ECOLOGICAL DIVERSITY AND BIODIVERSITY AS CONCEPTS FOR CONSERVATION PLANNING: COMMENTS ON RICOTTA

Sahotra Sarkar

Biodiversity and Biocultural Conservation Laboratory, Section of Integrative Biology and Department of Philosophy, University of Texas at Austin, 1 University Station, #C3500, Austin, TX 78712 –1180, USA.
E-mail: sarkar@mail.utexas.edu

Received 5 May 2006; accepted in final form 5 May 2006

ABSTRACT

Ricotta argues against the existence of a unique measure of biodiversity by pointing out that no known measure of α-diversity satisfies all the adequacy conditions that have traditionally been set for it. While that technical claim is correct, it is not relevant in the context of defining biodiversity which is most usefully measured by β-diversity. The concept of complementarity provides a closely related family of measures of biodiversity which can be used for systematic conservation planning. Moreover, these measures cannot be replaced by summary statistics but must rely on inventories of biodiversity surrogates at candidate sites for conservation.

Key Words: α-diversity, β-diversity, biodiversity, complementarity, systematic conservation planning

1. INTRODUCTION

Scientific concepts do not emerge in isolation. Rather, their emergence is context-dependent in two ways: (i) they have some role to play in enabling a discipline to achieve its intended goals; and (ii), typically, they are related to other concepts within the discipline. For "biodiversity" both contexts are clear. The term was introduced in 1986 as a contraction for "biological diversity" (Takacs, 1996). It ostensively referred to the feature of the living world that the new discipline of conservation biology was supposed to conserve (Sarkar, 2005). Within conservation biology, it is related to the suite of concepts used to select conservation areas (Sarkar, 2003), in particular, complementarity which will be discussed in some detail later in this note (Sarkar, 2002; Sarkar and Margules, 2002).

Ricotta (2005) argues that there is no single concept of biodiversity; rather we must use a set of summary statistics. What he seems to mean is that there is no single measure of biodiversity, the distinction between a concept and its possible measures not always being carefully maintained in his paper. Whether there is a single concept of biodiversity, and what it should include, is a topic that has generated much debate among conservation professionals. Most conservation biologists take biodiversity to be a descriptive feature of a system. However, biodiversity has sometimes been attributed normativity (Callicott *et al.*, 1999; Roebuck and Phifer, 1999) and it has often been supposed to embody socio-political values (Vermeulen and Koziell, 2002). Nevertheless, if we accept that

Acta Biotheoretica (2006) 54: 133–140
DOI: 10.1007/s10441-006-8259-z
© Springer 2006

biodiversity protection does not exhaust the goals of conservation biology (and environmental protection in general), then it is probably reasonable to consider it as a purely descriptive concept and, further, to restrict the concept to include the variety of living features and processes at all levels of structural, taxonomic, and functional organization, but not ecosystem services or culturally induced categories.

Thus, any conceptual ambiguity about the concept of biodiversity is at least partly easily removed. However, whether or not there is a unique (quantitative) measure is a different and more difficult question. The basic point that Ricotta wants to emphasize, the non-existence of such a unique measure, is correct. Nevertheless, his discussion can be questioned on three grounds: (i) the arguments and examples he discusses are rather beside the point because they address a type of ecological diversity that has little bearing on biodiversity and its conservation (namely, α-diversity); (ii) the existing measures of biodiversity that are used within conservation biology, in particular, within systematic conservation planning (namely, β-diversity) typically bear strong resemblances to each other and, thus, emphasizing their differences is misleading; and (iii) these measures are not summary statistics – indeed, summary statistics do not work as measures of biodiversity.

2. MEASURES OF ECOLOGICAL DIVERSITY

In an ecological context, the first quantitative index of diversity was proposed by Fisher *et al*. (1943) in an attempt to relate the number of individuals to the number of species in a sample drawn from a natural community. Starting in the late 1940s, Preston (1948, 1962a,b) extended and corrected Fisher's work. The statistical models used by Fisher *et al*. and Preston were all phenomenological, based on the fit of models with data, rather than being derived from biological principles. In contrast, MacArthur (1957) proposed a diversity measure based on the "broken-stick" model which began with the biological assumption that the different species in a community apportioned resources at random. (MacArthur also had two other models but, in these discussions, the broken-stick attained iconic status as a null model while the others were generally ignored.) These innovations paved the way for a resurgent theoretical ecology in the 1960s that went beyond population ecology, leading to the theory of island biogeography and, eventually, the diversity-stability question (see below). (Kingsland (1985) reviews much of this history; Drake (2005) focuses on the history of diversity measures.)

However, the diversity measures which Ricotta (2005) considers emerged during the same period from a different conceptual background. In 1949, Simpson (1949) introduced an index of "concentration" ($\sum_{i=1}^{n} \pi_i^2$; where π_i is the frequency of the i-the type and $\sum_{i=1}^{n} \pi_i = 1$) the inverse or complement of which both provide measured of diversity. Meanwhile, Margalef (1958) adopted Shannon's (1948) information index ($-\sum_{i=1}^{n} \pi_i \log \pi_i$) as a diversity index. (Earlier, MacArthur (1955) had used the same index but as a measure of stability.) Both belong to Rényi's (1960) family of entropy measures. The introduction of these two measures led to a variety of others and a large set of empirical studies in the 1960s that measured diversity (reviewed by Hutcheson's (1969)). Nevertheless, the most fundamental question – the one which still motivates Ricotta (2005)–remained open: what is the justification of these measures? Hurlbert (1971) posed the question forcefully and no fully satisfactory answer has yet been produced.

Conceptually there are two options for answering this question: (i) we could show that a proposed measure captures some unproblematic intuition about diversity by laying down explicit adequacy conditions and, ideally, proving that the measure in question is the only one satisfying these conditions; or (ii) we could try to connect the proposed measure to ecological processes. There are two ways in which the second option can be carried out: (a) the proposed diversity measure may describe a result of ecological processes; or (b) it may play a role in determining the outcome of ecological processes. Starting in the 1960s, all three strategies of justification have been tried, and a minor lacuna in Ricotta's (2005) argument is that he considers only (i) and (ii)b.

Proposed adequacy conditions for diversity measures have included the increase of: (1) richness; (2) evenness (or equitability); (3) abundance rarity (the level of occurrence); (4) geographical rarity; (5) distinctiveness; and (6) abundance transfer (Patil and Taillie, 1982; Vane-Wright *et al.*, 1991; Sarkar, 2002; Sarkar and Margules, 2002). Note that, with the exception of (4) all of these parameters are "local" in the sense that their assessment does not require access to information outside a given system; geographical rarity is global but the rarity of species within a system is still a feature of that system. The trouble with this justificatory strategy is that no measure satisfies all these adequacy conditions though this result apparently has not been proved in full generality within a unified mathematical framework. (Ricotta notes that condition (5), interpreted as Schur-concavity, and condition (6) alone leave only richness as a possible measure and this is unsatisfactory because there is obviously more to diversity than merely richeness.) This result may be interpreted as showing that there is no single concept of diversity, as Ricotta does. Alternatively, it may be interpreted as showing that no single measure of diversity will simultaneously optimize all intuitions. The second interpretation has two advantages: (i) it suggests that we examine our intuitions to see which are less dispensable than others; and (ii) it leaves open the option to choose a measure of diversity on the ground that it is connected to ecological processes.

Unfortunately, efforts to find such connections have also foundered. Patil and Taillie (1976, 1979, 1982) initiated an ambitious program of deriving diversity, interpreted as average rarity, from models of probable inter-specific and intra-specific encounters. The Shannon and Simpson indices then emerge from different ways to compute the average. (Even earlier, MacArthur (1972) had used similar models though not with an explicit agenda of justifying diversity measures.) Unfortunately, Ricotta (2005) ignores this work – as apparently have most commentators since the 1980s – which may provide some ground for cautious optimism about justifying measures of diversity using option (ii)a. The trouble is that these models seem to have no obvious bearing on other questions of ecology.

A richer–and still living–tradition attempts to connect diversity to ecological processes, such as productivity, and even more importantly, stability. The idea that diversity and stability are connected has a long and well-known history (May, 1974; Pimm, 1993). MacArthur (1955) is probably the first to have made the claim precise, with Elton (1958) and Pimentel (1961) providing initially promising empirical support. However, starting in the 1960s, the appropriate definition of ecological stability became as controversial as the definition of diversity. Lewontin (1969) introduced a variety of exact definitions, none of which captured all ecological intuitions.

Theoretical models produced results that seemed to depend on modeling strategies, when models could be mathematically analyzed at all. In particular, May (1973) analyzed

a large class of models in which increased diversity did not necessarily lead to increased stability and, moreover, was likely to decrease the set of conditions in which stability could be obtained. Recent work has also made empirical support for a diversity-stability relationships much more equivocal than before (Pimm, 1993), with most theoretical models practically impossible to test in the field (Levins, 1975). Recent positive results by Tilman and collaborators (Tilman, 1999; Lehman and Tilman, 2000), with diversity interpreted as richness and stability interpreted as constancy, have been followed by equally compelling negative ones with richness found to be inversely correlated with stability interpreted as resilience and resistance (Pfisterer and Schmidt, 2002; see, also, the commentary by Naeem (2002)).

These developments suggest that Ricotta is correct: there is no veridical concept of ecological stability and, consequently, no such concept of diversity related to stability. But this would be an unwise interpretation: the conclusion in the last sentence does not follow from the premise. In the context of biodiversity and its conservation, we have been using inappropriate concepts of ecological diversity, inventory-based concepts, referring only to what occurs within systems located at sites, rather than difference-based concepts. Whittaker (1960) elaborated the relevant distinctions back in 1960. He distinguished between α-diversity, the diversity within a site, β-diversity, that between sites, and γ-diversity, or the total diversity of a region, including both α- and β-diversity. The latter two are the only ones relevant to biodiversity (see below). The measures and adequacy conditions we have been considering are all related to α-diversity and restricted to what happens within a site; even geographical rarity of species at a site, as was noted earlier, refers directly only to what occurs at that site.

3. BIODIVERSITY

Turning now to conservation biology, the field has different goals at different scales, both geographic and taxonomic, and there is often considerable disagreement about them. However, at larger geographic scales, say beyond 10^3 km^2, it is relatively uncontroversial that a central task of conservation biology, sometimes called systematic conservation planning (Margules and Pressey, 2000; Sarkar, 2004, 2005), is to achieve *representation* of all relevant aspects of biodiversity (technically, what are called biodiversity *surrogates* (Margules and Pressey, 2000; Sarkar *et al.*, 2005)) in a conservation area network so that management plans can be devised for their *persistence* into the indefinite future. What constitutes relevant biodiversity depends on context since, in practice, we are never in a position to categorize – let alone conserve – diversity at all levels of structural, taxonomic, and functional organization (Sarkar, 2002; Sarkar and Margules, 2002). But Ricotta's claim is stronger than this: it is that there is no single measure of biodiversity.

Note that to represent *all* biodiversity surrogates in a conservation area network *ipso facto* requires the use of some quantitative measure even if it is not unique. What usefully constrains the set of possible measures is that the design of conservation area networks always occurs under a constraint that limits the amount of land that can be placed under a conservation plan: there are many other equally valid claims on land for all biologically interesting sites to be placed under conservation. The task of conservation planning is to represent all biodiversity surrogates in as few sites as possible, a problem long studied by the computer science and operations research communities, besides conservation biologists (Kingsland, 2002; Sarkar *et al.*, 2004a). The problem is thus one

of constrained optimization: the representation of surrogates must be maximized without violating the constraint that not too much land may be placed under conservation. Any solution to this problem requires attention to diversity between sites: it does not make sense, for instance, to conserve multiple sites with high α-diversity (by any measure) if the different sites have the same surrogate composition. Thus, β-diversity is the relevant concept of diversity in conservation biology, especially conservation planning. (For the same reason γ-diversity is also relevant but will not be further discussed here because it is yet to be explicitly used in conservation planning). It follows that the problems with measures of α-diversity noted in the last section are not relevant in the context of using a measure of biodiversity for conservation planning.

There have been many proposed measures of β-diversity (Wilson and Schmida, 1984; Koleff *et al.*, 2003). The one almost universally used in conservation planning (Justus and Sarkar, 2002) is based on the concept of complementarity: the complementarity value of a new site, relative to set of selected sites, is its quantitative contribution to the representation of surrogates that are not already adequately represented in the selected set. The simplest such measure is the number of surrogates (such as species) that are not present in the selected set. The use of complementarity goes back to the pioneering work of Kirkpatrick in Tasmania (Kirkpatrick, 1983; Kirkpatrick and Harwood, 1983; Pressey (2002) provides a historical assessment of Kirkpatrick's work). The importance of using complementarity was independently discovered at least three other times in the 1980s and 1990s (Ackery and Vane-Wright, 1984; Margules and Nicholls, 1987; Rebelo and Siegfried, 1990). Margules *et al.* (1988) developed the first explicit algorithm incorporating complementarity and most algorithms used today are variants of their approach. The term "complementarity" was introduced by Vane-Wright *et al.* (1991). Over the years it has replaced richness as the most common measure used to designate sites for conservation. (Justus and Sarkar (2002) review the history of the use of complementarity in practical conservation planning until 2000.)

Complementarity was not explicitly introduced as a concept of β-diversity though recent work on ecological diversity recognizes it as such. As Magurran (2003, p. 172) puts it: "Complementarity is . . . β-diversity by another name – the more complementary two sites are, the higher their β-diversity." Because complementarity is defined with respect to an existing selected set of sites, unlike traditional measures of β-diversity, it is not a symmetric concept except in the simplest (or mathematically degenerate) case in which the existing selected set consists of exactly one site. If sites are selected iteratively, as in many algorithms used in conservation planning, the complementarity value of a site changes with each iteration. In general distances based on complementarity measures are non-metric: they do not satisfy the triangle inequality. In the literature on algorithm design, the use of complementarity is known as the "greedy algorithm" (Moore *et al.*, 2003; Sarkar, 2005).

Since the quantitative contribution of surrogates to a conservation goal can potentially be assessed in a variety of ways, there is more than one measure of complementarity. Though this fact would support Ricotta's denial of any single measure of biodiversity, it is important to note that all such measures are strongly related to each other because they instantiate the same general definition given in the last paragraph. (Most measures of complementarity are also related to the Marczewski-Steinhaus distance which is the complement of the standard Jaccard index (Colwell and Coddington, 1995; Magurran, 2003) provided that these are interpreted asymmetrically.)

The final point to note is that complementarity measures are not usefully interpreted as summary statistics. The complementarity value of a site is only defined relative to a set of selected sites; thus, the exact composition of each site (what surrogates are present in it and, for many measures of complementarity, their absolute abundances) must be known in order to compute complementarity values. Summary statistics such as richness (and other measures of α-diversity) will not suffice for the purpose of selecting sites. At best, a complementary value may be viewed as a summary statistic for each combination of (i) possible existing set of sites and (ii) a potential new site. But, in any practical context, this would be an onerous computation to undertake because the set of such combinations is almost always intractably large in practice and most such combinations are of no value since they would not be used during a planning process (that is, selecting the most optimal final set of sites). Moreover, the set of possible sites for conservation is often open-ended and, in such a situation, such a computation would not even be possible. One critical practical lesson emerges from these observations: when distributional data on surrogates (such as species) are recorded in the field, replacing the lists of surrogates at each collection point by summary statistics will make these data useless for conservation planning.

REFERENCES

Ackery, P.R. and R.I. Vane-Wright (1984). Milkweed Butterflies. Cornell University Press, Ithaca.

Callicott, J.B., L.B. Crowder and K. Mumford (1999). Current normative concepts in conservation. Conservation Biology 13: 22–35.

Colwell, R.K. and J.A. Coddington (1994). Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society (London) B 345: 101–118.

Drake, J.M. (2005). The Background of Biodiversity: Quantitative Measures of Species Diversity. Unpublished mms, pp. 1943–1982.

Elton, C.S. (1958). The Ecology of Invasions by Animals and Plants. London, Methuen.

Fisher, R.A., A.S. Corbet and C.B. Williams (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12: 42–48.

Hurlbert, S.H. (1971). The nonconcept of species diversity: A critique and alternative parameters. Ecology 52: 577–586.

Justus, J. and S. Sarkar (2002). The principle of complementarity in the design of reserve networks to conserve biodiversity: A preliminary history. Journal of Biosciences 27(S2): 421–435.

Kingsland, S.E. (1985). Modeling Nature: Episodes in the History of Population Ecology. Chicago: University of Chicago Press.

Kingsland, S. (2002). Creating a science of nature reserve design: Perspectives from history. Environmental Modeling and Assessment 7: 61–69.

Kirkpatrick, J.B. (1983). An iterative method for establishing priorities for the selection of nature reserves: An example from Tasmania. Biological Conservation 25: 127–134.

Kirkpatrick, J.B. and C.E. Harwood (1983). Conservation of Tasmanian macrophytic wetland vegetation. Proceedings of the Royal Society of Tasmania 117: 5–20.

Koleff, P., K.J. Gaston and J.J. Lennon (2003). Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72: 367–382.

Levins, R. (1975). Evolution in communities near equilibrium. In: M.L. Cody and J.M. Diamond (Eds) Ecology and the Evolution of Communities. Harvard University Press, Cambridge, MA, pp. 16–50.

MacArthur, R.A. (1955). Fluctuations of animal populations and a measure of community stability. Ecology 36: 533–536.
MacArthur, R.A. (1957). On the relative abundance of bird species. Proceedings of the National Academy of Sciences (USA) 43: 293–295.
MacArthur, R.A. (1972). Geographical Ecology. New York, Harper.
Magurran, A. (2004). Measuring Biological Diversity. Blackwell, Oxford.
Margalef, R. (1958). Information theory in ecology. General Systems Yearbook 3: 36–71.
Margules, C.R. and A.O. Nicholls (1987). Assessing the conservation value of remnant habitat 'islands': mallee patches on the Western Eyre Peninsula, South Australia. In: Saunders, D.A., G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins (Eds) Nature conservation: The role of remnants of native vegetation. Surrey Beatty and Sons, Sydney, pp. 89–102.
Margules, C., A. Nicholls and R. Pressey (1988). Selecting networks of reserves to maximize biological diversity. Biological Conservation 43: 63–76.
Margules, C.R. and R.L. Pressey (2000). Systematic conservation planning. Nature 405: 242–253.
May, R.M. (1973). Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.
Moore, J.L., M. Folkmann, A. Balmford, T. Brooks, N. Burgess, C. Rahbek, P.H.Williams and J. Krarup (2003). Heuristic and optimal solutions for set-covering problems in conservation biology. Ecography 26: 595–601.
Patil, G.P. and C. Taillie (Eds) (1976). Biological diversity: Concepts, indices, and applications. In: Proceedings of the 9th International Biometric Conference. Raleigh, N.C.: Biometric Society, ???–???.
Patil, G.P. and C. Taillie (1979). An overview of diversity. In: Grassle, J.F., G.P. Patil, W. Smith, and C. Taillie (Eds) Ecological Diversity in Theory and Practice. Fairland, MD: International Cooperative Publishing House, pp. 3–27.
Patil, G.P. and C. Taillie (1982). Diversity as a concept and its measurement. Journal of the American Statistical Association 77: 548–561.
Pimentel, D. (1961). Species diversity and insect population outbreaks. Annals of the Entomological Society of America 54: 76–86.
Pimm, S.L. (1991). The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities. University of Chicago Press, Chicago.
Pressey, R.L. (2002). The first reserve selection algorithm – a retrospective on Jamie Kirkpatrick's 1983 paper. Progress in Physical Geography 26: 434–441.
Preston, F.E. (1948). The commonness, and rarity, of species. Ecology 29(3): 254–283.
Preston, F.W. (1962a). The canonical distribution of commonness and rarity: Part I. Ecology 43: 185–215.
Preston, F.W. (1962b). The canonical distribution of commonness and rarity: Part II. Ecology 43: 410–432.
Rebelo, A.G. and W.R. Siegfried (1990). Protection of Fynbos vegetation: Ideal and real-world options. Biological Conservation 54: 15–31.
Rényi, A. (1960). On measures of entropy and information. In: J. N. (Ed) Proceedings of the Fourth Berkeley Symposium on Mathematical Statistics and Probability. 1. University of California Press, Berkeley, pp. 547–561.
Ricotta, C. (2005). Through the jungle of biological diversity. Acta Biotheoretica, in press.
Roebuck, P. and P. Phifer (1999). The persistence of positivism in conservation biology. Conservation Biology 13: 444–446.
Sarkar, S. (2002). Defining "biodiversity": Assessing biodiversity. Monist 85: 131–155.
Sarkar, S. (2003). Conservation area networks. Conservation and society 1(2): v–vii.

Sarkar, S. (2004). Conservation Biology. In: E.N. Zalta (Ed) Stanford Encyclopedia of Philosophy. Winter 2004 ed. Available at: <http://plato.stanford.edu/archives/win2004/entries/conservation-biology/>.

Sarkar, S. (2005). Biodiversity and Environmental Philosophy: An Introduction. Cambridge University Press, New York.

Sarkar, S. and C.R. Margules (2002). Operationalizing biodiversity for conservation planning. Journal of Biosciences 27(S2): 299–308.

Sarkar, S., J. Justus, T. Fuller, C. Kelley, J. Garson and M. Mayfield (2005). Effectiveness of environmental surrogates for the selection of conservation area networks. Conservation Biology 19: 815–825.

Sarkar, S., C. Pappas, J. Garson, A. Aggarwal and S. Cameron (2004). Place prioritization for biodiversity conservation using probabilistic surrogate distribution data. Diversity and Distributions 10: 125–133.

Shannon, C.E. (1948). A mathematical theory of communcation. Bell System Technical Journal 27: 379–423, 623–656.

Simpson, E.H. (1949). Measurement of diversity. Nature 163: 688.

Takacs, D. (1996). The Idea of Biodiversity: Philosophies of Paradise. Johns Hopkins Press. Baltimore.

Tilman, D. (1999). The ecological consequences of biodiversity: A search for general principles. Ecology 80: 1455–1474.

Vane-Wright, R.I., C.J. Humphries and P.H. Williams (1991). What to protect? – systematics and the agony of choice. Biological Conservation 55: 235–254.

Vermeulen, S. and I. Koziell (2002). Integrating Global and Local values: A Review of Biodiversity Assessment. IIED, London.

Whittaker, R.H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30: 279–338.

Wilson, M.V. and A. Shmida (1984). measuring beta diversity with presence-absence data. Journal of Ecology 72: 1055–1064.