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## WHAT DO WE MEAN BY BIODIVERSITY?

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**ABSTRACT.** The use of the word 'biodiversity' has increased dramatically in the last decade in the popular press, governmental and intergovernmental reports, scientific papers and meetings. Here I discuss the challenge around operationalizing the concept of biodiversity to enable its incorporation into scientific theory. Multiple dimensions, levels of organization and components have been organized to create a conceptual framework were biodiversity research revolves. As an example, I describe how research on the functional dimension of biodiversity has developed and how concepts and theory have emerged along the way. The degree to which some overall level of biodiversity is required for the delivery of ecosystem services is still unknown. In this sense, the essential issue that has fuelled biodiversity research is yet unresolved. However, in a couple of decades of intensive research, the formalization of the theory behind the theory has progressed substantially.

**KEY WORDS:** Biological diversity, ecological science, operationalization, conservation science

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### A BRIEF HISTORY

The use of the word 'biodiversity' has increased dramatically in the last decade in the popular press, governmental and intergovernmental reports, scientific papers and meetings. Once a concept is so widely used in scientific and non-scientific environments it is important to determine its exact meaning. There is no single definition for this term; biodiversity refers to different things in different contexts and often it is used as a rather vague concept in political environments. The fact that there are several meanings associated with the word biodiversity is due, in part, to its rapid development.

The concept of biological diversity was being used as early as 1980 by authors like Lovejoy (1980) who defined it simply as the number of species, and Norse (1980) who included genetic diversity and species richness. A few years later Norse (1986) considered biological diversity as being comprised of three levels: genetic (within species), species (amongst species) and ecological (community) diversity. The word biodiversity, formed by

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the contraction of 'biological diversity', appeared for the first time in the Biological Abstracts database in 1988 with four references. By then it had acquired its current broad meaning (Lewis 1988). Despite its imprecise definition, biodiversity became very frequently used in scientific literature soon after its first appearance, reflecting its fundamental importance in ecological science. Today, only for the first three months of 2007, the number of records for biodiversity in the Current Contents databases is 827.

Owing to the close relationship between biodiversity and conservation issues, as scientists were beginning to define the term more precisely, the concept increasingly became the center of discussion in political and public arenas. In the Biodiversity Convention, signed in 1992 as a result of the UNCED Conference on the Environment and Development ('The Earth Summit') (Heywood et al. 1995), the term biodiversity became an official political concern for 156 nations. The definition of 'Biological diversity' produced as a result of the conference was broad and rather vague (see table 1 at the end of this text). Today biodiversity is seen in different contexts as a general concept (in the sense of an ecological paradigm), a political construct (to enhance nature conservation) or a measurable entity (Gaston 1996).

#### THE IMPORTANCE OF BIODIVERSITY

'Importance' is a human conception. When asking why is biodiversity important, a human dimension is automatically introduced to the question. In a sense, the question is the same as asking what is the relevance of the 'variety of life' to humans. Biodiversity, conceived as the variety of life on earth, constitutes the foundation of human existence. The ways in which biodiversity is important to humans can be organized into three categories: economical (mainly raw materials), environmental services (such as maintenance of gaseous quality of the atmosphere) and ethic and aesthetic values (Smitinand 1995). Many humans believe that all living forms, including humans, should have the same right to existence. This idea underlies the ethical value of biodiversity. Humans also place an aesthetic value on other forms of life and natural ecosystems; Wilson (1984) has named this innate appeal for the natural world to humans as 'Biophilia'. That is, affiliating with other forms of life is a basic human need, materially, intellectually and spiritually. Ironically, humans are eroding that very same biodiversity with the way they perform the vast majority of their every day and productive activities. This decline has made us aware of our dependence on biological diversity and the limits to the disruption that this natural machinery can endure. The degree to which some overall level of biodiversity is required for the delivery of ecosystem

services has been the greatest concern and, therefore, most biodiversity research has been devoted to this question.

#### DEFINITION OF BIODIVERSITY IN SCIENCE

Biodiversity can be regarded as a 'pseudocognate' (Salt 1979) because the meaning of the concept can be grasped intuitively, without the necessity of operational definitions. Probably, our instinctive affiliation with other forms of life has made us 'comfortable' with the idea of biodiversity in an irrational fashion. However, this intuitive meaning delays the search for a true rational definition. Worse, repetition and familiarity have made us so certain of the term that it has become blindly accepted as a concrete property of nature (Peters 1991).

In science theories are developed to be able to predict phenomena of the real world. All theories are built around concepts or variables. Many definitions of the concept of biodiversity have been produced, and all highlight the broad character of the concept: they cover at once all of life units and processes (table 1). Nevertheless, these definitions cannot be used in scientific practice, because by attempting to be comprehensive they end describing vague relationships (variability, variety or interrelatedness) between components (living organisms, genes, ecosystems or species). In other words, they fail to be operational. An operational definition requires the practical specification of the range of phenomena that a concept or term represents.

It has been said that science always begins with a concept that is often vague (Peters 1991). The presence of vague concepts such as biodiversity may be essential to both the process of operationalization and to the social discourse of young sciences like ecology. Even so, successful science goes beyond this primal stage to develop variables and theories. If biodiversity is to be incorporated into the theory of ecological science, the current concept must be considered more critically and focus on overcoming the multiple challenges encountered when trying to acquire an operational character.

#### CHALLENGES

Biodiversity is today associated with different phenomena by different scientists. The number of species in whole ecosystems (Laurance 2007), sensitive species to urban disturbance on a landscape (Mortberg, Balfors, & Knol 2007), the diversity of secondary compounds produced by different individuals of the same plant species (Sacchetti et al. 2007) or genetic diversification that leads to speciation (Wade 2007), for example. It applies to many levels of biological organization (ecosystems, communities or genomes) and components (genes, individuals, species or biochemical

compounds) within each of those levels. Anyhow, its meaning is not universal; it will vary across levels and components. By this stage biodiversity has so many different meanings that one can never be sure which is intended at any one time. Clarity can only be achieved if scientists, who use biodiversity in a technical sense at any level, specify what exactly they mean by it and why they are considering such definition. However, this immediate solution proliferates definitions and compounds the problem in the long run (Peters 1991).

For example, phylogenetic distance has been suggested as a surrogate variable of biodiversity at the organismal level (Harper & Hawksworth 1995) but cannot be included in genetic or ecological diversity. An operational definition of biodiversity must therefore indicate what levels and components are to be considered. The sort of theory that can be developed depends on this choice. Further, in theory, the definition of biodiversity not only should state its dimensions, levels and components but assert precisely how those dimensions, levels and components are related to one another, and only then biodiversity will become an operational concept that is defined in the form of a theory. For the last two decades, a number of scientists have been working to precise the definitions and measurability of biodiversity at different levels (Bisby et al. 1995; Gaston 1994, 1996; Kunin & Lawton 1996; Lawton & Brown 1993; Loreau et al. 2001; Lovejoy 1980; Martinez 1996; May 1995; McAllister 1991), yet less attention has been paid to the relationship between these levels. A great number of elements have been suggested as candidates for components of the definition of biodiversity. However, nobody has yet produced a compound definition of biodiversity that can be practically used in scientific research, and still retain the umbrella character of the definitions shown in table 1.

An example of the recurrent problem found in research papers is the use of biodiversity as a synonym of species number or species richness (May 1995). Species can be counted and the number of species present at a site might seem to be quantitative measures of its biodiversity and allow comparison with other sites. Then we must ask, if biodiversity means species richness, why do we need both concepts? Therefore, biodiversity must include more elements than the number of species. Species richness ignores other levels of biodiversity such as the genetic and the ecosystem. Also, it assumes, amongst other things, that all species at a site, within and across systematic groups, contribute equally to its species diversity. A measure of biodiversity (at the species level) of a site ought ideally to consider how different the inhabitants are from each other (phylogenetic distance; Harper & Hawksworth 1995), the biomass that each species contributes to the living pool of the site, and how many of the species found are endemic or rare.

## CURRENT APPROACHES

Most scientists performing biodiversity related research have left aside the problem of its definition and have found ways of avoiding it. Two of those common approaches are: (1) to keep biodiversity as a broad concept, and use other terms such as species richness, gene richness and phylogenetic distance, as surrogates that are assumed to reflect the overall biodiversity, and so can be included in a scientific theory; (2) to define biodiversity deliberately in an artificial and simplistic manner which is still relevant to the needs of the specific case. In the first approach, the concept is addressed in a tangential way, and the research's import relies in the assumption that it is possible to extrapolate findings to a broader scale. In the second, the concept of biodiversity is no longer addressed as a whole; authors select some of its components that are thought to be relevant to a specific problem, for example as the number of endemic mammals when choosing a site for a conservation area.

Many dimensions have been attributed to biodiversity—composition, structure, function (Noss 1990), time and space (May 1995)—that can be studied at different levels of biological organization—genetic, organismal and ecological. A number of schemes have been suggested by which the major features of biodiversity can be distinguished, and some sense made of what constitutes the 'variety of life' (Gaston 1996).

Noss (1990) pointed out that one of the crucial characteristics of biodiversity is that it is hierarchical, allowing measuring changes in variables at different levels of organization (figure 1) and obtaining a more comprehensive and multidimensional picture of environmental deterioration. Hierarchy theory suggests that higher levels of organization incorporate and constrain the behavior of lower levels (O'Neill et al. 1986). Therefore, global environmental problems such as greenhouse warming and stratospheric ozone depletion impose fundamental constraints on efforts to preserve particular natural areas or endangered species. Hence, the hierarchical nature of biodiversity suggests that environmental deterioration should be measured at multiple levels of organization and should cover its compositional, structural and functional dimensions. In this sense, biodiversity as a conceptual framework provides an ecological map for identifying specific, measurable indicators to monitor change and assess the overall status of biodiversity. Some debate exists over the limits to the basic concept of biodiversity. The most important of these relate to the extent to which the concept embraces processes such as energy and nutrient flow as components, rather than simply entities like individual organisms, taxa and habitat types. Most definitions of biodiversity are based primarily on entities and seem to ignore processes (Gaston 1996; Noss 1990).

A conventional division of biodiversity is the one that breaks it down into three levels of biological organization: genetic, organismic and ecological diversity (Harper & Hawksworth 1995). Noss (1990) elaborates on this division by pointing out that each of the levels can be studied at the structural, compositional and functional dimensions (figure 1). Composition is formed by the identity and variety of elements in the collection; it includes elements such as species lists or allelic richness. Structure refers to the physical organization or pattern of a system; components such as chromosomal polymorphism and habitat complexity are included in this dimension. Functional involves ecological and evolutionary processes; it includes elements such as gene flow, nutrient cycling or disturbance. Because the compositional, structural and functional aspects of nature are interdependent, the three dimensions are interconnected.

In terms of the genetic level of organization, the diversity of life can be considered fundamentally genetic since underlying phenotypic diversity is a diversity of genetic blueprints. Genes specify proteins, proteins form the basis of physiology, development, appearance and physiology of organisms. A variety of genetic methods can be used to measure the genetic variation underlying any of these functional levels, no matter if we are interested in biodiversity within or between populations, metapopulations, species or any taxonomic level (Mallet 1996).

Organismal diversity refers to diversity expressed at distinct taxonomic hierarchies and generally emphasizes the evolutionary origin of biodiversity (May 1995). Most authors consider species diversity as the most important measure at this level, yet higher taxonomic levels can also reflect this diversity. Harper et al. (1995) favor the term 'organismal' over 'species diversity' because it embraces other taxonomic categories above species. In order to place organismal diversity in a spatial context, the terms 'alpha', 'beta' and 'gamma-diversities' were introduced (Whittaker 1977). Alpha diversity has been defined as the diversity of species (or higher taxa) within local areas. Gamma diversity refers to the regional scale, and beta diversity is the ratio of gamma and alpha diversities, and it is intended to express community dissimilarity.

Species of organisms are not distributed uniformly over the surface of the planet but form spatial patterns of various sorts (Bisby et al. 1995). The level of ecological diversity is structured and characterized by the variety of associations that species form by interacting with each other and their physical environment. Complicated patterns of species clumping may originate from the operation and interaction of historical, physical and functional factors.

WHY ARE SCIENTISTS INTERESTED IN DEFINING BIODIVERSITY  
IN TERMS OF MEASURABLE VARIABLES?

The fact that an increasing number of scientific papers are concentrating on studying biodiversity reflects the belief that it is not simply an abstract concept but a measurable entity, that at least in some sense it can be made operational (Gaston 1996). The desirability of measuring biodiversity is posed on the grounds that it enables broad questions raised by this concept to be subjected to rigorous empirical enquiry (Harper & Hawksworth 1995), and therefore subject of scientific investigation. Scientific knowledge about biodiversity is crucial for comprehending and maintaining its relationship to the ecosystem structure and function; its understanding is also required for the management of resources and maintenance of their life support functions and productivity (Burley & Gauld 1995). If the rules that determine distribution, variety and abundance of life on earth were better understood, it would be possible to apply such knowledge to improve human interactions with the surrounding biosphere (Kunin & Lawton 1996). Nevertheless, several approaches to biodiversity measurement are probably required to address the multifaceted human-environment interactions.

How serious is the damage caused by human activities to the environment? The literature on biological diversity too often seems polarized between enthusiasts and skeptics; "crusaders devoted either to selling the cause of conservation or to sink it" (Kunin & Lawton 1996). If these arguments are to be objectively resolved, ways of measuring damage at all levels of organization and spatio-temporal dimensions ought to be developed. The heightened interest in biodiversity presents an opportunity to address environmental problems holistically, rather than in the traditional and fragmented species-by-species, stress-by-stress fashion (Noss 1990). Biodiversity as a hierarchical concept, allows measuring changes in variables at different levels of organization and obtain a more comprehensive and multidimensional picture of environmental deterioration. Furthermore, biodiversity is a desirable conceptual framework to investigate environmental deterioration because effects of environmental stresses at one level can be expected to reverberate through other levels often in unpredictable ways (Noss 1990). When natural landscape is fragmented, for example, overall species richness may stay the same or even increase, yet the integrity of the community has been compromised with the invasion of weed species and isolation of genetic populations (Burley & Gauld 1995). The extent and character of these effects will be demonstrated by diversity measurements at the genetic and ecological levels.

The hierarchical character of biodiversity also encompasses an approach from the top down, focusing efforts on crucial elements. Increasingly detailed measurements can be performed as lower levels of

organization are approached. For example, when attempting to identify biologically significant areas at high risk of impoverishment, it is possible to begin with a coarse-scale inventory of landscape pattern, vegetation, habitat structure and species distributions. Then intensive research at lower levels of organization can be focused on critical areas, while dedicating less monitoring to the total landscape under management (Noss 1990).

Another argument for making biodiversity a measurable entity is that agencies prefer to promulgate and enforce regulations based on quantitative criteria. Furthermore, publicly funded conservation programs that are intended to preserve or increase biodiversity will have to include monitoring instances in order to determine quantitatively the success or failure of any of funded action (Duelli & Orbist 1998). Biodiversity should enter the agenda of policy makers because all humans participate in its degradation. By entering laws and policies, biodiversity conservation will become the responsibility of all citizens, not only a scientific concern. If the majority of people are expected to be involved in decreasing the process of degradation, it is fundamental to provide them with tools to evaluate the loss (Kunin & Lawton 1996). Furthermore, the developed tools must be simple enough to be accessible to non-specialists since the monitoring task is so immense—for every human activity at all times (Janzen 1993)—that it cannot be all carried out only by scientists.

#### THE MEASURABILITY OF BIODIVERSITY

Whether biodiversity can be measured is a different question to whether its components or dimensions can be quantified (Gaston 1996). There is no doubt that biodiversity in the broadest sense of the Rio Convention cannot be measured (Duelli & Orbist 1998). Many studies are written in such a way as to imply that their findings, although based only on a single variable, concern biodiversity as a whole. Notwithstanding, the abstract concept of biodiversity across a range of hierarchical scales cannot be expressed by a single variable. The complexity is in this sense irreducible, and the search for an all-embracing measure of biodiversity, however desirable it might seem, will be a fruitless one (Gaston 1996; Noss 1990). Therefore, the choice of a measurement of biodiversity will depend fundamentally on the use to which it will be put.

A measurement of biodiversity must solve two problems. First, what, ultimately, is to be measured? Second, how, realistically, can appropriate data be obtained? (Williams & Humphries 1996). In general, measures are used to assess a selected aspect of biodiversity of one or more subsets of objects—a taxon or biota of an area, for example—in comparison either with the entire set (total diversity of the chosen aspect of biodiversity), or

with other subsets such as taxon or other area (Williams & Humphries 1996). The key point is how to choose the particular aspect or aspects of biodiversity that will be measured and how to do it.

To choose one particular aspect or process to be measure is to choose which aspect of biodiversity is hypothesized as to hold a key role in the perpetuation of the system or in being the most vulnerable to the deterioration by human activities. Consequently, deciding upon in which aspect of biodiversity to focus is a deeper problem than, for example, adjudicating among any inherent preferences of taxonomists to count beetle species, or of ecologists to study net primary productivity (Gaston 1996).

Most explicit attempts to quantify some component of biodiversity have concerned primarily with genetic and other specific levels of the hierarchy in biological phenomena. A large number of papers (Duelli & Orbist 1998) recognize that species richness is only one measure of biodiversity, yet do not explain why they have selected it and proceed to treat it as if it were the ultimate measure of biodiversity. Other levels included in definitions of biodiversity, such as ecosystem and landscape, have received little attention, and this perhaps reflects a lack of clarity as to what biodiversity means at this level, as well as the controversial stances associated to the definition of these entities themselves (Gaston 1996).

The measurement of diversity itself (as the way of quantifying a specific component of biodiversity, such as species) is complex. Some measurements simply count entities; others additionally attempt to incorporate some element of their difference (such as abundance). Much of what is known about diversity measurements in biology was garnered in the 1960's and early 1970's in the exploration of ecological measures of diversity, derived originally from the information theory, which combined the number of species and the evenness of their abundance (Grassle, Patil, Smith, & Taillie 1979; Magurran 1996). These indices have essentially fallen out of favor as they are difficult to interpret, and are sample size and sampling pattern dependent (Noss 1990). Whether developing these or new ones, innovative ways of measuring diversity need to be considered in the context of biodiversity (Gaston 1996).

#### DIFFERENT APPROACHES TO BIODIVERSITY MEASUREMENT

If a scientific study is intended to contribute to the understanding of biodiversity, whatever variable is being measured it is assumed as an indicator or surrogate of patterns at a larger scale. The dimensions, levels of organization and components of biodiversity are analogous to a web; their interrelatedness cannot be reduced without compromising the core meaning of the concept of biodiversity. In this sense, even the most comprehensive approach to measure any component of biodiversity re-

lays on the possibility of extrapolation, in the fact that changes in one dimension, level of organization or component will reverberate or be reflected on the others.

Different components, relationships and processes, at all levels of organization, have been suggested to be good indicators or surrogates for biodiversity. All of them provide different information about biodiversity and have proved to be more or less useful for extrapolation in different settings. For this reason, approach to measurement should be selected according to the necessities of specific problems and should carefully consider the hierarchical structure of biodiversity.

When selecting a surrogate for biodiversity there is an unavoidable compromise between precision and the possibility of extrapolation. More remote surrogates (higher levels of biological organization) represent a bigger portion of life forms and, therefore, integrate more of the functional processes that are important for maintaining both ecosystem services and ecosystem viability (Williams & Humphries, 1996), but provide little precision. Conversely, surrogates chosen amongst lower levels of organization are highly precise but their power of extrapolation to other levels is very limited. Furthermore, remote surrogates are easier to measure and have lower costs than proximate measures (Williams & Humphries 1996). Possibly the best approach is to start with distal measures and proceed down the hierarchy, using the information obtained at higher levels of organization to hypothesize which proximate measures will be most sensitive to disturbance.

Amongst the methods developed to measure some aspect of biodiversity, which have proved useful in different contexts, are molecular measurements, species richness estimates, phylogenetic distance assessments and functional diversity estimates. This text will focus on discussing the theory behind the measurement of the functional aspect of biodiversity, since these are directly related to the problem of the relationship between biodiversity and ecosystem services. For a thorough revision of the measurement of other dimensions of biodiversity refer to Janzen (1993), Beattie (1994), Pearson (1995), Harper (1995), May (1995), Stork (1995), Balmford (1996) and Williams and Humphries (1996).

#### THE FUNCTIONAL ASPECT OF BIODIVERSITY AS AN EXAMPLE

Ecosystems can usefully be regarded as 'machines' for many discussions of the way biological and physical processes entwine to maintain the biosphere as a place where life can flourish (May 1995). Particularly, in some discussions concerning ecosystem services, environmental deterioration and option value of resources, we do best by dealing with functional

aggregations to the functional dimension of biodiversity. For example, a pristine forest and a seriously degraded site may have identical numbers of species present, but the composition of those species might be quite different, and the degraded site may have lost many of the rare, highly restricted species that might be crucial for certain ecological processes (Burley & Gauld 1995). In this case it is more efficient to focus on the functional groups involved in the crucial process.

After discussing the multitude of concepts concerning biodiversity, or the variability of life, from genes to ecosystems, one might hope that selecting the functional aspect of biodiversity would improve the operationalization of the concept. However disappointing, functional aspects of biodiversity are broad and vague concepts that need substantial added specification in order to become scientifically more useful (Martinez 1996). In theory, all biological processes at all levels of biological organization can be regarded as functional components of biodiversity. Noss (1990) clearly separated the functional dimension of biodiversity and organized a wide variety of biological processes according to the level of organization at which they operate. However, scientific research on the functional aspect of biodiversity is barely two decades old and there is only a small and immature body of literature that explicitly addresses the topic. In general, the field still lacks widely accepted definitions of central terms such as 'function' itself.

Despite this lack of clarity, there are several consistent concepts, explicitly and implicitly embraced by investigators. With respect to the term 'function' there is a general acceptance that it is closely related to ecological processes (Martinez 1996). In common English language the word 'function' is used in numerous ways. The definition in *The Oxford Current English Dictionary* (Anonymous 1990) that most applies to the biodiversity context is "the activity by which a thing fulfils its purpose." The problem with the use of such a definition is that 'purpose' is a human notion that is foreign to natural systems and finds no foundation in science. The teleological implications of such a concept pervade discussions of function in biology and ecology, and have been discussed in detail elsewhere (Mayr 1988). Many theories that involve biodiversity and function can be interpreted to imply a 'purpose' in their conception. For example, the word 'redundancy' in its literal sense implies superfluous or unnecessary, and therefore the redundancy hypothesis could be interpreted as if species needlessly perform the same function in the ecosystem (Naeem 1998).

Following Lawton (1993), in this text the use of the word 'function' does not imply that ecosystems have goals or objectives; ecosystems simply process materials and energy. The replacement of 'purpose' with 'process' retains the essence that if something is functional, it must perform some action to participate in an ecological process. Therefore functional diver-

sity can be defined as the variety of interactions with ecological processes (Martinez 1996). If this definition is accepted then it follows that 'ecosystem function' and 'ecological process' are synonymous (Lawton & Brown 1993). Naeem (1998) proposes a more detailed definition that agrees with this rationale: "ecosystem function [comprises] the biochemical activities of an ecosystem or the flow of materials (nutrients, water, atmospheric gases) and processing of energy."

Living entities can be functional—participate—in an ecological process by directly performing (plants in primary production) or interacting indirectly (nitrogen fixing bacteria providing such element for primary production; Martinez 1996). In biological systems all entities are related in some way or another. This scheme sets the problem of drawing an arbitrary line to determine when the participation of an entity starts being too indirect to be considered functional in the process.

Two types of hypotheses can be tested when studying the functional dimension of biodiversity. First, the ones that describe the relationship between components of other dimensions of biodiversity with components of the functional dimension (species richness-ecological processes for example); and second, those hypotheses that describe relationships within the functional dimension, that is, relationships between ecological processes within or at different levels of organization of the functional dimension (functional group richness-ecosystem productivity, for example).

The study of the functional dimension of biodiversity requires more than measuring a particular interaction with a process (for example, the occurrence of pollination). It also involves distinguishing between different types of interactions with processes, which includes identifying functional groups and their frequency of occurrence (Martinez 1996). In addition, specification of the scale of interest is critical in understanding which theories and data may be reasonably employed to address the ecological process. Explicit scales of interaction are also very useful for clarifying the level of generalization that theories and observations warrant. The scientific challenge to investigators of functional diversity is to formulate hypotheses that apply to the broadest range of systems, with the widest variety of conditions, and yet performing the same function (Martinez 1996).

#### FUNCTIONAL GROUPS: THE COMPONENTS AT THE ORGANISMAL LEVEL OF THE FUNCTIONAL DIMENSION

It is possible to measure aspects of the functional dimension of biodiversity if it is defined in terms of biological processes and interactions between components that participate in those processes. Depending on the level of organization, the components performing processes could rank from

groups of genes to sets of ecosystems. However, most of the research of functional aspects of biodiversity has focused at the organismal level. At this level, the species or organisms—components—that interact to make biological processes possible may be aggregated under the category of functional groups. In other words, a functional group is formed by those organisms that share common biogeochemical attributes with respect to a particular ecosystem process (Naeem 1998). Functional diversity can be measured by determining which and how many functional groups are represented in an ecological system. First, a typology of functional groups should be developed based on a variety of interactions with an ecological process. Once this typology is achieved, the representation of a functional group is expressed by the occurrence of interactions with the process that defines the group. Membership of living entities in functional groups is evaluated quantitatively (e.g., prey consumed in predation process) by characterizing the interactions with a process both qualitatively (which prey were consumed) and quantitatively (how much was consumed). Standard statistical procedures can be used to quantify the similarity and difference between entities according to qualified and quantified functions (Martinez 1996). At least part of the option value of morphological characteristics may lie in the relationship to functional characteristics. When defined broadly, individual functional groups tend to comprise entire taxa. Thus there is probably some relationship between functional group richness of an area and its higher taxon richness (Gaston 1994).

#### THE THEORY BEHIND THE USE OF FUNCTIONAL GROUPS

The classification of living entities into functional groups has been suggested as a way of simplifying the assessment of ecosystem properties and to understand the complexity in ecological systems (Körner 1993). Functional groups are defined diversely in ecology (Naeem 1998). The membership of functional groups is commonly defined by functional similarity, which means that entities have similar interactions with the same process (Chapin, Schulze, & Mooney 1992), in other words, entities share common biogeochemical attributes (Vitousek & Hooper 1993). As with other grouping schemes in biology, any typology applied to the functional character of species will be, to some degree, arbitrary. Still, once the choices are made, the number of functional groups and their membership are useful parameters to understand ecological processes (Martinez 1996).

The interactions between functional groups and an ecological process may be specified qualitatively (decomposers that decompose the same type of organic matter) or quantitatively (decomposers that decompose similar amount of organic matter). Three main variables can be distinguished: (1) functional complexity (Naeem 1998, or diversity among func-

tional groups, sensu Vitousek and Hooper 1993) that is measured by the number of functional groups that interact with a process; (2) functional redundancy defined by the number of functionally similar entities within each functional group (Naeem 1998), and (3) functional diversity within functional groups, often based either on more finely resolved distinctions between entities or interactions and processes different than those that determined group membership (Martinez 1996).

Functional groups can be formed at many levels of organization and for any sort of function. As tools, their justification lies in the need for generalization across more detailed grouping systems of biological entities (such as species; Körner 1993) and across levels of organization. The reasoning behind research restricted to details of a single process in a single species is that if enough detail is accumulated, it will be possible to automatically arrive at a better understanding within the next level of organization. This may be true in some cases, but in most cases it is not, since the processes selected for study may turn out to be of limited significance, or may be overshadowed by other processes not investigated. Furthermore, the breakdown of diversity into functional groups also needs to account for this dilemma by refraining from too narrow group definition (Körner 1993).

Some research, particularly in the field of plant functional diversity (Körner 1993; Tilman, Knops et al. 1997), has defined functional groups on the basis of the physical characteristics of organisms. Such physical arrangements rather than process-oriented criteria are based on the structure-function relationship. However, structural and physical characteristics might be defined by several simultaneous functions, or there may be no clear association between the characteristics of a species and its net contribution to an ecosystem process (Naeem 1998). Therefore, the grouping produced by physical characteristics may not reflect precisely the relationships of entities with a particular ecological process.

As mentioned before, it has been recognized that the grouping of entities into functional groups is in some sense arbitrary. Species have been grouped based on their physiological, morphological, and phenological attributes with potential significance to a particular ecological process, leading to what might be termed as 'candidate' functional groups. These groups have to be tested experimentally to determine how close they are in terms of functional similarity. Zak (1994) measured functional similarity of soil organisms using cluster and principal component analyses based on Jaccard's similarity index. Other authors have used cluster analysis and multivariate analysis of variance in several forms (Naeem & Li 1997; Tilman & Downing 1994). A common problem encountered when delineating functional groups is deciding whether to include ontogenetic functional shifts. Immature and mature organisms of the same species

often function differently. The solution to this type of problems is somewhat arbitrary and involves the consideration of definitions, consistency and pragmatism (Martinez 1996).

Functional groups overlap with other concepts such as 'guilds' and 'trophic species'. Guilds were originally defined as groups of organisms that exploit environmental resources in a similar manner (Root 1967), and they are, in fact, a particular type of functional group. Anyhow, confusion between the terms guild and functional group arose largely due to the departure from the original resource exploitation emphasis of guilds towards the inclusion of other ecological processes such as primary productivity or pollination. 'Food webs' can be considered another approach to the typification of functional groups. Food webs depict trophic processes between classes of organisms that consume and then metabolize the biomass of another or the same classes of organisms (Naeem & Li 1997). Organisms that interact with this process are either consumers or resources, and therefore taxa may be aggregated into trophic species that are a particular type of functional groups that aggregate taxa that appear to share the same set of trophic consumers and resources (Martinez 1996). As oppose to guilds, trophic species include organisms that not only share the same type of resources consumed, but also share the same type of consumers. The strength of this typification, however, depends on the degree to which species aggregate clearly into trophic classes (Naeem & Li 1998).

#### THE RELATIONSHIP BETWEEN FUNCTIONAL DIVERSITY AND OTHER DIMENSIONS OF BIODIVERSITY

The relationship between biological entities and ecological processes is two-way: it includes the reaction of a process to changes in a biological entity and the reaction of the entity to a change in the process (Martinez 1996). Some components of other dimensions of biodiversity, such as species richness may increase, decrease, leave unaffected or stabilize the rate (Tilman & Downing 1994), even affect the temporal dynamics and spatial patterns (Martinez 1996) of ecological processes.

As mentioned before, most ecosystems are experiencing loss of species richness associated with the activities of human expansion, raising the issue of whether the biogeochemical functions of ecosystems will be impaired by this loss (Naeem et al. 1994). In relation to this interaction, a lot of debate has been centered on the questions of how species richness affect the rate of ecological process (figure 2) and if, in this sense, there are species that can be considered redundant. Walker (1992) introduced the concept of 'redundancy' for the purposes of assessing conservation priorities. He believes that conservation should be focused in those species that

are singular in their contribution to ecosystem function. The objection to the concept of redundancy is that it may be interpreted as to imply that no conservation effort should be placed on species that are considered redundant.

Naeem (1998) introduces a novel way of considering the term redundancy based on theory taken from reliability engineering. He proposed the theoretical relationship between the probability of an ecosystem 'failure' and the redundancy of its components. In his model, an ecosystem process can be seen as a machine where each component (functional group) has an independent, finite probability of failure (reliability) and all components are mutually dependent upon one another, as in the functioning of a machine. The more members a functional group has, the more reliable it will be, nonetheless, the more complex an ecosystem process is (the more functional groups it involves) its failure will be more likely, or, in other words, it will be less reliable. The validity of this hypothesis has important ecological, management and economic implications given the large-scale substitution of diverse natural ecosystems with less diverse managed systems (Naeem and Li 1997).

Walker (1992) proposed that species redundancy enhances ecosystem resilience (the speed of recovery of an ecosystem process after disturbance). Naeem (1998) suggests that this relationship is not guaranteed since, after local extinction of one component of the functional group, resilience of the system will depend on the compensatory ability of the redundant components in functional groups. Still, the importance of redundancy might be in its potential to buffer biogeochemical properties and processes against the failure of a single species, or group of species, to establish or to maintain itself in fluctuating environmental conditions (Naeem & Li 1997; Tilman & Downing 1994; Vitousek, Turner, Parton, & Sanford 1994). This has been called the 'biological insurance hypothesis for biodiversity' (Naeem & Li 1997), and holds that the more diverse ecosystems are, the more likely functional groups will contain some species that can thrive during a given environmental perturbation and thus compensate for other members that are reduced by that disturbance (Tilman & Downing 1994).

Before the concept of functional redundancy can be questioned, it is necessary to determine those living entities that are involved in a particular process. Species that do not interact with an ecological process cannot be considered as redundant in account that they are not repeating any function performed by other organisms (Martinez 1996). Lawton and Brown (1994) suggest that the apparent redundancy of species is also due to the fact that most investigations have been focused on the loss of individual species and not on the changes that involve addition of entire functional groups (Körner 1993). Therefore, ecosystems are likely to show

more sensitivity to changes in species richness when functional groups are represented by one or few species; then the net rate of an ecological process will show a significant relationship with the increase of species richness, until each functional group is represented, and then an asymptote is soon reached as more species are added (Naeem 1998). These are some of the reasons why the hypotheses illustrated in figure 2 are too simple to capture the true complexity of the relationship between ecosystem processes and species richness. However, they have served to motivate empirical evaluation of this relationship.

The absolute redundancy of a species cannot be asserted because it implies that all its functions have been demonstrated to be accounted for by other species. This seems to be a theoretical and practical impossibility. Not only are all processes impossible to investigate, but it is impossible to investigate one process at every level of organization and temporal scale (Martinez 1996). Furthermore, changing conditions or particular episodes can turn relatively unimportant species into critical ones in the future (Tilman, Knops et al. 1997). To measure functional redundancy the framework of the function of interest, particular scale, extent and resolution need to be specified (Martinez 1996).

The relationship between species richness, redundancy and ecosystem process has been tested in several settings. Ecological knowledge supports a wide range of views on the subject (Naeem, Thompson, Lawler, Lawton, & Woodfin 1994). Most studies have been performed in highly simplified conditions such as agricultural systems (Tilman & Downing 1994) and microcosms (Naeem & Li 1997; Naeem et al. 1994). Only a few have attempted some type of manipulation in the field (Vitousek et al. 1994; Wardle, Zackrisson, Hornberg, & Gallet 1997b). There has been a great deal of debate about the strength of the evidence produced by research in this area (Grime 1997; Huston 1997; Temperton, Mwangi, Scherer-Lorenzen, Schmid, & Buchmann 2007; Tilman, Naeem et al. 1997; Wardle, Zackrisson, Hornberg & Gallet 1997a).

#### SO, WHAT DO WE MEAN BY BIODIVERSITY?

The generation of a global concept that covers all the dimensions of the variety of life has not proven useful for its original purpose: to quantify the extent of human damage to fragile ecosystems. In this issue the very essence of the human predicament is reflected. The consequences of our actions reverberate in a multidimensional complexity that seems to overpass our capacity to comprehend it, to understand it in the scientific sense of the word: to be able to model the process so that predictions can be made. Most scientists performing conservation-related research have left aside the problem of defining biodiversity by devising ways of avoiding

it. Avoiding the integrative meaning of biodiversity when performing conservation-related science means to miss the very essence of conservation difficulties. Environmental impact is a problem only as the effects of environmental stresses will have different consequences at different levels of biological organization. Effects at one level can be expected to reverberate through other levels often in unpredictable ways.

Probably the most important outcome of the creation of a concept for biodiversity has been understated. As scientists search for a precise definition of the concept a rich body of theory has developed. Therefore, more useful than the definitions of biodiversity has been the conceptualization of its dimensions and levels of organization. This has converted biodiversity into a conceptual framework that allows us to focus conservation research to the identification of specific, measurable indicators to monitor change and assess human impact at different levels of organization, within a more feasible timeframe. What remains for scientists is to drive their research into this conceptual framework and base their choices of system, organism and scale on the hierarchical logic that it entails.

TABLE 1  
 Definitions of 'biological diversity' and 'biodiversity'  
 (modified from Gaston 1996).

TABLE 2  
 The levels of organization and components of biodiversity  
 (modified from Heywood V.H. 1995).

ECOLOGICAL DIVERSITY	GENETIC DIVERSITY	ORGANISMAL DIVERSITY	CULTURAL DIVERSITY
Biomes Bioregions Landscapes Ecosystems Habitats Niche Populations	Populations Individuals Chromosomes Genes Nucleotides	Kingdoms Phyla Families Genera Species Subspecies Populations Individuals	Human interactions at all levels

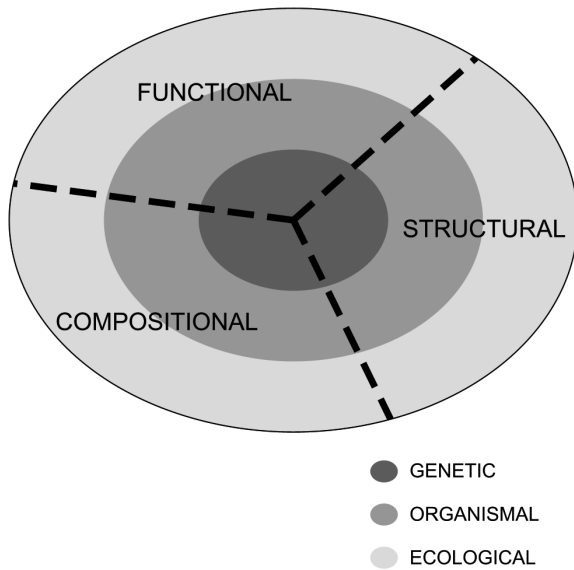


FIGURE 1  
Dimensions and levels of organization of biodiversity as a conceptual framework (modified from Noss 1990).

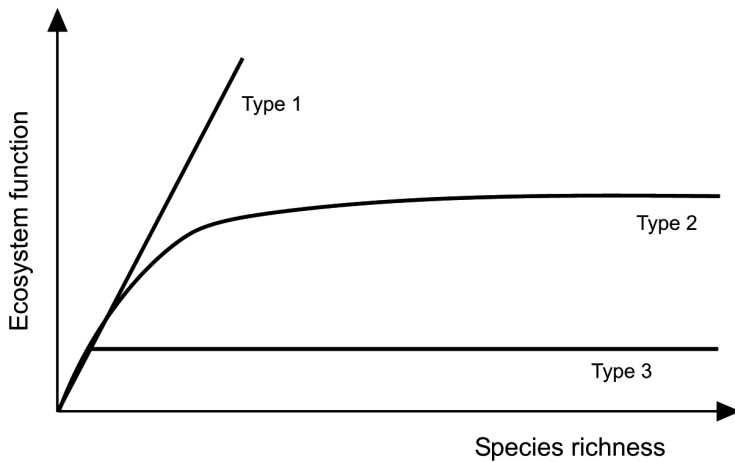


FIGURE 2  
Possible functional relationship between species richness and ecosystem level of biogeochemical functions. Type 1 curve implies a linear effect of richness, type 2 suggests an asymptotic relationship, and type 3 suggests that there is no effect of diversity (modified from Vitousek and Hooper 1993).

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