

Species Diversity Measurement: Choosing the Right Index

Steven H. Cousins

Species are by definition different from each other. This fact favours ranking rather than additive indices. In addition, new methods show how the degree of difference between species can be included in an index. The functional aspect of species diversity measurement is strengthened by incorporating other differences between species (such as body size, predator or parasite) as a component of diversity. The choice of index and measurement of diversity are influenced by these developments.

An independent re-evaluation of how to construct representations of species diversity is occurring in both conservation biology^{1,2} and functional ecology^{3,4}. The essence of these changes lies in reassessing the condition that all species are treated equally in a diversity index, and instead, substituting rules dependent on functional or taxonomic differences between species. Before assessing these new developments, it is worth considering the assumptions on which the conventional indices⁵ are based.

A typical use of a diversity index is Shannon's index (see Hill⁶) applied to a count of birds found at a particular location. In making the index, data for each species are added together, and the importance of each species is related to the count of individuals in each species. The two assumptions that are of interest here are (1) that the index is limited to one taxonomic group, i.e. birds rather than birds plus insects, and (2) that all species are equal (a sparrow is equivalent to a hawk in a count of species present).

It is ironic that species are treated as equal in conventional indices when the very basis of the identification of species is that they are different from each other. The saying that 'you can't add apples and pears' alerts us to this problem.

Are species different?

Sibling species are very similar, while species are increasingly different if they belong to different, increasingly higher, taxa. These higher taxa (family, order, class, etc.) reflect progressively greater differences in anatomy or body plan.

Steven Cousins is at IERC, Cranfield Institute of Technology, Cranfield, Bedfordshire MK43 0AL, UK.

As already noted, species diversity indices are typically applied to a clearly defined taxonomic group. The precise taxon level depends on the group being studied. Thus, for birds the indices are at the level of class, i.e. Aves, while for butterflies or moths the taxonomic level is the order, i.e. Lepidoptera. Plant diversity measurement is often made at the kingdom level, without reference to the plant divisions, but with observations limited to particular size categories, such as trees or field-layer plants. The use of different taxonomic break points for indices applied to different taxa can perhaps be seen as part of the problem raised earlier, namely, the treatment of species as being equal but only within apparently arbitrary limits of taxonomy.

The conservation dilemma

Much as they may hate doing so, conservationists are preparing methods to choose between species that may be conserved. May² asks, 'how do we go about making choices for the ineluctably limited number of places on the ark?' One possible approach is provided by Atkinson⁷: 'Given two threatened taxa, one a species not closely related to other living species and the other [related to a] widespread and common species, it seems reasonable to give priority to the most taxonomically distinct form.'

Vane-Wright *et al.*¹ have explored the implications of measures of taxonomic distinctiveness. They use the hierarchical taxonomic classification to calculate an 'information' index for species, based on the number of branch points of the classification tree (see Box 1). Vane-Wright *et al.* are able to show the value of their technique by a study of the world-wide distribution of bumblebees in the *Bombus sibiricus* group. If a simple species count is used to locate the grid square of maximal diversity then the Ecuador square, which has 10 species (23% of the world total), is selected. However, when taxonomic distinctiveness is allowed for, Gansu in China is selected, with 23% of the world total as against Ecuador's 15%.

Cardinal and ordinal diversity measures

At a more local scale, at least two types of diversity measure can be distinguished: those that treat each species as equal and then create the index by adding the species in some

way, and those that treat each species as essentially different and create a representation of diversity by ranking each species in an order of some kind. We can call these cardinal and ordinal diversity measures, respectively. Williams' alpha⁸ and Shannon's H' and J, as well as the related family of indices (see Hill⁶) including species richness and species density, are cardinal indices. Species abundance distributions, species size spectra and species lists are ordinal representations.

Cardinal indices are widely used for the environmental assessment of areas of habitat. As is argued below, ordinal measures may offer advantages for environmental assessment. Lauri Oksanen (pers. commun.) has proposed that the scale of observation, in a functional rather than a spatial sense, is key to the validity of using cardinal indices. He suggests that cardinal indices are suitable for describing the diversity of a guild of species but are unsuitable for description of communities where ranking the very different species found in a community is the better option.

While ordinal measures reflect the condition that species are different, the most commonly used of these – species rank abundance distributions – still have considerable limitations since they only recognize differences between species in terms of their abundances, and rank them on that basis. Thus, species rank abundance distributions again treat species as equal if their abundances are approximately equal.

May⁹ has outlined many of the properties of species abundance distributions arising from different assumptions about the manner in which species partition resources. Figure 1 illustrates how two communities containing the same number of species and individuals would have different relative abundances of individuals in species, depending on whether species divided resources on a 'broken-stick' or canonical basis. This leads to different values of S (species number) and N (individual number) being observed until the whole 'community' is enumerated. The observed distributions of natural communities can then in theory be described as being more or less similar to the broken-stick distribution or the canonical log-normal distribution (Fig. 1). But, as we have observed, it is assumed in constructing species abundance distributions that species are equal if their abundances are equal.

Since the objective of making the species abundance distributions has

been to distinguish between explanations of resource use, it is particularly relevant that species can differ in their resource demands. Body size is an important species variable here. This point is raised by Harvey and Godfray³, who point out that since the abundance of organisms is related to body size and energy expenditure is also related to body size, then, if numbers of individuals are canonically distributed in a community, the biomass and energy expenditure cannot also be canonically distributed. Sugihara¹⁰ has challenged this view, proposing that all three variables – numbers, biomass and energy expenditure – are canonical. This debate will no doubt continue, but it is timely to reflect that relative abundance distributions are not the only ordinal tool we have for analysing diversity. In addition, given May's criticism⁹ that the properties of relative abundance distributions derive from the central limit theorem, then new approaches do indeed seem desirable.

Diversity measurement based on body size

Counting the number of animal species (*S*) in a weight class and the number of individuals (*N*) in a weight class meets the above conditions by treating species as being different when they are in different weight classes. Thus, within weight classes, any of the cardinal diversity indices can be used; indeed, relative abundance measures have recently been applied within weight classes¹¹.

The direct plot of *N* and *S* against weight can be of particular interest. The distribution of individuals in weight classes forms the 'Eltonian Pyramid' that is at the root of energetics-based descriptions of ecosystems¹². Superimposing the numbers of species in those weight classes on the numbers of individuals allows a description of where diversity is located in a functional sense. It will indicate where, in the size spectrum, diversity is relatively high or low. Using body size to relate diversity and energetics phenomena has been discussed before^{4,13}. Some species will add to the diversity and numbers of individuals found in several size classes due to the development of individuals from young to adult.

Functional aspects

Although species diversity is a purely descriptive measure of an area or unit, there has long been an implicit assumption that the diversity measure captures some aspect of ecosystem or community function,

Box 1. The taxonomic information index

Systematics offers two ways of measuring taxonomic distinctiveness: group membership measures, based on hierarchies in which some common ancestry is assumed, and measures of genetic or phenetic distance. Vane-Wright *et al.*¹ adopt the first method.

The species that have the most branches between the stem and the tip are set equal to 1, then the sister group to this is given a score (*W*) equal to the sum of the existing branch values. This is repeated until all species have been included. The weightings can be expressed as percentages. However, this appears to overweight the value of the taxonomically distinct species, since the most distinct will always be equal in value to the sum of all the other species. To amend this approach, Vane-Wright *et al.* have proposed an 'information' index (*I*) based on the number of branchings in the tree that include the species whose characteristics are being measured. They then divide the sum of the *I* values by the value for the individual species itself. Finally, this is expressed as the percentage contribution that each terminal taxon makes to the total diversity as measured by *I*.

	<i>W</i>	%		<i>I</i>	$\frac{\sum I}{I}$	%
	1	6.25		4	3.5	10.7
	1	6.25		4	3.5	10.7
	2	12.5		3	4.67	14.3
	4	25		2	7	21.4
	8	50		1	14	42.9
Sum:	16	100	Sum:	14	32.7	100

May² has proposed amendments to this scheme, and Vane-Wright *et al.* are also refining the method having established¹ a general approach.

even if what it captures is only vaguely defined. The diversity-stability hypothesis^{14,15} provided a framework in which attention could be focused on diversity measurement under the presumed relevance of diversity to ecosystem stability.

The discovery¹⁶ that stability and species diversity were inversely related in certain model food webs indicated at the very least that diversity could no longer be assumed to be important to ecosystem stability. High species diversity may be desirable aesthetically, but links to ecosystem stability would plainly have to be clearly specified and then tested experimentally.

The possibility that trophic structure determines the number of species found in a location has been regularly raised^{17,18}. The mechanism proposed has varied, from the number of trophic levels¹⁸ to simple stochastic elimination of species whose populations are brought to low numbers by predation or starvation¹⁸. The major problem in relating species diversity to functional ecosystem parameters such as food-web structure, or energy flow, has been the incompatibility of the types of data used in the two fields⁴: diversity indices of various types on the one hand, and trophic-level analysis in either an explicit form¹⁹ or an implicit form using food webs²⁰ on the other. Compatible methods of measuring diversity and energy flow have been proposed⁴. These use

body size as the basis of trophic interactions, and number of species of different body sizes as a diversity distribution. As well as the theoretical justification for size-structured food webs²¹, empirical research has also demonstrated this phenomenon²², although the approach is most developed in marine ecology¹². It is likely that we are entering a new period of testing the diversity-stability hypothesis based on these size-structured methods of analysis.

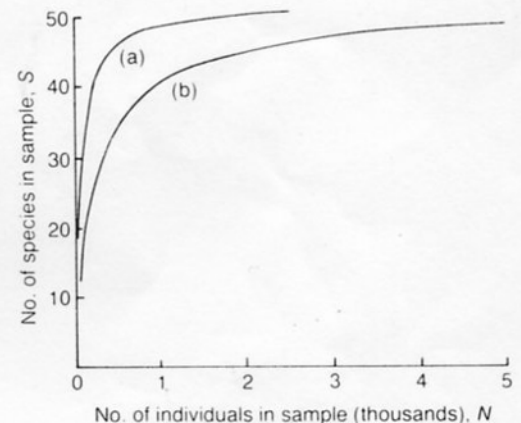


Fig. 1. The relationship between (a) 'broken-stick' and (b) canonical log-normal distributions for increasing sample size in a community containing 50 species. The broken-stick model assumes randomly allocated non-overlapping niches, while the canonical is a particular case of log-normal distribution of species abundances. Here, 25 species are encountered in the first 73 and 230 individuals, respectively, for curves (a) and (b). *Redrawn with permission from Ref. 9.*

Food webs and foraging theory

Food-web interactions appear to have important consequences for the measurement of species diversity. The different types of trophic activity, predation, parasitism, herbivory and so on are associated with different levels of species richness within the same taxon²³. The clues to the mechanism behind these observations may lie with foraging theory.

Conventional food-web studies have adopted few if any of the developments in foraging theory. One important result^{24,25} shows that, in general, any species will be included in the diet of a predator (regardless of the prey species abundance) provided that the predator encounters members of that species and that the rate of energy gain from eating it exceeds a particular value. Consequently, the species identity of the prey is of no importance to the predator. A spider will eat an individual of any species that is encountered in its web, provided the prey item is neither so small that it is below the energy-gain rate limit nor so large that it escapes.

This opportunism appears true for types of predation where the prey is an animal and capture is achieved by a physical or mechanical process that overpowers the prey. Parasitism and herbivory present different problems for the ingesting organism, leading to fundamentally different levels of species specificity in the diet. In the case of parasitism, it may be conjectured that the passage of energy from large to small organisms involves problems so great that the parasite has to specialize on a single species or single family of species. Herbivory presents problems of overcoming the plant's defense compounds and its defensive structures such as spines, waxes and hardened coatings. Thus, the interaction between herbivore and plant can be either a biochemical one or a physical one (as in predation), or both. In practice, the

species identity of herbivore and plant is important as there appears to be coupling between particular species of herbivore and particular plant species, as was shown classically by Southwood²⁶ for insects on British trees. Other taxa, such as birds and ruminants, are far less species-specific in their feeding.

Counting species and comparing diversities between ecosystems would perhaps be more meaningful if parasite diversity were separated out from predator diversity. Price²³, in a survey of the feeding habits of British insects, has shown that parasites (72.1% of the fauna) are much more numerous than predators (6.3% of the fauna, including non-parasitic herbivores), and could therefore swamp predator diversity data where combined. The remaining 21.5% are saprophages.

Conclusion

Taking the view that species diversity is contingent on how ecosystems are functionally organized – a view that is consistent with the traditional search for explanations of diversity in trophic structure – then size-based diversity distributions appear to be important developments. The distinction between diversity of parasites and predators also appears important for diversity measurement, since these two categories of organisms cannot be meaningfully summed.

After several decades of defining species diversity of a community based upon the assumption of species equivalence within the single taxon, there is now a recognition that the very difference between organisms that underlies the species concept favours ordinal (ranking) measures over cardinal (additive) indices. The use of diversity measurement for environmental assessment may need to be extended by showing where, in a functional sense, the diversity is located. A typology of diversity is emerging following the earlier models of types of stability¹⁶ and types of rarity²⁷. Distinguishing between predator and parasite diversity, as well as adopting body-size classes within the taxon and the measurement of taxonomic distinctiveness, are major components of such a typology.

One of the challenges of future research in this area will be to bridge the functional and the taxonomic distinctiveness lines of inquiry. Conservationists may need to take the functional nature of species into account for the ark, while functional ecologists²⁸ have already called for

an increase in understanding of taxonomic parameters in trophic studies. But even without these cross-links, the fields of functional ecology and conservation biology both stand to benefit significantly from the new developments in species diversity measurement.

Acknowledgements

Thanks to Kevin Gaston and Lauri Oksanen for comments on the manuscript.

References

- 1 Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) *Biol. Conserv.* 55, 235–254
- 2 May, R.M. (1990) *Nature* 347, 129–130
- 3 Harvey, P.H. and Godfray, H.C.J. (1987) *Am. Nat.* 129, 318–320
- 4 Cousins, S.H. (1980) *Proceedings of the 17th International Ornithological Congress*, pp. 1051–1055, Deutsche Ornithologen-gesellschaft
- 5 Pielou, E.C. (1975) *Ecological Diversity*, Wiley
- 6 Hill, M.O. (1973) *Ecology* 54, 427–431
- 7 Atkinson, I. (1989) in *Conservation for the Twenty-first Century* (Western, D. and Pearl, M., eds), pp. 54–69, Oxford University Press
- 8 Williams, C.B. (1964) *Patterns in the Balance of Nature*, Academic Press
- 9 May, R.M. (1975) *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 81–120, Belknap Press
- 10 Sugihara, G. (1989) *Am. Nat.* 133, 458–463
- 11 Morse, D.R., Stork, N.E. and Lawton, J.H. (1988) *Ecol. Entomol.* 13, 25–37
- 12 Platt, T. (1985) *Can. Bull. Fish. Aquat. Sci.* 213, 55–64
- 13 Cousins, S.H. (1989) *Nature* 340, 350–351
- 14 Elton, C.S. (1962) *The Pattern of Animal Communities*, Methuen
- 15 Odum, E.P. (1969) *Science* 164, 262–270
- 16 May, R.M. (1973) *Stability and Complexity in Model Ecosystems*, Princeton University Press
- 17 May, R.M. (1988) *Science* 241, 1441–1449
- 18 Hutchinson, G.E. (1959) *Am. Nat.* 93, 145–159
- 19 Lindeman, R.L. (1942) *Ecology* 23, 399–418
- 20 Pimm, S.L. (1982) *Food Webs*, Chapman & Hall
- 21 Cousins, S.H. (1980) *J. Theor. Biol.* 82, 607–618
- 22 Warren, P.H. and Lawton, J.H. (1987) *Oecologia* 74, 231–235
- 23 Price, P.W. (1977) *Evolution* 31, 405–420
- 24 Pulliam, H.R. (1974) *Am. Nat.* 108, 59–75
- 25 Charnov, E.L. (1976) *Am. Nat.* 110, 141–151
- 26 Southwood, T.R.E. (1961) *J. Anim. Ecol.* 30, 1–8
- 27 Rabinowitz, D. (1981) in *The Biological Aspects of Rare Plant Conservation* (Synge, H., ed.), pp. 205–217, Wiley
- 28 Hochberg, M.E. and Lawton, J.H. (1990) *Trends Ecol. Evol.* 5, 367–371

Organizing a Meeting?

Each month we publish brief details of forthcoming meetings. If you would like your conference or symposium to have a free entry in *TREE's Meetings Diary*, send the details to: The Editor, *Trends in Ecology and Evolution*, 68 Hills Road, Cambridge CB2 1LA, UK.

Each entry is included when received, and then repeated when space permits.