

III.1

Biodiversity: Concepts, Patterns, and Measurement

Robert K. Colwell

OUTLINE

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Life on Earth is diverse at many levels, beginning with genes and extending to the wealth and complexity of species, life forms, and functional roles, organized in spatial patterns from biological communities to ecosystems, regions, and beyond. The study of biodiversity encompasses the discovery, description, and analysis of the elements that underlie these patterns as well as the patterns themselves. The challenge of quantifying patterns of diversity at the species level, even when the organisms are known to science, is complicated by the problem of detecting rare species and the underlying complexity of the environmental template.

GLOSSARY

α , β , and γ diversity. The species diversity (or richness) of a local community or habitat (α), the difference in diversity associated with differences in habitat or spatial scale (β), and the total diversity of a region or other spatial unit (γ)

biodiversity. The variety of life, at all levels of organization, classified both by evolutionary (phylogenetic) and ecological (functional) criteria

diversity index. A mathematical expression that combines species richness and evenness as a measure of diversity

evenness. A measure of the homogeneity of abundances in a sample or a community

functional diversity. The variety and number of species that fulfill different functional roles in a community or ecosystem

rarefaction curve. The statistical expectation of the number of species in a survey or collection as a function of the accumulated number of individuals or samples, based on resampling from an observed sample set

relative abundance. The quantitative pattern of rarity and commonness among species in a sample or a community

richness estimator. A statistical estimate of the true species richness of a community or larger sampling universe, including unobserved species, based on sample data

species accumulation curve. The observed number of species in a survey or collection as a function of the accumulated number of individuals or samples

species–area relation. The generally decelerating but ever-increasing number of species as sampling area increases

species richness. The number of species in a community, in a landscape or marinescape, or in a region

1. WHAT IS BIODIVERSITY?

Although E. O. Wilson first used the term *biodiversity* in the literature in 1988, the concept of biological diversity from which it arose had been developing since the nineteenth century and continues to be widely used. Biodiversity encompasses the variety of life, at all levels of organization, classified both by evolutionary (phylogenetic) and ecological (functional) criteria. At the level of biological populations, genetic variation among individual organisms and among lineages contributes

to biodiversity as both the signature of evolutionary and ecological history and the basis of future adaptive evolution. Species that lack substantial genetic variation are thought to be more vulnerable to extinction from natural or human-caused changes in their environment.

It is at the species level that the term *biodiversity* is most often applied by ecologists and conservation biologists, although higher levels of classification (genera, families, orders) or patterns of evolutionary diversification are sometimes also considered, especially in paleontology. Species richness is the number of species of a particular taxon (e.g., birds or grasses) or life form (e.g., trees or plankton) that characterize a particular biological community, habitat, or ecosystem type. When data are not available at the community, habitat, or ecosystem level, political units (counties, states or provinces, countries) are often used as the basis of statements about species richness.

Within biological communities and ecosystems, functional diversity refers to the variety and number of species that fulfill different functional roles. A *food web* and some measure of its complexity and connectivity is one way to depict the functional diversity of a community. Another is the classification and enumeration of species representing different *functional groups*, such as primary producers, herbivores, and carnivores. Within forest communities, for example, plant functional groups that are often distinguished include fast-growing pioneer species that quickly colonize disturbed habitats, slower-growing species that characterize mature forests, and plants that fill special functional roles, such as those that fix atmospheric nitrogen. A marine biologist working on soft-bottom communities might categorize benthic organisms by the physical effect they have on the substrate as well

as by source of nutrients. In microbial communities, microbial taxa that depend on and transform different chemical substrates represent distinct functional groups.

At the level of landscapes, marinescapes, or ecosystems, biodiversity is conceived on a landscape or larger scale, often in terms of the number, relative frequency, and spatial arrangement of distinguishable ecosystem types, or *ecoregions*.

2. RELATIVE ABUNDANCE: COMMON SPECIES AND RARE ONES

The species that characterize any natural community differ in relative abundance, usually with a few species quite common and most species much less so. Another way of looking at it is that most individuals belong to the few common species in a typical community. For example, in a study of the soil “seed bank” in a Costa Rican rainforest, by B. J. Butler and R. L. Chazdon, the 952 seedlings that germinated from 121 soil samples included 34 species. The most common single species was represented by 209 seedlings, and the next most common had 109. In contrast, the least common 15 species each had 10 or fewer seedlings.

One way to plot such species abundance data (an approach originated by R. H. Whittaker) is a *rank-abundance curve*, in which each species is represented by a vertical bar proportional to its abundance. Figure 1 shows such a plot for the seed bank data. Notice the long “tail” of rarer species. A community with such striking disparities in abundance among species is said to have low evenness. A rank-abundance plot for a hypothetical community with perfect evenness would be flat instead of declining, indicating that every species had the same abundance.

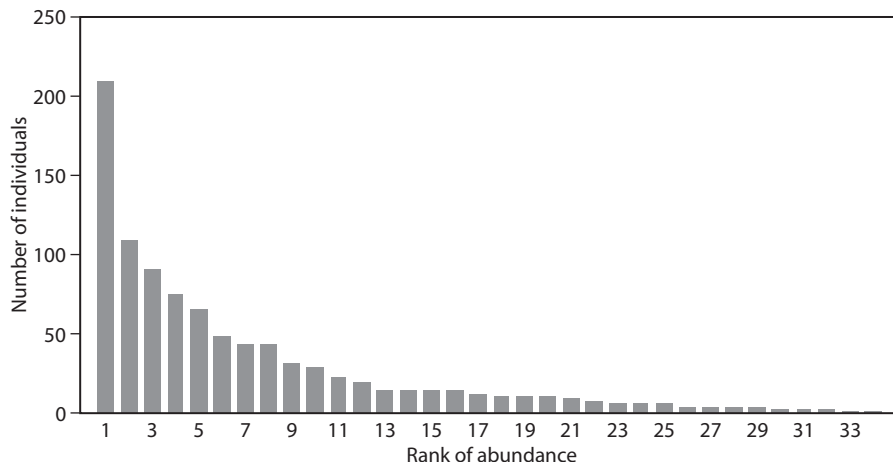


Figure 1. A rank-abundance curve.

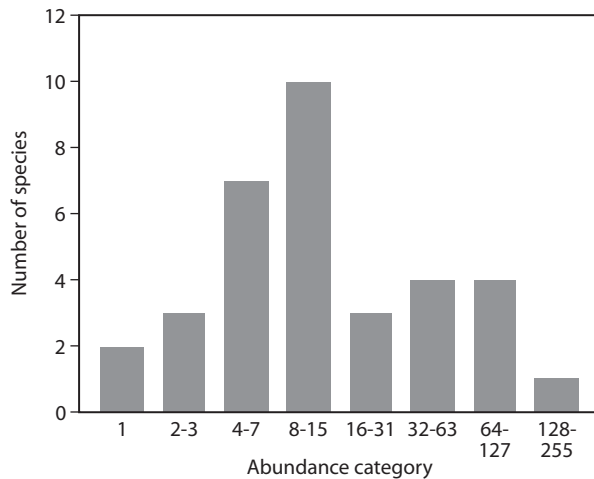


Figure 2. A log abundance plot.

Another way to plot the same species abundance data is to count up the number of species in each abundance category, starting with the rarest species, and plot these frequencies against abundance categories, as in figure 2. It is customary to use abundance categories in powers of two, which gives a *log abundance plot* (originated by F. W. Preston). When relative abundance distributions approximate a *normal* (bell-shaped) curve in a log abundance plot (the seed bank data in figure 2 come close), the statistical distribution is called *lognormal*. Lognormal distributions of relative abundance are common for large, well-inventoried natural communities. Many other statistical distributions have been used to describe relative abundance distributions, including the *log-series* distribution, which is described later in the context of diversity indices.

Conservation biologists are concerned with relative abundance because rare species are more vulnerable to extinction. Some species that are rare in one community are common in another (e.g., gulls are rare in many inland areas, but common along coasts), but some species are scarce everywhere they occur (e.g., most large raptors). In a classic paper, D. Rabinowitz classified species by three factors: (1) size of geographic range (not localized versus localized); (2) habitat specificity (not habitat specific versus habitat specific); and (3) local population density (not sparse versus sparse). She pointed out that there are seven ways to be rare, by this classification, but only one way to be common: not localized, not habitat specific, not sparse. Species that are rare by all three criteria (localized, habitat specific, and sparse), such as the ivory-billed woodpecker in the United States, are the most vulnerable to extinction.

3. MEASURING AND ESTIMATING SPECIES RICHNESS

On first consideration, measuring species diversity might seem an easy matter: just count the number of species present in a habitat or study area. In practice, however, complications soon arise. With the exception of very well-known groups in very well-known places (for which we already have good estimates of total richness anyway), species richness must generally be estimated based on samples. First of all, even for groups as well known as birds or flowering plants, not all species that are actually present are equally easy to detect. Although size, coloration, and—for animals—behavior can affect the detectability of individuals, relative abundance is the most important influence on the effort required to record a species. As every beginning stamp or coin collector soon discovers, the common kinds of coins or stamps are usually the first to be found. As the collection grows, the rate of discovery of kinds new to the collection declines steadily, as rarer and rarer kinds remain to be found.

For species richness, this process can be depicted as a *species accumulation curve*, sometimes called a *collector's curve*. The jagged line in figure 3 shows a species accumulation curve for the seed bank data of figure 1, as the 121 soil samples were added one at a time to the total. Because the order in which the soil samples were added to the collection was arbitrary, a smoothed version of such a curve, called a *rarefaction curve*, makes more sense. Conceptually, a rarefaction curve can be produced by drawing 1, 2, 3, . . . N samples (or individuals) at a time (without replacement) from the full set of samples, then plotting the means of many such draws. Fortunately, this is not necessary, as the mathematics of combinations allows rarefaction curves to be computed directly, along with 95% confidence intervals (the dashed lines in figure 3), based on work by C. X. Mao and colleagues. Rarefaction curves are especially useful for comparing species richness among communities that have not been fully inventoried or have been inventoried with unequal effort.

Richness estimation offers an alternative to rarefaction for comparing richness among incompletely inventoried communities. Instead of interpolating “backward” to smaller samples as in rarefaction, richness estimators extrapolate beyond what has been recorded to estimate the unknown asymptote of a species accumulation curve. Simple (regression-based) or sophisticated (mixture model) curve-fitting methods of extrapolation can be used, or nonparametric richness estimators can be computed. The latter depend on the frequencies of the rarest classes of observed species to

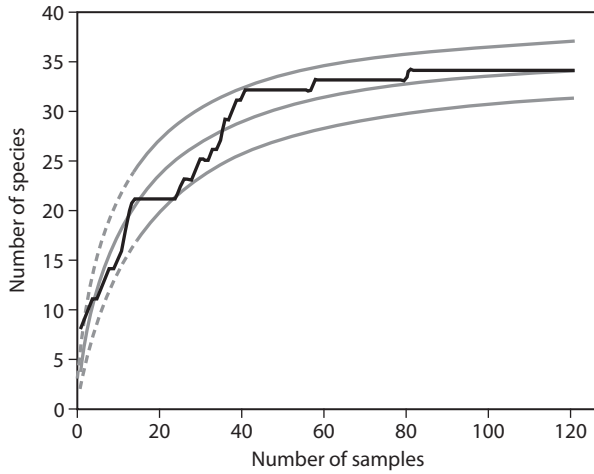


Figure 3. Species accumulation and rarefaction curves.

estimate the number of species present but not detected by the samples. The simplest nonparametric estimator, *Chao1*, augments the number of species observed (S_{obs}) by a term that depends only on the observed number of *singletons* (a , species each represented by only a single individual) and *doubletons* (b , species each represented by exactly two individuals):

$$S_{\text{est}} = S_{\text{obs}} + \frac{a^2}{2b}.$$

For the seed bank example of figures 1 and 2, when all samples are considered, 34 species were observed. Of these species, two were singletons, and two were doubletons, so that the estimated true richness is 35 species, confirming the visual evidence from the rarefaction curve that the inventory was virtually complete. The real utility of estimators, however, lies in their potential to approximate asymptotic species richness from much smaller samples. Figure 4 shows the same rarefaction curve (solid line) as in figure 3, with the estimated (asymptotic) species richness (shown by the dashed line) for the *Chao1* estimator, which begins to approximate true richness with as few as 20 samples. (The estimator curve shows the mean of 100 random draws for each number of samples.) It should be noted that richness estimators are not a panacea for problems of undersampling. Hyperdiverse communities with large numbers of very rare species, such as tropical arthropods, have so far resisted efforts to provide reliable nonparametric richness estimators.

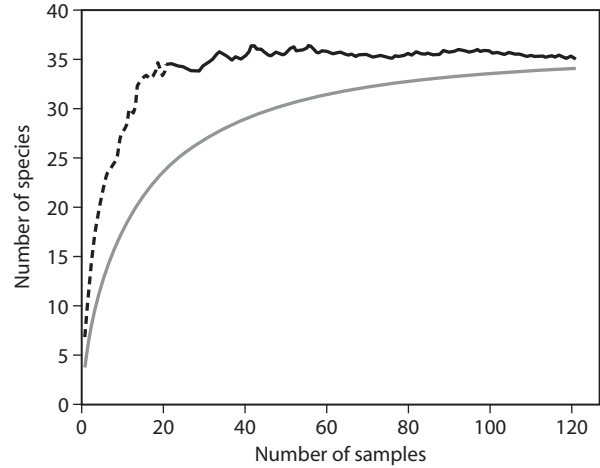


Figure 4. Estimated species richness and rarefaction curves.

4. SPECIES DIVERSITY INDICES

The concept of diversity, including biodiversity itself as well as the narrower concept of species diversity, is a human construct without any unique mathematical meaning. The simplest measure of species diversity is species richness, but a good case can be made for giving some weight to evenness as well. For example, the subjective sense of tree species richness is likely to be greater for a naturalist walking through a forest composed of 10 species of trees, each equally represented, than a forest of 10 species in which one species contributes 91% of the individuals and the others each 1%.

Diversity indices are mathematical functions that combine richness and evenness in a single measure, although usually not explicitly. Although there are many others, the most commonly used diversity indices in ecology are *Shannon diversity*, *Simpson diversity*, and *Fisher's α* . If species i comprises proportion p_i of the total individuals in a community of S species, the Shannon diversity is

$$H = -\sum_{i=1}^S p_i \ln p_i \text{ or, preferably, } e^H$$

and Simpson diversity is

$$D = 1 - \sum_{i=1}^S p_i^2 \text{ or, preferably, } D' = \left(\sum_{i=1}^S p_i^2 \right)^{-1}.$$

Both Shannon and Simpson diversities increase as richness increases, for a given pattern of evenness, and increase as evenness increases, for a given richness, but

they do not always rank communities in the same order. Simpson diversity is less sensitive to richness and more sensitive to evenness than Shannon diversity, which, in turn, is more sensitive to evenness than is a simple count of species (richness, S). At the other extreme, a third index in this group, the *Berger-Parker index*, depends exclusively on evenness; it is simply the inverse of the proportion of individuals in the community that belong to the single most common species, $1/p_i(\max)$. Because rare species tend to be missing from smaller samples, the sensitivity of these indices to sampling effort depends strongly on their sensitivity to richness. In practice, which measure of diversity to use depends on what one wishes to focus on (pure richness or a combination of richness and evenness), the relative abundance pattern of the data, comparability to previous studies, and the interpretability of the results. These four diversity measures (richness, the exponential form of Shannon diversity, the reciprocal form of Simpson diversity, and the Berger-Parker index) can be shown to be specific points on a diversity continuum defined by a single equation based on the classical mathematics of Rényi entropy, as first shown in the ecology literature by M. O. Hill in 1972 and periodically rediscovered since then. L. Jost, in 2005, reviewed these relationships and provided compelling arguments for preferring the exponential version of Shannon index and the reciprocal (D') version of the Simpson index.

Fisher's α is mathematically unrelated to the Rényi family of indices. It is derived from the log-series distribution, proposed by R. A. Fisher as a general model for relative abundance:

$$\alpha x, \alpha x^2/2, \alpha x^3/3, \alpha x^4/4, \dots, \alpha x^n/n,$$

where successive terms represent the number of species with 1, 2, 3, ..., n individuals, and α is treated as an index of species diversity. Estimating α from an empirical relative abundance distribution, however, depends only on S (the total number of species) and N (the total number individuals) but nevertheless requires substantial computation because iterative methods must be used. Fisher's α is relatively insensitive to rare species, and the relative abundance distribution need not be distributed as a log-series.

5. THE SPATIAL ORGANIZATION OF BIODIVERSITY

Imagine walking through a forest into a grassland or snorkeling across a coral reef beyond the reef edge toward the open sea. The testimony of our own eyes confirms that the biosphere is not organized as a set of smooth continua in space but rather as a complex

“biotic mosaic” of variably discontinuous assemblages of species. On land, the discontinuities are driven in the shorter term by topography, soils, hydrology, recent disturbance history, dispersal limitation, species interactions, and human land use patterns, and in the longer term and at greater spatial scales by climate and Earth history. The same or analogous factors structure biodiversity in the sea.

If you were to keep track of the plant or bird species encountered, in the form of a species accumulation curve, during a long walk in a forest followed by a long walk in an adjacent grassland, the curve would first rise quickly, as the common forest species were recorded, leveling off (if the walk is long enough) as the rarest forest species are finally included. The number of species accumulated at that point (or a species diversity index computed for the accumulated data) is called the α diversity (or local diversity) for a habitat or community, a concept originated by R. H. Whittaker. (Note that α diversity has nothing to do with Fisher's α , in terms of the names, although the latter may be used as one measure of the former.) As you leave the forest and enter the grassland, the curve will rise steeply again, as common grassland species are added to the list. Once rarer grassland species are finally included, the curve begins to level off at a new plateau. The increment in total species (or the change in a diversity index) caused by the change in habitat is one measure of β diversity, in Whittaker's terminology (sometimes called *differentiation diversity*), although there are many ways to quantify β diversity and little agreement about which is best. The total richness or diversity for both habitats combined (the second plateau in the species accumulation curve) is the γ diversity (regional diversity) for this hypothetical forest-grassland landscape.

The forest-to-grassland example presents a classic illustration of β diversity, as originally conceived by Whittaker, but the concept has been generalized to include spatial differentiation of biotas within large expanses of continuous, environmentally undifferentiated habitat as well as between isolated patches of similar habitat. Within expanses of homogeneous habitat, β diversity is usually considered to be the result of *dispersal limitation*—the failure of propagules (fruits, seeds, juveniles, dispersive larval stages, migrants, etc.) to mix homogeneously over the habitat—but in practice, it is often hard to rule out subtle differences in environment as a cause of biotic differentiation.

6. ESTIMATING β AND γ DIVERSITY FROM SAMPLES

Estimating β or γ diversity for a region or landscape, from samples, is a daunting prospect for any but the

best-known groups of organisms. Over larger spatial or climatic scales, the “patches” of the mosaic can be better viewed as ordered along gradients, in either physical or multivariate environmental space. Unfortunately, the geometry of the biotic mosaic is remarkably idiosyncratic (although it may be properly *fractal* for some organisms at some scales), which means that designing a scheme for estimating richness at large spatial scales is likely to require many ad hoc decisions—it is more like designing trousers for an elephant than finding yourself a hat that fits.

A common approach to coping with idiosyncratic biotic patterns is to take advantage of biotic discontinuities to define “patch types” in the mosaic for sampling purposes. For example, the vegetation of treefalls in a forest might be distinguished from the riparian (streamside) vegetation and from the mature forest matrix. Or the fish fauna of isolated patch reefs might be distinguished from the fish fauna of fringing reefs. An alternative is to select sampling sites along explicit gradients, such as elevational transects on land or depth and substrate gradients in the sea. Both strategies represent forms of stratified sampling in which the strata are the patch types or gradient sites, and multiple samples within them are treated as approximate replicates, meaning, in practice, that samples within patch types or gradient sites are expected to be more similar than samples from different types or sites.

Any particular definition of patch types and the scale that underlies them is inevitably somewhat arbitrary. A seemingly less arbitrary alternative would be spatially random sampling over the entire region of interest, analyzed using a multivariate approach to assess the relationship of richness and species composition to underlying environmental and historical factors. But, given limited resources (are they ever otherwise?), random sampling over heterogeneous domains is often highly inefficient because of the uneven relative abundance of patch types: the biota of common patch types are oversampled compared to the biota of rarer patch types, which may even be missed entirely. If one accepts a within- and between-patch-type design framework, the definition of patch types (or sample spacing on gradients) is best made at the design phase based on expert advice and whatever prior data exist, with the possibility of later iterative adjustment.

Although comparisons of α diversity among patch types by rarefaction are interesting in their own right, they fail to provide the information needed to estimate γ diversity because some species are likely to be shared among patch types and some species may be missed by the sampling in all patch types. If we had full knowledge of the biota (complete species lists) for all patch

types within a region, it would be simple to determine the total biota for two, three, . . . all types combined, computing some measure of (average or pair-specific) β richness (species turnover) along the way. For sampling data, the problem is much more difficult. Undetected species within patch types are not only undetected, they are unidentified, so that that we do not know whether the same or different species remain undetected in different patch types.

Nonetheless, it is possible in principle to estimate lower and upper bounds for γ (regional) richness. The union of detected species lists for all patch types, pooled, provides a lower-bound estimate of total domain richness, on the assumption that every species undetected in one patch type is detected in at least one other patch type. The sum of total richness estimates over all patch types (including undetected species from each patch type, using nonparametric estimators or extrapolation techniques), adjusted for the number of observed shared species, is an approximate upper-bound estimate of total regional richness, assuming that undetected species included in the estimates are entirely different for each patch type and were detected in none.

The truth inevitably lies between these bounds, for data from nature. To estimate the true regional richness, we need information about the true pattern of shared species among patch types. Statistical tools for estimating the true number of species shared by two sample sets, including species undetected in one or both sets, are scarce, and this is an area in which much more work is needed. Many studies have attempted to address the problem of estimating β diversity, or pooling samples (between patch types or random samples) by using similarity indices, such as the Sørensen or Jaccard indices. Unfortunately, the number of observed, shared species is almost always an underestimate of the true number of shared species because of the undersampling of rare species. This means that species lists based on samples generally appear proportionally more distinct than they ought to be, similarity indices are routinely biased downward, and slope estimates for the decline in similarity with distance (“distance decay of similarity”) are likely to be overestimated. Recently, A. Chao and others have developed estimation-based similarity indices that greatly reduce undersampling bias and promise to help correct this longstanding dilemma. These indices are based on the probability that two randomly chosen individuals, one from each of two samples, both belong to species shared by both samples (but not necessarily to the same shared species). The estimators for these indices take into account the contribution to the true value of this probability made by species actually present at both sites but not detected in one or both samples.

7. SPECIES-AREA RELATIONS

Ecologists and biogeographers have long documented a striking regularity in the pattern of increase in the species count as larger and larger geographic areas are considered. When the number of species or its logarithm (depending on the case) is plotted against the logarithm of area, an approximately linear relationship is revealed. With either plot (a log-log power curve or a semilog exponential curve), the pattern on arithmetic axes is a decelerating but ever-increasing number of species as area increases. This pattern, known as the species-area relation (SAR), has been called one of the few universal patterns in ecology, but its causes are not simple.

There are many variants on SARs, but the primary dichotomy separates plots based on nested sampling schemes from plots in which the areas of increasing size are distinct places, such as islands in lakes or seas, habitat islands on land, or simply political units (states, countries) of different areas. There are two important causes for the increase in species count with increasing area. The first cause is undersampling. Especially in the case of nested sampling schemes, in which smaller areas lie within larger ones, the smaller units may be too small or too poorly sampled to reveal all species characteristic of the habitat(s) they represent. In this case, the supposed SAR for the smaller areas is better described as a species accumulation curve or rarefaction curve. B. D. Coleman and colleagues pointed out that, even for a completely homogeneous species pool, larger areas will have more species because they contain more individuals; the model they proposed is virtually indistinguishable from a rarefaction curve.

The second cause of increasing species count with area is β diversity, in all its varieties. (1) Within large expanses of homogeneous habitat, species composition may vary spatially simply because of dispersal limita-

tion, so that larger areas contain more species. (2) Larger areas are more likely to include a greater number of habitat types or ecoregions, each with its own distinct or partially distinct biota. (3) For very large areas, on continental scales, ecologically similar biotas may have very different evolutionary histories. For example, the lizard fauna of coastal Chile and coastal California share many ecological similarities but have no species (or even genera) in common. Such cases could be viewed as an extreme form of dispersal limitation, as we discover to our dismay when alien species from similar biomes on other continents become local invasives (e.g., California poppy, *Eschscholzia californica*, in Chile, and the Chilean ice plant, *Car-pobrotus chilensis*, in California).

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Indices of diversity and evenness*

Carlo H.R. HEIP, Peter M.J. HERMAN & Karline SOETAERT

Netherlands Institute of Ecology
Centre for Estuarine and Coastal Ecology
PO Box 140
4400 AC Yerseke
The Netherlands
heip@cemo.nioo.knaw.nl

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Abstract

An overview is given of the different indices used, since their introduction in the 60's, for the determination of diversity in biological samples and communities. The most commonly used indices are based on the estimation of relative abundance of species in samples. Relative abundance can also be used for either a graphical or a mathematical representation of species-abundance relationships, from which diversity indices can be deduced as well. Most common in the literature are indices either describing the richness or species number and the evenness or partitioning of individuals over species or a combination of both. The most commonly used diversity indices can be grouped in a coherent system of diversity numbers developed by HILL (1973) that includes species richness, the Simpson index and a derivation of the Shannon-Wiener index as special cases. In this system species are different only when their abundance is different. Therefore, during the last decade a number of indices have been developed that take into account the taxonomic position, trophic status or body size of the species. There is as yet no consensus as to the use of evenness indices. We apply the condition that evenness should be independent of species richness (HEIP, 1974). The number of potential evenness indices is then strongly reduced. It is

*These lecture notes are in part an update of the paper "Data Processing, Evaluation and Analysis". Carlo Heip, Peter Herman & Karlien Soetaert, 1988. *In*: Introduction to the Study of Meiofauna (R.P. Higgins & H. Thiel eds). Smithsonian Institution Press, Washington D.C., London. Publication nr 2459 of the Netherlands Institute of Ecology.

argued that the calculation of diversity or evenness indices should simply serve as descriptors of community structure and be complemented with information on ecological functioning.

Indices de diversité et régularité

Mots clés : diversité, richesse spécifique, régularité, relations espèce-abondance

Résumé

Les différents indices servant à déterminer la diversité dans les échantillons biologiques et les communautés sont passés en revue, depuis leur introduction dans les années 1960. Les indices les plus souvent employés se basent sur l'estimation de l'abondance relative des espèces dans les échantillons. L'abondance relative peut également être utilisée pour la représentation graphique ou mathématique des relations espèce-abondance, desquelles peuvent être déduits les indices de diversité. Les indices les plus souvent rencontrés dans la littérature sont ceux qui soit décrivent la richesse ou le nombre d'espèces, soit la régularité ou le regroupement des individus dans les espèces, ou bien une combinaison des deux. Les indices les plus utilisés peuvent être regroupés dans un système cohérent développé par HILL (1973), qui inclut la richesse spécifique, l'indice de Simpson et un dérivé de l'indice de Shannon-Wiener pour des cas particuliers. Selon ce système, les espèces sont différentes seulement quand leur abondance est différente. Cependant, au cours des dix dernières années, ont été développés un certain nombre d'indices qui prennent en considération la position taxonomique, le statut trophique ou bien la taille corporelle des espèces. Il n'y a pas encore de consensus sur l'utilisation des indices de régularité. Nous appliquons les conditions où la régularité devrait être indépendante de la richesse spécifique (HEIP, 1974). Le nombre d'indices de régularité potentiel est alors fortement réduit. Il est démontré que le calcul de la diversité ou des indices de régularité devrait seulement servir en tant que descripteurs de la structure d'une communauté et être complété par des informations sur le fonctionnement écologique.

1. Introduction

It is common practice among ecologists to complete the description of a community by one or two numbers expressing the "diversity" or the "evenness" of the community. For this purpose a bewildering diversity of indices have been proposed and a small subset of those have become popular and are now widely used, often without much statistical consideration or theoretical justification. The theoretical developments on the use of diversity indices have been mostly discussed in the 60's and 70's. Although the subject continues to be debated

to this day, by the 90's their popularity in theoretical ecological work had declined. In contrast to this loss of interest from theoretical ecologists, diversity indices have become part of the standard methodology in many applied fields of ecology, such as pollution and other impact studies. They have entered environmental legislation and are again attracting attention at the turn of the century because of the surge of interest in biodiversity and the never ending quest for indicators of the status of the environment.

The basic idea of a diversity index is to obtain a quantitative estimate of biological variability that can be used to compare biological entities, composed of discrete components, in space or in time. In conformity with the "political" definition of biodiversity, these entities may be gene pools, species communities or landscapes, composed of genes, species and habitats respectively. In practice, however, diversity indices have been applied mostly to collections or communities of species or other taxonomic units. When this is the case, two different aspects are generally accepted to contribute to the intuitive concept of diversity of a community: species richness and evenness (following the terminology of PEET, 1974). Species richness is a measure of the total number of species in the community (but note already that the actual number of species in the community is usually unmeasurable). Evenness expresses how evenly the individuals in the community are distributed over the different species. Some indices, called heterogeneity indices by PEET (1974), incorporate both aspects, but HEIP (1974) made the point that in order to be useful an evenness index should be independent of a measure of species richness.

Because comparison is often an essential goal, a diversity index should in principle fulfil the conditions that allow for a valid statistical treatment of the data, using methods such as ANOVA. This also requires that estimates from samples can be extrapolated to values for the statistical population. The statistical behaviour of the various indices that have been proposed is therefore a point of great importance. In practice a number of problems arise such as the definition of the entities of variability (which species, life-stages or size classes within species, functional groups, etc.?), problems of delimitation of communities and habitats, sample size, etc. that, when not accounted for, prevent the correct application of univariate statistics.

The major starting point for nearly all computations is a matrix containing stations as columns and species as rows and of which the entries are mostly abundance or biomass data. Diversity indices are univariate (and therefore do not contain all the information present in the species $\times$ stations matrix), but the same matrix can be used as the starting point for either a univariate (using other summary statistics) or a multivariate analysis. In modern ecological

practice diversity indices are therefore nearly always used in conjunction with multivariate analyses.

The main problem in obtaining estimates of diversity is the basic but often painstaking effort necessary to collect the samples in the field and to sort, weigh and determine the organisms present in the sample. The cost and effort of the calculations are now minor in comparison. The general availability of large computing power and the wide array of easily available software has made the computations that were tedious only twenty years ago extremely easy now. The danger is that often the conditions for application of the software, *e.g.* checking the assumptions and conditions required for using specific statistical tests against the characteristics of the available data, are not considered.

2. Species-abundance distributions

2.1. Introduction

Nearly all diversity and evenness indices are based on the relative abundance of species, *i.e.* on estimates of p_i in which

$$p_i = N_i/N \quad (2.1)$$

with N_i the abundance of the i -th species in the sample, and

$$N = \sum_{i=1}^S N_i \quad (2.2)$$

with S the total number of species in the sample.

If one records the abundances of different species in a sample (and estimates them in a community), it is invariably found that some species are rare, whereas others are more abundant. This feature of ecological communities is found independent of the taxonomic group or the area investigated. An important goal of ecology is to describe these consistent patterns in different communities, and explain them in terms of interactions with the biotic and abiotic environment.

One can define a “community” as the total set of organisms in an ecological unit (biotope), but the definition used must always be specified as to the actual situation that is investigated. There exist no entities in the biosphere with absolutely closed boundaries, *i.e.* without interactions with other parts. Therefore, some kind of arbitrary boundaries must always be drawn. PIELOU (1975) recommends that the following features should be specified explicitly:

1. the spatial boundaries of the area or volume containing the community and the sampling methods;

2. the time limits between which observations were made;
3. the set of species or the taxocene (*i.e.* the set of species belonging to the same taxon) treated as constituting (or representing) the community.

The results of a sampling program of the community come as species lists, indicating for each species a measure of its abundance (usually number of individuals per unit surface, volume or catch effort, although other measures, such as biomass, are possible). Many methods are used to plot such data. The method chosen often depends on the kind of model one wishes to fit to the data. Different plots of the same (hypothetical) data set are shown in figure 1.

It can readily be seen that a bewildering variety of plots is used. They yield quite different visual pictures, although they all represent the same data set. Figures 1A–D are variants of the Ranked Species Abundance (RSA) curves. The S species are ranked from 1 (most abundant) to S (least abundant). Density (often transformed to percentage of the total number of individuals N) is plotted against species rank. Both axes may be on logarithmic scales. It is especially interesting to use a log-scale for the Y-axis, since then the same units on the Y-axis may be used to plot percentages and absolute numbers (there is only a vertical translation of the plot).

In so-called “ k -dominance” curves (LAMBSHEAD *et al.*, 1983) (figure 2A–D), the cumulative percentage (*i.e.* the percentage of total abundance made up by the k -th most dominant plus all more dominant species) is plotted against rank k or log rank k . To facilitate comparison between communities with different numbers of species S , a “Lorenzen curve” may be plotted. Here the species rank k is transformed to $(k/S) \times 100$. Thus the X-axis always ranges between 0 and 100 (figure 2C).

The “collector’s curve” (figure 2D) addresses a different problem. When one increases the sampling effort, and thus the number of animals N caught, new species will appear in the collection. A collector’s curve expresses the number of species as a function of the number of specimens caught. Collector’s curves tend to flatten out as more specimens are caught. However, due to the vague boundaries of ecological communities they often do not reach an asymptotic value: as sampling effort (and area) is increased, so is the number of slightly differing patches.

The plots in figure 3A–D are species-abundance distributions. They can only be drawn if the collection is large, and contains many species (a practical limit is approximately $S > 30$). Basically, a species-abundance distribution (figure 3A) plots the number of species that are represented by $r = 0, 1, 2, \dots$ individuals against the abundance r . Thus, in figure 3A there were 25 species with 1 individual, 26 species with 2 individuals, etc. More often than not,

the species are grouped in logarithmic density classes. Thus one records the number of species with density *e.g.* between 1 and $e^{(0.5)}$, between $e^{(0.5)}$ and $e^{(1)}$, etc. (figure 3B). A practice, dating back to PRESTON (1948), is to use logarithms

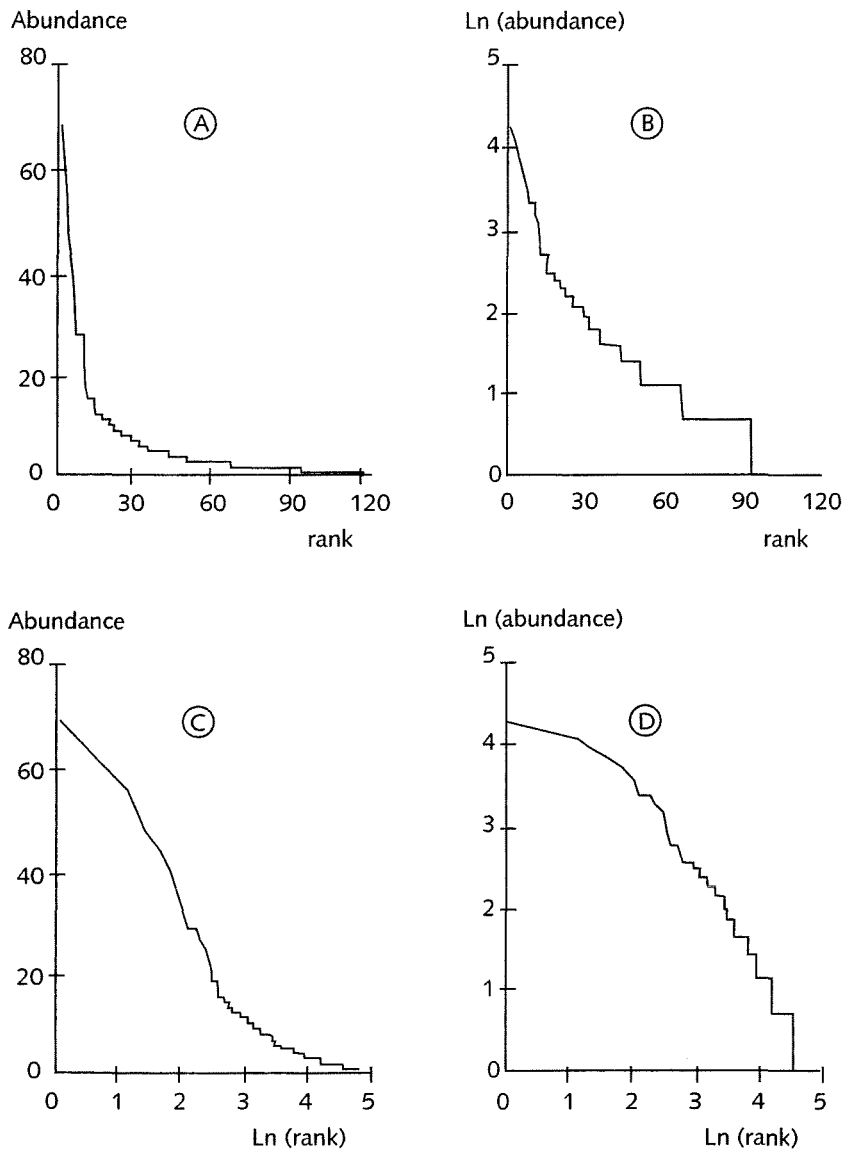


Figure 1: Ranked species abundance curves, representing the same data, with none, one or both axes on a logarithmic scale.

to the base 2. One then has the abundance boundaries 1, 2, 4, 8, 16, etc. These so-called “octaves” have two disadvantages. The class boundaries are integers, which necessitates decisions as to which class a species with an abundance

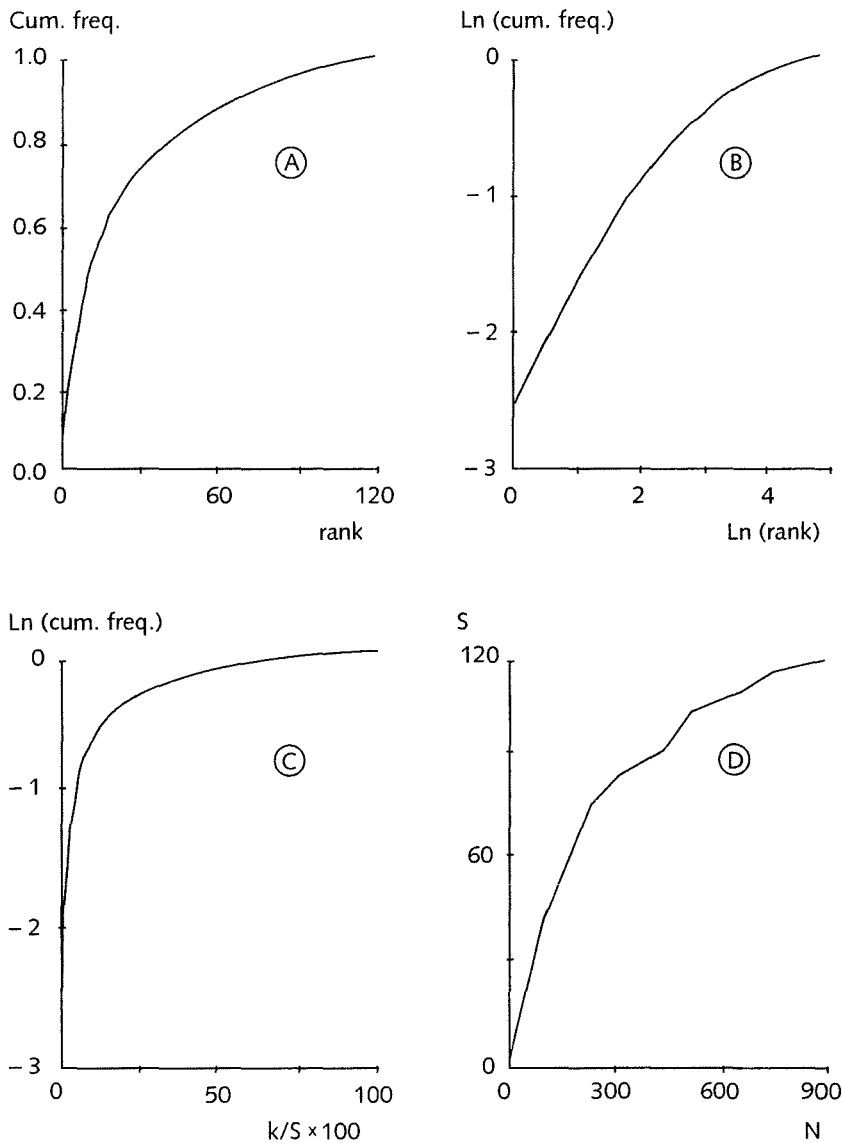


Figure 2: The same data set represented as a k -dominance curves (A-B), the Lorenzen curve (C) and the collector's curve (D).

equal to a class mark belongs; and, the theoretical formulation of models is “cluttered” (MAY, 1975) by factors $\ln(2)$, which would vanish if natural logs were used.

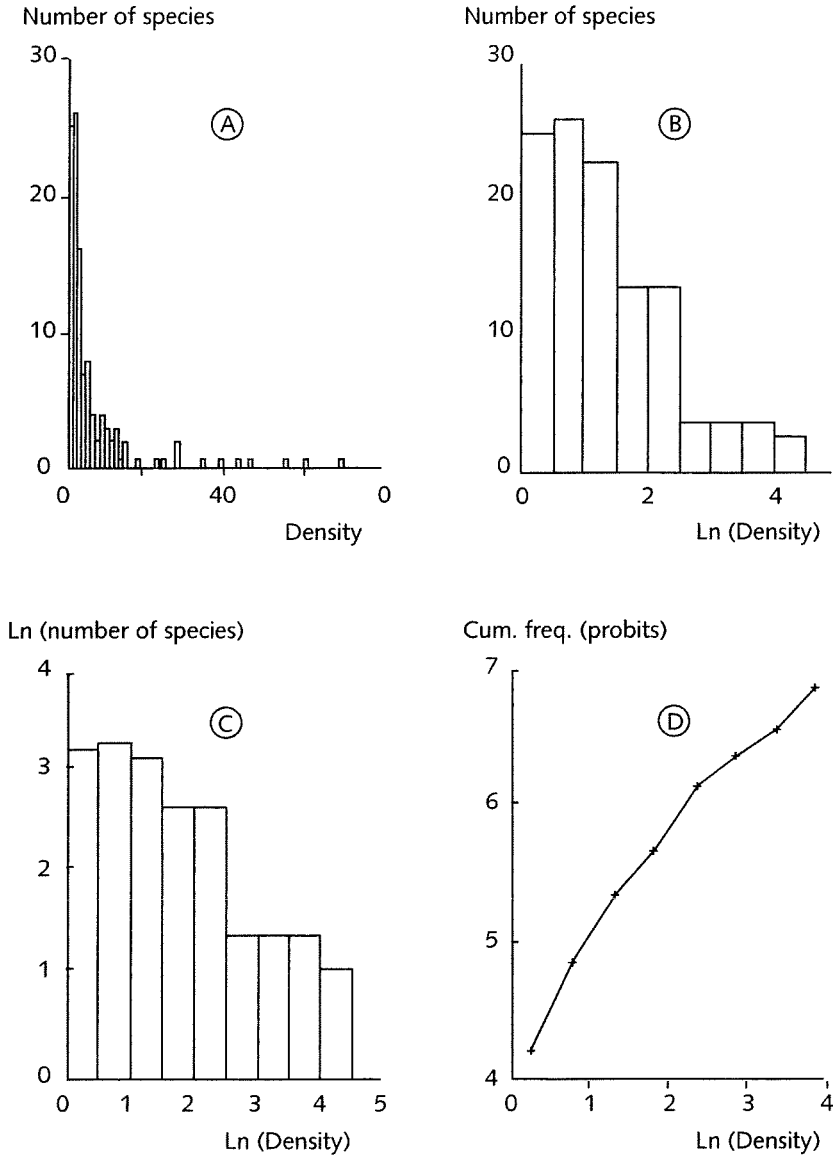


Figure 3: The same data set represented as species abundance distributions (A-C), and cumulative species abundance on a probit scale (D).

The ordinate of species-abundance distributions may be linear or logarithmic. Often one plots the cumulative number of species in a density group and all less abundant density groups on a probit scale (figure 3D).

2.2. Species-abundance models

Two kinds of models have been devised to describe the relative abundances of species. "Resource apportioning models" make assumptions about the division of some limiting resource among species. From these assumptions a ranked abundance list or a species-abundance distribution is derived. The resource apportioning models have mainly historical interest. In fact, observed species-abundance patterns cannot be used to validate or discard a particular model, as has been extensively argued by PIELOU (1975, 1981). One should consult these important publications before trying to validate or refute a certain model fortuitously!

"Statistical models" make assumptions about the probability distributions of the numbers in the several species within the community, and derive species-abundance distributions from these.

2.2.1. The niche preemption model (Geometric series ranked abundance list)

This resource apportioning model was originally proposed by MOTOMURA (1932). It assumes that a species preempts a fraction k of a limiting resource, a second species the same fraction k of the remainder, and so on. If the abundances of the species are proportional to their share of the resource, the ranked-abundance list is given by a geometric series:

$$k, k(1 - k), \dots, k(1 - k)^{(S-2)}, k(1 - k)^{(S-1)} \quad (2.3)$$

where S is the number of species in the community. MAY (1975) derives the species abundance distribution from this ranked abundance list (see also PIELOU, 1975).

The geometric series yields a straight line on a plot of log abundance against rank. The communities described by it are very uneven, with high dominance of the most abundant species. It is not very often found in nature. WHITTAKER (1972) found it in plant communities in harsh environments or early successional stages.

2.2.2. The negative exponential distribution (broken-stick model)

A negative exponential species abundance distribution is given by the probability density function:

$$\psi(y) = Se^{-Sy} \quad (2.4)$$

Stated as such, it is a statistical model, an assumption about the probability distribution of the numbers in each species. However, it can be shown (WEBB,

1974) that this probability density function can be arrived at *via* the “broken-stick model” (MACARTHUR, 1957). In this model a limiting resource is compared with a stick, broken in S parts at $S - 1$ randomly located points. The length of the parts is taken as representative for the density of the S species subdividing the limiting resource. If the S species are ranked according to abundance, the expected abundance of species i , N_i is given by:

$$E(N_i) = \frac{1}{S} \sum_{x=i}^S \frac{1}{x} \quad (2.5)$$

The negative exponential distribution is not often found in nature. It describes a too even distribution of individuals over species to be a good representation of natural communities. According to FRONTIER (1985) it is mainly appropriate to describe the right-hand side of the rank frequency curve, *i.e.* the distribution of the rare species. As these are the most poorly sampled, their frequencies depend more on the random elements of the sampling than on an intrinsic distribution of the frequencies.

PIELOU (1975, 1981) showed that a fit of the negative exponential distribution to a field sample does not prove that the mechanism modelled by the broken-stick model governs the species-abundance pattern in the community. Moreover, the broken-stick model is not the only mechanism leading to this distribution. The same prediction of relative abundance can be derived by at least three other models besides the niche partitioning one originally used (COHEN, 1968; WEBB, 1974).

The observation of this distribution does indicate (MAY, 1975) 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).

2.2.3. The log-series distribution

The log-series was originally proposed by FISHER *et al.* (1943) to describe species abundance distributions in large moth collections. The expected number of species with r individuals, E_r , is given as:

$$E_r = \alpha \frac{X^r}{r} \quad (2.6)$$

($r = 1, 2, 3, \dots$). α (> 0) is a parameter independent of the sample size (provided a representative sample is taken), for which X ($0 < X < 1$) is the representative parameter. The parameters α and X can be estimated

by maximum likelihood (KEMPTON & TAYLOR, 1974), but are conveniently estimated as the solutions of:

$$S = -\alpha \ln(1 - x) \quad (2.7)$$

and

$$N = \frac{\alpha X}{1 - X} \quad (2.8)$$

The parameter α , being independent of sample size, has the attractive property that it may be used as a diversity statistic (see further). An estimator of the variance of α is given as (ANSCOMBE, 1950):

$$\text{var}(\alpha) = \frac{\alpha}{\ln X(1 - X)} \quad (2.9)$$

KEMPTON & TAYLOR (1974) give a detailed derivation of the log-series distribution. It was fitted to data from a large variety of communities (e.g. WILLIAMS, 1964; KEMPTON & TAYLOR, 1974). It seems, however, to be in general less flexible than the log-normal distribution. In particular, it cannot account for a mode in the species-abundance distribution, a feature often found in a collection. According to the log-series model, there are always more species represented by 1 individual than there are with 2. The truncated log-normal distribution can be fitted to samples with or without a mode in the distribution.

CASWELL (1976) derived the log-series distribution as the result of a neutral model, *i.e.* a model in which the species abundances are governed entirely by stochastic immigration, emigration, birth and death processes, and not by competition, predation or other specific biotic interactions. He proposes to use this distribution as a “yardstick”, with which to measure the occurrence and importance of interspecific interactions in an actual community. Other models have been proposed to generate the log-series distribution (BOSWELL & PATIL, 1971) but they all contain the essentially neutral element as to the biological interactions. However, the proof that any form of biological interaction will yield deviation from the log-series is not given. Neither is it proven that “neutral” communities cannot deviate from the log-series. Therefore we think that the fit of this distribution cannot be considered as a waterproof test for species interactions.

2.2.4. The log-normal distribution

PRESTON (1948) first suggested to use a log-normal distribution for the description of species-abundance distributions. It was shown by MAY (1975) that a log-normal distribution may be expected, when a large number of independent environmental factors act multiplicatively on the abundances of the species (see also PIELOU, 1975).

When the species-abundance distribution is log-normal, the probability density function of y , the abundance of the species, is given by:

$$\psi(y) = \frac{1}{y\sqrt{2\pi V_z}} \exp \frac{-(\ln y - \mu_z)^2}{2V_z} \quad (2.10)$$

The mean and variance of y are:

$$\mu_y = \exp \left(\mu_z + \frac{V_z}{2} \right) \quad (2.11)$$

$$V_y = (\exp(V_z) - 1) \exp(2\mu_z + V_z) \quad (2.12)$$

where μ_z and V_z are the mean and variance of $z = \ln(y)$.

If the species abundances are lognormally distributed, and if the community is so exhaustively sampled that all the species in the community (denoted S^*) are represented in the sample, the graph of the cumulative number of species on a probit scale (figure 3D) against log abundance will be a straight line. This is not normally the case.

In a limited sampling a certain number of species $S^* - S$ will be unrepresented in the sample (S being the number of species in the sample). The log-normal distribution is said to be truncated. In the terminology of PRESTON (1948) certain species are hidden behind a "veil line". It follows that it is not good practice to estimate the parameters of the lognormal distribution from a cumulative plot on a probit scale. In fact if one does not estimate the number of unsampled species, it is impossible to estimate the proportion of the total number of species in a particular log density class. Species abundances that are lognormally distributed will not yield straight lines if one takes into account only the species sampled. Note also that the normal regression analysis is not applicable to highly correlated values such as cumulative frequencies. (If the frequencies are replaced by evenly distributed random numbers, their cumulative values on probit scale still yield very "significant" correlations with log abundance).

In fitting the log-normal two procedures are used (apart from the wrong one already discussed). The conceptually most sound method is to regard the observed abundances of species j as a Poisson variate with mean λ_j , where the λ_j 's are lognormally distributed. The probability, p_r , that a species contains r individuals is then given by the Poisson log-normal distribution (see BULMER, 1974). p_r can be solved approximately for $r > 10$, but must be integrated numerically for smaller values of r . BULMER (1974) discusses the fitting to the data by maximum likelihood. PIELOU (1975) argues that the fitting of the Poisson lognormal, though computationally troublesome, is not materially better than the alternative procedure, consisting in the direct fitting of the

continuous lognormal. The complete procedure in recipe-form is given in PIELOU (1975).

2.3. On fitting species-abundance distributions

Ever since FISHER *et al.* (1943) used the log-series, and PRESTON (1948) proposed the log-normal to describe species-abundance patterns, ecologists have been debating which model is the most appropriate. Especially the log-normal and the log-series have (had) their fan-clubs (*e.g.* SHAW *et al.*, 1983; GRAY, 1983 and other papers). In our opinion, these debates are spurious. As PIELOU (1975) remarked, the fact that *e.g.* the log-normal fits well in many instances, tells us more about the versatility of the log-normal than about the ecology of these communities. Although most of the distributions have a kind of biological rationale (to make them more appealing to a biological audience?) the fact that they fit does not prove that the “biological” model behind them is valid in the community. The fitting of a model to field data is meaningful if the parameter estimates are to be used in further analysis. This is analogous to the use of the normal distribution in ANOVA: in order to perform an ANOVA, the data should be normally distributed. Of course this must be checked, but only as a preliminary condition. No one draws conclusions from the fit or non-fit of the normal distribution to experimental data, but from the test performed afterwards. Similarly, if a particular model fits reasonably well to a set of field data, the parameter estimates can be used, *e.g.* in respect to the diversity of the communities

3. Diversity indices derived from species-abundance distributions

Historically, the first diversity measure was derived by FISHER *et al.* (1943) as a result of the derivation of the log-series distribution. The parameter α of the log-series distribution is independent of sample size. From equation (2.7) it is easily seen that α describes the way in which the individuals are divided among the species, which is a measure of diversity. In adopting the log-series model for the species-abundance distribution, the evenness is already specified, so that α only measures the relative species richness of the community. α , as determined by the fitting of the log-series model to the sample, is only valid as a diversity index when the log-series fits the data well. The same reasoning can be extended to the log-normal distribution. PRESTON (1948) expressed the diversity (richness) as the (calculated) total number of species in the community, S^* .

The use of the log-series α was taken up again, and extended by KEMPTON & TAYLOR (1974). TAYLOR *et al.* (1976) showed that, when the log-series fits the data reasonably well, α has a number of attractive properties. The most important of these are that (compared to the information statistic H' and Simpson's index; see below) it provided a better discrimination between sites, it remained more constant within each site (all sites were sampled in several consecutive years), it was less sensitive to density fluctuations in the commonest species, and it was normally distributed. On the other hand, when the data deviate from the log-series, α is more dependent on sample size than the other indices.

4. Rarefaction

An obvious index of species richness is the number of species in the sample. However, it is clear that this measure is highly correlated with sample size, an undesirable property. SANDERS (1968) proposed a method to reduce samples of different sizes to a standard size, so as to make them comparable in terms of the number of species. The formula used by SANDERS (1968) was corrected by HURLBERT (1971), who showed that the expected number of species in a sample of size n is given by:

$$ES_n = \sum_{i=1}^S \left(1 - \frac{\left[\frac{N - N_i}{n} \right]}{\left[\frac{N}{n} \right]} \right) \quad (4.1)$$

where N_i is the number of individuals of the i -th species in the full sample, which had sample size n and contained S species. The notation in square brackets $\left[\frac{A}{B} \right]$ indicates the number of permutations of A elements in groups of size B . Alternatively, random samples can be drawn by computer from the original sample (SIMBERLOFF, 1972). For an example of application of this method to deep-sea benthos see SOETAERT & HEIP (1990).

5. Hill's (1973) diversity numbers

HILL (1973) provided a generalized notation that includes, as a special case, two often used heterogeneity indices. Hill defined a set of "diversity numbers"

of different order. The diversity number of order a is defined as:

$$H_a = \left(\sum_i p_i^a \right)^{1/(1-a)} \quad (5.1)$$

where p_i is the proportional abundance of species i in the sample. In the original notation N is used instead of H , but to avoid confusion with abundance N , we propose to use H (Hill) instead. For $a = 0$, H_0 can be seen to equal S , the number of species in the sample. For $a = 1$, H_1 is undefined by equation (5.1). However, defining

$$H_1 = \lim_{a \rightarrow 1} (H_a) \quad (5.2)$$

it can be shown that

$$H_1 = \exp(H') \quad (5.3)$$

where H' is the well-known Shannon-Wiener diversity index:

$$H' = - \sum p_i \ln p_i \quad (5.4)$$

This is the most widely used diversity index in the ecological literature.

Note that in the usual definition of the Shannon-Wiener diversity index logarithms to the base 2 are used. Diversity then has the peculiar units "bits·ind⁻¹". The diversity number H_1 is expressed in much more natural units. It gives an equivalent number of species, *i.e.* the number of species S' that yields H_1 if all species contain the same number of individuals, and thus if all $p_i = 1/S'$. This can be seen in equation (5.3), which in this case reverts to:

$$H_1 = \exp(-\ln(1/S')) = S' \quad (5.5)$$

An additional advantage of H_1 over H' is that it is approximately normally distributed.

It has been argued (see *e.g.* PIELOU, 1975) that for small, fully censused communities the Brillouin index should be used. This index is given by:

$$H = \frac{1}{N} \log \frac{N!}{\prod N_i!} \quad (5.6)$$

in which $\prod N_i = N_1 \cdot N_2 \cdots N_S$.

We do not recommend this index. The theoretical information argument for its use should be regarded as allegoric: it has no real bearing to ecological theory. PEET (1974) showed with an example that the Brillouin index has counter-intuitive properties: depending on sample size, it can yield higher values for less evenly distributed communities.

The next diversity number, N_2 , is the reciprocal of Simpson's dominance index λ , which is given by:

$$\lambda = \sum_i p_i^2 \quad (5.7)$$

for large, sampled, communities. If one samples at random and without replacement 2 individuals from the community, Simpson's index expresses the probability that they belong to the same species. Obviously, the less diverse the community is, the higher is this probability. In small, fully censused communities, the correct expression for Simpson's index is:

$$\lambda = \sum_i \frac{N_i(N_i - 1)}{N(N - 1)} \quad (5.8)$$

where N_i = number of individuals in species i , N is the total number of individuals in the community.

In order to convert Simpson's dominance index to a diversity statistic it is better to take reciprocal $1/\lambda$, as is done in Hill's H_2 , than to take $1 - \lambda$. In that way the diversity number H_2 is again expressed as an equivalent number of species.

HILL (1973) pointed out that λ is a weighted mean proportional abundance, as it can be written as:

$$\lambda = \sum w_i p_i / \sum w_i \quad (5.9)$$

where the weights are equal to the relative abundance $w_i = p_i$.

The diversity number of order $+\infty$, $H_{+\infty}$, is equal to the reciprocal of the proportional abundance of the commonest species. It is also called the "dominance index". MAY (1975) showed that it characterises the species-abundance distribution "as good as any, and better than most" single diversity indices. It is also the most easily estimated diversity number since its calculation only requires distinction between the commonest species and all the others.

HILL (1973) showed that the diversity numbers of different orders probe different aspects of the community. The number of order $+\infty$ only takes into account the commonest species. At the other extreme, $H_{-\infty}$ is the reciprocal of the proportional abundance of the rarest species, ignoring the more common ones. The numbers H_0 , H_1 , and H_2 are in between in this spectrum. H_2 gives more weight to the abundance of common species (and is, thus, less influenced by the addition or deletion of some rare species) than H_1 . This, in turn, gives less weight to the rare species than H_0 , which, in fact, weighs all species equally, independent of their abundance. It is good practice to give diversity numbers of different order when characterising a community. Moreover, these numbers are useful in calculating evenness (see below).

6. The subdivision of diversity

6.1. Hierarchical subdivision

In the calculation of diversity indices, all species are considered as different, but equivalent: one is not concerned with the relative differences between species. However, in nature some species are much more closely related to some other species than to the rest of the community. This relation may be considered according to different criteria, *e.g.* taxonomic relationships, general morphological types, trophic types, etc. It may therefore be desirable to subdivide the total diversity in a community in a hierarchical way. PIELOU (1969) shows how the Shannon-Wiener diversity H' can be subdivided in a hierarchical way. The species are grouped in genera, and the total diversity equals:

$$H'_T = H'_g + H'_{wg} \quad (6.1)$$

where H'_g is the between genera diversity given by:

$$H'_g = - \sum_i q_i \log q_i \quad (6.2)$$

and

$$H'_{wg} = \sum_i q_i \left(- \sum_j r_{ij} \log r_{ij} \right) \quad (6.3)$$

is the average within-genus diversity. The same procedure may be repeated to partition the between-genera diversity into between-families and average within-family diversity. This approach was generalised by ROUTLEDGE (1979) who showed that the only diversity indices that can be consistently subdivided are the diversity numbers of HILL (1973) (of which H' can be considered a member, taking into account the exponential transformation).

The decomposition formula is:

$$\left(\sum_i \sum_j t_{ij}^a \right)^{1/(1-a)} = \left(\sum_i q_i^a \right)^{1/(1-a)} \left(\left(\sum_i q_i^a \sum_j r_{ij}^a \right) / \sum_i q_i^a \right)^{1/(1-a)} \quad (6.4)$$

for $a \neq 1$.

In equation (6.3) q_i = proportional abundance of group (*e.g.* genus) i , r_{ij} = proportional abundance of species j in group i , t_{ij} = proportional abundance of species j (belonging to group i) relative to the whole community.

It can be seen that the community diversity is calculated as the product of the group diversity and the average diversity within groups, weighted by the

proportional abundance of the groups. Note that this is consistent with Pielou's formulae (eq. (5.9)) since $H_1 = \exp(H')$.

The hierarchical subdivision of diversity may be useful to study the differences in diversity between two assemblages, and to investigate whether a higher diversity in one assemblage can be attributed mainly to the addition of some higher taxa (suggestive of the addition of new types of niches), or of a diversification of the same higher taxa that are present in the low-diversity assemblage.

It may also be useful to study other than taxonomic groups. Natural ecological groupings, such as the feeding or body types may be particularly interesting. HEIP *et al.* (1984, 1985) used θ as a "trophic diversity index" to describe the diversity in feeding types of nematodes,

$$\theta = \sum_{i=1}^n q_i^2 \quad (6.5)$$

where q_i is the proportion of feeding type i in the assemblage and n is the number of feeding types.

6.2. Spatio-temporal diversity components

All ecological communities are variable at a range of spatio-temporal scales. Thus if one examines a set of samples, (necessarily) taken at different points in space, and possibly also in time, and calculates an overall diversity index, it is unclear what is actually measured. Whereas diversity may be small in small patches at a particular instant, additional diversity may be added by the inclusion in the samples of diversity components due to spatial or temporal patterns.

Following WHITTAKER (1972) one often distinguishes between α -diversity, the diversity within a uniform habitat (patch), β -diversity, the rate and extent of change in species composition from one habitat to another (*e.g.* along a gradient), and γ -diversity, the diversity in a geographical area (*e.g.* the intertidal range of a salt marsh). These are useful and important distinctions.

The subdivision of total diversity H' in ecological components is discussed by ALLEN (1975). He treats a sampling scheme where S species are sampled in q sites, each consisting of r microhabitats. The problem is different from a hierarchical subdivision, since the same species may occur in different microhabitats and sites (it can, of course, only belong to one genus, one family, etc. in hierarchical subdivision). ALLEN (1975) presents two solutions. One can treat the populations of the same species in different microhabitats as the fundamental entities. Total diversity is then calculated on the basis of the

proportional abundance (in relation to the total abundance in the study) of these populations. This total diversity can then be subdivided hierarchically.

Alternatively, one can subdivide the species diversity in the total study in average within microhabitat diversity, average between microhabitat (within site) diversity, and average between site diversity components. The latter computations are generalised for HILL's (1973) diversity numbers by ROUTLEDGE (1979).

6.3. Cardinal and ordinal diversity measures

Species are different and fulfil different roles in ecosystems, and within species individuals are different as well. Since most diversity indices are based on the relative abundance of the different species representing the community, abundance is the only trait of species that is considered to differ between them. COUSINS (1991) distinguishes between indices that treat each species as equal (cardinal indices) and those that treat each species as essentially different.

Species that are taxonomically more similar are also more similar in their morphology, and often in their behaviour and their ecological role in the system, than species that belong to different higher taxa. In practice diversity indices are often applied only to certain taxonomic groups (taxocenes) and the precise taxon level depends on the group being studied. VANE-WRIGHT *et al.* (1991, see also MAY, 1990) have explored the implications of measures of taxonomic distinctiveness. They have used the hierarchical taxonomic classification to calculate an "information index" for species that is based on the number of branch points in the classification tree.

The idea has been taken one step further by WARWICK & CLARKE (1995) who introduced two new indices. In the first one, called taxonomic diversity, the abundance of a species is weighed with the taxonomic path length linking the species with the other species. Taxonomic diversity is the average (weighted) path length in the taxonomic tree between every pair of individuals. A second index, called taxonomic distinctness, is defined as the ratio between the observed taxonomic diversity and the value that would be obtained if all individuals belong to the same genus. This index was shown to be very sensitive to changes in community composition of macrobenthos around drilling platforms in the North Sea.

When diversity is represented by ranking each species in an order of some kind, the resulting index is called an ordinal index by COUSINS (1991). The classical indices, such as Shannon-Wiener and Simpson's index, are cardinal, whereas species abundance distributions, size spectra and species lists are ordinal representations. Cardinal indices are proposed to be useful for describing the diversity of a guild of species or the species within certain classes of body

size or weight, but are considered unsuitable for description of entire communities, where ranking the species is the better option.

7. Sampling properties of diversity indices

Since estimates of the true population (in a statistical sense) value are based on sampling that population it is necessary to pose the question what the sampling properties of diversity indices are. The sampling method itself has to fulfil a number of conditions and usually requires randomness. A good estimator of an index must be unbiased with minimum variance. As already pointed out a number of indices are biased, *e.g.* all indices based on estimates of S , the number of species in the community. The estimator of the Shannon-Wiener index is also biased. Estimators of the Simpson index and the rarefaction measure on the contrary appear to be unbiased. Species must be distributed at random and independent of other species. This is not usually the case and there is as yet no method that will produce unbiased diversity indices with low sampling variance and sampling distributions not influenced by species distribution patterns in the field.

Two methods that have become increasingly popular to overcome some of these difficulties are the jackknife and the bootstrap methods. These are resampling methods and are discussed in more detail by DALLOT (this issue).

In the jackknife method pseudovalues are computed for the parameter of interest (*e.g.* species number, or Hill H_1) which measure the weighted influence of each sample. The i -th pseudo-value is

$$g_i = ng_0 - (n-1)g_{-i} \quad (7.1)$$

in which g_0 is the parameter computed with the n samples pooled and g_{-i} the corresponding value omitting the i -th sample.

In the bootstrap method the parameter is computed using a set of observed values drawn with replacement from the original set.

8. Evenness

The distribution of individuals over species is called evenness. It makes sense to consider species richness and species evenness as two independent characteristics of biological communities that together constitute its diversity (HEIP, 1974).

Several equations have been proposed to calculate evenness from diversity measures. The most frequently used measures, which converge for large samples (PEET, 1974) are:

$$E = \frac{I - I_{\min}}{I_{\max} - I_{\min}} \quad (8.1)$$

and

$$E = \frac{I}{I_{\max}} \quad (8.2)$$

where I is a diversity index, and $I_{\min}$ and $I_{\max}$ are the lowest and highest values of this index for the given number of species and the sample size.

To this class belongs Pielou's J :

$$J = H'/H'_{\max} = H'/\log S \quad (8.3)$$

The condition of independence of evenness measures from richness measures is not fulfilled for the most frequently used evenness indices, such as J' (surprisingly, this is still the most widely used evenness index despite twenty years of literature describing its poor performance). As discussed by PEET (1974) such measures depend on a correct estimation of S^* , the number of species in the community. It is quasi impossible to estimate this parameter. Substituting S , the number of species in the sample, makes the evenness index highly dependent on sample size. It also becomes very sensitive to the near random inclusion or exclusion of rare species in the sample.

HILL (1973) proposed to use ratios of the form:

$$E_{a:b} = N_a/N_b \quad (8.4)$$

as evenness indices (where N_a and N_b are diversity numbers of order a and b respectively). Note that $H' - H'_{\max} = \ln(N_1/N_0)$ belongs to this class, but that $J' = H'/H'_{\max}$ does not. These ratios are shown to possess superior characteristics, compared with J' . HILL (1973) also showed that in an idealised community, where the hypothesised number of species is infinite and the sampling is perfectly random, $E_{1:0}$ is always dependent on sample size. $E_{2:1}$ stabilises, with increasing sample size, to a true community value. However, in practice all measures depend on sample size.

$$E_{1:0} = \frac{e^H}{S} \quad (8.5)$$

HEIP (1974) proposed to change the index to

$$E'_{1:0} = \frac{e^H - 1}{S - 1} \quad (8.6)$$

In this way the index tends to 0 as the evenness decreases in species-poor communities. Due to a generally observed correlation between evenness and number of species in a sample, $E_{1:0}$ tends to 1 as both $e^H \rightarrow 1$ and $S \rightarrow 1$. However this index falls into the same category as J , being dependent on an estimate of S .

A whole series of evenness indices can be derived from Simpson's dominance index λ . Since the maximum value of λ is $1/S$ (S = number of species), an evenness index can be written as

$$E = \frac{1/\lambda}{S} \quad (8.7)$$

This corresponds to $E_{2:1}$ of HILL (1973)

$$E_{2:1} = \frac{1/\lambda}{e^H} \quad (8.8)$$

which was modified by ALATALO (1981) in the same way as HEIP (1974) modified $E_{1:0}$.

$$E'_{2:1} = \frac{1/\lambda - 1}{e^H - 1} \quad (8.9)$$

Even in the recent literature (SMITH & WILSON, 1996) it is recognized that the measurement of evenness is still very much a matter of debate and the literature continues to be "plagued" by new propositions (MOLINARO, 1989; CAMARGO, 1992; NEE *et al.*, 1992; BULLA, 1994). If the criterion of independence of measures for species richness and evenness (HEIP, 1974) is accepted, the choice of indices becomes more restricted. A good discussion is given by SMITH & WILSON (1996) who applied a series of additional requirements, *e.g.* that the index should decrease by reduction in abundance of minor species, decrease by addition of one very minor species, be unaffected by the units used, etc. These authors concluded that the independence of richness criterion is the only sensible one and only five indices passed this test.

However, SMITH & WILSON's (1996) comparison is valid for samples only and several of the indices proposed are still dependent on the number of species S in the community and therefore on sample size. Still, their idea to use the variation in species abundance is attractive (HILL, 1997). If one uses Hill's number $H_2 = 1/\lambda$ a simple statistic is the weighted mean-square deviation from the proportional abundances that would be expected for H_2 equally abundant species. A measure of evenness is then:

$$D_{MS} = \frac{\sum w_i (p_i - \lambda)^2}{\sum w_i} \quad (8.10)$$

in which MS = mean square, λ is Simpson's index (eq. (5.9)) and $w_i = p_i$ (eq. (2.2)).

HILL (1997) also shows that the expected mean and variance of the relative abundance p_i are given by

$$E(p_i) = \lambda \quad (8.11)$$

$$\text{Var}(p_i) = D_{MS} \quad (8.12)$$

A measure of the shape of the species abundance relation is given by

$$D_{MS}^* = D_{MS}/\lambda^2 \quad (8.13)$$

and a measure of evenness by:

$$E_{MS} = 1/(1 + D_{MS}^*) \quad (8.14)$$

In general, species-abundance distributions show more information about the evenness than any single index. On the other hand, statistics describing these distributions can also be used as measures of evenness. Examples of indices that perform well are the one proposed by CAMARGO (1992), based on the variance in abundance over the species and the one proposed by SMITH & WILSON (1996).

$$E_q = (-2/\pi) \arctan b' \quad (8.15)$$

in which b' is the slope of the scaled rank of abundance on log abundance fitted by least square regression. The reader is referred to SMITH & WILSON (1996) for further details.

9. The choice of an index

The choice of an index has to be considered with care. In our opinion Hill's diversity numbers present a coherent system for diversity estimates. They provide numbers that are equivalent to species numbers and include the simplest measure of species richness, the number of species in the sample as a special case. They also include variants of the Shannon-Wiener and the Simpson indices to which most use of diversity indices has converged. These indices reflect both the evenness (as they are based on the relative abundance of the species considered p_i) and species richness (as they sum up over all the species in the sample). They have even been called evenness indices in the recent literature (WILSEY & POTVIN, 2000), an idea that is worth exploring but very much in contrast to established use of the term.

LAMBSHEAD *et al.* (1983) have noted that, whenever two k -dominance curves do not intersect all diversity indices will yield a higher diversity for the

sample represented by the lower curve. In such a case one could even try using Hill's diversity number $+\infty$ (the relative abundance of the most dominant species), for instance in monitoring or impact studies where the need for "quick and dirty" measures is often required for reasons of cost. Equivocal results arise as soon as the k -dominance curves intersect.

The different measures of diversity are more sensitive to either the commonest or the rarest species). An elegant approach to the analysis of this sensitivity is provided by the response curves of PEET (1974). In order to summarise the diversity characteristics of a sampled community, it is advisable to provide the diversity numbers N_0, N_1, N_2 , possibly also $N_{+\infty}$, the dominance index. If permitted by the sampling scheme, one can use these indices in a study of hierarchical and/or spatio-temporal components of diversity. In any case, it should be remembered that the indices depend on sample size, sample strategy (*e.g.* location of the samples in space and time), spatio-temporal structure of the community, and sampling error. Although formulae for the estimation of the variance of H' have been proposed, these do not include all these sources of error (HEIP & ENGELS, 1974; FRONTIER, 1985).

Evenness indices should still be regarded with caution, but the latest propositions by SMITH & WILSON (1996) and HILL (1997), although perhaps conflicting, deserve further study. It is always advisable to use species-abundance plots to study evenness.

Finally, we should stress the possibilities and limitations of diversity and evenness indices. An index must be regarded as a summary of a structural aspect of the assemblage. As has been stressed throughout this article, different indices summarise slightly different aspects. In comparing different assemblages, it is useful to compare several indices: this will indicate specific structural differences. A diversity index summarises the structure, not the functioning of a community. It is thus very well possible that two assemblages have a similar diversity, whereas the mechanisms leading to their structures are completely different (*e.g.* COULL & FLEEGER, 1977). Often these functional aspects cannot readily be studied by observing resultant structures, and may require an experimental approach.

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