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Issues in the Measurement of Biological Diversity

*Andrew R. Solow**
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ABSTRACT

There are many national and international efforts to conserve biological diversity. However, since conservation resources are scarce, they must be used as effectively as possible. This Article examines recent developments in the definition and measurement of biological diversity. The authors explore the advantages and disadvantages of various measures of biological diversity, and the sensitivity of the optimal allocation of conservation resources to alternative measures. This Article demonstrates the importance of the choice of a biological diversity measure while simultaneously indicating that this choice is only one part of the ultimate goal of conservation.

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I. INTRODUCTION

Although direct evidence is scarce, it is widely believed that human activities—most notably tropical deforestation—are

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contributing to a loss of biological diversity through the extinction of plant and animal species.[1] As a result, a number of national and international efforts are underway to conserve biological diversity. It is also widely recognized—although only reluctantly in some circles—that the resources available to conserve biological diversity are limited. These resources include both direct expenditures on conservation and foregone economic growth. Because conservation resources are scarce, it is important that they be allocated as effectively as possible. To do this, it is necessary to specify exactly what is meant by biological diversity and how it should be measured. This paper outlines some recent work in this area.

II. A DECISIONMAKING FRAMEWORK

Dr. Solow has outlined a decisionmaking framework for the conservation of biological diversity.[2] While this framework is too general to be of much practical use, it is useful for focusing the discussion. Let $S = (S_1, S_2, \ldots, S_n)$ be the set of species under consideration, s be an arbitrary subset of S, and $D(s)$ be the diversity of s. In principle, S may contain all the species on Earth. Let $A = (A_1, A_2, \ldots, A_m)$ be the set of possible conservation activities, a be an arbitrary subset of A, and $C(a)$ be the cost of undertaking a. Conservation activities are assumed to alter the survival probabilities of the species in S. The expected diversity that results from undertaking the subset of conservation actions (a) is:

$$E_a = \Sigma\, D(s)\, p_a(s)$$

where the summation is over all possible subsets s and where $p_a(s)$ is the probability under a that s is the surviving set of species. The optimal subset of conservation activities a^* maximizes E_a subject to the budget constraint $C(a^*) \leq B$, where B is the total budget available for conservation activities.

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1. For the conventional, if somewhat extreme, view, see Norman Myers, *Tropical Deforestation and a Mega-Extinction Spasm*, *in* CONSERVATION BIOLOGY: THE SCIENCE OF SCARCITY AND DIVERSITY 394 (Michael E. Soulé ed., 1986) (arguing that present trends of forest exploitation could lead to the extinction of millions of species).

2. Andrew Solow et al., *On the Measurement of Biological Diversity*, 24 J. ENVTL. ECON. & MGMT. 60 (1993).

Three points should be made about this formulation. First, the issue of measuring biological diversity is separate from the issue of survival probabilities. Survival probabilities depend on a number of ecological factors.[3] In many cases, little is known about these factors and the best way to ensure the survival of a species is simply to preserve the habitat in which it lives.[4] In this sense, habitat preservation can be viewed as an instrument for achieving the goal of conserving a maximally diverse set of species. Second, as formulated, biological diversity changes only with the extinction (or origination) of species and not with changes in abundance. On the other hand, survival probability and, consequently, expected diversity do depend on abundance. Third, as illustrated below, the optimal subset of conservation activities depends on the way in which diversity is measured. It is for this reason that a formal consideration of the measurement of biological diversity is important. Without such a measure, it is not possible to know whether one allocation of conservation resources is more effective than another.

III. MEASURING BIOLOGICAL DIVERSITY

Perhaps the simplest measure of the diversity of a set of species is the number of species in the set.[5] This is called species richness. As a measure of biological diversity, species richness has been criticized for failing to account for genetic or taxonomic differences between species.[6] A set consisting of five species of ant is, in some sense, less diverse than a set consisting of three species of ant and one species of elephant. Let d_{ij} be the distance between species S_i and S_j. The distance between species can be based on morphological, behavioral, genetic, or other differences.[7] Suppose that the distance between each pair of species in S is known. The problem of measuring biological diversity is to

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3. *See* Michael E. Soule, *What Do We Really Know About Extinction?*, *in* GENETICS AND CONSERVATION: A REFERENCE FOR MANAGING WILD ANIMAL AND PLANT POPULATIONS 111-24 (Christine M. Schonewald-Cox et al. eds., 1983) (reviewing such factors).

4. *See, e.g.*, RICHARD PRIMACK, ESSENTIALS OF CONSERVATION BIOLOGY 301-69 (1993) (discussing the establishment, design, and management of protected areas to preserve species).

5. *See, e.g.*, Robert May, *Conceptual aspects of the extent of biological diversity*, 345 PHIL. TRANSACTIONS ROYAL SOC'Y LONDON B. 13, 14 (1994) (discussing the reasons why this measure of diversity is the most commonly used).

6. *Id.* at 18.

7. A recent review emphasizing genetic distance is given in MASATOSHI NEI, MOLECULAR EVOLUTIONARY GENETICS (1987).

incorporate these distances into a measure of the diversity of a subset of *S*.

It is natural to measure the diversity of a set consisting of two species by a nondecreasing function of the distance between them. In this way, a set consisting of two species of ant is less diverse than a set consisting of one species of ant and one species of elephant. A diversity measure extends this notion to more than two species. At first glance, this may appear to be a straightforward problem. For example, why not measure the diversity of a set of species by the average distance between them? In fact, this is a poor measure because diversity could be increased by driving a species to extinction.

To avoid absurd results of this kind, it is useful to set down some axioms that a diversity measure must satisfy.[8] One obvious axiom is that diversity cannot be decreased by the addition of a species to a set. A related axiom is that diversity cannot be increased by the addition to a set of a species that is identical (in the sense of being at zero distance) to a species already in the set. A third axiom is that the diversity of one set should be greater than the diversity of a second set if the distances between the species in the first set are unambiguously greater than those in the second set.

These axioms do not define a unique measure of diversity. The first measure that satisfied these axioms was proposed by Martin L. Weitzman.[9] The basic reasoning behind this measure is the following: define the diversity of a single species to be zero. Also, define the distance between a set of species s and a single species S_0 as the distance between S_0 and the nearest species in s. It seems natural to define the diversity of the union of s and S_0 as the diversity of s plus the distance between s and S_0. This would also be extremely convenient, because it would provide a simple algorithm for calculating the diversity of an arbitrary set of species: build up the set by starting with a single species in it, add the other species one at a time, and increment the diversity by the distance between the current set and the added species. Unfortunately, as a little thought will show, the final result of this operation depends on the order in which the species are added in building up the set. To avoid this ambiguity, Weitzman's measure equals the maximum possible result of this operation.

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8. *See* Martin L. Weitzman, *On Diversity*, 107 Q.J. ECON. 363 (1992); Andrew Solow & Steven Polasky, *Measuring Biological Diversity*, 1 ENVT'L & ECOLOGICAL STAT. 95 (1994) (discussing such axioms).

9. Weitzman, *supra* note 8.

Weitzman's measure has a number of attractive features. However, it also has some disadvantages. One is that, loosely speaking, it does not exhibit diminishing returns to distance. As a result, Weitzman's measure tends to favor sets consisting of maximally unusual species.

Solow and Polasky took quite a different approach to constructing a diversity measure.[10] They considered a simple model of the benefits that species provide in terms of their option value (i.e., the possibility that they will provide future pharmaceutical or other benefits). Because genetically similar species also tend to be similar in terms of their provision of benefits, it is optimal under such a model to conserve a diverse collection of species. By formalizing this idea, Solow and Polasky derived a simple measure of the option value of a set of species. Not only is this measure connected to utilitarian considerations, but it also satisfies the three axioms outlined above; therefore, it is a diversity measure as well. This measure is equal to one when the species are all at zero distance from each other; it is equal to species richness when the species are all at infinite distances from each other; and it falls between one and species richness for intermediate cases. For this reason, the measure can be interpreted as the effective number of species in the set. Unlike Weitzman's measure, this measure does exhibit diminishing returns to distance.

Weitzman's measure and the measure proposed by Solow and Polasky are both based solely on the distances between species. If the phylogenetic relationships among the species under consideration are known, and if a model of the descent of features such as the provision of benefits is available, then it is possible to construct a phylogeny-based measure.[11] Clearly, the information requirements of phylogeny-based measures exceed those of distance-based measures. Provided this information is available, however, phylogeny-based measures are preferable.

IV. AN EXAMPLE

To illustrate the sensitivity of alternative measures of biological diversity to the optimal allocation of conservation resources, consider the following simple example. Suppose that

10. Solow & Polasky, *supra* note 8.

11. *See, e.g.*, Daniel P. Faith, *Phylogenetic Pattern and the Quantification of Organismal Biodiversity*, 345 PHIL. TRANSACTIONS ROYAL SOC'Y LONDON B.45 (1994) (proposing one such measure).

three species S_1, S_2, and S_3 are under consideration and that their current survival probabilities are 0.8, 0.1, and 0.5, respectively. That is, S_1 is relatively safe, S_2 is highly threatened, and S_3 is of intermediate status. Suppose that the outcome (i.e., extinction or survival) for each species is independent of the outcomes of the others. Suppose that the total budget for conservation is 0.5 and that the cost of increasing survival probability by an amount δ is equal to δ. For example, if the entire budget is expended on S_2, its survival probability would be increased to 0.6. Finally, suppose that $d_{13} = d_{23} = 1$ and that $d_{12} = \alpha$.

It is easy to show that the expected species richness in this case is simply given by the sum of the survival probabilities. Thus, any allocation of the budget across the three species is equally good. The situation is more complicated for Weitzman's measure. For example, if $\alpha = 0.2$, so that S_1 and S_2 are relatively closely related, the optimal allocation is to spend 0.06 on S_1 and the remaining 0.44 on S_3. This allocation attempts to ensure that S_3 and at least one of the closely related pair S_1 and S_2 survive. Incidentally, the worst possible allocation in this case is to spend the entire budget on S_2. In this simple example, the optimal allocation is relatively insensitive to α. For example, if $\alpha = 0.8$, the optimal allocation is to spend 0.09 on S_1 and the remaining 0.41 on S_3. Qualitatively similar results hold when diversity is measured by the effective number of species.

V. DISCUSSION

In broad terms, there are two possible interpretations of the call to conserve biological diversity. The first is a general admonition to take into account the effect on species in planning development projects. The second is a specific goal of conservation. While the former may be the more sensible interpretation, the main point of this article is that, if it is to be the latter, then it may be important to be specific about the meaning and measurement of biological diversity.

Much of the early work on the measurement of biological diversity was motivated by a narrow problem in the conservation of cranes.[12] The complete set of distance data is available for this

12. *See, e.g.*, Solow et al., *supra* note 2, at 65-67 (applying formulas for the measurement of diversity to the 14 species of cranes).

group,[13] which contains only fourteen species. A similar problem concerning the twenty-six species of glucosinolate-producing plants was considered by Solow and Polasky.[14] In contrast, many practical conservation decisions involve a large (commonly unknown) number of species, many of which are unidentified. In such situations, only the most fragmentary information about the distances between species is available and it is impossible to calculate the kinds of diversity measures described in this article. Even in these situations, the development of these measures is useful, if only to underline the fact that numbers alone may be inadequate.

Incidentally, the need to think carefully about the goal of conservation extends far beyond the choice of a diversity measure. For example, if the goal of conservation is to maximize expected species richness, the bottom-up approach embodied in the Endangered Species Act (in which conservation expenditures are allocated to equalize extinction probabilities from the bottom up) is inefficient. Instead, conservation expenditures should be allocated to equalize the marginal effect on extinction probability.

VI. CONCLUSION

Conservation resources are scarce. Therefore, it is of the utmost importance that those that are part of the effort to conserve biological diversity use these resources as effectively as possible. In order to know which allocations of conservation resources are the most effective, a formal consideration of the measurement of biological diversity is important. A diversity measure must satisfy certain axioms in order to be useful. Diversity cannot be decreased by the addition of a species to a set; diversity cannot be increased by the addition to a set of species that is identical to a species already in the set; and the diversity of one set should be greater than the diversity of a second set if the distances between the species in the first set are unambiguously greater than those in the second set. There are various diversity measures, each with its own advantages and disadvantages. However, as the provided example illustrates, there is sensitivity of the optimal allocation of conservation resources to alternative measures. One may interpret the goal of conserving biological diversity as an admonition to include the

13. Carey Krajewski, *Phylogenetic Relationships Among Cranes (Gruiformes: Gruidae) Based on DNA Hybridization*, 106 AUK 603, 616-18 (1989).

14. Solow & Polasky, *supra* note 8.

effect on species in planning development projects or as a specific goal of conservation. If it is the latter goal, there is a need to be specific about the meaning and measurement of biological diversity. However, to accomplish the ultimate goal of the conservation of biological diversity, there is a need to consider more than the choice of a diversity measure.