a particularly species rich community.

The classical, direct approach to calculate the expected number of species is well-known. In the case of a spatially completely random community the species richness of a sample containing  $m$  individuals can be calculated in the following way:

$$ES_{\text{klassisch}}(m) = ST - \sum_{i=1}^{ST} (1 - p_i)^m.$$

In a 4-species community with 130, 45, 17 and 9 individuals the expected species richness in a sample containing  $m = 8$  individuals is the following:

$$ES_{\text{klassisch}}(8) = 4 - \left(1 - \frac{130}{201}\right)^8 + \left(1 - \frac{45}{201}\right)^8 + \left(1 - \frac{17}{201}\right)^8 + \left(1 - \frac{9}{201}\right)^8 \approx 2.686.$$

In the case of indirect approach we calculate the expected number of species in a very different way. Plots were randomly placed in, and count how many species they contain. In the case of a 4-species community there are 32 species combination. The set of the vectors of species combination is as follows:

$$SC = \{ (0\ 0\ 0\ 0), (1\ 0\ 0\ 0) (0\ 1\ 0\ 0), (1\ 1\ 0\ 0) (0\ 0\ 1\ 0), (1\ 0\ 1\ 0) (0\ 1\ 1\ 0), (1\ 1\ 1\ 0), \\ (0\ 0\ 0\ 1), (1\ 0\ 0\ 1), (0\ 1\ 0\ 1), (1\ 1\ 0\ 1), (0\ 0\ 1\ 1), (1\ 0\ 1\ 1), (0\ 1\ 1\ 1) (1\ 1\ 1\ 1) \}$$

The number of species combinations of  $v$  is denoted by  $Card(v)$ . In this way, the expected value of species richness, for this plot size using the indirect approach, is the following:

$$ES_{\text{indirekt}}(m) = \sum_{v=1}^{2^{ST}} p(v) \cdot Card(v).$$

It is evident that this is not really an economical way of calculateing the expected number of species even in the case of species poor communities; it increases by the power of 2 as  $S$ , the number of species of the community increases. The parameter  $m$  in this case may be interpreted as the expected size of individual in a plot (or sample).

Let's create a model for the indirect approach to calculate the model number of species known to be calculated av species combinations  $p(v)$  frequency. If the species  $i$  ( $i = 1, \dots, ST$ ) is the total female piece of the total sampling area, and plot size of the total area of  $p$ -ad section, look for the answer to the question how much the probability that a given species does not occur in the plots. It is obvious that the opposite event, that at least one individual of the species found in the plots. Select the number of species of animals, such as random variables, with, and then look for the probabilities. is the probability that the plots the number of individuals of the species is zero, while the probability that at least one specimen of the species which occur in the plots. Since each individual was likely to be the  $p$  kvadrata and certain specific kvadrata coming to an independent, so a binomial distribution can be described as:

$$P(\xi_i = k) = B(n_i, p) = \binom{n_i}{k} p^k (1 - p)^{n_i - k},$$

ie, the probability of that species will not occur in a random way kvadrata END:

$$P(\xi_1 = 0) = B\left(130, \frac{8}{201}\right) = \left(1 - \frac{8}{201}\right)^{130} \approx 0.00509,$$

This probabilistic model can also be interpreted statistically, due to many kvadrata kihelyezve give them-just not of the species will occur.

8 Specifically, the head of the plot plots containing the size of the total area mintegy 1/25-ödrésze containing 201 individuals, whereas the proportion of individuals are distributed over the area, to be exact,  $p = 8/201$ -ed part. Thus, the first race of the 130-depleted 1000 is placed will have a plot, around 5, which does not occur in this species. It is clear that  $n_4 = 9$  egyedes this species is much more likely:

$$P(\xi_4 = 0) = B\left(9, \frac{8}{201}\right) = \left(1 - \frac{8}{201}\right)^9 \approx 0.6938.$$

This means that it plot of 1000 more than 690 will be empty.

The relative frequency of the species combinations can be calculated as follows:

$$\begin{aligned} p(1,1,0,0) &= P(\xi_1 > 0) \cdot P(\xi_2 > 0) \cdot P(\xi_3 = 0) \cdot P(\xi_4 = 0) \\ &= (1 - P(\xi_1 = 0)) \cdot (1 - P(\xi_2 = 0)) \cdot P(\xi_3 = 0) \cdot P(\xi_4 = 0) \\ &= (1 - 0.00509) \cdot (1 - 0.1608) \cdot 0.5014 \cdot 0.6938 \approx 0.2904. \end{aligned}$$

This means that (1,1,0,0) is the species combination almost 30% of the plots.

The model for ingestion so far to calculate the expected number of species, because we know that  $v = (1,1,0,0)$  fajkombinációjú plots relative frequency  $p(v) = p(1,1,0,0) \approx 0.2894$ . As the number of species in the plots Card  $(v) = S_v = 2$ , so the relative share of the test size plots fajszámának development. All 16 of these fajkombinációra calculated szorzatokát and summarizing them to obtain the expected number of species. This is based on the binomial distribution model

$$ES_{\text{szorzatok, Binomiális}}(m) = \sum_{v=1}^{16} p(v) \cdot \text{Card}(v) = 2.642.$$

This is an extremely sophisticated way of calculating the expected number of species.

It should be noted that the binomial distribution is used instead of the Poisson distribution, which under certain conditions, the binomial distribution is used for proxy. Then

$$P(\xi_i = k) = \frac{(\lambda_i)^k}{k!} e^{-\lambda_i},$$

and

$$P(\xi_i = 0) = e^{-\lambda_i},$$

where  $l_i$  is the average number of individuals, ie. Like in the past to  $p = 8 / 201$ , ie the ratio of plot size of the full study area. Thus, the most common and the rarest species, the proportion of empty plots formed in the following manner:

$$P(\xi_1 = 0) = e^{-\left(\frac{130 \cdot 8}{201}\right)} = 0.00566 \quad \text{and} \quad P(\xi_4 = 0) = e^{-\left(\frac{9 \cdot 8}{201}\right)} = 0.6989.$$

The Poisson distributions based on the approximation of the expected (average) species richness

$$ES_{\text{indirect, Poisson}}(m) = 2.625.$$

Shows that the direct and indirect approach to the analysis of the results of the full three-dimensional randomness nearly identical, and are close to one another indirect approach to the case presented the results of models. Great care would also, if this does not happen. The indirect approach is exactly the significance of the methods to field conditions is very suitable tool for the assurance that from the kölcsönhatásmentes, random null-space model, the extent and manner in which the community structure and pattern.

## 9. Density dependent and density independent representations

It is evident from the previous sections, that an  $ES(m)$  curve plotted against  $m$  can be regarded as a diversity profile. Therefore, it can be used for diversity ordering of communities. Diversity profiles of the studied communities are displayed by Figure 4. The result is generally the same as with the Rényi diversity index family with the technical exception, that this method is sensitive to the dominant species when the value of the scale parameter is low and it is sensitive to the dominants for large scale parameter values.

We can argue, however, that the number of species is plotted against the same number of individuals for each sample. The number of individuals, however, is different on the leaves in the communities. Therefore, we can argue that we should have taken into account this difference of the densities. To plot the number of species that way, the result is significantly different: community Cm3 is more diverse than Cm4 for the whole range of the scale parameter; Figure 5. We prefer to mentioned the first plot (Figure 4) as a density independent representation, because we ignored the differences in the densities of the communities. The second one will be mentioned as a density dependent representation. This is a crucial point of measuring and especially comparing diversities.

## 10. Numerical example

An important property of  $ES(m)$  diversity (as well as the species-individual diversity plot) that the scale parameter has a direct biological interpretation. It is the number of individuals in a sub-sample. When  $m$  is small, just the frequent species can be found in the sub-sample, therefore  $ES(m)$  is small. Increasing the sub-sample size, the expected number of species also increases. Plotting  $ES(m)$  against  $m$ , a diversity profile is received. In fact, this is a species-area curve. It is well-known that the number of species in the sample depends on the number of individuals. This relationship, however, is not linear.

Let see a numerical example. Compare the number of species of three plant communities. Suppose that the number of individuals is 10 for the total study area, which is the same for each studied community. The first community is denoted by E, the second one by F, and the third one by G. The relative abundance structure of the community G is totally identical with that of E. The only difference is that the density of the community G is less than the density of community E. The ratio is

$$\text{density}(E) : \text{density}(G) = 2.5 : 1 .$$

The abundance vectors are as follows:

$$n(E) = (1000, 500, 250, 250, 150, 100, 100, 75, 50, 25),$$

$$n(F) = (1100, 625, 263, 175, 125, 75, 50, 37, 27, 23),$$

$$n(G) = (400, 200, 100, 100, 60, 40, 40, 30, 20, 10).$$

We use a plot size that a plot contains 25 individuals for the communities E and F. The density of community G is less than the density of E or F. Therefore, the number of individuals for the same plot size is just 10, because

$$N(E) : N(G) = 25 : 10.$$

We can calculate the number of species for that plot size for each community using ES(m) diversity:

$$ES_{\{E\}}(25) = 10 - \{(1-0.4)^{25} + (1-0.2)^{25} + \dots\} = 7.071 \approx 7,$$

$$ES_{\{F\}}(25) = 10 - \{(1-0.44)^{25} + (1-0.25)^{25} + \dots\} = 6.185 \approx 6,$$

$$ES_{\{G\}}(10) = 10 - \{(1-0.4)^{10} + (1-0.2)^{10} + \dots\} = 4.862 \approx 5.$$

So, the communities can be ordered according to their species richness in the following way:

$$ES(E) = 7 > ES(F) = 6 > ES(G) = 5.$$

When we compare the species richness by ES(m) for the same number of individuals, then

$$ES_{\{G\}}(25) = 10 - \{(1-0.4)^{25} + (1-0.2)^{25} + \dots\} = 7.071 \approx 7.$$

Now, the order is quite different:

$$ES(E) = ES(G) = 7 > ES(F) = 6.$$

Even this simple example illustrates clearly that the density dependent and density independent representations may produce very different conclusions. The interpretation of the results is certainly not simple. Sometimes a density independent comparison is justified and sometimes certainly not. I would like to mention an example for each interpretation.

We are comparing two communities, where the individuals are distributed randomly and independently of each other, and the relative abundance vectors of the communities are identical. The only difference is that the density of the second community is the double. Using the same plot size, we find that the community with the higher density is more diverse. In this particular case this looks not entirely true, because the relative abundance vectors (i.e., the ratio of the species) and the spatial structures of the communities are identical. The only difference is the density. We may say, that in this case the comparison based on the same number of individuals is more advised. (I'd like to mention a simple, non-biological example. We have a detailed street-map of a big city - just like a vegetation map. We have random plots on the map, and the "number of species" is the number of streets in the plot. Using a xerox machine, we can make a copy of the map using 1:0.5 zoom. Then, using the same plot size we compare the number of streets in the plots of the original size, and the conclusion is that the diminished map is more "species/street rich". Is it? Or, just we have compared them on a wrong scale?

Another example is, when we are comparing animal communities of water bodies; e.g. ponds. The number of individuals supported by the pond is characteristic to the trophic status of the pond. Therefore, in this case we may argue that there is no reason to "eliminate" this information from the data set. The density dependent interpretation fits better to the ecological goals of the study.

Specialists of different sub-disciplines of ecology are using traditionally different representations. In botany always entirely density dependent representation is applied, because plots of the same size is used for the comparison. In algology frequently 100 or 1000 individuals are counted and the number of species is determined in that way. In soil zoology also a similar technique is used to determine species richness. This is a density independent representation of the number of species.

## 11. Effect of spatial and/or temporal pattern

In the case of the previously analysed data sets, the abundances characterizing communities C3 and C4 were based on pooled samples of the stands. It frequently happens in ecological studies. There are many reasons of pooling. The separate samples are too "small" or we would like to characterize the flora of an area, therefore we

pool the samples of a region or a time period, etc. All of the presented calculations were based on pooled samples. Frequently it is worth to look into the details of the separate samples.

Tóthmérész (1996) has produced the following, rather surprising example. He has compared two communities based on pooled samples of 10 plots. Community A was more species diverse than community B (20 vs. 11 species). His conclusion was that, in some respect, it is an artifact because neither of the plots of the community A is richer than the plots of B. The average number of species was 4.7 for the plots of community A and 9.4 for the plots of community B. The much higher number of species was resulted in just by the rather high variability of species composition from plot-to-plot. Sometimes it is mentioned as  $\beta$ -diversity, while the diversity of a plot is mentioned as  $\alpha$ -diversity or just simple as diversity. In the case of the epiphyllous liverworts, a very similar situation arises. The diversity of a moss stand on a leaf may be mentioned as  $\alpha$ -diversity, while the stand-to-stand variability of the community as a  $\beta$ -diversity. The total diversity of the community is composed of by the  $\alpha$ - and  $\beta$ -diversity. There are a few difficulties, however, with the measuring  $\beta$ -diversity. The simplest one is that there is no standard, generally accepted measure of  $\beta$ -diversity. The more sophisticated one is that all of the measures of  $\beta$ -diversity looks to be related to the study problem and to the rather general problem of community organisation. Therefore, it is not possible to measure automatically the  $\beta$ -diversity of a community as in the case of  $\alpha$ -diversity. It always involves some modelling.

As a vital conclusion, it should be emphasized that the pooling of samples may be dangerous in the presence of definite temporal and/or spatial pattern, because it mask the variability and may produce artificially high diversity. Naturally there is no such danger, when we would like to know just the total species pool, etc.  $\{ \text{species pool} \}$

## 12. List of animation, audio files and movies

animation Ecological Succession Animation.flv

## 13. Questions

- What is a species-accumulation plot?
- How the species-area curve is plotted?
- What is measured by beta-diversity?
- What is the difference between density dependent and density independent representations?

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# 15. fejezet - Chapter 14 Indirect analysis of patterns

## 1. Biodiversity: The economist's view

Economists use diversity measures at least as frequently as ecologists. This motivates the following review of the economist's view of diversity. Apart from the level at which biodiversity is regarded, the writer's background also plays a role. In recent developments biodiversity has received attention from economists as well as ecologists. Although the latter may be considered as the founders of the concept (after all both Lovejoy and Wilson were ecologists) economists have introduced other ways of thinking about biodiversity. Because biodiversity has economic value, economists want to measure it. Probably the most straightforward method to measure the actual value of biodiversity is the Contingent Valuation Method (CVM).

The general idea is that to measure biodiversity value one holds a survey on what people are willing to pay (WTP) to preserve it or how much they need to be paid to be willing to accept the loss (WTA). This WTP or WTA can then be used in a Cost-Benefit analysis. The CVM has several drawbacks: apart from ethical problems of valuing organisms there are several biases. The strategic bias: people are trying to influence the final result or they tend to show free rider behaviour, the information bias: do people have enough information to value the subject? and the hypothetical bias: because the market is hypothetical, the respondent may not take the survey seriously. Furthermore since people are less willing to give things up they already have than they are willing to pay for things they don't have yet, the WTA is often much higher than the WTP (Callan & Thomas, 1996). The advantage of the CVM is that it takes into account all the values of biodiversity (i.e. the use value as well as the non-use values).

Several other methods are used like the travel cost method, the hedonic pricing method and estimating household production functions. These methods all measure the direct use of biodiversity only, by valuing it according to the time spent to travel to a reserve, or the prices of real estate in the neighbourhood. Another objection against the previously mentioned value estimations is that these methods estimate the value indirectly and based on the use of biodiversity as a resource thus not representing its real value (Pearce & Moran, 1994).

Looking at biodiversity as a genetic resource is also a popular viewpoint taken by many economists. For example: Sedjo and Simpson (1995), Swanson (1996), Cabo (1999) and Goeschl and Swanson (2002) state that the northern economies rely for their research and development (mostly in the field of biotechnology and medicines) on the southern economies' biodiversity. With this in mind, they have calculated the value of (southern) biodiversity and developed several trade models.

A problem that became especially clear from these trade models is the problem of property rights. The problem is that one cannot claim property rights on biodiversity (although states can claim property rights if they have signed the Biodiversity Convention) but patents can be placed on biological altered organisms. The problem arising from this is that organisms are often retrieved from the South, and then modified in the North. The North then places a patent on the organism and earns the money for it.

In 1992 Weitzman introduced a more bottom up way of measuring biodiversity. In a series of articles in 1992, 1993 & 1998 Weitzman argues that the value of a species is in direct utility and the diversity it adds to the diversity pool. He argues that the more diversity is conserved the more value we conserve and proposes to measure this diversity by measuring genetic distances between species. He does not attach a monetary value to the genes but does provide a ranking criterion with which several projects can be ranked.

In his 1992 paper 'On Diversity' Weitzman first of all introduces a measure of diversity by taking the distance of species  $j$  to collection of species  $Q$  both out of the total collection  $S$ . This distance is equal to the nearest species  $i$  in  $Q$ :  $d(i,j)$ . Weitzman then works this distance measure out to a measure of diversity by relating this distance of a species to its closest relative to the length and branches it adds to the evolutionary tree.

In 'What to preserve?' Weitzman uses this formula, with genetic distances as the distance  $d(i,j)$  and the extinction probabilities of a family of cranes to calculate each crane species' marginal diversity. He then uses this marginal diversity to analyse on which species the conservation money should be spent. In 1998 Weitzman describes this subject in a more extensive paper called 'The Noah's Ark Problem' and introduces a ranking criterion  $R_i$  as follows:

$$R_i = (D_i + U_i)(DP_i/C_i)$$

In this equation stands  $R_i$  for the “the expected marginal distinctiveness plus utility per dollar of species  $i$ ”,  $D_i$  is the distinctiveness of species  $i$ ,  $U_i$  is the direct utility of species  $i$  (including its existence value),  $DP_i$  is the increase in probability that species  $i$  will survive at cost  $C_i$ .

Weitzman then builds a formula to calculate the *expected* diversity under uncertainty. He then sums up the exogenous utility from the conserved species. Finally he introduces a budget constraint and combines the three formulas to a decision rule.

Several arguments have been put forward against the view of Weitzman. Mainwaring (2001) argues that the view of Weitzman is too narrow and pleads for a broader view on biodiversity, including ecosystem services and the role of a species in its habitat. Weitzman’s view may be part of the decision, but his ranking criterion should not be the only thing to consider.

Weikard (2002a) does agree with Weitzman on the idea of measuring diversity but argues that measurement should not be on the species level but on the ecosystem level, because there is very little information on the genetics of species. He then shows that using Weitzman’s framework on the ecosystem level boils down to counting species in ecosystems.

Conservation strategies should according to Weikard be aimed at conserving species-rich ecosystems that are highly dissimilar from other ecosystems. In this case those ecosystems would probably be the before mentioned hot-spots of the world. Brock & Xepapadeas (2004) state that the method of Weitzman in his Noah’s article in 1998 is nice but that the direct utility is exogenous and not linked to the diversity itself. They state that the utility should be endogenous instead and linked to diversity itself, and therefore they develop a welfare-maximising problem under genetic constraints.

The view of economists is fairly different from the view from the one of the ecologists. From the views of the economic side Weitzman’s view is probably most related to the ecologists. Although the distinctiveness doesn’t play a large role in the ecologists view the first signs of interest in this region begin to appear as is shown by the index of Ricotta, who combines taxonomic distance with a parametric index.

If Weitzman’s index doesn’t prove to be a special case of a parametric family, then it might be possible to combine his index with a parametric family in the same way Ricotta has done.

Besides when we lift Weitzman’s criterion to a higher level it boils down to the number of species as Weikard (2002a) has shown. The number of species (species richness) is most of the time related to the indices ecologists use. If there’s no a relation on the species level there’s always the possibility of looking at the problem on the ecosystem level.

The other ways of biodiversity measuring proposed by economists are less useful to try to combine them with the ways of ecologists. The focus is too much on the value and not on the extent of biodiversity itself in case of the CVM, the same goes for the TCM and hedonic pricing method.

The focus on trade and pharmaceutical use is also too value related and the view is too broad to combine them with the ecological indices that measure in general small communities. The method of Brock and Xepapadeas (2004) finally is too theoretical and is in practice hard to use when working with larger communities.

## **2. Weitzman & parametric indices connections**

The main theory of Weitzman has been described in his article ‘On Diversity’ in this article Weitzman builds a main framework, which would be the foundation of his later work on diversity in the articles ‘What to preserve?’(1993) and ‘The Noah’s Arc Problem’(1998). In this chapter I will try to show the connections between the Rényi index and Weitzman’s criterion. I will move from a very theoretical viewpoint with very strict assumptions to a more realistic viewpoint with realistic assumptions.

It all starts with the notion that diversity should be based on the differences between species, arguing that the more different a species is from the others, the more diversity it adds.

If we have a set of species  $S$  with  $n$  number of species and  $i$  and  $j$  are species within this set  $S$  then the distance  $d(i,j)$  should according to Weitzman be a good measure of diversity. The starting point is:

$$d(i,j) \geq 0$$

$$d(i,i) = 0$$

$$d(i,j) = d(j,i)$$

With these distance and rules in mind, Weitzman develops a diversity measure  $V(S)$  of the species set  $S$  with the  $d(i,j)$  as a base. The first measure of diversity developed from this is one that holds only under certain circumstances, i.e. under perfect taxonomy, when the distances between species are ultrametric. Ultrametric distances mean that for any 3 points  $i, j$ , and  $k$  in  $S$  the following is true:

$$\max\{d(i,j), d(i,k), d(j,k)\} = \max\{d(i,j), d(i,k), d(j,k)\} \quad (2)$$

If distances are ultrametric, then the following proposition holds:

$$V(Q \cup j) - V(Q) = d(j, Q) \quad (3)$$

where  $Q$  is a proper non-empty subset from  $S$ . This can be used as a diversity measure. Unfortunately in practise distances are seldom ultrametric.

Because this equation only works when distances between species are ultrametric another equation is filled in, one that works under all circumstances.

$$V(S) = \max_{i \in S} (V(S \setminus i) + d(i, S \setminus i)) \quad (4)$$

The solution for this equation can be obtained once a  $d_0$  has been specified. This  $d_0$  should be an outgroup species, a species not available in set  $S$ , which has an equal distance to all species in  $S$ , for

$$d(i, 0) = d_0 \quad \forall i \in S \quad (5)$$

with for convenience,  $d_0 > d(i,j) \quad \forall i, j \in S$

The most simple form of the Weitzman index appears when the distance  $d(i,j)$  between all species  $n$  of the set  $S$  is equal and a constant:  $d(i,j) = c$ . In this case the Weitzman formula is reduced to:

$$V(S) = (n - 1) * c + d_0 \quad (6)$$

The formula  $V(S) = \max_{i \in S} \{V(S \setminus i) + d(i,j)\}$  implies that to calculate the diversity  $V(S)$  one has to search the  $\max d(i,j)$  of the smallest  $d(i,j)$  per pair of species in the set  $S$  and that this distance is added to the diversity, and then the next species is eliminated from the set until one species remains. Eliminating of this species will add  $d_0$  and complete the total diversity.

But because  $d(i,j)$  is equal for all species, each species adds  $c$  except for the last one which adds  $d_0$ .

Rewriting the formula (6) we get:

$$n = ((V(S) - d_0) / c) + 1 \quad (7)$$

In other words for certain cases Weitzman's formula can be transformed to the number of species, and if  $d_0=c=1$  then Weitzman's algorithm is equal to the number of species.

Now let's turn to the ecological view, and the Rényi index in particular. Rényi's index was first described by Rényi in 1961. It is a parametric index and an extension of the already mentioned index. As the index it used to be an index for the measurement of entropy and was later on adopted by ecologists for the measurement of diversity. It takes the following mathematical form:

$$H_a = (1 / (1 - a)) \log \sum p_i^a \quad \text{with } a \neq 0 \text{ and } a \neq 1 \quad (8)$$

where  $a$  is the scale parameter and  $p_i$  is the relative abundance  $p$  of species  $i$  from the set  $S$ .

If  $a = 0$  this formula becomes the logarithm of the number of species.

*proof:* If  $a = 0$  then  $1 / (1 - a) = 1$  and  $\sum p_i^a = \sum 1 = n$

If we fill in the rewritten Weitzman's formula (7) for  $n$  in (8) we get:

$$H_a = \log \left[ \frac{(V(s) - d_0)}{c} + 1 \right] \text{ if } a = 0 \text{ and } d(i,j) \text{ is equal and constant } "i,j \quad (9)$$

In this situation where  $d(i,j)$  is equal and a constant  $"i,j$  and  $a=0$  Weitzman can be converted to a specific case of the Rényi's index.

Weitzman (1992) does not specify in which way  $d(i,j)$  should be measured, though he seems to prefer genetic distances. Genetic distances between species will never be equal in practise. These distances are based on the fractions of mismatches between DNA-strings from the species. This number increases as the species has been split of the ancestor for a longer time. As species don't split off all exactly at the same time, the distances are very different between species. Apart from that genetic distances are empirical data so there's always a certain random factor included (Graur & Li, 2000).

If the distances between species are measured as the distance in the Linnean taxonomic tree, the only way the distance between species can be constant and equal is at certain forms of the tree. For example when all species are placed in the same genus, or all species are placed in the same family, but all in a different genus within that family.

Another special case, in which the Weitzman formula equals the Shannon-index divided by two, is mentioned by Weitzman (1992) himself: We interpret an ecological community as a set of species  $S(1,2,.. r)$  and the total resources allowing for a total of  $N$  individuals, with  $N_j$  being the number of individuals of species  $j$ . The distance between individuals within a species is zero, the distance between individuals of different species is equal for all individuals in those species and positive.

$N$  is modelled as a line segment from  $[0, N]$  along which each species takes it own niche  $N_j$  and within each niche  $N_j$ , each individual of species  $j$  takes a niche of 1 unit. In mathematical terms:

$$\int_0^N S = \sum S_j, \quad N = \sum N_j \quad (10)$$

Furthermore  $N_j$  and  $N$  satisfy:

$$\lim_{N \rightarrow \infty} N_j/N = p_j > 0 \quad "j = (1,2,..k) \quad (11)$$

where  $\sum p_j = 1$ . Now consider, for the case, that each individual is considered to be a species, whose ecological distance is set by how far it is from other species along gradient  $N$ . Then

$$V'(S;N)$$

represents the "inflated" diversity function obtained from counting each individual as a separate species. Next let

$$V'(S_j;N)$$

be the diversity function for  $S_j$  (in isolation) obtained from considering each individual a separate species. This should of course be zero since all individuals within  $S_j$  are equal, but it is not zero if individuals are considered to be species.

It then seems natural to define the "true" diversity per unit of biomass:

$$V^* = \lim_{N \rightarrow \infty} (1/N) \{ V'(S;N) - \sum V'(S_j;N) \} \quad (12)$$

This function corrects the "inflated" function by subtracting the sum of the diversity added by the individuals considered to be species that are from the same species.

The index is

$$H = - \sum (p_j \log p_j) \quad (13)$$

Now it can be proven that  $V^* = H/2$

To do so we start with a Lemma: Suppose we have a collection  $A$  of  $M$  species-individuals spaced 1 unit apart from each other along a line of length  $M-1$ . Suppose furthermore that:

$$M = 2^K + 1 \tag{14}$$

for some positive integer K, then

$$V(A) = ((M - 1)/2) * \log_2 (M - 1) + (M - 1) \tag{15}$$

The minimum distance between 2 neighbours is one. If we use the elimination procedure, the first time (M - 1)/2 species/points are eliminated, adding ((M-1)/2) x 1 to the diversity. What remains are ((M-1)/2) + 1 species separated by a distance of 2. The next elimination takes care of (M-1)/4 species, adding ((M-1)/4) x 2 (= (M-1)/2) to the diversity. What then remains are (M-1)/4 + 1 species separated by a distance of 4.

This elimination procedure can take place  $\log_2 (M-1)$  times each time adding (M-1)/2, until finally 2 points remain with a distance of (M-1).

Now to continue the proof that  $V^* = H/2$  define that:

$$K_j(N_j) \leq \log_2 (N_j - 1) \tag{16}$$

and

$$K(N) \leq \log_2 (N-1) \tag{17}$$

In the limit as  $N \rightarrow \infty$  and remembering (11) that  $N_j/N$  then goes to  $p_j$ ;  $K(N)$  and  $K_j(N_j)$  can be accurately approximated by integer values.

Applying the lemma to (12) we get:

$$V^* = \lim_{N \rightarrow \infty} 1/N * [((N-1)/2) * \log_2 (N-1) + (N-1) - \sum_j ((N_j-1)/2) * \log_2 (N_j-1) + (N_j-1)]$$

if we use (10) and rearrange we get:

$$V^* = \lim_{N \rightarrow \infty} * [ \{ (2(r-1)/N) + (N-1)/N \log_2 (N-1) \} - \{ \sum_j (N_j-1)/N \log_2 (N_j-1) \} ]$$

If we apply this limit and remember that in  $\lim_{N \rightarrow \infty} N_j/N = p_j$ . We get:

$$V^* = * * (- \sum p_j \log_2 p_j)$$

Which is what we wanted to prove, except for the base of the logarithm, but this can be varied without any real differences, and easily recalculated.

The index is also a special case of the Rényi's index. In fact Rényi's index is an extension of the index. The Rényi index is equal to the index for  $a \rightarrow 1$  as shown by Hill in 1973. Evidently  $\lim_{a \rightarrow 1} 1/(1-a) \log \sum p_i^a = \lim_{a \rightarrow 1} - \sum p_i \log p_i$  (using l'Hospital). In this case under the mentioned presumptions  $V^* = H_a$  only if  $a \rightarrow 1$ . Although these conditions are as theoretical as the previous ones, they are more realistic.

Another way to approach this problem is in the limit of adding 1 species to the already existing set Q (1, 2, 3, ... n). Weitzman's index behaves as follows: adding one species b to the set Q will increase the diversity at least (i.e.: if the elimination path is not changed) with  $d(b,i)$  where  $d(b,i)$  is the distance of species b to its nearest neighbour in Q.

Rényi's index increases depending on a. Species b will add  $p_b^a$  but it will also subtract a little from other species  $p_i^a$ . After all: the total  $\sum p_i^a$  must remain equal to 1. If  $a < 1$  the total  $\sum p_i^a$  will increase and so will Rényi. If  $a > 1$  the total  $\sum p_i^a$  will decrease but due to the logarithm and negative  $1/1-a$  this is transformed into an increase. There is however no general rule on how much exactly this increase is, because this depends on which species' abundances are decreased.

Both indices thus move in the same direction but not with the same speed. Since there is no general rule on how much Weitzman or Rényi increases (Weitzman with at least  $d(k,i)$  and Rényi with some  $p_k^a$  but also decreases a little in the other  $p_i^a$ ), there is no general way of equalling both unless some strict (not realistic) assumptions are made.

Tóthmérész mentioned one other family of indices to be very useful for diversity ordering. This is the logarithmic dominance ordering. This type of ordering is in fact a line connecting sums, in descending order along a logarithmic x-axis. Its mathematical description is:

$p_i = (\log i, \sum_{j=i+1}^S p_j)$  for  $j = i+1$  to  $S$  with all  $p_j$  put in descending order

If the descending order of the species, is the same as the elimination procedure of Weitzman's algorithm and it is plotted against the logarithmic species number and there is a direct, clear connection between the decrease of the sums and  $d(i,j)$  then Weitzman both formula's are each other counterparts. After all  $V(S)$  would then increase with each  $i$  eliminated and the logarithmic dominance plot would decrease.

If distances between species for the Weitzman index are set to be one constant, Weitzman's index collapses to the number of species. If the distances between species is treated as a gradient along which species lie and within the species individuals exist with all equal niches Weitzman's formula collapse to " index. In general both indices are not equal but they move in the same direction. This also goes for the logarithmic dominance index.

### 3. The parametric indices

The indices Tóthmérész (1995) described as the best indices were the Rényi's index and the logarithmic dominance index. Both indices were calculated with Divord 1.70, the program written by Tóthmérész to calculate these indices.

Other indices were calculated as well but their results were less clear. The exp (Rényi), Daróczy, Patil & Taillie and Right-tail-sum diversity all pressed the curves more toward each other so the intersections were hard to distinguish.

The species-individual and species-area curves produced clear results for sample-community relations but diversity ordering was not retrieved from it (both as described by Tóthmérész, 1995).

### 4. The comparison

Because Rényi doesn't have one ordering but a series of orderings I considered the ordering of Rényi's index at intervals. The closest match was for  $a = [0, 0.5]$  and the years separated. This is the result as shown in table 3. As soon as the years are combined the picture becomes more complicated and the results are not exactly the same anymore. A Spearman rank correlation test is still easily passed, though.

In the follow up tables we see the ordering of the Rényi index change further as the scale parameter increases and the results start to differ more and more from Weitzman's index. As the scale parameter increases a Spearman rank correlation test is less and less easily passed.

The orderings provided in table 4 are more or less the same, but the differences that are there, are quite large (as can be seen in the graphs). H05 1986 is by far the most diverse in Weitzman's graph while in Rényi's graph H05 2000 is clearly the most diverse.

The difference is not that large however that correlation can be denied. A Spearman rank correlation test is easily passed at  $a = 0.005$  significance level (not to be mixed up with scale parameter  $a$ ). There definitely is a correlation between the two at this stage of Rényi's index but what about later stages?

The orderings, which are provided by table 8, even fail a Spearman rank correlation test at a 0.05 significance level. Only for values  $>0.05$  than this it's not failed, but this would be a rather high significance level.

So for this case study Weitzman's algorithm and Rényi's index are correlated for the parameter values of  $a = [0, 2]$ . At higher values correlation is only proven for higher significance levels. Especially at the level of  $a = [2, 4]$  the correlation becomes doubtful.

This is rather logical: as the scale parameter increases the index becomes more sensitive to abundance patterns and this is completely ignored by Weitzman's index. At the beginning of the index Rényi's index is more sensitive to species numbers, and these are not ignored by Weitzman's algorithm.

## Chapter 14 Indirect analysis of patterns

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Interesting point is furthermore that most communities are not comparable according to the parametric indices, there are many intersections between the communities. Apparently the stands were quite the same.

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# 16. fejezet - Discussion and Conclusions

This research started with the problem of biodiversity and the indices that are available to measure biodiversity. There are many indicators and indices of biodiversity. In the EU alone an inventory of biodiversity indicators reached the number of 665 indicators (EU, 2002).

Of course indicators is not the same as indices and there are probably fewer indices than indicators (after all indicators are used in general to use simpler things than indices) but the fact that there are whole books written about the subject of diversity indices and there are conferences on the subject does indicate the importance that science confers to the topic.

Because there are so many indices, it is important to know which indices are the same and whether we use more or less the same measures.

The relations between indices are also important because they are often developed from different views on (bio)diversity. If there are relations between indices or they prove to be the same then perhaps we can capture more aspects of biodiversity with one index.

The purpose of this research was neither to make an inventory of all biodiversity indices nor to show all the relations between them. Rather it makes a small contribution to the world of indices and tries to show the relations between two indices that spring forth from rather different viewpoints on biodiversity.

One of the major differences between these viewpoints is the different goals of the diversity indices have. The ecological indices are designed to compare areas at the level of which one has the highest diversity. This is not necessarily true for economic indices, since economy does not focus on diversity per se but on utility, or to be exact on the utility of diversity. A high diversity does not automatically imply a high utility.

This is the reason that Weitzman (1993, 1998) in his follow up articles includes discounting and the utility of separate species, to make his algorithm more economically viable. These modifications however, separate this algorithm further from the ecological indices.

Another consequence of the difference in viewpoints between ecologists and economists is that Weitzman's algorithm violates an ecological axiom about diversity indices. This is the axiom that the maximum diversity is reached in a community in which all species of that community are equally abundant. This is true for the Rényi, Simpson and Shannon index, but not necessarily for the Weitzman index since it completely ignores abundance patterns.

The literature review of this research merely touches upon the vast number of indices there are to measure biodiversity in this world. Nonetheless it tries to show the origin of some of the oldest indices on diversity and the origin and some of the viewpoints of the developers of the indices that are compared in this research.

Besides the history of indices in the literature review, it also tries to touch upon the current state of affairs of biodiversity indices. Although indices become more complicated as time goes by, we have modern computers to help us with the calculations nowadays.

The theoretical framework is a piece of maths in which is shown that under very strict constraints Weitzman's algorithm equals Rényi's index. Unfortunately when these constraints are released this is no longer true. The ordering can still be the same nonetheless, as both indices keep on increasing as the number of species increases, but the amount is not the same.

Perhaps there are other possibilities to link Weitzman's algorithm to the index of Rényi that I didn't find. The subject is interesting enough to look into a bit further.

The case study then finally illustrates the aspects that partially came out of the theoretical framework. It also adds the Spearman rank correlation test to the result, which adds a point to the fact that both indices produce more or less the same results, or that their results are at least correlated.

As the scale parameter  $a$  increases the ordering of Rényi starts to differ more and more from the ordering of Weitzman. The Spearman rank correlation test fails as soon as the value of the scale parameter became larger than 2, unless the significance level is increased (larger than 0.005).

The correlation is most clear in the beginning, but this is logical for Rényi's index is close to species count there and Weitzman's algorithm heavily relies on species numbers (and under constraints is equal to the number of species). Weitzman's algorithm is under constraints also related to the index, which is also in the beginning of the Rényi index ( $a \rightarrow 1$ ).

One has to keep in mind that all data for the case study were taken from the same forest. Although the circles were different it might be interesting to see how both indices work out on larger and different scales, for example when comparing for example a meadow with a forest.

## 1. Conclusions

The research questions of this research were:

- Is there a mathematical relationship between the Weitzman-index and the families of Tóthmérész?
- Is the Weitzman-index part of the parametric families of diversity?
- Can the parametric families of Tóthmérész be considered as a special case of the Weitzman index?
- Does the Weitzman-index provide the same answers concerning biodiversity, as do the families of Tóthmérész?
- Can the indices be combined to one index for biodiversity?

In answer to the first question: Yes there is a relationship between Rényi's index and Weitzman. This does not mean that there is a relation between Weitzman and all the families described by Tóthmérész but that there is at least a relation between one of the families and Weitzman. Weitzman and Rényi are, under very strict constraints, the same.

In answer to question two: Again yes but only under very strict constraints (see theoretical framework)

In answer to question three: This question was only raised in case question two would be answered with a no. Since the two are equal for some special cases, both are the same. So yes but only under strict constraints.

In answer to question four: The answers provided by Weitzman and the families of Tóthmérész are more or less the same. On some parts they differ but the difference is not enough to fail a Spearman Rank Correlation test for this particular example.

In answer to question five: Under strict constraints both indices are the same and can thus be combined. If this is not enough one can combine Weitzman with a family as Ricotta (2004) does. One has to keep in mind though that as soon as Weitzman's algorithm is introduced that the ecological axiom about abundance patterns is violated.

## 2. List of animation, audio files and movies

animation Food Chains.flv animation Save Biodiversity.flv animation Sustainability explained.flv

## 3. Questions

- What is Rao index?
- Define the Weitzmann index
- Explain the economic view of diversity

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# 17. fejezet - Chapter 15 Space Series Analysis

## 1. Functional diversity

Functional diversity has attracted considerable interest; the positive relationship between ecosystem functioning and species richness is often attributed to the greater number of functional groups found in richer assemblages (Diaz & Cabido 1997, Tilman 1997, Hector et al. 1999, Chapin et al. 2000, Loreau et al. 2001). It is not always obvious how functional groups should be delineated, nor which species should be assigned to them. Petchey and Gaston (2002a, 2002b) have recently proposed a new method for quantifying functional diversity (FD). This approach is conceptually similar to the phylogenetic diversity (PD) measure of May (1990b), Vane-Wright et al. (1991), Faith (1992, 1994), and Williams et al. (1994). Both measures are based on total branch length. However, whereas phylogenetic diversity is estimated from a phylogenetic tree, functional diversity uses a dendrogram constructed from species trait values. One important consideration is that only those traits linked to the ecosystem process of interest are used. Thus a study focusing on bird-mediated seed dispersal would exclude traits such as plumage color that are not related to this function. A trait matrix, consisting of  $S$  species and traits is assembled, and then converted into a distance matrix. Standard clustering algorithms are used to generate a dendrogram, which in turn provides the information needed to calculate branch length (Petchey & Gaston 2002b). The resulting measure is continuous and can be standardized so that it falls between 0 and 1. The method makes intuitive sense. For example, a community with five species with different traits will have a higher FD than a community of equal richness but where the species are functionally similar. And, as the complementarity of the species increases, the value of FD becomes more strongly associated with species richness. The measure appears robust and provides qualitatively similar results when different distance measures and clustering techniques are used. FD has been shown to be a powerful technique for evaluating the functional consequences of species extinctions (Petchey & Gaston 2002a) and has the potential to shed light on a number of key issues in ecology, such as species packing and community saturation. To date it has been evaluated using well-censused assemblages in which the functional roles of the member species have been extensively documented. It will be interesting to see how it performs when samples are incomplete and where the functional dynamics are less well understood.

## 2. Body size and biological diversity

In contrast to taxonomic and functional diversity measures, traditional diversity measures treat all species as equal. Species abundances provide the only weighting in heterogeneity and evenness statistics. Other differences are ignored. Species abundance, typically measured as the number of individuals or biomass, is an intuitive measure of species importance. Indeed, niche apportionment models are built on the assumption that relative abundance is a surrogate for the manner in which resources are distributed amongst species. Species abundance data can be time consuming to collect. Oindo et al. (2001) have devised a new index which makes inferences about the relative abundances of species from their body size. It is based on the observation (Damuth 1981) that there is a predictable relationship between body size and abundance. Different guilds have different values of  $k$ . Oindo et al.'s (2001) index uses this relationship to estimate diversity. The new index performed well when tested using assemblages of mammalian herbivores in Kenya and has potential in rapid biodiversity assessment. Further evaluation would be useful, particularly in circumstances where species have been disproportionately harvested.

Diversity indices, sometimes referred to as heterogeneity measures, distil the information contained in a species abundance distribution into a single statistic. Heterogeneity measures fall into two categories: parametric indices, such as log series  $a$ , that are based on a parameter of a species abundance model, and nonparametric indices, such as the Simpson index, that make no assumptions about the underlying distribution of species abundances. Nonparametric measures can be further divided into those that emphasize the species richness component of diversity, for example the Shannon index, and those, for instance the Berger-Parker index, that focus on the dominance/evenness component. Although nonparametric measures are not linked to specific species abundance models the underlying distribution of species abundances can influence their performance. One of the most popular diversity statistics, the Shannon index, has properties that can impede the interpretation of results. On the other hand, the Simpson index performs well, both as a general purpose diversity statistic and when recast as an evenness measure. Communities may be identical in terms of richness and evenness but differ

in the taxonomic diversity of their species. A new class of measures takes this aspect of biological diversity into account. One promising method, the Warwick and Clarke taxonomic distinctness measure, is an extension of the Simpson index and has the advantage of being robust against variation in sampling effort. Confidence limits can be applied to many of these measures.

### 3. Number of Species and Intermediate Disturbance Hypothesis

The intermediate disturbance hypothesis postulates that for any ecological system the diversity of species will be highest when, or where, disturbance is at some intermediate level. The hypothesis simply overlays environmental disturbances that negatively impact one or more species onto the temporal process of community development or succession. Starting with a new, unoccupied patch of habitat the number of species in it will increase as it is colonized. As population densities and species diversity continue to increase, resources will eventually become limiting and the species will compete for these resources. With increased competition, inferior competitors will be displaced and eventually lost. At some point species losses should be greater than gains and the number of species will decline and, in the extreme, end with a single dominant species remaining. Thus, the temporal pattern of diversity can be represented by a unimodal or quadratic curve in which diversity initially increases and then declines over time. Any disruption or disturbance of this process will likely reset the community to some earlier state. High rates of disturbance will keep the community in an early stage with few species and low rates of disturbance will allow competitive exclusion to reduce diversity. Therefore, some rate or magnitude of disturbance should exist that maintains the community in an intermediate developmental state of highest diversity.

At its core the hypothesis makes four principal assumptions: (1) populations and the communities that they form are constantly changing; (2) these changes can result in the gain or loss of species; (3) the process of community change can be disturbed or disrupted by any number of physical and biological events that remove individuals, populations, species, or the whole community; and (4) the change in the number or diversity of species is nonlinear as a consequence of the interaction between species recruitment and the limits placed on continued increases by finite available resources. The first three of the assumptions are straightforward. First, normal processes of individual birth, growth, and mortality will produce change. These changes may be limited to replacement of individuals in stable populations with little measurable change at the community level. It is more likely that populations will fluctuate in size and produce changes in species' relative abundances including complete loss of some species. Second, for any community, there is always some probability of new species immigrating or existing species emigrating or going extinct locally. Third, disturbances that produce losses certainly can occur in any system, but their effects will vary based on their magnitude, frequency, and spatial extent. The fourth assumption is probably the most contested. The increase in species as a habitat is colonized clearly must occur and the rate of increase will decline as both available resources and the pool of available new species decrease with the addition of each new species. Thus the critical aspect is whether after some period of time competition for limiting resources or some other process results in sufficient species losses to cause a decline in diversity.

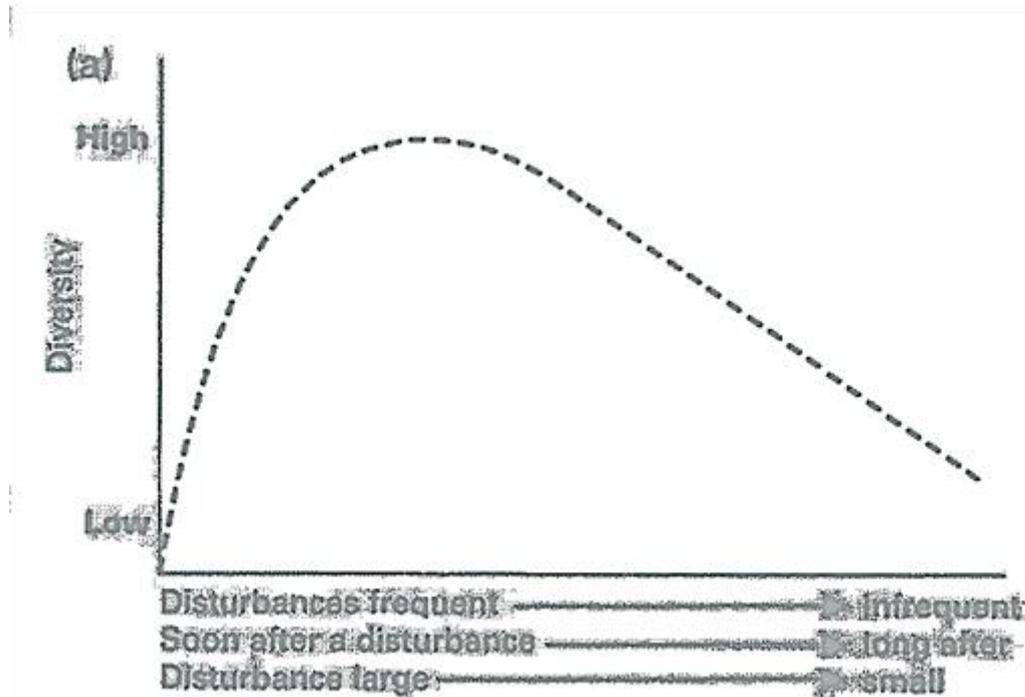


Figure 1. Simple demonstration of the effect of disturbance to diversity after Connell (1969)..

Although the intermediate disturbance hypothesis is most often tied to changes in species associated with succession, it is not really dependent on any particular process of community development. The process can be interrupted or perturbed by weather, fire, flood, drought, herbivores, predators, disease, tree falls, waves, etc. These disturbances can affect any or all species, randomly or selectively. When diversity increases and then decreases as the community develops through time, then some level of disturbance is likely to maintain the community at a state of maximum diversity.

Because of its apparent generality the intermediate disturbance hypothesis has been studied and tested in a vast array of empirical studies of most types of natural communities and habitats, in experimental communities in small laboratory chambers, and in larger ecosystems and landscapes that can include multiple habitats and communities. There have also been a substantial number of theoretical and modeling studies that have tried to develop and test constraints on the hypothesis and its applicability. As a consequence, there is a diversity of opinions about when, where, and to what systems the hypothesis should be applied. Before limiting the hypothesis to one extreme of catastrophic disturbances that remove all species in fragments or patches within a landscape or to the other of noncatastrophic disturbances across homogeneous habitat that maintain high diversity by reducing populations to noncompetitive levels, it is important to examine the historical context of the hypothesis and how it has evolved.

## 4. Background of the disturbance hypothesis

The idea that an intermediate level of disturbance can lead to the highest diversity within a system has been proposed independently by numerous ecologists based on their observations of a variety of communities. Although observations of the phenomenon can be found in studies from at least the early 1900s, J. H. Connell is usually credited with giving the first formal definition and description of this idea as the intermediate disturbance hypothesis in his 1978 Science paper. Connell found the intermediate disturbance hypothesis to be the best of six explanations for the high diversity of species found in the tropical coral reefs and rainforests that he was studying. Alternate explanations included equal chance in which all species are equal and diversity is a function of the environment and species available in a region, 'gradual change' in which environmental changes prevent competitive exclusion; 'niche diversification' or the finer division of resources among competing species; 'circular networks' in which competition is not hierarchical; and 'compensatory mortality' in which noncompetitive mortality is greatest for dominant species. Connell was careful to limit the scope of the intermediate disturbance hypothesis to the main structural species of these two systems, corals and trees. He saw them as representative of communities of sessile, often long-lived, species with dispersal largely limited to the

larval and seed life stages produced through reproduction. He specifically excluded more motile species which have the potential to avoid or quickly adjust to the impacts of disturbance.

In this context, Connell described these diverse systems as dynamic, nonequilibrium communities that did not approach maximal diversity by the coexistence of species which have divided available resources on finer and finer scales. Rather than a balance or equilibrium among coexisting species each with their unique way of using some portion of the available resources, species contested limiting resources with those superior competitors ultimately pushing out the inferior. Within long-lived coral reef and forest communities competitive exclusion is not instantaneous and may take decades to centuries. In these long time periods any number of events can disrupt the competitive process, remove or reduce the abundance of dominants, and make resources more available. Although one can imagine how disturbances such as disease, wind, or waves might exclusively or disproportionately affect large dominant coral or tree species, such types of disturbance are not necessary for disturbance to contribute to higher diversity. Disturbances that randomly remove individuals or parts of the habitat will create areas available for colonization with available resources and reduced competitor abundance. New or previously lost species have the opportunity to colonize these areas with the potential of increasing local diversity.

At its core the intermediate disturbance hypothesis is recognition that environmental change can alter ecological processes and patterns, particularly when the change is of sufficient magnitude, frequency, or spatial extent to cause mortality and the local loss of populations, species, or whole communities. How disturbance disrupts processes, the nature of the processes being disrupted, and ultimately, the consequences for diversity have had their own diversity of interpretations. The most dominant view has been that of physical processes operating at variable frequencies causing interruptions of a successional sequence that progresses from good colonizers to competitive dominants. Even with these constraints intermediate disturbance can be viewed differently. At one end of the spectrum intermediate disturbance can be seen as some frequency of catastrophic or complete removal of the community in patches within a fragmented landscape. If this produces patches of different ages, disturbed at different times then some intermediate frequency of disturbance will maximize the cumulative diversity of all patches. At the other end of the spectrum intermediate disturbance can be seen as part of secondary succession in which noncatastrophic disturbances operating in a homogeneous system keep abundances sufficiently low and resources sufficiently available to prevent competitive exclusion from occurring. In this context intermediate disturbances provide the environmental variability and temporal diversity in resource availability that can produce opportunities for a greater diversity of species life histories or adaptations.

Alternately, the link between high diversity and intermediate levels of diversity can be maintained independent of any of the specific interspecific relationships that are part of succession. For example, island biogeographic theory as proposed by R. H. MacArthur and E. O. Wilson presents an alternate scenario for the colonization of an island or patch of habitat that is neutral to species identities. The number of species present will be a function of the number of species immigrating minus the number of species lost or going extinct locally. Immigration rate will be a declining function of the number of species present, reaching zero when all species in the available pool of species are present. With all species having some probability of being lost, the cumulative extinction rate will increase as the number of species present increases. Therefore, some balance or equilibrium in species number should exist when immigration and extinction rates are equal. Species extinction rates should also be higher when they begin interacting or when population sizes are limited by available resources. Thus there should be a higher noninteractive equilibrium species number that might be expected to precede a lower interactive equilibrium species number. In patchy environments, the catastrophic random disturbance of individual patches will produce a distribution of patches with a mean age equal to the mean disturbance rate. At some intermediate rate of disturbance, the majority of patches will be at an age when they are at or near the noninteractive equilibrium number of species creating the overall highest diversity for the system. Likewise, noncatastrophic disturbance can lower extinction rate by opening resources and keep individual patches at the highest diversity. This approach is not limited to specific types of species, makes no assumptions about competitive dominance or the relative strengths or directions of any interactions. It relies only on the system reaching some dynamic balance between species losses and gains that will change once resources become limiting. Regardless of whether the probabilities of both immigration and extinction are equal or variable among species, some intermediate level of disturbance should produce the highest number of species.

An important question arises as to whether the intermediate disturbance hypothesis is a logical tautology that is unfalsifiable because intermediate disturbance cannot be defined independently of diversity. First, the hypothesis can be falsified if it can be shown that no decrease in diversity occurs as a community develops over time. In this case no intermediate frequency or magnitude of disturbance can increase diversity. Second, disturbance can be defined relative to the life histories or generation times of the species within a community for

disturbance frequency or the degree of mortality for disturbance magnitude. In this sense the extremes of high and low disturbance can be defined with an array of intermediate disturbance rates or magnitudes in between. If diversity is not higher at a reasonable suite of the definable intermediate rates or magnitudes, then the hypothesis is falsified. If however, the extremes cannot be defined, then intermediate cannot be defined and falsification is not possible. This may be a problem for slow-developing communities of long-lived organisms for which it may be difficult to test the hypothesis over an adequate range of measurable intermediate disturbances within one's life span. Nevertheless, if maximum diversity is hypothesized to develop before resources become limiting or interactions increase mortality rates, then the intermediate rate or magnitude of disturbance may be defined as that which limits the use of available resources to some measurable level such as less than 90% of the space that can be occupied.

## 5. Elements of Intermediate Disturbance

There are two principal elements of the intermediate disturbance hypothesis: a temporal sequence of community development or change, and a set of one or more environmental changes that are seen as disrupting the temporal sequence. A nonlinear change in the number of species in a community or any other ecological system is a necessary component of the intermediate disturbance hypothesis. This change is usually seen as unimodal or quadratic with a peak in diversity at some intermediate point in time. This is in contrast with two other potential patterns, a continuous increase in species number over time and an asymptotic increase with species number reaching and stabilizing at some maximum. Assuming that there is some finite pool of available species, then stabilization at this number of species represents the upper limit to diversity. It follows that if over time diversity increases or increases to an asymptote without any decrease, then no frequency or magnitude of disturbance can result in higher diversity and the intermediate disturbance hypothesis would be rejected.

Beyond a pattern of increasing and then decreasing diversity over time, the process by which a community develops is unimportant. If development proceeds in an orderly successional sequence of species or through random colonization, the aspect critical to the intermediate disturbance hypothesis is that diversity peaks at some intermediate stage of the process. On the other hand, the characteristics of the system, especially the taxa or species included, the variability in their life histories, and their trophic relationships, have important consequences to the application and testing of the hypothesis.

Connell was careful to restrict the intermediate disturbance hypothesis to particular types of species when he applied it to the structural tree and coral species in forest and reef systems. It is logical to assume that within these taxa there will be a limited range of life histories such that high to low rates of disturbance can be defined. However, if we included all species from bacteria to vertebrates that might be considered to be part of tropical reef or forest systems, then imposing a single meaningful scale of disturbance is difficult. Disturbance is relative to the taxa being examined and their life histories or generation time. An intermediate rate of disturbance for a bacterial community may be on the order of hours to days while it may be decades or more for corals or trees. A similar argument can be made for the size of a disturbance with large disturbances to a bacterial community being too small to be disturbances to trees. In such complex systems it may be necessary to classify disturbances in terms of frequency, magnitude, and spatial extent simultaneously and identify a combination that maximizes overall diversity. For example, if an intermediate disturbance frequency for trees is on the order of decades, smaller magnitude daily intermediate disturbances for bacteria will occur multiple times within the period of highest tree diversity. This would produce a set of multiple intermediate disturbances of specific frequencies and magnitudes that result in several diversity maxima.

Including multiple trophic levels within the system being considered produces a similar set of problems. Modeling has demonstrated that the degree to which disturbances affect each trophic level can influence the overall impact on diversity. If a disturbance affects all levels equally then an intermediate level producing the highest diversity will exist. Alternatively, if the impact of a disturbance is disproportional there may not be an intermediate level producing the highest diversity. For example, if a disturbance principally causes mortality in a lower trophic level this would open resources at this level and some intermediate disturbance rate should lead to higher diversity at this trophic level. At the same time herbivores or predators in the next trophic level would experience reduced resources because of the lowered overall abundances of prey. This should lead to greater competition, lower diversity in the higher trophic level, and an unknown change in overall diversity. If species at higher trophic levels are more selective in their prey then the changes in their resources with disturbance and the effect on overall diversity are even more difficult to predict.

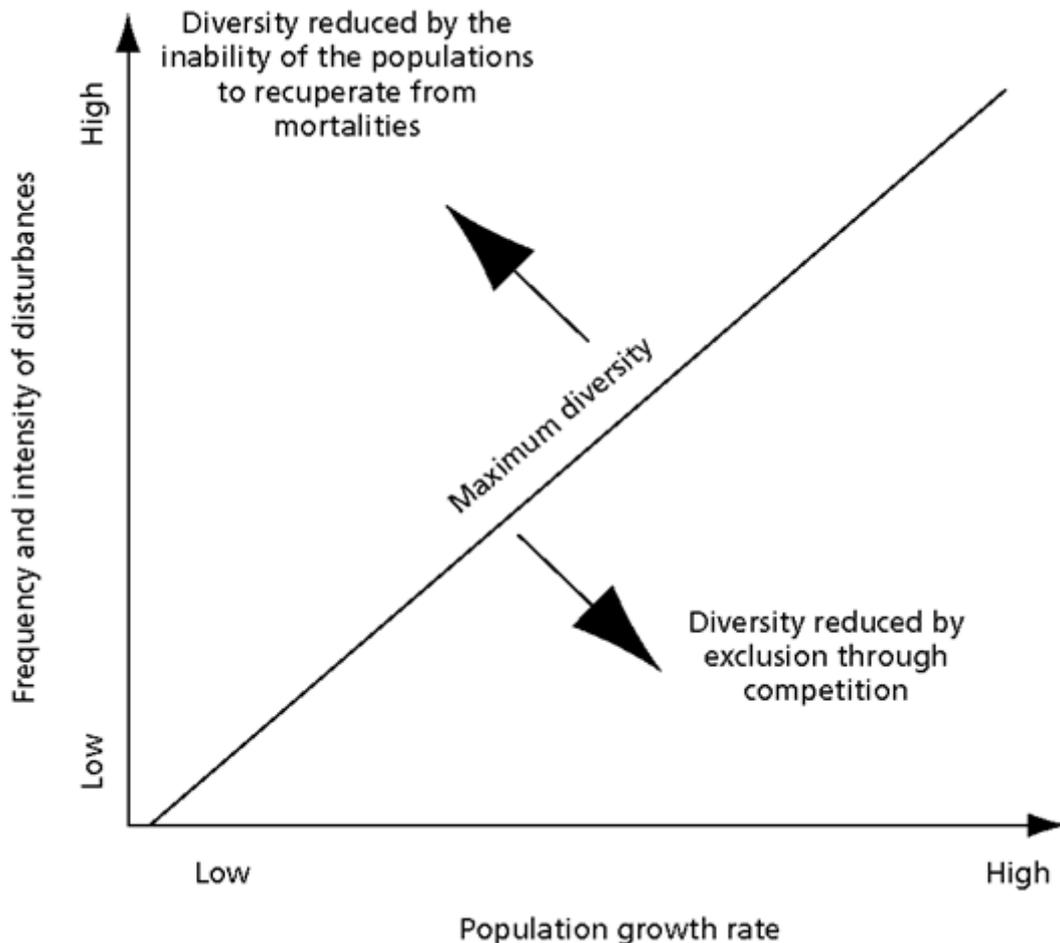
In a similar manner, the degree or number of positive symbiotic interactions within any system may affect directly the relationship between disturbance and diversity. At its core the intermediate disturbance hypothesis

depends on resources becoming limiting and resulting negative effects on abundances and the survival of species. If a significant number of interspecific interactions within a system are positive, then disturbances may actually reduce available resources or the ability of species to utilize them. For such a system no level of disturbance may increase diversity.

## 6. Types of Disturbances

In intermediate disturbance hypothesis, disturbances are any events or processes that produce mortality. Disturbances will vary in frequency, magnitude, and spatial extent and they are usually viewed as unpredictable. Frequency is the most common attribute associated with intermediate disturbances and the effects of changes in disturbance frequency are, perhaps, those most easily seen. In part, this results because the rate at which disturbances occur can be imposed directly onto the temporal change in a system's diversity. Disturbance rate translates directly into a mean age of the community and its diversity.

The magnitude of a disturbance is measured in terms of the mortality it causes which can vary between catastrophic, with complete loss of all individuals of all species, and noncatastrophic with the loss of only a few individuals and possibly no loss of species. Secondary succession is often seen as resulting from disturbances of low to intermediate magnitude. Disturbances of intermediate magnitude and frequency may reduce abundances without causing the loss of any species. The lowered abundances of some or all of the species can free resources, reduce or eliminate competition, and allow coexistence and high diversity.



**Figure 2.** The effect of population growth rate to frequency and intensity influencing the diversity.

Finally, disturbances can vary in spatial extent, affecting all or only certain parts of a system. Because species are usually not distributed evenly, the spatial extent and location of a disturbance can result in the complete loss of some species regardless of the magnitude or frequency of the disturbance. Spatial extent of disturbances is particularly important in patchy environments. In a patchy system, the community within each patch may develop independently and the age and diversity of communities can differ among patches as a function of their

disturbance histories. Within such systems there may be two or more disturbance levels that promote the highest diversity, one for each patch which may vary with size and a mean disturbance rate for the whole system that maximizes the differences in species composition among patches and thus overall diversity. The degree to which the patches are in phase or disturbed at the same time and to the same degree will affect the impact of patchiness on intermediate disturbance.

Disturbances can result from physical or biological processes and the source of a disturbance will determine its impact on diversity. Physical disturbances are the most common ones associated with intermediate disturbance. A long list of physical phenomena including wind, flooding, waves, fire, exposure to extreme heat or cold, increased UV radiation, low dissolved oxygen or anoxia, drought, extreme pH, etc., can cause various degrees of mortality and disturbance. Although the probability of any of these occurring may vary predictably with location or season, we usually see physical disturbances as unpredictable in the degree to which they affect populations and as being fairly unselective in terms of which species are affected. Species will differ in their tolerances to any of these and other physical phenomena, but these disturbances do not target particular species. Biological disturbances most commonly result from disease, herbivory, or predation all of which may target particular species and result in selective disturbance. If the targeted species are dominants then an intermediate level of disturbance is likely to produce higher diversities by making resources available to other species. If biological disturbances cause a disproportionate loss of rare or competitively inferior species, diversity could be lowered by exacerbating the rate at which dominants monopolize resources. This is not to say that biological disturbances are all selective. For example, a grazing limpet might remove all species from all or part of rock, regardless of whether they are food items. This disturbance would not differ from a similar removal through physical scraping.

## **7. Gradients and Landscapes**

The intermediate disturbance hypothesis has been applied and tested in larger systems, in particular to spatial patterns of diversity along gradients and within landscapes. Gradients and zonation patterns often have communities dominated by different species at opposite ends with a mixture often with higher diversity at intermediate locations. The diversity pattern is consistent with the effects of intermediate disturbance, but other factors can contribute to this pattern. Gradients can result not only from unidirectional variations in disturbance but from variations in one or more environmental variables. Gradients in factors such as temperature, light, pH, nutrients, soil type, rainfall, or salinity can result in different communities at the extremes based on species tolerances with the potential for a mixture of species or an ecotone between the two. Diversity will likely be higher at intermediate sites, producing a pattern consistent with the intermediate disturbance hypothesis but not resulting from an actual gradient in disturbance. Gradients in diversity with high intermediate values are not by themselves proof of the intermediate disturbance hypothesis.

Ecological landscapes represent complex spatial variation in habitats or communities and disturbance can be an element in producing these patterns. The relationship of landscape pattern to disturbance is clearest when disturbance acts to fragment a mature homogenous system into a terrain of patches in different ages or states of recovery from disturbances of different magnitudes. Some intermediate level of disturbance should produce a landscape of greatest diversity. Given the potentially large spatial extent of landscapes, they can be a mixture of habitat types in which overall diversity results from habitat diversity and not disturbance or the landscape can be influenced by multiple types of disturbances that affect only some subset of habitats or fragments. If the landscape consists of habitable fragments or patches imbedded within an unsuitable matrix, such as ecological reserves within an urban area, then the intermediate disturbance hypothesis may not apply.

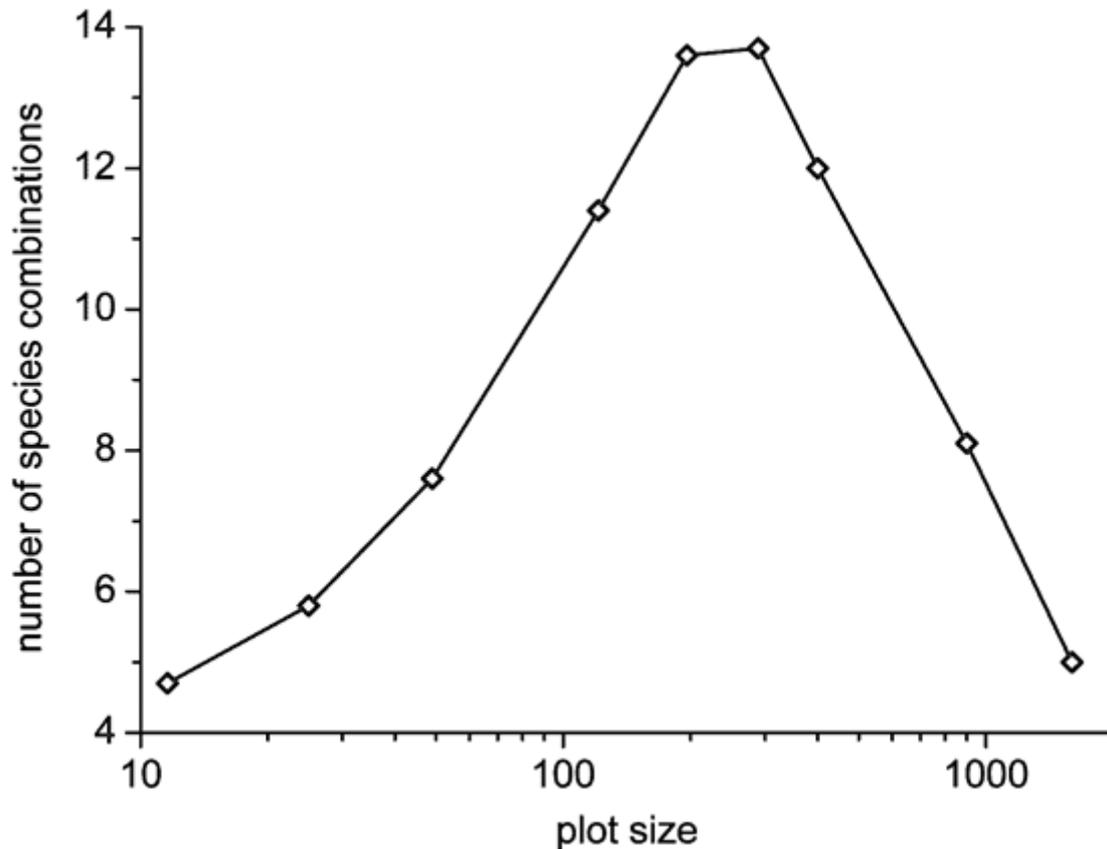


Figure 3. Changes of the number of species combination from the plot size.

## 8. Variations and Alternatives

The attractiveness of the intermediate disturbance hypothesis is its deceptive simplicity of applying some form of disruption to the observable process of community development. Clearly as a barren patch of habitat is colonized, species richness should increase regardless of whether one envisions the community developing as a defined succession or as a random accumulation of species. Eventually resources should become scarce with competition causing some decline in diversity. It follows that if this process of change can be halted at the right time diversity will be maintained at the highest level. Reality, however, is not so tractable. Even within a homogeneous habitat, community development will vary as a consequence of random recruitment as well as differences in competitive ability or susceptibility to predators. Recruitment, itself, may vary with season, distance from source, interspecific differences in productivity, etc., and not be random. Together these can result in delaying any competition for resources and a decline in diversity. Likewise, the simultaneous variability in the magnitude, frequency, and spatial scale of disturbances, whether they operate catastrophically or noncatastrophically, whether they are seen as operating within or among patches, or whether one or more types occur, all create a complexity that makes testing the hypothesis difficult.

This has resulted in both empirical and theoretical challenges to the hypothesis. For most of these, it is intermediate disturbance as a causal mechanism that is challenged not the pattern of highest diversity at some intermediate state in community development. Two types of alternatives based on empirical studies are the importance of considering interacting processes and the control of the recolonization of disturbed sites by external rather than internal processes. The importance of environmental gradients is an example of the former and recruitment limitation of the latter.

Although physical disturbance may produce light gaps in forest or overturn rocks and boulders in the rocky intertidal, these habitats, as well as others can be subject to gradients in environmental variables that produce a similar unimodal or quadratic pattern in diversity. Within the rocky intertidal, desiccation and high temperatures in the high intertidal and predation and herbivory in the low intertidal can result in different communities at the two extremes with an intermediate zone that mixes both sets of species and has a higher diversity. Disturbances

from rock turnover resulting from wave action can also produce a similar gradient of diversity based on rock size in the same location. Separating the impact of these processes based on pattern alone is difficult, if not impossible. Even patterns produced by disturbance may not be a consequence of some intermediate level of disturbance. For example, the colonization of an abandoned old field next to a forest can result in an ecotone community of highest diversity between the field and forest. The field may have been created by disturbance, but the pattern results from a gradient of environmental conditions between two extremes rather than ongoing differences in disturbance rates or magnitude.

Recruitment limitation, unlike intermediate disturbance does not rely on limiting resources within a disturbed patch to control diversity. Differential recruitment from the species surrounding or closest to the patch controls the development of the community within the patch, making colonization by species more distant or excluded from that part of the landscape much less likely. Colonization is not a lottery and disturbances do not create sites or resources for early-succession species that would be outcompeted over time. Species diversity is maintained in the system by the overall patchiness of the system and the inability of superior competitors to reach and colonize distant disturbed sites with poorer competitors. It is not clear how recruitment limitation operates over long time periods in which rare events of superior competitors colonizing distant sites might eventually occur.

Theoretical and modeling studies have led to variations and modifications of the intermediate disturbance hypothesis, including variations in the community or ecological system, variations in disturbance characteristics, and linking or contrasting other environmental parameters with disturbance. For example, when the complexity of the community is increased by the inclusion of multiple trophic levels or groups of species with very different life histories, intermediate disturbance becomes harder to define. A single frequency or magnitude of disturbance is unlikely to affect species of vastly different sizes and generation times in the same way or necessarily be intermediate for all. Likewise, disturbances that maintain higher diversity and presumably lower population levels of prey may have the opposite effect on predators. Characteristics of disturbance such as the timing or phasing of disturbances among patches can also modify the overall effect of disturbance. Even at the same magnitude and frequency, whether a disturbance affects one or all patches at the same or different times will determine its impact and what level of disturbance produces the highest diversity. Other parameters such as recruitment or productivity can also have a nonlinear impact on diversity and change the effect of disturbance. Low and high levels of recruitment may minimize the effects of disturbance. At low recruitment resources may not be limiting and disturbance would have little effect while at high recruitment levels any effect of disturbance would be quickly overwhelmed. Only at intermediate levels would differences in disturbance affect diversity.

## **9. List of animation, audio files and movies**

animation The Greedy Inc.mp4

## **10. Questions**

- What is the relationship between ecosystem functioning and species richness ?
- Explain how the functional diversity is measured?
- Which are the principal elements of the intermediate disturbance hypothesis?
- Mention a few types of disturbance?
- What does intermediate means?

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# 18. fejezet - References

## Videos:

An Indonesia Picture Show: [http://youtu.be/a\\_Yfl05U7B0](http://youtu.be/a_Yfl05U7B0)

Biodiversity World Map: <http://youtu.be/udSm33V-2ek>

Global Biodiversity Outlook: [http://youtu.be/\\_xe6ukoCZ90](http://youtu.be/_xe6ukoCZ90)

How Ecosystems Work: [http://youtu.be/HGDUk1neX\\_Y](http://youtu.be/HGDUk1neX_Y)

International Year of Biodiversity: [http://youtu.be/\\_JiFYifch58](http://youtu.be/_JiFYifch58)

Why Biodiversity Matters: [http://youtu.be/RPrnWJil\\_D8](http://youtu.be/RPrnWJil_D8)

## Animations:

Adopt a seed, save a species animation: <http://youtu.be/HhyCuPWJOK4>

Beer and Biodiversity: [http://youtu.be/UC\\_c4O6WbQg](http://youtu.be/UC_c4O6WbQg)

Biodiversity and Conservation: <http://youtu.be/YFTkbG1WDWg>

Biodiversity begins: <http://youtu.be/Tm6BHzaLYmQ>

Biodiversity Cartoon: <http://youtu.be/b8Fa3FfZs7Q>

Biodiversity Richness Evenness and Importance: [http://youtu.be/YEA2\\_zWLY\\_g](http://youtu.be/YEA2_zWLY_g)

BioDiversity: <http://youtu.be/1yL42VuTfdo>

Biodiversity cube: <http://youtu.be/DtZzHDbtqcU>

Biogeography Evidence for Evolution: <http://youtu.be/tnY7GpsFPJM>

Climate change energy action: <http://youtu.be/wsBiiI4zVBY>

Conserving Biodiversity: <http://youtu.be/NbolP79cEuE>

Diversity: <http://youtu.be/0PbSXVCDMvo>

Ecological Succession Animation: <http://youtu.be/KiSrHzqNYq8>

Food Chains: <http://youtu.be/2zGbYEzBJYE>

Green roofs explained: [http://youtu.be/Xq-72\\_nBR1Q](http://youtu.be/Xq-72_nBR1Q)

Island Biogeograph: <http://youtu.be/ngsvzaKmfiv>

Launch of the International Year of Biodiversity: <http://youtu.be/BJOa4xq55v0>

Loss of Biodiversity: <http://youtu.be/Mo7uGbxA6H8>

Population Growth: <http://youtu.be/C973AYIcnzI>

Save Biodiversity: <http://youtu.be/JdgKKH63QKc>

Sustainability explained: <http://youtu.be/JhFYkyyJz8>

The Greedy Inc: <http://youtu.be/SORUXtsv2-g>

Threats to Biodiversity: <http://youtu.be/t6LsfeHDGs8>

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Urban Biodiversity: <http://youtu.be/A8wp6oqXmm4>

Using Excel to Calculate Biodiversity: <http://youtu.be/QJkcvpiM-oo>

### Voices:

Biodiversity-Introduction: <http://sdrv.ms/16AcXQX>

Human Pollution Ecology : <http://sdrv.ms/1dJSWNZ>

Human Water Pollution: <http://sdrv.ms/16AdqCP>

Identifying Priority Sites for Biodiversity Conservation: <http://sdrv.ms/16AdrGH>

Island Biogeography: <http://sdrv.ms/16AdthT>

Symbiotic Relationship Aphids and Ants: <http://sdrv.ms/16AdwtT>

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