Diversity as a Concept and its Measurement: Comment

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Pattil and Taillie have given us a lucid and well-defined analytic framework for studying the mathematical properties of diversity indices. By defining ecological diversity very sensibly as average species rarity and by establishing a set of general criteria for measures of diversity, they are able to bring rigor to issues such as the ambiguity of diversity orderings and the sensitivity of indices to rare species. A similar although less comprehensive attempt at a unifying notation has been made by Hill (1972), who insightfully derived the family $\Delta_n$ based on Renyi's entropy. Whereas Hill's essay was aimed at an ecological audience, Pattil and Taillie's paper is clearly aimed to provide signpost entry into the subject for statisticians. For this reason I thought that it might be useful here to enumerate a few criticisms and philosophical nitpickings that many ecologists and even born-again mathematical ecologists have raised about the study of species diversity and especially the proliferation of diversity indices in the literature. These should be taken less as criticisms of this particular paper, than as counsel for statisticians who may be interested in contributing to the literature on species diversity.

WHY DIVERSITY?

There are two broad reasons why attention has been focused on characterizing the diversity of an ecological assemblage. These depend on whether one treats diversity as an abstract phenomenological property or a specific biological one. That is, whether one treats diversity in its general sense, as a property in itself, or as an indicator of the functioning and organization of communities. First, diversity per se, as a phenomenological property, contains intrinsic interest, and as a fundamental quality of perception seems to demand quantification. It is not surprising, therefore, that one finds diversity measures emerging in such varied disciplines as genetics, linguistics, and economics. The special significance of species diversity as a phenomenological property arises from its association, in a political context, with human values and environmental quality. Such species diversity indices have the practical importance of enabling one to speak precisely (albeit no less arbitrarily) about the qualitative effects of human disturbance on the environment. Here justification for a particular index rests more on philosophy than science, since the primary purpose of the index is to reflect a human value rather than to capture an important property of state in the functioning of communities. This does not detract from the significance of the problem, however, as underscored by the multitude of indices that have been proposed.

Apart from politics there are the more ontological concerns of diversity as a biological property. To the ecologist, diversity is interesting as a property of state in so far as it has the potential to reflect the nature of the underlying processes and organization that structure the community. Therefore, beyond arbitrary or weakly motivated definitions, the scientific interest in and importance of ecological diversity hinges directly on its possible connection with the functioning and organization of communities. The principal aim of such scientific study, therefore, is to find a characterization of species diversity that most clearly reveals this functional connection.

One can group approaches to this problem into three alternative strategies, depending on whether preliminary emphasis is given to the index, the model, or the data. Choosing initially to focus on the index necessarily invokes a phenomenological view of diversity. One does not know whether the index chosen is capturing interesting phenomena or is the best one for revealing the nature of the underlying community structure. To take this approach is in some sense putting the cart before the horse, since the analysis that follows can only have meaning after the index has been justified with a functional model and established with data. The problem of diversity ordering for example, as considered by Pattil and Taillie, is really an epistemological one, and it is only when diversity is related to a functional model that the question of "what is more diverse" becomes more than sterile controversy.

In view of how little is known about the connection between diversity patterns and community processes, it seems premature at this early stage to restrict attention to indices and risk losing information by condensing the complete abundance vector into a single statistic. It would be more prudent in these initial stages to consider the complete abundance vector as represented by ranked abundance plots or species frequency distributions (see May 1975 or Pielou 1975). Regularities in these empirical distributions may then be found (Fisher et al. 1943; Preston 1948; May 1975; Kempton 1979) that could provide insight into the underlying processes that structure the community. Only after obtaining a verified model can one

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properly derive an appropriate diversity index that reveals the connection between process and pattern.

Fitting data to theoretical distributions has the added advantage of enabling one to make inferences about the community from incomplete samples. In this sense, the title of Patil and Tailie's essay is somewhat misleading, in that they do not address the crucial practical concerns of inferring community diversity measures from samples. All of the indices discussed are in general sample-size dependent. Questions of the philosophy of approach aside, historical inertia in the wide usage of indices suggests that this is a problem that in the future could benefit from the sort of systematic treatment given to the question of ordering. Simpson's index, for example, can be shown to be independent of sample size if the underlying pattern of abundances has a logseries distribution (May 1975).

Although Patil and Tailie have, for the most part, focused on diversity as a phenomenological property, it is notable that some attempt was made to motivate Simpson's index, species count, and the information-theoretic measure in terms of interspecific encounter probabilities, waiting times, and niche theory. None of these interpretations, however, has yet proved to be very fruitful, as they suffer from such real-world concerns as spatial patchiness and clumping in species distributions, differential mobility, and problems associated with interpreting niche overlap between species from their spatial covariance. Approaching the study of species diversity through a priori models is a valid enterprise, but requires a clear intuition of how communities operate, which thus far seems to be lacking.

In closing, I believe that Patil and Tailie's paper, although interesting and useful in its own right, will be regarded by ecologists not so much as a contribution to the theory of species diversity as a constructive and insightful essay in tidying up a messy literature on diversity indices. Truly ground-breaking contributions to the theory of species diversity are not likely to arise in vitro from a mathematical analysis of indices but will most probably depend on an interplay of analysis with real data.

REFERENCES


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Rejoinder

G. P. PATIL AND C. TAILLIE*

1. INTRODUCTION

We greatly appreciate the comments by I. J. Good and George Sugihara. In this rejoinder, we simply review recent literature on diversity. In so doing, we hope to have touched base with some of the comments of Good and Sugihara.

2. DIVERSITY IN CONSERVATION AND MANAGEMENT

The National Forest Management Act of the United States (Federal Register 44(181), 219.13(6), 1979) requires that the management practices should maintain the diversity of the forest ecosystems. These regulations further require quantitative comparisons of the diversities of the natural and the managed forests.

The Committee to Review Methods for Ecotoxicology of the Environmental Sciences Board of the U.S. National Academy of Sciences (1981, John Cairns, Jr., Chairman) has concluded in their report on testing for effects of chemicals on ecosystems that "diversity is a system property that is likely to be a sensitive measure of ecosystem contamination." The Committee has further recommended that "methods should be developed

* The rejoinder is written by the authors while they are partially supported by the National Marine Fisheries Service, Woods Hole, for studies in Stochastics and Statistics in Marine Fisheries Research and Management.

© Journal of the American Statistical Association
September 1982, Volume 77, Number 379
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