Commentary

How relevant are the concepts of species diversity and species richness?*

Biodiversity is a science that is still in its infancy or, in the words of Ernst Mayr (1997), at the 'what' stage. The inventorying and monitoring of biological diversity have just started for a few taxonomic groups and have yet to be initiated for most taxa. As biodiversity equals variety at the species level of biological organization, the terms species richness and species diversity have become key concepts in conservation biology. Both concepts are important characteristics of community structure. Therefore, much has been published on the measurement of the species richness and species diversity of communities (MacArthur 1955; Hurlbert 1971; Peet 1974; Pielou 1975; Magurran 1988, 2004; Schluter and Ricklefs 1993; Colwell and Coddington 1994; Krebs 1999). However, a certain looseness in the use of these terms is still found in the literature, for example when they are used interchangeably (see Cotgreave and Harvey 1994; Harrison *et al* 2000). This has led to a some confusion. In this Commentary, the concepts of species richness and species diversity are discussed in the light of recent developments. It is suggested that a clear distinction needs to be made between the two if we are to avoid further confusion surrounding these terms. We also introduce a simple diagram through which species number, species abundance, and species diversity can be represented in an integrated manner.

1. Species diversity

Species diversity is an appropriate term for ecologists who are interested in understanding the mechanisms and effects of certain ecological phenomena, such as pollution, environmental disturbances, etc. It is a function of the number of species present (i.e. species richness or number of species) and the evenness with which the individuals are distributed among these species (i.e. species evenness, species equitability, or abundance of each species) (Margalef 1958; Lloyd and Ghelardi 1964; Pielou 1966; Spellerberg 1991). This definition may be the best one that is available at this moment; and the concept of species diversity should be restricted to this extent (Hurlbert 1971). "Species richness" is neither a synonym nor a measure of species diversity. Species richness is easy to measure and understand, whereas the measuring of species diversity is complicated because measures of diversity vary in the relative emphasis they place on the number of species (i.e. species richness) and their relative abundance (i.e. species evenness). As there are innumerable ways of emphasizing different aspects of the species abundance relationship, the number of diversity indices is, in principle, infinite (Molinari 1996). However, because all measures must emphasize one or the other factor of diversity (i.e. species richness or species evenness), no single perfect diversity index is possible that can distil the information contained in a species abundance distribution into a single statistical number (Clarke and Warwick 2001). Nonetheless, ecologists have invented a number of indices over the years, each of which has its own limitations (Magurran 2004).

Moreover, species diversity, as it is usually measured, is an aspect of community structure. Structurally, many rare species are minor components of a community. For example, Shannon's index is insensitive to rare species, which, however, are very important in studies of biodiversity. Since species diversity has never had a single, unequivocal definition, it is possible to muddle along with a plethora of indices, each supported by at least one person's intuition and a few recommended by fashion

*Dedicated to Dr Colin J Bibby.

(Hurlbert 1971). One among these indices is the Shannon-Wiener index (generally known as the Shannon index; Shannon and Weaver 1949), which is notoriously dependent on sample size and is weighted towards species richness. Another measure is Simpson's index (Simpson 1949) that is weighted towards species evenness.

2. Species richness

McIntosh (1967) was the first to coin the term species richness, but the concept itself is the oldest and most fundamental concept of biological diversity (Peet 1974). Species richness can refer to the number of species present in a given area or in a given sample, without implying any particular regard for the number of individuals examined in each species. Species richness can be numerical (or simply "species richness"; Hurlbert 1971) or be related to area (or simply "species density", namely the number of species present in a given area; Simpson 1964).

Certain limitations of species diversity indices led to the invention of many species richness measures. Notable among these is the "rarefaction methodology" as suggested by Sanders (1968), which calculates the expected number of species $E(Sn)$. Rarefaction is a way of comparing the relative species richness of plots with incomplete sampling and varying levels of sampling effort. $E(Sn)$ can also be calculated by using a refined form of the rarefaction methodology that was developed by Hurlbert (1971). However, the rarefaction methodology also has some limitations, as it is notoriously dependent on sample size and can, therefore, misinterpret the data of very small samples. Other notable measurements are capture-recapture methods (Burnham and Overton 1979), the jacknife procedure (Heltshe and Forrester 1983), and the species accumulation curve (Colwell and Coddington 1994). In addition, the randomization option of the program EstimateS (Colwell 1997) calculates the species abundance curve based on the model of linear dependence of Soberon and Llorente (1993) and predicts a species richness asymptote. The Species-Area (SA) relationship (Rosenzweig 1995) posits that "the number of species that can exist in a given land area is a function of the area: smaller areas have fewer species and larger areas have more species, all other things being equal". Finally, the direct measure of the species number (NO) seems to be one of the simplest and best methods for expressing species number relations.

Since species richness simply denotes the number of species, it is an un-weighted measure of species number relations. In species diversity, species are weighted by some measure of their abundance, productivity, or size. Because the conservation of biological diversity is a meaningful reason for the study of biodiversity, this particular branch of science is dominated by conservation biologists whose interest is focused on the few rare species that characterize most biota. We opine, therefore, that species richness is the best tool for conservation biologists because it de-emphasizes the many common dominant species in a community. A consistent feature that emerges when biodiversity is examined in the context of species richness is that most taxonomic groups are species-poor with a large number of monotypic taxa, relatively few groups are species-rich, and frequency distributions have the shape of a hollow curve (see Scotland and Sanderson 2004). Another useful measure of patterns of species distributions is the spatial and temporal a, b and g diversities (Whittaker 1970, 1972). Since most of these measurements use the species presence-absence data, it is also suggested that it will be much clearer if we use the terms a, b and g richness.

3. Our species abundance curve

This is a line diagram constructed by plotting the number of individuals on the y-axis and the species rank on the x-axis (exemplified by data collected on avian biodiversity from the Loktak lake, 24°25′–24°42′N; 93°46′–93°55′E, Manipur, Northeast India, between January 2000 and December 2002). Species ranks are calculated using the number of individuals for each species. The species that has the largest number of individuals is ranked first and the species that has the least number of individuals is ranked last. The resultant curve can be compared to two hypothetical species diversity lines (maximum SD line and minimum SD line) made on the graph (i.e. the lines representing species diversity

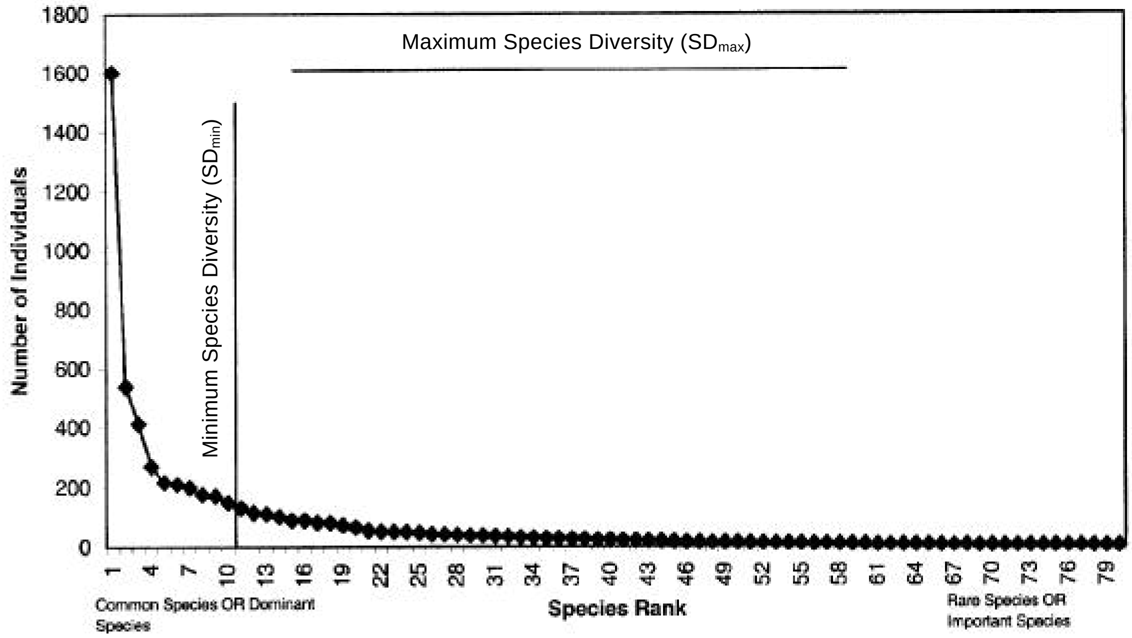

Figure 1. Species abundance curve. The figure also includes two hypothetical species diversity lines (maximum SD line and minimum SD line). The curve's parallelism to either of the two hypothetical lines shows its affinity towards either $SD_{max.}$ or SD_{min}.

qualitatively). The curve's parallelism to either of the two hypothetical lines shows its affinity towards the SD maximum line or the SD minimum line. This diagram is a simple approach to demonstrate the species number, species abundance and species diversity in an integrated manner (figure 1). The species abundance curve shows the presence of many rare species that had less than ten individuals during three years' sampling in the Loktak lake and the dominance by a few abundant species that may act as an ecological indicator of the lake's changing ecosystem.

4. Conclusion

The concept of species richness (i.e. the number of species) gives as much information that is related to biodiversity as the concept of species diversity. This has led to both terms being used interchangeably, which in turn leads to a confusion of the concepts. It is suggested, therefore, that ecologists apply more direct approaches to the study of species-numbers relations by relying on direct measures of the number of species (i.e. species richness) rather than applying several diversity indices that are simply derived variables.

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LAISHANGBAM SANJIT
DINESH BHATT*
Avian Biodiversity and Bioacoustics Lab,
Department of Zoology and Environmental Sciences,
Gurukula Kangri University,
Haridwar 249 404, India
**(Email, dd_bhatt@yahoo.com)*

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