# DIVERSITY AND BIODIVERSITY: WHAT MIGHT BE THEIR SIGNIFICANCE IN THE SCOPE OF SUSTAINABLE DEVELOPMENT?

By JOÃO CARLOS MARQUES<sup>1</sup>

With 1 figure

ABSTRACT. Difficulties involved in understanding the dynamics of diversity are discussed, aiming to show that it has not been possible to find any "diversity index" capable to express the dynamics of mixed populations, exhibiting stabilized values through space and time. Diversity and Biodiversity, as working concepts, are analyzed in terms of their meaningful differences. It becomes clear why biologists put at present less emphasis in the interpretation of Diversity as a "descriptor" of representative segments of the biosphere, Biodiversity appearing instead as a much more "saleable" term, and therefore much more appealing to decision-makers. It is appraised if the novelty in Biodiversity concerns only this "marketing" idea, showing that although more holistic, this concept is relatively more intuitive, allowing to relieve the pressure towards quantitative measurements that prevailed for many years in connection to the more conventional concept of Diversity. In other words, the previous Diversity concept has been split, giving origin to Biodiversity. Such split was afterwards helpful to precise the meaning of diversity, since this concept had previously been side tracked to a kind of static statistical problem, instead of expressing the dynamics of ecosystems as a whole. On the other hand, the new emphasis on biodiversity revitalized taxonomic studies providing better tools to assist the analysis of the structure and dynamics of the biosphere. The two concepts, Diversity and Biodiversity, are analyzed through a simple dynamic model, and it is discussed how they capture natural cyclic changes. A major conclusion is that Diversity appears to develop from the stores of Biodiversity. Finally, the two concepts are discussed in terms of what might be their significance in the scope of sustainable development.

Bol. Mus. Mun. Funchal, Sup. N.º 6: 349-361, 2001

<sup>1</sup> IMAR - Instituto do Mar, Departamento de Zoologia, Faculdade de Ciências e Tecnologia, Universidade de Coimbra, 3049 Coimbra, Portugal. E-mail: jcmimar@cygnus.ci.uc.pt

*RESUMO*. As dificuldades envolvidas na compreensão da dinâmica da diversidade e sua medida são discutidas, visando ilustrar que não foi ainda possível criar um "índice de diversidade" capaz de expressar, por meio de valores estabilizados em termos espaciais e temporais, a dinâmica de populações misturadas.

Enquanto conceitos de trabalho, Diversidade e Biodiversidade são analisados em termos das suas diferenças significativas. São tornadas claras as razões que levam presentemente os biólogos a colocar menos ênfase na interpretação da Diversidade como "descritor" de segmentos representativos da bioesfera, surgindo em alternativa a Biodiversidade como um termo mais muito mais "vendável" e, por conseguinte, mais apelativo para os decisores políticos. É discutido se a novidade da Biodiversidade reside apenas nesta ideia de "marketing", mostrandose que, embora mais holístico, este conceito é, todavia, relativamente mais intuitivo, o que terá permitido aliviar uma clara pressão, ligada ao conceito mais convencional de Diversidade, que prevaleceu durante muitos anos, no sentido de efectuar medidas quantitativas. Por outras palavras, o prévio conceito de Diversidade foi dividido e deu origem ao de Biodiversidade. Esta divisão foi útil no sentido de precisar o significado de Diversidade, uma vez que este conceito, anteriormente, havia sido abordado como uma espécie de problema estatístico estático, em vez de expressar a dinâmica dos ecossistemas como um todo. Por outro lado, esta nova ênfase na Biodiversidade ajudou a revitalizar, em novos moldes, a investigação em taxonomia, melhorando por conseguinte a panóplia de instrumentos utilizáveis na análise da estrutura e dinâmica da bioesfera. Os dois conceitos, Diversidade e Biodiversidade, são analisados por meio de um modelo dinâmico muito simples, sendo discutida a forma como cada um deles captura as mudanças cíclicas naturais. Uma das principais conclusões parece ser que a Diversidade, enquanto medida, se desenvolve como expressão activa da Biodiversidade, subjacente nos sistemas. Finalmente, os dois conceitos são discutidos em termos de qual possa ser o seu significado no contexto do desenvolvimento sustentável.

Diversity is usually defined as biological variety in nature, which can be perceived in an intuitive way, quantified, and adequately expressed in any appropriated manner. Diversity appeared as an interesting concept since we noticed the regular way individuals fall into species, which could be observed for instance through the study of insect collections, marine invertebrate samples, or birds counting during surveys. In random collections, a few species always appear represented by many individuals, while decreasing numbers of individuals usually represents the rest of it, and many species are even represented by single specimens. An attempt to generalise such representation easily justified for instance to characterise a rocky shore as being of higher diversity than a sandy beach. Of course, in practice, the approach will be strongly dependent on the taxonomic characteristics of the group on which diversity estimations are tentatively based, and it is clear, as an example, that algae pose different problems than invertebrates or fish.

Through time our view of diversity changed, and nowadays this concept may be regarded better as the amount of genetic non-redundant information existent in a defined ecological (biological) system. From a quantitative point of view, the diversity of a given genetic pool (G) may be expressed as a function of the number of species (S), of the biomass (B), or of the total number of individuals (N). Moreover, ecologists know quite well that they should expect more constancy in ratios than in absolute numbers, and they also familiar with the properties of logarithmic relations (e. g. allometric). The expression of diversity could therefore be tentatively approached, as a start, assuming that  $G \approx S^k \approx B^{k'} \approx N^{k''}$ .

Other mathematical functions, more complex, were used to express the same kind of relations. For instance, VOLTERRA (1926) proposed a reasonable approach to what is basically the same problem and FISHER *et al.* (1943) explored in what extent it was adequate to use expressions based on statistical hypothesis, but we may say that, since then, statisticians were never contented with the concept of diversity. This might be due to the dynamics of diversity, which is permanently altering the information content, making it a trouble in any set of definable probabilities. In fact, it's not possible to stabilise variance in samples, since the entire model suffers from the typically irregular dynamic change almost always found in nature. Such dynamics combines a general tendency to increase diversity along different ways, with the occurrence of unexpected declines, which are often spatially extensive. Therefore, although we can measure diversity, it can hardly be considered as a static property of samples proceeding from a given system.

A few relations regarding the composition of natural communities exhibit relatively low spatial (local) and temporal variability, and constitute therefore suitable possibilities to be used as diversity measures. That's the case, for instance, of measures of information or of "entropy", like the Shannon-Wienner index (see MAGURRAN, 1988):

$$H' = -\sum_{i}^{n} p_i \log_2 p_i$$
$$i = 1$$

This one is quite equivalent to the Brillouin index (1962 in KAESLER & HERRICKS, 1976):

$$H = (1/N) Log_2 (N!/N_1! N_2! N_i!)$$

It is easy to demonstrate that diversity, when expressed by Brillouin's formula, will increase by  $(1/N) \log_2 (N_a/N_b+1)$  if in a sample one individual of a common species (a) is removed, being replaced by one individual of a more rare species (b). This is not too different from Volterra's formula (VOLTERRA, 1926; SCUDO, 1971), which introduces a function of the sum  $\sum a_i N_i \log N_i$ .

This brief synopsis gives one an approximate idea of the difficulties involved in understanding the dynamics of diversity. It is not pessimistic if we say that it is impossible to find a "diversity index" capable to express the dynamics of mixed populations, exhibiting stabilised values through space and time. The difficulties may be summarised in the following way:

a) The increase of diversity through time is inevitably gradual, usually associated with the emergence and transformation of an organised system, but its decrease is most frequently abrupt.

b) If we consider the spatial characteristics of ecosystems, we are forced to conclude that it is impossible to have stabilised variance, which may lead us to favour any kind of spectral expression taking into account the way diversity may shift as a function of the space considered. The problem in this case is that each spatial enlargement provides a different spectrum as a function of the characteristics of new sites added to the sample.

c) Since the biosphere is a continuous, it is not satisfactory to set apart "local" diversity (called  $\alpha$  diversity) from diversity estimated by pooling discontinuous patches ( $\beta$  diversity) or measured at larger spatial scales or by ( $\gamma$  diversity), although, in a certain extent, such description might helpful to approach the biodiversity concept.

It as been tried to discriminate between the two components of diversity, *i. e.*, the number of species in presence (species richness) and the uneven representation of the different species (eveness). Nevertheless, the two properties are correlated, since they emerge from an artificial division of the same distribution pattern, and therefore we may argue that there is no reason why we should expect any clear advantage from such approach. Another attempt is represented by "rarefaction methods" (extrapolation procedures), which seek for estimating an "expected number of species". The statistical properties in the natural sets assumed by such methods are interesting but not proven, and therefore we cannot recommend it.

Even the simplest way to express diversity, the rank frequency diagrams (FRONTIER, 1985) may be criticised, namely when certain features of the sequences, like "convexities" or "concavities" are interpreted as an effect of prevailing biological interactions. Although this might be possible, the most probable, and perhaps more realistic, rationale of such characteristics is that the initial conditions of the average pattern may simply reflect transient population oscillations affecting the species living

concurrently in a given community. Actually, this constitutes an interesting starting point regarding the issue of seasonal variation and its irreversibility.

An additional problem in estimating diversity must be examined, which consists on the fact that modular organisms, for instance large marine macrophytes, cause difficulties in defining and counting individual organisms as such. Consequently, it becomes much more complicated to calculate diversity when we deal with systems that combine big vegetal species or colonial animals with isolated individuals, often belonging to a great number of different size strata, and to perform estimations based on biomass provides only a partial solution. In fact, modular species are of great importance, namely because they behave as quite conservative genetic pools. In other words, nature is too complex to be successfully described by simple indices, and all the tries proposing new ways to estimate diversity couldn't provide any tangible conceptual progress (see MAGURRAN, 1988).

At present, we may say that biologists put less emphasis in the interpretation of diversity as a descriptor of representative segments of the biosphere. Instead, the interest turned to "biodiversity". This new term suddenly emerged and its use expanded rapidly, although it's difficult to say where it came from. Beyond any doubt, biodiversity is much more "saleable" and therefore much more appealing to decision-makers, but let's appraise if the novelty restricts only to this "marketing" idea.

For some authors biodiversity may be seen as the full range of biological diversity from intraspecific genetic variation to the species richness, connectivity and spatial arrangement of entire ecosystems at a landscape level scale (see for instance SOLBRIG, 1991). This means that biodiversity concerns much less the existent numerical proportions among different taxonomic units and much more the absolute number of such taxonomic units or, in other words, genetic richness. In this sense, biodiversity represents a more holistic approach to ecosystem's properties than the old diversity concept.

The biodiversity concept becomes especially interesting with regard to high diversity ecosystems, where the two properties, in their ultimate form, are not necessarily related with higher biological or metabolic activity, rather the contrary. We may find good examples of this in estuarine environments (see MARQUES *et al.*, 1993b; 1997). On the other hand, this may explain, for instance, why we should expect to find profuse biological diversity in environments like the deep sea. The reason is that what drives diversity developing is the balance between the energy flow, usually expressed in turnover, and the genetic differentiation related with a hard survival in such environment.

Although more holistic, the biodiversity concept is relatively simple, which allowed to relieve the pressure towards quantitative measures that prevailed for many years following the more conventional concept of diversity. On the other hand, such different perspective emphasised the goal of finding simple and comprehensive regularities that may relate the total number of species found in samples with environmental changes at smaller (local) scales through speciation, migration, and extinction processes. So to say, the previous diversity concept has been split, giving origin to biodiversity, which finally helped in precise its meaning. In fact, somehow, the old concept of diversity had been side tracked to a kind of static statistical problem, which it is not, since it finally expresses the dynamics of ecosystems as a whole. On the other hand, the emphasis on biodiversity allowed revitalising taxonomy studies (this was actually one of the ideas behind the switch) and provides a better tool to assist the analysis of the structure and dynamics of the biosphere. The relations between the two concepts are therefore significant and will be further analysed.

## Analysis of the concepts of diversity and biodiversity through a simple dynamic model

Let us consider a first scenario, corresponding to an extreme situation: a chemostat or flow culture, submitted to a strong selection for yielding. The stock able to multiply faster will become the lasting one, and the final situation will be a monospecific population with minimal diversity. Let S be the number of species, i. e. discernible genotypes, and N the number of individuals, or total biomass. The final scenario referred above represents the situation where the turnover or flow are maximised and diversity is minimal, which can be described by  $S = N^k$ , and when  $k \rightarrow 0$  we have a suitable index of minimal diversity (MARQUES, 2001).

In practice, what the chemostat does is to help in selecting genotypes able to adhere to the walls, having as a result that a fraction of the individuals escapes the risk of being washed out from the system. This essentially resembles to the selective and evolutive processes that take place in rivers, where the capacity of species to resist being drifted away usually favours a lower investment in reproduction. This evolutive pattern is actually common in rivers, and as a consequence of different possibilities open to slow down drift benthic diversity is usually higher than plankton diversity.

As an example of the opposite situation we may imagine an artificial system, e.g. a zoological garden, which keeps receiving new specimens but from where we remove all the extra individuals from species already represented. As a result, a situation of maximum diversity would be created. In such case  $S = N^1$  and therefore the value of k, as proposed above, would be 1. The idea of proposing a scale of diversity between 0 (all specimens belonging to the same species) and 1 (all specimens belonging to different species) obviously appears as the immediate step, and k appears as a potential diversity index (MARQUES, 2001).

Keeping in mind the concept of biodiversity, these examples may be interpreted as showing that a system with maximal diversity (biodiversity) is somehow artificial and needs to be supported from the outside. In a certain extent, we may extrapolate that this supports the opinion that conservation undertaken in protected areas, botanical and zoological gardens will finally lead towards obsolescence and extinction. Although this view is indeed very pessimistic, it is in agreement with the experience that some ecosystems with high diversity often exhibit low turnover and low P/B ratios. Moreover, they receive in many cases a significant matter supply from external sources, as exemplified by the dynamics and composition of deep-sea communities (GRASSLE & MACIOLEK, 1992).

MARGALEF (1991; 1997) proposed a very simple model comparing two feedback loops. The first feedback concerned the total biomass or the total number of individuals,  $dN/dt = aN^h - bN^{h'}$ . Margalef's model uses not the entire powers 1,2, as it is done in the usual "demographic approach", but any values, h, h', provided that h' > h, necessary to have regulation. The second feedback loop concerned the changes in number of species,  $dS/dt = cS^m - dS^m$ , and was inspired in the hypothesis of island biogeography (MacARTHUR & WILSON, 1967).

Let us assume that a relative steady state may be approached, where  $dS/dt \rightarrow 0$ . In such case, the diversity index  $k = \log S/\log N$  or k = B (h'-h) / (m'-m), after making  $B = \log (bc/ad)$ , and therefore k expresses the relative efficiency of two feedback loops, which regulate respectively the total biomass or number of individuals and the total number of species. The differences between the powers, h'-h and m'-m, define how diversity will stabilise. It is obviously that more correct, although more complicated too, mathematical expressions may be proposed, and besides it is not likely at all that the assumed constants are really so. The aim of this simple approach was merely to show that:

a) If it's easier to increase biomass than to split genetically the populations then local diversity will decline.

b) If the biomass or number of individuals cannot increase, but genetic splitting can pursue, or colonisation from outside is likely to occur, then local diversity will increase.

For instance, the old time-stability hypothesis (SANDERS, 1968) may be interpreted in conformity to the model. According to Sanders, the characteristics of marine communities modify in space and time as a function of changing environmental stress. That way, at local level, a long period of low environmental stress would make possible the development of what he called "biologically accommodated" communities, while in more highly stressed environments we should expect to find "physically controlled communities", up to a level of stress beyond any possible adaptation of living organisms. Estuaries constitute a paradigm of "physically controlled communities", corresponding to the situation described in a), while deep-sea and rockyshore infralittoral communities are good examples of "biologically accommodated" communities, corresponding to the situation described in b).

But the same model may be applied to other situations. Natural succession change, for instance, tends to evolve from a type a) to a type b) situation in a rapid way, and biogeographically speaking, from high to low latitude ecosystems also change according to the same pattern (MARGALEF, 1997; MARQUES, 2001).

## How diversity and biodiversity capture natural cyclic changes

Diversity of ecosystems suffers normally a cyclical change, namely in seasonally fluctuating climates, which may be described through a series of irreversible loops on a system of coordinates relating for instance S and N, or S and B (see above). Let us use as example the Mondego estuary benthic communities (see Marques *et al.*, 1993a; 1993b), located in a temperate climate. During spring, both number of individuals and biomass tend to increase, but at the very beginning of the season only a smaller number of species are present, or at least only a few of them are able to start reproducing fast, taking profit from the new available resources. The result is that diversity is low, independently on the measure we may use. As summer moves onwards diversity rapidly increases and later, during fall, many species still persist in the system, although presenting rather low densities. Finally, during winter, when many species are dormant, diversity decreases very much. Nevertheless, in computing it, we are usually not taking into account eggs, algae spores, resting stages found in the mud etc., as actually we should do. Many other examples could be found in the literature illustrating this pattern of variation in temperate ecosystems.

Consideration of the annual cycle of diversity in ecosystems from the Temperate Zone is very helpful in understanding the relations and differences between the concepts of diversity and biodiversity. It appears reasonable to say that diversity comes closer to biodiversity during winter. In fact, diversity is usually an expression of the representation of species in the active ecosystem, while biodiversity is rather closer to the winter situation of any clearly seasonal ecosystem. Let us take another example, a temperate forest. In this case, seeds in the soil of the forest surely comprehend many potentialities that do not have any expression in diversity measures effected based on winter samples. The same goes for the aquatic species, or their resting stages, present in river banks, where they wait for the proper occasion to recolonise the benthos. In other words, they constitute a reserve of biodiversity that may show up when environmental conditions allow ecological succession to continue.

## Diversity develops from the stores of biodiversity

Let us use another example to make clearer the relations between the concepts of diversity and biodiversity as they generally used. It is well known that, independently from the local diversity of the marine plankton community, plankton blooms associated

with upwelling, developing successively or in different places, concern only a few species. This is in many aspects alike what we described with regard to cyclic changes in temperate terrestrial and aquatic ecosystems. Since in biodiversity we comprehend the reserve of genotypes (see above), such marine plankton blooms may be interpreted as experiments in evolution which borrow genotypes from the reserve of biodiversity, play with it and, genetically changed or unchanged, return it back to the general store. The major interest of ecologists typically focus on the most active segments of the yearly spectrum, associated with moderate or high biological activity, here referred as experiments in evolution. From this perspective, it might be suggested that in temperate regions we should usually find a significant difference between actual diversity and total potential (bio)diversity, while for instance in equatorial climates, where there is no seasonal variation, the difference between diversity and biodiversity might be not so large (MARGALEF, 1997).

To look upon biodiversity as a dynamic reserve containing a part of the results from past evolutionary processes, acting as a genetic information pool and providing the potential substratum for existent diversity is quite helpful in enlightening the relations between the two concepts (Fig. 1). Ecosystems continuously accede to genetic materials from the biodiversity store, and natural selection acts upon their active expression. If some new valuable genetic acquisition occurs, eventually new information provided by the reworked materials returns to the biodiversity store, enriching it. On the other hand, through time, the parts of the biodiversity store that have less and less actual active expression become obsolescent and eventually disappear, together with much larger fractions of information that are removed as a result of major environmental changes (e. g. orogenic processes, climatic change, human impact). The events that occur in the active parts of ecosystems are obviously constrained within limits that depend on the biodiversity store, and must be seen as experiments in evolution that provide a rather important loop, necessary to understand the reciprocal relations between the complementary concepts of diversity and biodiversity.

## Diversity, biodiversity and sustainability

Sustainability and sustainable development are two recent concepts that have been more and more used in the last decade, although their meaning remains somehow vague. In fact, if development should imply an indefinite increase of human population and /or in the consumption of energy, obviously there will be no way to sustain it. But let us assume optimistically that an increase in quality of life, as we understand it nowadays, do not necessarily imply a substantial increase of energy consumption, and therefore that there is such a thing as the possibility of sustainable development.

There is no clear definition of what a sustainability niche might be, but as a rough approach it is commonly accepted that the present human population should use

natural resources in a such a way that these remain a patrimony for the future generations. Under the risk of an irreversible destruction of most of our actual renewable resources, therefore compromising the future, this will imply to preserve the integrity of natural ecosystems.

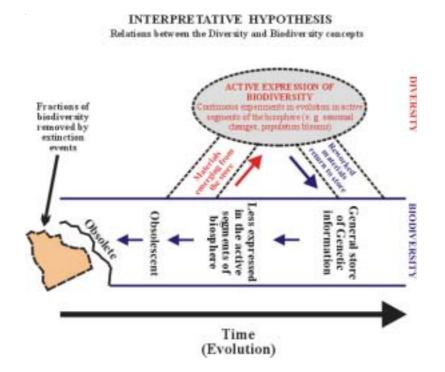


Fig. 1 - Relations between the concepts of diversity and biodiversity (MARQUES, 2001).

Let us consider some of the definitions of ecosystem integrity found in the literature, although try to define the concept might be, in a certain extent, contradictory to the meaning of the concept it self:

"Biological integrity is the maintenance of the community structure and function characteristic of a particular local or deemed satisfactory society" (CAIRNS, 1977 in KAY, 1993);

"Biological integrity is the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition and functional organisation comparable to that of the natural habitat of the region" (KARR & DUDLEY, 1981 in KAY, 1993);

"If a system is able to maintain its organisation in the face of changing environmental conditions then it is said to have integrity" (KAY, 1989 in KAY, 1993).

These different definitions, formulated during more than a decade, evolved from a more motionless to a more dynamic notion of integrity, but the systems capabilities

#### 2001 Marques, Diversity and Biodiversity: Is there a meaningful difference?

to maintain organisation and function remain the central concept. A decrease in available organic information, as is associated with a loss of biodiversity, may impair somehow the capacity for obtaining an optimised rate of change in any future recovery from disasters caused by human population pressure. Actually, it is surely not possible to prevent that a fraction of the organic information available in the biosphere becomes obsolescent and finally is lost, as a consequence of changes introduced by humankind. According to the approach presented in this paper, we should expect human pressure to cause a decrease in diversity, in first place, and after a short delay in biodiversity as well. To this effect should be added the result of disturbances of more catastrophic character, natural or human made, taking away large fractions of biodiversity. At short term this will endanger the capacity of present ecosystems to maintain organisation and function, so to say, their integrity. And the loss of ecosystem's integrity definitely doesn't fit in the concept of sustainable development. Therefore, the preservation of biodiversity is perhaps one of the best indicators we may use to fix boundaries that help us in defining in a more precise way the meaning of this concept.

### REFERENCES

#### FISHER, R. A., A. S. CORBERT & C. B. WILLIAMS:

1943. The relation between the number of animals and the number of species in a random sample of animal population. *Journal of Animal Ecology*, **12**: 42-58.

#### FRONTIER, S.:

1985. Diversity and structure in aquatic ecosystems. Oceanography and Marine Biology Annual Review, 23: 253-312.

### GRASSLE, J. F. & N. O. MACIOLEK:

1992. Deep-sea richness: Regional and local diversity estimates from quantitative bottom samples. *The American Naturalist*, **139**: 313-341.

### KAESLER, R. L. & E. E. HERRICLS:

1976. Analysis of data from biological survey of streams: Diversity and sample size. *Water Resources Bulletin*, **12** (6): 125-135.

### KAY, J. J.:

1993. On the nature of ecological integrity. In: *Ecological integrity and the management of ecosystems* (eds.: S. Woodley, J. Kay & G. Francis), pp. 201-213. St. Lucie Press, Canada.

#### MacARTHUR, R. H. & E. O. WILSON:

1967. The theory of island Biogeography. Princeton University Press, Princeton.

#### MAGURRAN, A. E.:

1988. Ecological diversity and its measurement. Croom Helm, London.

#### MARGALEF, R.:

- 1991. Reflexiones sobre la diversidad y significado de su expresión cuantitativa. In: Simposium Diversidad Biològica – Biological Diversity, pp. 105-112. Fundación Areces, ADENA-WWF y SCOPE, Madrid.
- 1997. Our biosphere. In: *Excellence in Ecology*. Ecol.Inst., Odendorf/Luhe, Germany. 175 p.

### MARQUES, J. C., P. MARANHÃO & M. A. PARDAL:

1993a. Human impact assessment on the subtidal macrobenthic community structure in the Mondego estuary (Western Portugal). *Estuarine Coastal and Shelf Science* 37: 403-419.

MARQUES, J. C., L. B. RODRIGUES & A. J. A. NOGUEIRA:

1993b. Intertidal benthic communities structure in the Mondego estuary (western Portugal): Reference situation. *Vie Milieu*, **43** (2-3): 177-187.

MARQUES, J. C., M. A. PARDAL, S. N. NIELSEN & S. E. JØRGENSEN:

1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. *Ecological Modelling*, **102**: 155-167.

### MARQUES, J. C .:

2001. Diversity, Biodiversity, Conservation and Sustainability. *The Scientific World*, 1: 534-543.

#### SANDERS, H. L.:

1968. Marine benthic diversity: a comparative study. *The American Naturalist*, **102**: 243-282.

#### SCUDO, F. M.:

1971. Vito Volterra and theoretical ecology. *Theoretical Population Biology*, **2**: 1-23.

### SOLBRIG, O. T. (Ed):

1991. *From genes to ecosystems: A research agenda for biodiversity.* IUBS-SCOPE-UNESCO, Cambridge, Mass, 124 p.

## 2001 Marques, Diversity and Biodiversity: Is there a meaningful difference? 361

## VOLTERRA, V.:

1926. Variazioni e flutuazioni nel numero d'individui in specie animali conviventi. Memorie della Accademia dei Lincei, 6 (2): 31-113.

Date received: 15-05-1998.