"Every aspect of the assessment of biological diversity is controversial". Review this statement with particular emphasis on techniques for the measurement of diversity.

Themis Nasopoulou
(Reg. N. 377290)

University of Plymouth

School of Science

MSc/PGDip Biological Diversity

Academic Year: 2004-2005

Module: EAR 5102
(Multivariate Analysis for Environmental Science Research)

Module Leader: Professor Martin Kent

19th November 2004

INTRODUCTION

The absence of uniformity among organisms, the overall complexity of live, combined with the evolutionary processes among organisms and ecosystems, affected, inevitably, by human presence and activities, are facts that inspired philosophers, poets, artists, theologists and scientists. Throughout time they expressed their amazement, such as a variety of different theories on how this complex diversity of organisms arose, whether it can be maintained and by which factors it is being ruled.

Despite the impression given by recent international policy processes, biological diversity and its conservation are not new subjects. Herodotus in 450 BC was aware of the importance of intraspecific variation in tree species, although he did not know the word "genetic" and Aristotle in the 4th century BC was the first to describe and classify different species of flora and fauna (Howes, 1997). Theophrastus, follower of Aristotle produces the 'Enquiry into Plants', a detailed description and classification of plants and their properties. Charles Darwin in the middle of the nineteenth century was well aware of biological diversity and its importance for evolution and ecosystem stability.

Scientists realized that in order to deal with such complicated issues, they had to measure biodiversity, by objective means. Many different ways have been proposed, without reaching agreement on which parameters accurately assess biodiversity.

Moreover, the recent advances in genetics, introduced the element of genetic diversity, in the study of recognizing and comparing discrete units, adding complexity to the organisms and ecological diversity among species (Martin & Salamini, 2000).

"*Biological Diversity, means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they area part; this includes diversity within species between species and of ecosystems*".

Although many different definitions of the terms "biodiversity" and "biological diversity" have been published, the most comprehensive, seems to be the above statement, contained in the Article 2 of the "Convention on Biological Diversity", signed by more than 150 nations on the 5th June 1992, at the United Nations Conference on Environment & Development, held in Rio de Janeiro (Gaston & Spicer, 1998).

Meaning variability among living organisms, biodiversity has to be quantified. The keystone in quantifying, "measuring" biological diversity is the abundance of species in a defined unit. Species have become the "common currency" in almost all methods measuring biodiversity.

Biodiversity being a comparative study, the investigator typically wants to know if one domain is more diverse than another, or whether biodiversity has changed over time (Magurran, 2004). It's assessment is complex and varies according to the objectives of the assessor.

The term "**species richness**", represents the oldest and most intuitive measure of biodiversity. Species richness is simply the number of species in the unit of study (Magurran, 2004).

However, there are many other methods to measure biodiversity for example "**species evenness**" is the degree to which the number of individual organisms are evenly divided between different species of the community. Evenness is a measure of the relative abundance of the different species making up the richness of an area (Cox & Moore 2000; Leveque & Mounolou, 2003).

Harper and Hawksworth (1995) defined three elements of biodiversity: **Organismal or species biodiversity**, which represents the number of species, **ecological biodiversity,** defined as the diversity of communities and **genetic biodiversity**, representing the within species diversity.

Earlier (Whitaker 1972) five scales of biodiversity had been introduced:

α-diversity: the diversity of a clarified assemblage or habitat

β-diversity: a measure of the extent to which two or more spatial units differ, in terms of their species composition. It represents the diversity between areas of α diversity.

γ-diversity: is the diversity (usually measured as species richness) of a landscape or other large area

ε-diversity: the diversity of a biogeographic province

δ-diversity: the change in species between units of γ-diversity within an area of ε-diversity

Following Lande (1996), γ- diversity can be treated as mean α- diversity plus β- diversity. Thus, the larger the areas of α-diversity, relative to γ-diversity, the smaller the contribution of β-diversity to overall diversity (Lande, 1996).

Gray (2000) advocates the recognition of four scales of species richness: point species richness, sample species richness, large area species richness and biogeographic province species richness.

The controversy begins. Which is the type of biodiversity we want to measure? What do we have to measure? How are we going to measure it? How do we project our measurements into conclusions?

DATA COLLECTION –"SAMPLING"

The most important factor in measuring biodiversity, is of course data collection: sampling.

Collectors vary in their efficiencies and sampling is usually more challenging in some habitats and weather conditions, than in others.

Organisms, especially mobile ones, can be sampled at certain times of the day, or may show seasonal variation in abundance. We are aware that species are distributed unevenly across the earth. The invertebrate fauna is less well documented, whereas birds and mammals are most thoroughly enumerated. Many individual species, like bats, have not yet been formally surveyed. The most popular organisms are easily identified, where as others are not identified at all.

Unless an assemblage has been sampled exhaustively, species richness study will underestimate species richness to an unknown degree (Coddington et al, 1991).

Since time and money is in short supply and the number of species on earth unpredictable, we need to accurately predict the total species richness of assemblages, using as small samples as possible. On the other hand abundance distribution of species in nature, is variable and unpredictable among different biogeographical areas and habitats.

How can the investigator be confident that his data collection is accurate and offers a correct estimate of biodiversity?

Is his sampling effort intensive enough?

Is his sample adequate, to provide an accurate estimate of the size of the assemblage?

Is there a "stopping rule" in sampling?

Does a universe minimum sample size or sampling effort exist, ruling all possible species richness estimation attempts?

Probably not. It has been proposed, that the number of individuals needed for a reasonable estimate of diversity is in the region of 200-500 (Hayek & Buzas, 1996). In temperate regions for example, all but the rarest species will represent in a sample of 300-500 individuals. However, predetermined sample sizes of a few hundred individuals are for example inappropriate for megadiverse assemblages, such as tropical arthropods (Hammond, 1994).

Generally, standardizing measurements by the number of individuals collected and standardizing by area or sampling effort, can lead to different conclusions regarding species richness (Gotelli & Colwell, 2001).

Many small sampling units will result in a low α and a high β- diversity, while the converse will hold if there are fewer but larger samples. It is however accepted that repeated sampling and replication are keys to a correct species richness estimation. It is better to have many small samples, than a simple large area (Magurran, 2004).

ABUNDANCE MODELS

Which is the most reliable abundance model to use?

Abundance models were initially developed using data from groups of animals, such as birds, where individuals are readily identifiable. There are however circumstances, plant assemblages for example, where it can be difficult to decide where one individual ends and where the next begins.

A universally applicable measure of abundance is **biomass**. It is time consuming to estimate and is destructive (Kent and Coker, 1994), but is a direct measure of resource use and facilitates comparisons between taxa in which population sizes are markedly different (Guo & Rundel, 1997).

The area that plants or other sessile organisms cover can also been used as an abundance measure. It can be easily measured (Nohr & Jorgensen, 1997) but problems arise when organisms overlap one another, or where there is a combination of erect and prostrate growth forms.

Frequency or incidence, being the number of sampling units in which a species occurs, is another method of abundance measurement. An obvious disadvantage is that the abundance of widespread species in underestimated, whereas rare species abundance will be overestimated.

Species Richness

Species richness is often treated as the iconic measure of diversity, although it is not the only measure. It is the simplest way to describe community and regional diversity (Magurran, 1988; Hammond, 1994), and this variable - number of species - forms the basis of many ecological models of community structure (Stevens, 1989). Maximizing species richness is often an explicit or implicit goal of conservation studies (May, 1988), and current and background rates of species extinction are calibrated against patterns of species richness (Simberloff, 1986).

There are two methods of expressing estimates of species richness: a) **numerical**, which is the number of species per specified number of individuals or biomass and b) **species density**, which is the number of species per specified collection area or unit (especially favored in botanical studies) (Magurran, 2004).

Numerical species richness on the other hand lends itself to animal taxa, where individuals are readily identifiable and where the investigator has the option of continuing sampling until a certain minimum number of individuals are reached.

Species richness assessment protocols can be individual –based (individuals sampled sequentially) and sample –based (sampling units identified and all individuals within them enumerated). The sampling approach itself can implicate richness estimation. The major problem with species richness estimates, is their dependence on sampling effort (Gaston, 1996), which is rarely documented. This also impedes the comparison of the richness between different localities.

There are three approaches to estimating species richness from samples:

- Species accumulation curves
- Parametric methods
- Non-parametric methods

Species accumulation curves

Although species richness is a natural measure of biodiversity, it is an elusive quantity to measure properly (May, 1988).

Species accumulation curves, plot the cumulative number of species recorded as a function of sampling effort, representing a sample-area relationship (Colwell & Coddington, 1994). They are noted to move from left to right as new species are added and provide an estimate of the total richness of the assemblage. They illustrate the rate at which new species are added. But unless sampling has been exhaustive, these curves do not directly reveal total species richness. More effort, uncovering more species,

will lead accumulation curves to creep upwards. Sampling curves rise relatively rapidly at first, then much more slowly in later samples as increasingly rare taxa are added.

The curve for a thoroughly sampled fauna will reach a plateau, with few or no species being added with additional sampling (Magurran, 1988).

Samples should be taken in a systematic way, restricted to areas of reasonably homogenous habitat rather than being based on large-scale biogeographic zones.

There are three general methods of estimating species richness: extrapolating species accumulation curves, fitting parametric models of relative abundance and using non-parametric estimators. Species accumulation curves can be fit to equations that contain an asymptote, and the asymptote becomes the estimated species richness of the community. A difficulty with fitting asymptotic curves is that there are many different asymptotic equations and multiple methods of fitting curves to them. This results in a variety of different estimated richness values for the same observed species accumulation curve. Which of the different equations or curve-fitting methods is best is a subject of controversy (Longino, 2000).

Species richness curves, asymptotic or non-asymptotic, mainly have a role to predict the increase in species richness for additional sampling effort, rather than to estimate total species richness (Magurran, 2004).

Parametric methods

If the shape of a species abundance distribution can be satisfactorily described, it is theoretically possible to estimate overall species richness, or at the very least the increase in species richness for an additional sampling.

The two species abundance models with the greatest potential in this context are the log series and log normal distributions (Coldwell & Coddington, 1994). The log series is the easiest to apply. These authors also suggest that if the total number of individuals in a target area can be estimated, a good estimation of total species richness is possible.

Using the log normal distribution on the other hand, is probably inappropriate, there only few natural distributions are perfectly symmetric (Magurran, 2004).

Non parametric methods

A number of non parametric methods, provide a promising method of deducing total species richness, using tractable sample sizes. They represent one of the most important advances in diversity measurements over the last years.

These methods are called non parametric: They are not based on the parameter of a species abundance model, that has previously been fitted to the data. Their performance depends on the underlying distribution. These methods were introduces by Chao (1984) and their accessibility was further developed by Colwell (2000).

DIVERSITY INDICES

Diversity statistics are conventionally classified as either species richness measures (MacIntosh, 1967), or heterogeneity measures (Magurran, 2004).

McIntosh's diversity index (U)

A community can be envisaged as a point in an S-dimensional hypervolume and the Euclidean distance (U) of the assemblage from its origin can be used as a measure of diversity (Kent and Coker, 1994). U is calculated by the formula:

$$U=\sqrt{\Sigma\ n_i^2}$$

where, Σ = the number of species and
n = the number of individuals or abundance of the ith species in the quadrat / sample.

Heterogeneity measures are those that combine richness and evenness components of diversity and fall into two categories: A parameter of a species abundance model (parametric, like log series a) or a measure such as Simpson diversity index, that makes no assumption about the underlying species abundance distribution (non parametric diversity indices).

Non parametric measures of diversity

Shannon index

The Shannon index (H') can be some times found as Shannon-Wiener index, but elsewhere it is mistakenly identified as Shannon-Weaver index (Kent and Coker, 1994). This measure takes into account species richness and proportion of each species within a community. It assumes that individuals are randomly sampled from en infinitely large community (Pielou 1975) and that all species are represented in the sample.

Mathematically, it is one of the most sophisticated of biodiversity measures. This index, H, measures the order or disorder within a community. Order is determined by the number of individuals observed for each species or order (taxa) in a sample plot, calculating the Pi for each species and then multiply it by the natural log of that value. The index is calculated by the formula:

$$H = -\ sum\ (Pi\ log\ [Pi])$$

where, Sum = the number of species and
Pi = the proportion of individuals or the abundance of the ith species expressed as a proportion of total cover.

One of the problems with the Shanon index is that it confounds two aspects of diversity: species richness and evenness. This is often viewed on a disadvantage. An increase in the index may arise either as a result of greater richness or greater evenness, or even both (Kent and Coker, 1994; Magurran, 2004).

The Brillouin index

When the randomness of a sample cannot be guaranteed, for example when different species are differently attracted to stimuli, the Brillouin index (HB) is the appropriate. It is calculated as follows:

$$HB = (\log N - \Sigma \log n_i)/N$$

The Brillouin index describes a known collection about which there in no uncertainty. The Shanon index, by contrast must estimate the diversity of the unsampled, as well as the sampled portion of the community.

An important difference between the Brillouin and the Shannon indices, is that the Shannon index will always provide the same answer so long as the number of species and their proportional abundances are held constant. The Brillouin index is more time consuming than the Shannon index, less familiar and its dependence on sample size can lead to unexpected results. It cannot be used when abundance is measured as biomass or productivity (Magurran, 2004).

Shimpson index

The Shannon index emphasizes the species richness component of diversity. On the other hand, another group of diversity indices are weighted by abundances of the commonest species and are usually referred to as either **dominance or evenness** measures. Probably the best known is the Simpson's index. Simpson gave the probability of any two individuals drawn at random from an infinitely large community belonging to the same species.

It is heavily weighted towards the most abundant species in the sample, being less sensitive to species richness. It is one of the most meaningful and robust diversity measures available. It captures the variance of the species abundance distribution. Analysis of variance can be used to accurately estimate the total diversity in a region.

Simpson Index (**D**) is one of the most meaningful diversity measures available. In essence it captures the variance of abundance distribution. There are two versions of the formula for calculating **D:**

$$D = \Sigma p_i^2$$

where p_i = the proportion of individuals in the ith species.

The form of the index appropriate for a finite community, is:

$$D = \Sigma \{ [n_i(n_i-1)] / [N(N-1)] \}$$

where n_i = the number of individuals in the ith species and

N = the total number of individuals

D takes values between 0 and 1. Alternatively the (1-D) or the reciprocal (1/D) values can be measured, so that the value of the measure rises as the assemblage becomes more even. The 1/D value is the most widely used.

As species richness and evenness increase, so diversity increases. Simpson Diversity Index is a measure of diversity which takes into account both richness and evenness.

Other less frequently used non- parametric indices, are the Berger-Parker index (expresses the proportional abundance of the most abundant species), the Nee, Havey and Cotgreave's evenness measure, the Carmago's eveness index and the Smith-Wilson evenness index (1996). The latter 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.

Smith and Wilson (1996) conducted an extensive set of evalutions of available measures using a range of criteria. These included four requirements (essential) and ten desirable features of measures, as follows:

Requirements:

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

The desirable ten features are:

1. The maximum value of the index is reached 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 the 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.

According to the above criteria, the recently proposed Smith –Wilson index seems to be the most satisfactory evenness measure, shaving a slight superiority, to the most widely accepted, "traditional" Simpson's index (Magurran, 2004).

Taxonomic diversity

Taxonomic diversity indices have been introduced in order to assess the most taxonomically varied assemblages. Moreover these can be used in conjunction with species richness and rarity scores in the context of conservation.

Variations in taxonomic distinctness measures the evenness with which the taxa are distributed across the hierarchical taxonomic tree. These tests can be used in situations where sampling is uncontrolled and where the data are in the form of species presence/absence (Clarke &Warwick, 1998).

Clarke and Warwick (1998) taxonomic distinctiveness index is an extension of Simpson's index. It describes the average taxonomic distance, between two randomly chosen organisms throughout the phylogeny of all the species in the assemblage.

Functional diversity

Functional diversity has attracted considerable interest as a consequence of the current debate on ecosystem performance. The positive relationship between ecosystem functioning and species richness if often attributed to the greater number of functional groups found in richer assemblages.

Petchey and Gaston have proposed a way to quantify functional diversity (2002). Functional diversity uses a dendrogram constructed from species trait values, whereas phylogenetic diversity is estimated from a phylogenetic tree.

One important consideration is that only those traits linked to the ecosystem process of interest are used. Functional diversity has proved to be a useful tool for evaluating the functional consequences of species extinction (Magurran, 2004).

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.

Species abundance (typically measured as the number of individuals or biomass) is an intuitive measure of species importance.

Oindo et al (2001) have proposed a new index which makes inferences about the relative abundances of species from their body size. It is based on the observation that there is a predictable relationship between body size and abundance.

DISCUSSION - CONCLUSIONS:

Ecologists and conservation biologists may want to measure diversity for a number of reasons: (1) to characterize the community so that the ecological and evolutionary processes generating the community can be investigated; (2) to see if two or more communities differ; and (3) to see if the community is changing over time.

Concepts of species diversity such as α (diversity within a community), β (diversity across communities) and γ (diversity due to differences among samples when they are combined into a single sample) have been developed (Whittaker, 1972).

Diversity has two components: variety of forms, and relative abundance. Ecological processes generate a true relative abundance distribution for a set of species in a particular place at a particular time. Ecological sampling of that community produces an observed distribution that is a function of two patterns: the true distribution in nature and sampling artefacts. Sampling artefacts may include random deviations from the true distribution due to under-sampling, and sampling bias in which the sampling method favours the capture of some species over others (Rosenzweig, 1995).

The process of measuring biological diversity contains several steps. In any step, the investigator will have to choose between different options. The optimal is usually not well enough established.

What to sample?

How to sample?

When to stop sampling?

How to estimate abundance?

Which methods/tests to perform to extrapolate the data?

Which measure is more appropriate, species richness or species density?

The answer to each one of these questions can be controversial, each method offering some benefits and having drawbacks.

In other words, should communities be compared on the basis of a standardized number of individuals (species richness) or a standardized area or sampling unit (species density)? For conservation purposes and applied problems that focus on large areas, species density is probably of more interest because it measures the number of species within a specified area. On the other hand, for testing models and evaluating theoretical predictions in ecology, species richness may be more appropriate. Most theoretical models in community ecology do not contain explicit terms for area or density. Instead, the currency of these models is abundance and population growth rates. Probably, neither species density nor species richness is necessarily the "correct" way to measure diversity, but that patterns of diversity will be very sensitive to which measure is used (Gotteli & Colwell, 2001).

The rate of species accumulation is observed with a species accumulation curve. A species accumulation curve has some measure of effort, usually number of samples, on the horizontal axis, and cumulative number of species on the vertical axis. A particular ordering of samples produces a particular species accumulation curve. The last point on the curve will be the total number of species observed among all the samples. Changing the order of samples may change the shape of the curve, but not the endpoint. A smoothed or average species accumulation curve can be produced by repeatedly randomising sample order, calculating a species accumulation curve for each randomisation, and averaging the resultant curves. The curve for a highly undersampled fauna will be nearly linear, with each new sample adding many new species

to the inventory. The curve for a thoroughly sampled fauna will reach a plateau, with few or no species being added with additional sampling (Longino, 2000).

Common diversity measures are sample species richness, like the Shannon's Index and the Simpson's Index. These measures vary in how they are influenced by the species abundance distribution. Species richness, a measure that ignores evenness all together, is strongly influenced by the often long tail of rare species. "Dominance" indices, such as the Simpson's, are strongly influenced by the few most abundant species. The Shannon's Index is influenced by both species richness and by the dominant species.

Generally, we can agree that:

- There is no single overall measure of biodiversity; rather there are multiple measures of different facets (Gaston & Spicer, 1998).
- The measure of biodiversity chosen may reveal something about the values of the investigator. What you measure and how you measure, reveals on what you most value.
- Different measures may suggest different answers.
- A variety of methods can be used to measure abundance. The number of individuals and biomass are the most commonly used.
- Despite its significant limitations **species richness** is one of the most commonly used surrogates as it "intergrates" many different facets (genetic, organismal, ecological) of biodiversity. It is relatively easy to measure and has to some extent become the "common currency" of the study of biodiversity. Is dependent however on sample size and sampling effort, on the investigator's skills the accessibility of habitats and the detectability or rarity of species within habitats.
- Species accumulation curves, species richness indices, parametric and non-parametric methods, have been created in order to estimate species richness accurately.
- As a general rule it is better to have a number of small samples, than a single large one.
- The Simpson's index is recommended for it's ability to consistently rank assemblages, when sample is small.
- A community dominated by one or two species is considered to be less diverse than one in which several different species have a similar abundance.

Finally, assemblages can be compared using t-test and ANOVA, provided replicate samples have been taken, taking in account that estimates of diversity produced by the Shannon's, Simpson's indices and other widely used methods, are often approximately normally distributed.

However with 75% of species on earth, not yet formally described (Cox & Moore, 2000; Gaston & Spicer 1998), it remains in doubt whether current techniques in measuring biodiversity are efficient enough and if at all, species richness estimation, offers a successful tool in measuring biodiversity.

Both the magnitude and the urgency of the task of assessing global biodiversity require improvement of the use of estimation and extrapolation. Future biodiversity inventories need to be designed around the use of effective sampling and estimation procedures, especially for "hyperdiverse" groups of terrestrial organisms, such as arthropods, nematodes, fungi, and microorganisms (Hammond, 1994; Cox & Moore, 2000).

If diversity is recognized as an evolutionary product, it may cause no surprise that no single measurement serves all purposes.

REFERENCES

- Buzas, M.A. and Hayek, L.A-C. (1996) Biodiversity resolution: an integrated approach. Biodiversity Letters (3), 40-43.
- Chao, A. (1984). Non-parametric estimation of the number of classes in the population. Scand J Stat 11, 265-270.
- Clarke, K.R. and Warwick, R.M. (1998) A taxonomic distinctiveness index and its statistical properties. J Appl Ecol 35,523-531.
- Coddington, J.A., Griswold, C.E., Davila, D.S., Penarada, E. and Larcher, S.F. (1991). Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In: The uity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology. Ed. E.C. Dudley . pp. 44-60. Portland OR. Diocorides Press.
- Colwell, R.K. & Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. Phil. Trans. Royal Soc. London B, 345, 101-118.
- Colwell, R.K. (2000). Estimates: Statistical Estimation of Species Richness and Shared Species from Samples (Software and User's Guide), Version6.http://viceroy.eeb.uconn.edu/estimates
- Cox, C.B. and Moore, P.D. (2000). In: Biogeography. A biological and evolutionary approach. Pp. 10-31. Sixth Edition. Blackwell Science.
- Gaston, K.J. (1996). Spatial covariance in the species of higher taxa. In: Aspects of the genesis and maintenance of biological diversity (Ed. M.E. Hochenberg, J.Clobert & R.Barbault) pp. 221-242. Oxford, U.K. Oxford University Press.
- Gaston, K.J. and Spicer, J.I. (1998). Biodiversity: An introduction.
- Gaston, K.J. (2000). Global patterns in biodiversity. Nature, 405, 220-227.
- Gray, J.S. (2000). The measurement of marine species diversity, with an application of the benthic fauna of the Norwegian continental shelf. J Exp Mar Biol Ecol 250, 23-49.
- Gotteli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4(4): 379.
- Guo, Q. and Rundel, P.W. (1997). Measuring dominance and diversity in ecological communities: chosing the right variables. J Veg Sci 8, 405-408.
- Hammond, P.M. (1994). Estimating diversity in speciose groups. Phil Trans R Soc Lond B, 345, 119-136.
- Harper, J.L. and Hawksworth, D.L. (1995). Preface. In: Biodiversity measurement and estimation. Ed. D.L.Hawksworth. pp. 5-12. London. Chapman & Hall.
- Howes, C. (1997). Mapping a World of Disorder. In: The Spice of Life: Biodiversity and the extinction crisis. Pp 12-13. Blandford, 1997.
- Kent, M. and Coker P. (1994). In: Vegetation Despcriprion and Analysis. A Practical Approach. Pp. 72-112. Ed. John Wiley & Sons Ltd. England 1994.
- Lande, R. (1996). Statistics and partitioning of species diversity and similarity among multiple communities. Oikos 76, 5-13.
- Lawton, J.H., Bignell, D.E., Bolton, B. (1998). Biodiversity inventories, indicator taxa, and effects of habitat modification in tropical forest. Nature, 391, 72-76.
- Leveque, C. and Mounolou, JC. (2003). Biodiversity. Pp. 26-36. Ed. John Wiley & Sons, Ltd, 2003.
- Longino, J. T. 2000. What to do with the data. Pages 186-203 in D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, editors. Measuring and monitoring biological diversity: standard methods for ground-living ants. Smithsonian Institution Press, Washington, D.C., USA.
- Magurran, A.E. (1988). Ecological Diversity and its Measurement. Princeton University Press, Princeton, U.S.A.
- Magurran, A.E. (2004). Measuring Biological Diversity. Ed. Blackwell Science Ltd. 2004.
- Martin, W. and Salamini F. (2000). A meeting at the gene. Biodiversity and Natural History. European Molecular Biology Organization Reports, 1(3): 208-210.
- May, R.M. (1988). How many species on earth? Science, 241, 1441-1449.
- Nohr, H. and Jorgensen, A.F. (1997). Mapping of biological diversity in sahel by means of satellite image analysis and ornithological surveys. Biodiversity Conservation 6, 545-566.
- Oindo, B.O., Skidmore, A.K. and Prins, H.H.T. (2001). Body size and abundance relationship: an index of diversity for herbivores. Biodiversity Conservation 10, 1923-1931.
- Petchey, O.L. and Gaston K.J. (2002). Functional Diversity, species richness and community composition. Ecol Lett 5, 402-411.
- Pielou, E.C. (1975). Ecological Diversity. Wiley Interscience, New York, NY,U.S.A.
- Rosenzweig, M. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Simberloff, D. (1986). Are we on the verge of a mass extinction in tropical rain forests? In: Dynamics of Extinction, ed. Elliott D.K., pp. 165-180. John Wiley & Sons, New York.
- Simpson, G.G. (1964). Species density of North American recent mammals. Syst. Zool., 13, 57-73.
- Smith, B, and Wilson, J.B. (1996). A consumer's guide to evenness measures. Oikos 76, 70-82.
- Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am. Naturalist, 133, 240-256.
- Taylor, L. R. 1978. Bates, Williams, Hutchinson - a variety of diversities. Pp. 1-18 in L. A. Mound and N. Waloff, eds. Diversity of insect faunas: 9th symposium of the Royal Entomological Society. Blackwell, Oxford, U.K.
- Theophrastus. Enquiry into Plants. Volumes I and II. English translation by Sir Arthur Hort. Ed. William Heinemann Ltd., London 1968.
- Washington, H.G. (1984). Diversity, biotic and similarity indices. Water Res., 18, 653-694.
- Whittaker, R.H. (1972). Evolution and measurement of species diversity. TAXON, 21(2/3): 231-251.