THE USE OF COMMUNITY DIVERSITY FOR MONITORING TRENDS IN WATER POLLUTION IMPACTS

B. Dennis and G. P. Patil

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Draft of the Final Project Report on the Use of Community Diversity for Monitoring Trends in Water Pollution Impacts - Environmental Protection Agency, Program Evaluation Division, Washington, D. C.
Project Officer: William V. Garetz
Contract No: WA-6-99-2448-A.

A WORKING DRAFT

December 3, 1976

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PART A

IS COMMUNITY DIVERSITY A USEFUL CONCEPT FOR MONITORING TRENDS IN WATER POLLUTION IMPACTS?

PART B

LITERATURE REVIEW OF COMMUNITY DIVERSITY AND BIOMONITORING

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CERTAIN QUOTABLE QUOTES

"For top management and general public policy development, monitoring data must be shaped into easy-to-understand indices that aggregate data into understandable forms. I am convinced that much greater effort must be placed on the development of better monitoring systems and indices than we have in the past. Failure to do so will result in sub-optimum achievement of goals at much greater expense" . . . Russell E. Train.

"Monitoring the environment requires a working knowledge of all its parameters and regular sampling of at least the most important ones. There are often insufficient funds or staff for this to be done properly by human agencies, but the plants and animals which spend their lives there necessarily carry out a continuous monitoring program, reporting on conditions by their presence or abundance" . . . D. Reish.

"It is only as a result of thorough and continuous study of an environment and the species living in it that one can venture to describe the quantitative changes in the natural environment by changes in the quantitative abundance of specific kinds of species" . . . R. Patrick.

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IN WATER POLLUTION IMPACTS

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PART A

IS COMMUNITY DIVERSITY A USEFUL CONCEPT FOR MONITORING TRENDS IN WATER POLLUTION IMPACTS?

1. INTRODUCTION AND SUMMARY

Man's activities are having important and little understood impacts on aquatic communities. There is great need for the development of an applied science of ecology. Ecological systems analysts currently are constructing complex mathematical models in efforts to predict the responses of population sizes to environmental disturbances. But the efforts have had only limited success so far, as the biological processes at work in a community are complicated. The need for environmental action, though, is critical, and existing technology should be put to work. The understanding of ecosystems that is available at present is fragmented at best, but what understanding there is must be assembled and put to use in coping with environmental problems. By some ecologists (eg. Hurlbert, 1971) community diversity is considered an empty concept and, an imperfect technology; but the use of diversity in biomonitoring is state-of-the-art knowledge that will find valuable if stopgap, applications.

A collection of individuals of the same species is called a population; a collection of populations is termed a community. Each species population consists of organisms that have become adapted to their habitat over a long evolutionary history. Typically each species has its own range of tolerances to environmental factors. The organisms in the population will thrive if these factors, such as temperature, pH, and dissolved oxygen, never exceed lethal extremes. Other species are also important environmental factors, as the abundance of a population will be affected by interactions with other species in the community. These interactions may take such forms as predation, parasitism, competition, and grazing.

Pollutants as well as most other environmental factors, actually act at the level of the individual organism. If an organism is not adapted to thrive in an environmental disturbance, that organism's ability to grow, reproduce, or compete in the community will be affected. The cumulative effects of environmental perturbations on many organisms will result in changes in population sizes in the community. The impacts of pollutants on an aquatic community are manifested as shifts in population sizes in that community. Some species that are pollution intolerant may decline, perhaps to extinction, while other pollution tolerant species, perhaps newcomers, may increase in abundance in response to environmental disturbances.

If it were possible, a community would be best characterized at any given time by a vector of population sizes. Monitoring water pollution impacts would then amount to following the changes in population sizes as the organisms responded to the various environmental factors. However, obtaining estimates of all the population sizes in a community would be a massively difficult task, and the cost and manpower necessary to obtain these estimates make this approach prohibitive for biomonitoring.

The concept of community diversity is useful now in biomonitoring essentially because of the limitations of current field sampling procedures. It is difficult if not impossible to monitor absolute population sizes in a biological community. But through a sampling of a portion of a community we may obtain good estimates of the relative abundances of the populations in that community. We characterize the community by a vector of percentages or fractions of the total community abundance with one element for each species:

$$\underset{\sim}{\pi} = (\pi_1, \pi_2, \ldots, \pi_s) = (\frac{n_1}{n}, \frac{n_2}{n}, \ldots, \frac{n_s}{n})$$

where n_i = absolute abundance of the ith species in the community; $n = \sum_i^s n_i$; $\pi_i = \frac{n_i}{n}$; and s = total number of species in the community. This vector of relative abundances, $\underset{\sim}{\pi}$, will obviously change in response to changes in the population sizes n_i.

Measures of community diversity, at least the ones most important to biomonitoring, are basically indexes which signal when changes in the vector $\underset{\sim}{\pi}$ occur. Diversity measures are of greatest value to pollution impact assessment when the measures indicate that shifts in relative abundances of the species in the community are taking place, as these shifts are results of changes in the absolute population sizes themselves.

The question of whether community diversity is a useful concept for biomonitoring should be considered on both theoretical and empirical grounds. Ecological theory is needed in order to interpret a diversity change in terms of impact of environmental stress on a community. A diversity fluctuation itself is not a direct impact of pollution, but an indicator which can signal that events are taking place in the community which should be studied more carefully. It will be emphasized in this report that a diversity index is not a substitute for skilled field biological work, but diversity can be a useful warning to the investigators to examine the community in depth. The response of diversity to water pollution must also be backed by empirical evidence if the technique is to be meaningful. Preferrably, controlled tests should be performed to answer specific hypotheses about the relationships of community diversity and environmental pollutants. Investigators must also be able to distinguish pollution-caused diversity changes from those of natural causes through attention to sampling methods (see Energy Resources Company report for a thorough review) and statistical methods. Usefullness of diversity will depend furthermore on the practicality of gathering data in a routine fashion. Finally, whether diversity is useful or not will depend on whether the concept is applicable to the vast assortment of organisms of many different phyla that are typically present in aquatic communities.

The first section of this report contains some comments on the variety of diversity indices that are available, and calls attention to some recent work which shows how certain diversity indices are conceptually similar. The second and third sections of this report are reviews of the theoretical and empirical justification of using community diversity for monitoring trends in water pollution impacts. Other sections consider the sampling of different taxa or trophic levels, the use of biomass versus the numbers of individuals, artificial substrates, sampling different habitats, and the importance of identification of species.

The broad conclusions of this report are based on a careful study of the existing literature on ecological diversity and biomonitoring. These conclusions are as follows:

1. Community diversity is a useful concept for monitoring the impacts of water pollution on biological communities. The application of diversity in a biomonitoring program is justified both theoretically and empirically.

2. Community diversity may not be taken as a direct index of water quality as such, but can be used to study the impact of water quality on aquatic organisms.

3. Trained field ecologists will be needed to gather data and interpret diversity changes in terms of environmental impact. Investigators should be able to design simple experiments on-location, as some basic research will be needed at many stations to familiarize the investigators with the local community processes. Taxonomic work is unavoidable, but workers can become familiar with the species at a specific locale in a few months time.

4. Diversity alone is not adequate for assessing the overall biological impact of water pollution, but diversity can be invaluable in signalling when or where further work is needed.

2. MATHEMATICAL FORMULATIONS OF COMMUNITY DIVERSITY

There is no shortage of literature on the various mathematical formulations and statistical methodology of diversity indices. Statisticians and ecologists alike have proposed many diversity formulas for use in ecology, to the extent that the concept of ecological diversity must be defined in terms of the particular index in question. Indeed, the number of measures of community diversity that have been proposed have outstripped the need for such measures in ecological theory and practice.

The Energy Resources Company report gives an account of the properties of several of these indices; Pielou (1975, 1974, 1969) has written extensively on the subject and her works, along with the ERCO report should be consulted. We will not duplicate that material here, but wish to point out that certain diversity indices which are important to biomonitoring have a common conceptual basis.

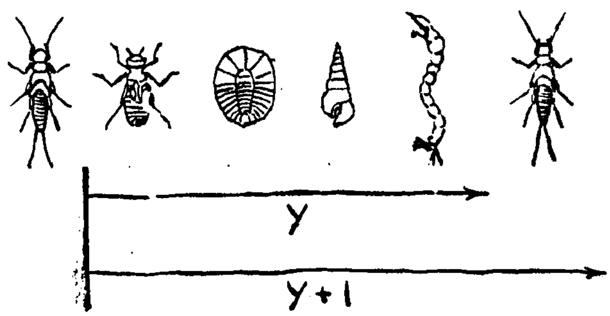
One of these diversity indices is simply the number of species in the community, S. This quantity, sometimes referred to as "species richness," is equated conceptually with diversity by some field ecologists (Whittaker 1972). The number works better as an index if the diversity is computed as S-1, so that the diversity is 0 when the number of species in the community is only 1. If the number of species in the community is large (above 50 or so) and the community has a lognormal abundance distribution, then the Shannon diversity formula will be almost totally dependent on this number of species (May, 1975). Such large numbers of species and lognormal distributions are common in diatom communities (Patrick et al., 1954).

Another diversity index is Simpson's formula, $1-\Sigma_i \pi_i$, where π_i is the relative (percentage) abundance of the ith species. This quantity is of particular importance to biomonitoring as the quantity can be estimated with the sequential sampling method of Cairns (1968), which involves little or no taxonomic training (see Patil and Taillie

1976 and the ERCO report). Simpson's index has the disadvantage of "saturating" at values very close to 1 as the number of species in the community increases above 50 or so (ERCO report).

The index most often used by ecologists in field studies is the Shannon formula $-\Sigma_i \pi_i \log \pi_i$. This function has many desirable properties which make it useful in field research and biomonitoring (ERCO report, Pielou 1975). However, ecologists have felt somewhat uncomfortable with the conceptual basis of this function; the relevance of "information theory" to a living community has been questioned (Pielou 1975).

Patil and Taillie (1976) have recently shown that these three diversity indices have a common conceptual basis. A single species, say species i, will be rare in a community to a greater or lesser extent compared with other species. The "rareness" of species i could be thought of as some decreasing function, $R(\pi_i)$, of that species' relative abundance, π_i. Here are some possible candidates for the exact functional form of $R(\pi_i)$ (see figure):



Starting with species i, an investigator randomly encounters individual members of the community (as in Cairns' sequential sampling method). Y is the number of encounters needed to find another individual of species i and is a random variable. Then $R(\pi_i)$, the rareness of species i, might take these forms:

1.) $R_1(\pi_i) = E[Y/\pi_i] = (1-\pi_i)/\pi_i$; or

2.) $R_2(\pi_i) = E[Y/\pi_i]/E[Y+1/\pi_i] = (1-\pi_i)$; or

3.) $R_3(\pi_i) = E[\frac{1}{Y+1}/\pi_i]E[Y/\pi_i] = -\log \pi_i$.

According to Patil and Taillie, the diversity of a community is the average rareness of that community, depending on how rareness is measured.

1.) $E[R_1(\pi_i)] = \Sigma_i \pi_i R_1(\pi_i) = S-1$, the species count;

2.) $E[R_2(\pi_i)] = \Sigma_i \pi_i R_2(\pi_i) = \Sigma_i \pi_i (1-\pi_i)$, Simpson's index;

3.) $E[R_3(\pi_i)] = \Sigma_i \pi_i R_3(\pi_i) = -\Sigma_i \pi_i \log \pi_i$, Shannon's index.

Thus, these three diversity indices arise from the same concept of average rareness. In particular, ecologists need not invoke "information theory" as a conceptual basis for the Shannon formula.

Summary and Recommendations

1. Certain references, in particular Pielou (1975) and the ERCO report, have thoroughly delineated the properties of many diversity indices.

2. Three indices are of particular importance to biomonitoring; they are the species number, Simpson's index, and Shannon's formula. These indices are linked by an underlying concept of average rareness.

3. ECOLOGICAL THEORY AND COMMUNITY DIVERSITY

It is helpful to briefly examine the current state of ecological theory on diversity. The critical task in the use of community diversity for biomonitoring is that of interpretation; fluctuations in community diversity may arise from a large number of ecological causes. The ups and downs of a diversity index plotted on a chart will provide little information on the actual impact of water pollution on the community. But those fluctuations will provide signals that events in the community are taking place. If unexpected or long-term diversity shifts occur, then the specific ecological factors which are causing the diversity change can be determined.

Diversity indexes such as the Shannon and Simpson formulas will be sensitive to those community changes which will alter the relative abundance vector $\underset{\sim}{\Pi}$, with one or two exceptions. These diversity indexes will not be sensitive to these possible, but unlikely, community changes:

1. The abundances of species change according to some constant proportion. This would happen if for some reason a pollutant killed a constant fraction of each species present; that is, if

$$\underset{\sim}{\Pi} = (\frac{n_1}{n}, \frac{n_2}{n}, \ldots, \frac{n_s}{n}) = (\pi_1, \pi_2, \ldots, \pi_s),$$

and this community is affected by pollution such that $n_1, \ldots, n_s$ are killed off in some fraction k, then the total number of individuals in the changed community is

$$n^1 = kn_1 + kn_2 + \ldots + kn_s = k\Sigma n_i = kn.$$

Then the relative abundance vector, $\underset{\sim}{\Pi}^1$, for the changed community is

$$\underset{\sim}{\Pi}^1 = (\frac{kn_1}{kn}, \frac{kn_2}{kn}, \ldots, \frac{kn_s}{kn}) = (\frac{n_1}{n}, \frac{n_2}{n}, \ldots, \frac{n_s}{n}) = \underset{\sim}{\Pi}.$$

Such a change would not be detected with either the Shannon or Simpson diversity formulas. However, it is very unlikely that a pollutant would affect the different species in exactly the same amounts. Species for the most part will differ in their pollution tolerance.

2. The abundances of species change so as to permute the elements, π_i, of the relative abundance vector. For instance, if a community had the abundance vector

$$\underset{\sim}{\pi} = (\frac{50}{100}, \frac{30}{100}, \frac{20}{100}) = (\frac{1}{2}, \frac{3}{10}, \frac{2}{10}),$$

and species 1 declined by 20 individuals and species 2 gained 20 individuals, then the resulting community vector would be

$$\underset{\sim}{\pi}^1 = (\frac{30}{100}, \frac{50}{100}, \frac{20}{100}) = (\frac{3}{10}, \frac{1}{2}, \frac{2}{10}) .$$

The Shannon or Simpson indexes would be the same for $\underset{\sim}{\pi}$ and $\underset{\sim}{\pi}^1$. But this event is also very unlikely in a community.

3. New species replace old species in such a fashion as to leave the $\underset{\sim}{\pi}$ vector unaltered. If for some reason a new species had established itself in the community in exactly the same abundance as a species that had gone extinct. Again, such an event is unlikely.

4. The community alters such that change in species number offsets change in "evenness." If this occurred the community vector $\underset{\sim}{\pi}$ with s elements would become a new vector, $\underset{\sim}{\pi}^1$, with some different number of elements; corresponding changes in the evenness of the elements make up for any diversity difference. This has happened in at least one field study. Logan and Mauer (1975) reported the diversities of stations located above and below a thermal effluent; stations below the effluent showed a slight (not significant) diversity increase. The species numbers at the below-effluent stations were low, however, and the diversity had been kept high by the increased evenness of the remaining species.

Thus it is important for the investigator to be aware of the nature of the community changes and how they are affecting the diversity index. Important changes in the community conceivably could go undetected if diversity is the only item being looked at. And when a diversity shift does occur the specific community changes that are responsible for the shift should be examined.

What kinds of community events are picked up by a diversity index? Formulas such as the Shannon or Simpson will be responsive to events such as these:

1. Irregular changes in the absolute abundance of species in the community. The vast majority of such changes will affect the evenness of the community vector, and hence affect the diversity index.

2. Net changes in the number of species in the community. This would happen if the number of colonizing species did not equal the number of extinctions in the community.

Are there any patterns to be expected in these community events? Whittaker (1972) has given an extensive review of ecological diversity and the factors which affect it in communities. According to Whittaker, the process of competition is very important to the evolution of a given diversity level in an ecosystem. Resources in communities are essentially scarce and species must compete for resources to survive. Given a resource gradient, such as prey size, substrate type, or light intensity, species gradually evolve to utilize different portions of this gradient, that is, species become specialized enough to out-compete other species for portions. Species which are so adapted can establish themselves in a community by "fitting in" between other species on the same resource gradients and commanding those portions for themselves. This is known as "species packing" in the ecological literature.

As the resources are divided up among species, the portions or amounts that a species can preempt for itself may be reflected in that species' absolute abundance in the community. Thus the relative abundance distribution of a community may reflect a mechanism by which the resources are being divided in the community. When the elements in the $\underset{\sim}{\pi}$ vector are ordered from largest to smallest, mathematical series formulas can be used as models for relative abundance. Two models in particular have been found to closely represent field data for a wide variety of communities (see Whittaker 1972 and May 1975 for extended discussions):

1. The geometric series is often the form of the relative abundance distribution for communities in harsh or marginal environments; it occurs also when a perviously unexploited resource is being colonized. This distribution arises when a first or dominant species preempts a fraction k of a resource, the next species takes the same fraction of the remainder, and so on.

2. The broken stick series is the form of the relative abundance distribution when a group of species apportion a resource essentially at random. It is found most often only for closely related species.

Both the above patterns of relative abundance only occur for the most part in communities with few numbers of species. A different pattern is found in communities with large numbers of species that are not closely related in resource use. It is the lognormal distribution (again see Whittaker 1972 and May 1975) and it is a species abundance distribution. This pattern has been found in many communities in nature (Preston 1948, 1962, Patrick et al 1954; Whittaker 1965). The distribution reflects the fact that large numbers of relatively independent factors may be governing the abundances of the species in the community (May 1975). In biomonitoring, samples of large numbers of species of diatons will likely have this pattern (Patrick et al 1954).

In the event of an environmental disturbance, shifts in abundance patterns may be expected to occur in a community. Ruth Patrick has developed a method of biomonitoring for use with diatoms which involves fitting a lognormal curve to the species abundance data, rather than (or in addition to) computing diversity (see Patrick, et al, 1954).

According to current ecological theory, if pollution - intolerant species decline in abundance, resources may be left unutilized. The pollution tolerant organisms then find themselves with a lack of competition for space, nutrients, or other resource, and they can rapidly increase in numbers. Also, new pollution tolerant organisms may be able to colonize the community, but many more sensitive species generally go extinct altogether. The resulting community abundance pattern of heavy dominance and fewer species gives the characteristic decline in diversity observed so often in the field (see section).

Disruptions in community food chains can cause shifts in relative abundance. Paine (1966) has found that predation may allow high diversity levels to be maintained if a predator eats a dominant competitor in the community. The predator ("keystone species") regulates the growth of the competitor by eating it, thus making available resources for other species.

In contrast, Kushlan (1976) found that predators could actually reduce the diversity of species at lower trophic levels, simply by eating the prey species to extinction.

Investigators in biomonitoring programs should look for community events such as these when a change in diversity occurs. The information thus gathered will help greatly in forming more detailed, applied theories of the impact of pollution on aquatic communities.

SUMMARY AND RECOMMENDATIONS:

1. Investigators should be aware of the types of community fluctuations that can occur, and should try to explain diversity change in terms of its component events. Diversity is seen as an indicator that a biological community is experiencing environmental impact; diversity itself is not seen as an impact.

2. Investigators should be aware that certain types of community events could go undetected if only diversity is used for monitoring the community. Perhaps more importantly, the investigators should become very familiar with the specific habitats being monitored as each habitat will have its own peculiar ecological events.

4. EMPIRICAL STUDIES AND COMMUNITY DIVERSITY

According to the ecologic theory in the pervious section, pollutants will generally cause adjustments and alterations in species abundances and community species composition. Furthermore, these adjustments should be detectable through use of an appropriate diversity measure.

Is this assertion supported by field evidence? Investigators have reported diversity index responses in a scattered but growing literature. The studies indicate that diversity measures are indeed sensitive in general to the addition of various pollutants to aquatic systems.

Howell and Gentry (1974) have shown that thermal effluents from a nuclear power plant decreased the diversity of aquatic insects in the Savannah River in South Carolina. Coutant (1962) reported a decline in diversity of macroinvertebrate riffle organisms in the Delaware River due to heated-water effluents. Temperature shifts in water are known to cause major alterations in the communities of algal flora in streams (Patrick et al 1969); presumably these changes would be detectable if the data were used to compute diversity. Johnson and Schneider (1976) have found that slight long-term temperature alteration can cause significant changes in entire communities; again such changes should likely show up in a diversity measure.

Wilhm (1967) concludes from a study that populations of benthic macroinvertebrates can be used to assess pollution in a stream receiving organic wastes, and that a diversity index is a clear and brief way to summarize the data.

Wilhm and Dorris (1966) studied the physicochemical conditions and benthic macrionvertebrate diversity in a stream receiving domestic and oil refinery effluents. They concluded that information theory diversity measures were more precise measures of stream conditions as reflected by benthic macroinvertebrate populations than traditional methods.

Oil spills have been shown to reduce macroinvertebrate diversity in streams in two field studies (Hoen et al 1974, 1975; Nauman and Kernodle 1975).

Williams (1964) reported the results of an extensive study that was conducted at 103 stations scattered on the Great Lakes and the major rivers of the United States. The numbers of species of diatoms at eutrophic stations were found to be generally lower than the numbers at "clean" stations. Diversity measures were not used in this report, but such community differences could probably be seen if the measures were used.

Heavy metals and other toxic constituents of industrial and domestic waste water significantly altered diversity of benthic organisms in a lake and stream in Maine (Davidson 1974).

The species diversity of the benthic oligochaete fauna in a lake polluted by acid mine drainage are significantly lower than the species diversity of a comparable unpolluted lake (Orciari and Hummon 1975).

Swartz et al (1975) report the decreased diversity of marine macrobenthos as an impact of sewage sludge.

The ERCO report cites several studies in the literature which appear to give conflicting or contradictory evidence on the use of diversity in biomonitoring. These papers merit closer attention here, for in reality no such conclusions should be drawn from these studies about the use of diversity:

ERCO cites Ewing and Dorris (1970) as supportive of the usefulness of diversity indexes, whereas this study was inconclusive. Ewings' and Dorris' study was performed in artificial ponds, and they found that in general, algol species diversity was not positively correlated with the nutrient concentrations in the ponds. But the nutrient concentrations (dissolved nitrate, nitrite, phosphorous) were not significantly different in the ponds and so no conclusions should be drawn about diversity indices from this study.

The study by Winner (1972) was cited in the ERCO report as evidence against the use of the diversity concept in biomonitoring. Winner was evaluating various indexes of eutrophy and maturity in lakes of different ages in effect testing various assertions by E. Odum and Margalef that diversity, P/B ratio, pigment ratio, and assimilation number will be affected as a lake undergoes its natural succession. Margalef's and Odum's theories of ecological succession have not been supported by field data through the years (Colinveaux, 1973) and seem to be less accepted now among ecologists. Note that Winner was not investigating the response of the lake biota to man-induced or sudden environmental stress. The aquatic community could respond differently to a sudden or artificially high nutrient load as compared to the nutrient buildup of a gradual system aging process.

ERCO pointed out that Logan and Maurer (1975) found an increased diversity of macroinvertebrates in a thermal effluent. But Logan and Maurer may have been dealing with very different communities at each of their sampling sites. Their four sites (one above, 3 below the thermal outflow) were located in an estuary along an increasing salinity gradient. The species compositions at the sites were somewhat different from each other. And the site locations varied from close to shore in a relatively narrow river to out in the middle of a bay, which suggests that the investigators were sampling different habitats. Finally, though diversity as measured by Shannon's formula did not decrease significantly in the thermal effluent, the number of species did decrease. This indicates that one aspect of diversity, the evenness or equitability, actually increased while the species number aspect of diversity decreased. The study is an example of one of the exceptional community events mentioned earlier which might go undetected if the data aren't analyzed further than merely computing diversity.

We wish to point out that there is a fundamental distinction between two potential uses of diversity in biomonitoring. The first use of diversity occurs when an investigator is interested in this question: given that a known pollutant is present in the system, are there consequences taking place in the natural community? Diversity is used in this case to assess impact of pollution on aquatic communities. The other question that might be of concern to an investigator is: "given that changes have taken place in the community, is there a pollutant present in the system?" Diversity here is used as an indicator of water quality.

The field studies mentioned above generally support the use of community diversity in the first sense. The investigators in these studies usually measured diversity above and below pollution outflows, so that a pollutant was known to be present in the water for these studies. In almost all cases clear community impacts could be demonstrated with the use of diversity measures. We conclude that diversity measures are among the best tools available for monitoring water pollution impacts on biological communities.

The validity of the use of diversity in the second sense, i.e., as a water quality index, still remains an open question. Wilhm and Dorris (1968) go so far as to propose the establishment of water quality criteria by the evaluation of biological conditions in receiving streams. They claim that values of diversity less than 1 (Shannon formula with logs taken to base 2) have been obtained in areas of heavy pollution, values from 1 to 3 in areas of moderate pollution, and values exceeding 3 in clean water areas. On the other hand, Swartz et al (1976) state that structure analysis provides an exceptionally good method for assessing ecological alterations at specific sites, but quantitative criteria such as diversity indices should not be used as universal regulatory standards.

On the basis of available data the position of Swartz et al seems preferrable to that of Wilhm and Dorris. Aquatic habitats are extremely varied in their environmental conditions from one area to another, and the natural communities present in each area consist of organisms uniquely adapted to these local conditions. Thus what may be a high diversity figure for one stream may be a low figure to another stream with different conditions and organisms. The natural diversities of two completely different areas are essentially uncomparable quantities; establishing water quality criteria on the basis of diversity indices seems unwarranted at this time.

Additionally, the number of studies which use diversity to evaluate pollution impacts is remarkably small to date. There are a vast number of chemical substances which pollute water at a great many concentrations, and quantitative field studies using diversity have been performed for relatively few of these contaminants. In this regard much of the data gathered in a biomonitoring program will be new information for ecologists.

The ERCO report concludes, as a result of their own evaluation of the literature: "Because of the contradictory nature of some of the diversity studies, it is highly doubtful whether diversity indices in their present form will serve as useful indicators of water quality." Perhaps this statement by ERCO is too pessimistic, for the field work done to date on diversity measures seems to give fairly consistent results. It is reasonable to think that an aquatic ecologist could very well monitor water quality trends in a particular area after the investigator had become thoroughly familiar with the local biota and natural conditions. To quote Ruth Patrick: "It is only as a result of thorough and continuous study of an environment and the species living in it that one can venture to describe the quantitative changes in the natural environment by changes in the quantitative abundance of specific kinds of species." (Patrick 1963).

SUMMARY AND RECOMMENDATIONS

1. Empirical studies performed to date indicate that diversity measures are indeed sensitive to the addition of various pollutants to aquatic systems.
2. Diversity measures are an excellent method of monitoring whole community impacts of water pollution.
3. Diversity measures have not been studied enough to be used as indicators of water quality.

5. SELECTED GROUP OF ORGANISMS VERSUS ALL TAXONOMIC GROUPS

Should all taxonomic groups in a community be sampled, or may the sampling effort be confined to a selected group of organisms? This complex question is of obvious practical concern in a biomonitoring program. Invariably, decisions at the present time on this question will involve a conflict between biological concerns and costs. The reason for this is the question has not been adequately researched.

The work done up to the present time indicates that as many taxonomic groups should be sampled as are possible under the constraints of cost and time. The investigations of Winner (1972) and Kushlan (1976) show that the diversities of different taxonomic groups or different trophic levels may behave in contradictory ways.

The diversity computations, however, should be confined to within these groups, that is, diversity should be calculated separately for each group. A diversity index calculated across a vast community of unrelated organisms may not be sensitive to environomental impacts that affect some groups but not others. The changes in numerical abundance that take place in zooplankton are on a totally different scale from the changes in abundance of, say, fish.

The work of Dickman (1968) illustrates the problems associated with computing diversity across many different taxonomic groups. Dickman included bacteria, phytoplankton, and zooplankton species in the diversity computations. He used the Shannon formula $H = - \Sigma \pi_i \log \pi_i$ as a diversity index: interestingly he defined the π_i values three separate ways. The first definition used numbers of individuals to compute π_i values, the second definition used biomass, and the third used relative productivity.

When biomass or numbers were used in the computations, the diversity index failed to be sensitive to changes in the higher trophic levels in the community. Dickman noted that over two thirds of the species encountered in a typical plankton sample had no significant effect on the diversity of that sample when numbers of individuals were used. However, the diversity index did respond to changes in the higher trophic levels when the relative abundances π_i were defined in terms of productivity.

The way Dickman used productivity in this study is misleading and is not recommended for biomonitoring purposes. Dickman failed to take into account the important distinction between growth and reproduction in computing the diversity of productivity: the relative abundance of the ith species π_i was defined as pr_i/PR where pr_i was the productivity of species i and PR was the total sample productivity. Productivity was calculated by multiplying the mean sample density and biomass for species i and then multiplying that product by the number of times that species i reproduced in one year. This ignores the possibility that the mean mass per individual in microbial proulations may undergo drastic fluctuations of many orders of magnitude. Cell growth research has indicated that there is only a loose connection between cell mass and cell division (Williams 1971). Obtaining the true productivity values for many species in an aquatic system would require techniques which are too costly and involved for use in biomonitoring. In addition the use of true productivity values in diversity indices is unresearched.

Dickman concluded that the Shannon-Weaver diversity formula fails to reflect significant changes in a community's structure because it is only sensitive to changes in relative abundance of a few of the trophic levels of a community. This conclusion is somewhat incorrect; if the organisms at all trophic levels happened to have comparable abundances then the diversity index would be sensitive to changes in community structure. Most often, though, the organisms on the first level or two of the trophic pyramid tent to vastly outnumber and outweigh the higher level carnivore populations. Obviously, if diversity is computed across a whole community of many phyla and several trophic levels certain organisms will swamp the diversity index with their relative abundance. This is what occurred in the Dickman study when diversity was computed across a community of bacteria, phytoplankton, and zooplankton.

Dickman's study indicates that the diversity calculations should be confined to within single groups of organisms. Diversity as a concept is most meaningful when applied to a "guild" of organisms. Guild refers to a set of species which are utilizing a specific type of resource (Root 1967). Generally the species in a guild are competing for the resource, or partitioning the resource in some way such as along a gradiant. For the purposes of biomonitoring groups which are naturally sampled as a unit such as diatoms or benthic insects may be considered guilds. Each species outcompetes the others in the guild only along a certain portion of the resource gradient; the resources are apportioned by competition. An environmental perturbance such as a pollutant may kill intolerant species or may reduce their ability to compete in the community. Pollution tolerant or unaffected species would then increase in abundance because lack of competition would allow them to broaden their resource utilization. A diversity index computed for a single guild or group of taxonomically close species will likely reflect these sort of changes in community structure.

But knowledge of diversity trends within one group of organisms may not reflect the diversity trends within other groups in the same aquatic system. Until difinitive research shows otherwise as many guilds should be sampled and studied as are possible under cost constraints. Diversities of phytoplankton, zooplankton, benthic insects, and fish should be computed separately and monitored. An investigator may wish to split these groups further when cost and effort constraints permit as these broad groups contain a large variety of organisms and are not strictly guilds as such.

Winner (1972) reported lack of correlations between phytoplankton and zooplankton diversities in five Colorado lakes. The lakes were all different in their relative degrees of eutrophication. Winner concluded that measurement of diversity in one community of an ecosystem does not necessarily indicate what diversities are in other communities of that ecosystem.

Further evidence that different groups of organisms should be monitored separately is given by Kushlan (1976). Kushlan studied changes in fish species diversity in the Everglades marshes and how such diversity was affected by the degree of water level stability. The overall fish species diversity increased during a prolonged period of high water and decreased during regimes of fluctuating water levels. Kushlan looked further into these trends by dividing the fish community into "functional groups." He placed each species into one of three categories: small omnivores and herbivores, small carnivores, and large carnivores. The separate diversities of these groups responded differently to water level stability; combined as one fish community the diversities summed to the overall results mentioned above. The diversity of the small omnivores and herbivores decreased during the stable high water period and increased during the fluctuating water periods. The diversity of both carnivore groups increased during the stable period and decreased during the fluctuating periods . Thus the diversities of different guilds within the overall fish community responded differently to environmental change.

More research is needed on this question of which taxonomic groups to sample. Information on the effects of specific pollutants on specific groups in aquatic communities will probably be available only after a national monitoring effort has been underway for some time. In this sense field workers in a biomonitoring program should be capable of conducting on-site research projects.

SUMMARY AND RECOMMENDATIONS

1. In a biological monitoring program, what little research there is indicates that several guilds, taxonomic groups, or trophic levels should be studied instead of just one group.
2. Diversity need not be computed across all these groups as the abundances of different phyla are generally not comparable numerically or conceptually.
3. Productivity - based measures of diversity are impractical in a biomonitoring program.
4. Diversity should be computed separately within each of the groups; each group diversity should be monitored and studied.
5. The information collected by field workers in a biomonitoring program will be valuable for its research purposes as well as its applied purposes.

6. BIOMASS VERSUS NUMBERS OF INDIVIDUALS

In studying a biological community an investigator must decide whether to use numbers of individuals or biomass in computing diversity. At first glance the problem seems a trivial one: if n_i is the number of individuals in species i and m_i is the total biomass of the species then these two quantities are related to each other at any given time by the relation

$$\frac{m_i}{\bar{m}_i} = n_i$$

where $\bar{m}_i$ is the mean biomass per individual of species i. It would seem then that biomass-diversity and individuals-diversity would be closely related measures in a community.

In fact, a biomass-diversity and individuals-diversity may behave very differently from each other. Field studies by Wilhm (1968) and Kushlan (1976) have shown that knowledge of trends in biomass-diversity is generally insufficient to predict trends in individuals-diversity, and vice-versa. The two statistics yield complimentary information about the aquatic life; an investigator may wish to gather the data to compute both. In biological monitoring the critical task is to interpret a diversity change in terms of an impact on the community. Knowledge of both biomass- and individuals-diversity will aid an investigator in this interpreting task.

One reason why these two diversity measures are different is the fact that the mean biomass per individual of species i, $\bar{m}_i$, varies from one species to the next. The relative abundance of the biomass of species i, therefore, may be substantially greater than or less than the relative abundance of individuals of species i:

$$B_i = \frac{m_i}{m} = \pi_i \frac{m_i}{m\pi_i} = \pi_i \frac{m_i n}{m n_i} = \pi_i \frac{\bar{m}_i n}{m} ,$$

where B_i is relative abundance of biomass; π_i is relative abundance of numbers; me is total community biomass; n is total numbers of individuals in the community. The $B_i < \pi_i$ when $\bar{m}_i n < m$ and $B_i > \pi_i$ when $\bar{m}_i n > m$. Both these cases are biologically meaningful; the B_i values for all species $i = 1,2,\ldots, s$ will be greater than or less than the π_i values depending on the corresponding $\bar{m}_i$ values. This means that the community biomass vector $\underset{\sim}{B} = (B_1, B_2, \ldots, B_s)$ may be practically unrelated to the individuals vector $\underset{\sim}{\pi} = (\pi_1,\pi_2,\ldots,\pi_s)$, other than the fact that both contain the same number of elements and that all the elements in each sum to unity. Any diversity index for which evenness or equitability is important will likely be different for both $\underset{\sim}{B}$ and $\underset{\sim}{\pi}$.

Another important problem arises from the fact that the mean biomass per individual, $\bar{m}_i$, may vary through time for any given species. To complicate matters the changes seen in $\bar{m}_i$ are often not related to the changes in numbers of individuals n_i. Individuals of a species could become larger in size but less abundant; thus n_i would decrease when $\bar{m}_i$ was actually increasing. To illustrate the effects of this process on ecological diversity consider a community of n total individuals and m total biomass. The relative abundance vector using numbers would be

$$\underset{\sim}{\pi} = \left(\frac{n_1}{n} \; \frac{n_2}{n} \ldots \frac{n_s}{n} \right) = (\pi_1 \; \pi_2 \ldots \pi_s).$$

Similarly, the relative abundance vector using biomass would be

$$\underset{\sim}{B} = \left(\frac{m_1}{m} \frac{m_2}{m} \ldots \frac{m_s}{m} \right) = (B_1 \; B_2 \ldots B_s).$$

We assume that both vectors have their elements arranged in order of relative abundance, that is

$$n_1 \geq n_2 \geq \ldots \geq n_s \text{ , and } m_1 \geq m_2 \geq \ldots \geq m_s.$$

Then suppose the biomass of species 1 decreases by an amount over a time interval, while the biomass of species 2 increases by that same amount :

$$\underset{\sim}{B}' = \left(\frac{m_1 - \varepsilon}{m} \quad \frac{m_2 + \varepsilon}{m} \quad \frac{m_3}{m} \ldots \frac{m_s}{m} \right) .$$

This would mean that the diversity of $\underset{\sim}{B}'$ had become larger than that of $\underset{\sim}{B}$ according to the criteria of Patil and Taillie (1976) for diversity indexes. But it is entirely possible that species 1 could increase in numbers during the same interval, with the average mass per individual declining. The diversity of the vector $\underset{\sim}{\pi}$ would then decline; that is, if

$$\underset{\sim}{\pi}' = \left(\frac{n_1 + k}{n+k} \quad \frac{n_2}{n+k} \ldots \frac{n_s}{n+k} \right) ,$$

then the diversity of $\underset{\sim}{\pi}'$ is less than that of $\underset{\sim}{\pi}$ if an evenness-sensitive index is used. In general, if the diversity of one of the vectors $\underset{\sim}{B}$ or $\underset{\sim}{\pi}$ changes, the other vector may not change in the same fashion.

Very little attention has been paid to this question of biomass versus numbers by ecologists. The underlying problem is that <u>growth</u> and <u>reproduction</u> are different processes in living things. These processes are affected differently by the various environmental factors. In particular, there seem to be no studies which have looked at specific pollutants and distinguished their effects on biomass- and individuals-diversity.

Wilhm (1968) gives empirical evidence that biomass- and individuals-diversity may change in different fashions. Wilhm studied a benthic macroinvertebrate community in a small Tennessee spring. Essentially two habitats existed in the spring for benthic organisms; one area of the spring was choked with vegetation and the other area was open. Wilhm sampled each of the two habitats monthly; the benthic organisms were sorted by species, counted, and weighed.

Wilhm stated that "differences were noted when biomass units were used instead of numbers." In the open areas of the spring, one species tended to increase its total biomass and decrease the biomass diversity. That same species also increased its mean weight per individual, so that its numbers did not increase very much. As a consequence, individuals-diversity tended to be higher in the open areas. In the vegetation-choked areas, the biomass- and individuals-diversity changed in the same directions. However, individuals-diversity showed much more pronounced fluctuations, while the biomass diversity in the choked area remained relatively constant. Finally, Wilhm noted that biomass per individual tended to vary monthly within many species.

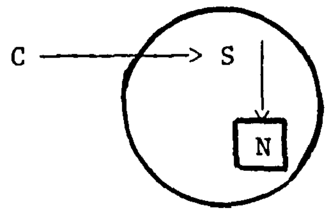
Kushlan (1976) has recently reported more differences in individuals- and biomass-diversity trends, this time in the fish community of the Everglades marshes. Kushlan's study suggests that both biomass- and individuals-diversity should be obtained when possible, for they both contain important and complimentary information about changes in a biological community. Kushlan found that during a several year period of stable environmental conditions, individuals-diversity tended to increase among the fish. However, biomass-diversity decreased, and the mean weight per fish increased over the same period. These trends all reflected a shift of the fish community to a large predator dominated system; stable water levels allowed large carnivore fish to thrive in the community. Kushlan states: "The different pattern of biomass diversity shows that the changes were more complicated than the mere redistribution of relative abundances."

Kushlan paid particular attention to interpreting the diversity changes in the Everglades fish community. He separated the fish into trophic groups (see section) and followed the diversity trends of each group separately. He measured the changes in average fish size as well as kept track of the species composition. In this way he was able to sort out the ecological processes or events that were taking place in the community which were causing the community diversity to shift.

What ecological processes cause changes in $\bar{m}_i$? The mass of an organism increases through uptake and assimilation of materials (nutrients) and decreases with processes such as respiration and excretion. Numbers of individuals in a population are affected by births, deaths, immigration and emmigration. Any environmental perturbation which affects these processes differentially will probably cause discrepancies between the biomass- and the numbers-diversity in the community.

Almost nothing is known about the relationships between numbers and mass of organisms. What little is known comes from research on populations of single cells. Williams (1971) proposes this concept of a cell:

> The cell comprises two basic portions, a synthetic portion and a structural/genetic portion.
>
> 1. The synthetic protion (s) increases by uptake of externally available nutrient (c).
> 2. The structural/genetic portion increases in turn from the materials in the synthetic portion.
> 3. Total cell mass $M = S + N$
> 4. The cell divides into d daughter cells only when the N-portion of the cell has become d times its initial size.



This means that the size of the S portion of the cell, and hence the overall size of the cell at division, is not uniquely determined. Results of cell growth experiments indicate that the N and S portions of cells are only loosely coupled. The implication is that growth and reproduction in populations are loosely related processes. These statements hold true for single cell populations; the statements may or may not be true for multi-celled organisms.

Further research will be needed to delineate the effects of specific environmental pollutants on biomass- and individuals-diversity, as well as to delineate the relationships between growth and reproduction in communities. Investigators will then be able to make decisions between use of biomass or use of individuals on the basis of which index is the most sensitive to the specific pollutant. For instance, in single cell populations the process of reproduction is affected by changes in temperature far more than growth is affected (Williams 1971). It is possible then that individuals-diversity may be a more sensitive indicator of thermal pollution than biomass-diversity, but this question will need testing. The data from a biomonitoring program in which both biomass and numbers are used will be invaluable in addressing these problems.

Summary and recommendations

1. Theory as well as field studies by Wilhm (1968) and Kushlan (1976) indicates that biomass-diversity and individuals-diversity can often behave in different fashions in a biological community.

2. The differences in response of these two diversity measures is largly due to changes in $\bar{m}_i$, the average mass of an individual of species i. Shifts in species composition of a community can also cause discrepancies between biomass- and individuals-diversity.

3. The quantity $\bar{m}_i$ is affected by two fundamentally different processes: growth and reproduction.

4. Growth and reporduction are probably loosely related, and are affected differentially by various environmental factors.

5. An investigator in a biomonitoring program should compute both biomass diversity and individuals diversity if possible. The investigator should also keep track of $\bar{m}_i$ for each species as well as the community species composition. These efforts will:

    a) aid in the task of interpreting biological impact of pollutants, and

    b) be invaluable in answering basic ecological questions on growth and reproduction.

7. ARTIFICIAL SUBSTRATES VERSUS NATURAL SAMPLING

Artificial substrates can only be used for those aquatic organisms that will colonize various surfaces by attaching, rooting, or burrowing. This rules out fish, zooplankton, and phytoplankton that do not attach themselves to substrates. Various types of algae, such as diatoms, and bottom dwelling organisms can be sampled with artificial substrates.

Several considerations must be weighed in deciding to use an artificial substrate for biomonitoring:

1) The technique must be scientifically defensible, that is, the effects of pollution on the substrate organisms should be comparable with the effects on the natural community. The investigators must determine that the artificial substrates are not propagating "artificial communities."

2) The convenience or savings on cost must be substantial enough to warrant using an artificial substrate instead of some other sampling method. This consideration, however, must be subservient to 1).

3) The colonization time will have to be taken into account. An unutilized substrate will require a certain amount of time before enough species have established themselves for a good sample. This colonization period will cause delays in the gathering of the data.

Diatoms can be sampled with ordinary glass microscope slides that are placed in the water for two weeks. This method was developed by R. Patrick and has been extensively tested (Patrick et al. 1954; Patrick 1963; Patrick 1968). The costs of this method are minimal and the colonization time (about 14 days) is reasonable for most purposes. J. Cairns has described a modification of the sequential sampling technique for estimating diversity which can be used while scanning the diatom slides with a microscope (Cairns 1968).

Benthic organisms can be sampled with baskets or trays of bottom materials such as rocks, mud, and sand (Cummins 1962, Cooke, 1956, Wene and Wickliff 1940), or with mats of artificial moss made out of string (Glime and Clemons 1972). These artificial substrate techniques for benthic organisms have several drawbacks. First, a long colonization time of up to 30 days may be necessary (Wene and Wickliff 1940). Second, the number of individuals on the artificial substrates tends to be less than on the natural substrate (Glime and Clemons 1972). Third, the techniques have not been tested as biomonitoring tools. Finally, there are effective alternatives in sampling methods available for the natural sampling of benthic organisms (ERCO report, Cairns 1971).

Summary and Recommendations

1. Artificial substrate sampling methods are available for periphyton (particularly diatoms) and benthic organisms.
2. The sampling of diatoms with glass slides is a technique that has been well developed and should play a prominant role in a biomonitoring program.
3. Artificial substrates are not a recommended technique for use with benthic organisms.

8. SAMPLING MANY HABITATS VERSUS SAMPLING FEW HABITATS

The habitat of a species is the environment of that species, as characterized primarily by physical and chemical qualities rather than position within a community (Whittaker 1972). For instance, a lake might have several habitats for benthic organisms such as rocky areas, sandy areas, and muddy areas. Whittaker defines the diversity found within a specific habitat as the alpha diversity; under natural conditions the alpha diversity is essentially the "species packing level" for that habitat. Beta diversity, according to Whittaker, is the between habitat diversity of an area. Beta diversity will determine the rate that the community composition will change as an observer travels from one habitat to the next.

A biomonitoring sample typically will be concerned with the alpha diversity of a given habitat. Beta diversity is mostly a concept of ecological theory and has been actually measured for very few communities (mostly terrestrial). The effect of pollution on beta diversity in aquatic systems is virtually uninvestigated at this time. If data is collected for many different habitats in a biomonitoring program, the data will be a valuable contribution to basic ecological research on beta diversity.

The question as to how many different habitats will be sufficient for biomonitoring purposes will have to be determined with on-site studies. Each lake or river has a particular set of environmental conditions, habitat combinations, and pollution problems; the investigators should study many habitats at first to get an idea of species compositions and to get an overall view of the sort of changes to expect in the diversities. If it turns out that the species compositions are similar for several habitats or that communities within different habitats respond similarly to changes in water quality then sampling only one of those habitats would probably be sufficient. If, however, the communities within habitats are quite different in their species composition or responses to pollution then many habitats will have to be monitored.

Allan (1975) studied the distributional patterns and diversity of benthic insects in a Colorado stream; this study contains some encouraging results for biomonitoring. Allan found that most of the species diversity of these insects was found within habitats rather than between habitats at the microhabitat level. This may indicate that investigators in a biomonitoring program will be able to be somewhat broad in their designations of habitats for sampling purposes. However, more information such as this for many different bodies of water is needed to form definite conclusions about habitat monitoring.

Summary and Recommendations

1. Investigators in a biomonitoring program should study many different habitats at first to achieve an overall view of the environmental problems peculiar to the specific body of water.
2. Data gathered for many habitats at once will constitute new knowledge for both basic and applied ecology.

9. THE IMPORTANCE OF TAXONOMY

Identification of species is perhaps the major technical problem in sampling for community diversity. Two groups of organisms, the diatoms and the benthic insects, are considered promising organisms for use in diversity monitoring, because of their ease of collection, large numbers of species, and sensitivity to water quality.

Both these groups, however, are notoriously hard to identify. Keying out a single individual to species can be a time consuming challenge to a PhD systematist. The alternatives to species identification are of mixed promise:

One idea is to simply not identify the organisms to species, but key them out to a higher taxonomic level such as genus or family. The diversity measure would then be computed using a vector of relative abundances of genera or families. According to Resh and Unzicker (1975) this approach is of dubious value. Resh and Unzicker point out that much of the variation in pollution tolerance is within genera rather than between genera for benthic insects. They found that out of 89 genera for which water quality tolerances ("tolerant", "facultative", or "intolerant") have been established for more than a single species, the component species fell into different tolerance categories in 61 of those genera.

Though Resh and Unzicker were specifically examining the "indicator species" method of water quality monitoring, their conclusions about species identification apply to diversity monitoring. Important community shifts in abundance at the species level could take place and not be detected if only genera figures were available for computing diversity.

The second alternative to species identification is to use the sequential sampling method developed by J. Cairns (Cairns et al. 1968). In this method individual specimens are taken sequentially and at random from a sample; each specimen is compared with the previous one as to whether it is the "same" or "different." The more times the comparisons are "different" for a given sample, the greater the biological diversity. Cairns proposed using #"runs"/#specimens as a diversity index; the sampling technique is now known to yield an estimate of the Simpson index (see Patil and Taillie 1976 and the ERCO report). According to Cairns this method of assessing the biological consequences of pollution would be useful for preliminary surveys or when results of some sort must be made available without delay.

There are some drawbacks to this sampling method. One drawback is that the data gathered in this fashion cannot be used for anything else. Another drawback is that changes in community composition would not be evident. Additionally, the investigator could not monitor changes in abundances of "indicator species" with this method. Finally, the Simpson diversity index has disadvantages when there are a large number of species (as is likely the case with diatoms or benthic insects), or when a few species are dominant in the community (see ERCO report for discussion of this). Taxonomic effort will be required if the investigator wishes to use another diversity index besides Simpson's.

Nonetheless, this is an easy and rapid method of sampling for diversity, and Cairns gives convincing data that indicate that the method can be used by non-biologists. Cairns had a non-biologist and a biologist both estimate the number of species of benthic organisms that were in several collections;the estimates of the two did not differ significantly. The method was also employed to assess pollution impacts above and below an outflow; Cairns' index showed the characteristic diversity decline for experiments of this sort. More field testing will be needed, but this method should have a significant role in a biomonitoring program.

Detailed community knowledge will be necessary many times, however, as the task of interpreting pollution impacts requires more information than a diversity figure . One possibility is that B.S.-level personnel could be trained to identify the species found in a local area within a few month's time. Another possibility lies in the perfection of optical identification devices (Cairns 1972). Much work will be necessary to carry out these possibilities.

Summary and Recommendations

1. Identifying the organism only to family or genus is not a recommended alternative to obtaining species diversity.
2. The sequential sampling method of J. Cairns is a rapid method of estimating diversity that should prove especially useful for preliminary surveys. Studies should be done on the effectiveness of this method for routine monitoring and on the effectiveness of training non-biological personnel to use this method.

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PART B

LITERATURE REVIEW OF COMMUNITY DIVERSITY AND BIOMONITORING

PART B

Section I

AN ANNOTATED BIBLIOGRAPHY OF COMMUNITY DIVERSITY AND ITS APPLICATIONS TO BIOLOGICAL MONITORING OF WATER QUALITY

Section II

A SELECTED LIST OF PUBLICATIONS ON COMMUNITY DIVERSITY

Section 1

AN ANNOTATED BIBLIOGRAPHY OF COMMUNITY DIVERSITY AND ITS APPLICATIONS TO BIOLOGICAL MONITORING OF WATER QUALITY

LITERATURE REVIEW OF COMMUNITY DIVERSITY AND BIOMONITORING

I. INTRODUCTION

Human use of aquatic ecosystems invariably creates impacts on those environments, if even only slight impacts. Though such human use must continue, careful management of the use is necessary as water is a finite resource and a limiting factor in many parts of the globe. Much attention has been given recently to the question of assessment of impact on water quality, and also the assessment of impact on water as a habitat for living things.

The diversity of an aquatic community is a measure of the variety of the types of organisms which thrive there. The species which characterize a lake or a stream are found there due to a vast assortment of ecological forces, including nutrient availability, colonizing ability, co-evolution, competition, environmental stability or predictability, and predation. In general, a community, if left undisturbed, will become more complex, that is, acquire a greater variety of species over an evolutionary time period. Human use of acquatic systems often perturbs the environment of these organisms. The resulting extinctions and changes in abundance of species will be reflected in a change in the diversities of the communities.

Use of ecological diversity in biomonitoring then will require an integration of a wide spectrum of scientific literature. Some of the topics of relevance to the use of diversity are niche theory and species packing, evolution, mathematical formulations, statistical methods, field sampling methods, and the field biology of aquatic systems. To aid in locating publications of relevance to diversity, this bibliography has been compiled from a variety of sources in different fields.

The bibliography is presented in two parts. The first part provides an annotated bibliography of ecological diversity and its applications to biological monitoring. Approximately fifty publications are listed in this first part. For each, a summary has been given of the results, methods, or discussions that will be of interest for biomonitoring applications. The publications have been selected for inclusion in this part on the basis of whether they will be of primary importance to the current project.

The entries in the annotated bibliography can be categorized into three basic topics. First, approximately ten publications have been included which delineate the current state of ecological theory in community diversity. They cover the time-stability-diversity hypotheses, species packing, and species abundance modeling among other topics. This basic research should be examined carefully by investigators interested in applying diversity measures to their problems. This theoretical work is needed to draw conclusions about what a diversity index can or cannot reveal about an ecological community.

The second topic is applied ecological diversity, which includes papers directly concerned with biomonitoring. These publications often report studies in which a community is sampled, data are gathered, a diversity index computed, and conclusions are drawn from the results. Such work is valuable to biomonitoring for reasons of data, field sampling methods, or basic field biology of aquatic organisms of interest.

The third topic in the annotated bibliography concerns the statistical treatment of data. This category includes mathematical formulations, properties and implications of different diversity indices, and problems of sampling and estimation.

The publications in the annotated bibliography have been numbered, and at the end of this first part, they are listed by number under the topic(s) to which they are relevant. The three topics are identified as: (I) ecological theory and concepts; (II) ecological applications including biomonitoring; and (III) statistical methodology.

The second part, which comes after the annotated bibliography, consists of a selected list of publications on ecological diversity. Over three hundred entries appear here. These have been included on the basis of their general interest to the broad subject of community diversity. It is hoped that this collection of titles will aid present investigators and others who are attempting to cope with the vast array of different journals in which diversity information is published.

The authors wish to note in passing that the number of papers directly concerned with biological monitoring is small compared with the numbers in other diversity areas. This list calls attention to the paucity of data and field studies, which directly test water quality monitoring hypotheses (with notable exceptions in the work of R. Patrick and J. Cairns). The authors would welcome any additional information, unpublished or otherwise, which would relate to monitoring problems.

ANNOTATED BIBLIOGRAPHY

1. ALLAN, J. D. 1975.

The distributional ecology and diversity of benthic insects in Cement Creek, Colorado.

Ecology, 56:1040-1053.

A brief review: Distributional patterns and species diversity of benthic insects in an alpine stream in Colorado were investigated on several levels of spatial scale, from faunal replacement over 1000 vertical m to microdistribution within the stony substratum. Most Most of species diversity as measured by H' was found within habitats rather than between habitats at the microhabitat level.

A comment: This material will be useful for biomonitoring purposes, as it gives general information on the ecology of benthic insects and sampling methodology. The within-and-between-habitat concept is a specific case of a heirarchial classification system.

2. BALL, R. C. and J. G. BAHR. 1975.

Intensive survey: Red Cedar River, Michigan.

In River Ecology.

A brief review: This is an integrated study of a Michigan watershed, including abiotic ecosystem components such as water chemistry, climate, discharge, and biotic components such as periphyton, aquatic macrophytes, macroinvertebrates, and fish. The study includes data on benthic diversity; the authors conclude that information theory indices of species diversity appear to be one of the more sensitive measures of changes in community structure caused by human perturbation.

A comment: The ERCO report cites a handful of contradictory studies on the usefulness of diversity indices, concluding that it is highly doubtful whether diversity indices in their present form will serve as useful indicators of water quality. This is a drastic conclusion on the basis of such a small sample of the literature. Revised conclusions will have to take into consideration research such as this of Ball and Bahr.

3. BARBOUR, C. D. and J. H. BROWN. 1974.
Fish species diversity in lakes.
Amer. Nat., 108:473-489.

A brief review: Barbour and Brown use stepwise multiple regression to obtain preliminary insights into the environmental parameters which influence the number of fish species occurring in lakes. Among their results: for a sample of 70 lakes and inland seas from throughout the world, surface area and latitude account for about one third of the variability in fish species diversity.

A comment: This is an investigation of fish species diversity on a global scale, with a view toward confirming a prediction of MacArthur and Wilson's island biogeography model. There may be useful material here for biomonitoring purposes in terms of methodology: a problem with using diversity in biomonitoring is to statistically "filter" the naturally-caused diversity fluctuation from the human caused fluctuation.

4. CAIRNS, J. et al. 1968.

The sequential comparison index--a simplified method for non-biologists to estimate relative differences in biological diversity in stream pollution studies.

J. Water Pollution Control Fed., 40:1607-1613.

A brief review: A simple and rapid method is reported by which a non-biologist can estimate species diversity of benthic invertebrates or diatoms for the purpose of water quality monitoring. Individual specimens are taken sequentially and at random from a sample; each specimen is compared with the previous one. The more "runs" for a given number of specimens, the greater the biological diversity. Examples of use of this technique are reported for diatoms and invertebrates collected at varying distances from a sewage outfall.

A comment: The problem of taxonomic training is one of the most critical in using diversity indices in water quality monitoring. The organisms considered most suitable for biomonitoring use are diatoms and benthic invertebrates, as large samples are easily collected and these organisms are sensitive to changes in water quality. However, keying these organisms to species can be a taxonomic challenge to a trained Ph.D. biologist. Dr. Cairns' sequential sampling technique is a major alternative to laborious and difficult keying work that should be considered when time, cost, or personnel limit a water monitoring effort. Cairns proposes using # runs/# specimens as a diversity index; the sampling technique has been subsequently shown to be an estimate of the Simpson's diversity index (see Patil & Taillie, 1976, and ERCO report). The drawback of this method is that the data so gathered cannot be used for anything else. A diversity index presented without any other information may conceal changes in species composition of the community when it is compared to a value computed for the community at an earlier time. To monitor changes in species composition, changes in abundances of "indicator species," or changes in diversity indices other than Simpson's same taxonomic effort will be required.

5. DeBENEDICTIS, P. A. 1973.
On the correlations between certain diversity indices.
Amer. Nat., 107:295-302.

A brief review: DeBenedictis points out that positive correlations are to be expected between a number of different diversity indices due to the ways in which the indices are defined. He notes that obtaining the expected values of the correlation coefficients would be impossible without postulating probability distributions to describe the indices. In a mathematical appendix, he derives an expected correlation coefficient between S (species number) and H' (Shannon-Weiner).

A comment: The main argument is rather self-evident; however, this paper should be examined along with the work on correlations between indices which was done by ERCO. (ERCO used data.)

6. EWING, M. S. and T. C. DAVIS. 1970.
Algal community structure in artificial ponds subjected to continuous organic enrichment.
Amer. Mid. Nat., 83:565-582.

A brief review: Nine artificial ponds, each subjected to one of three experimental treatments of organic enrichment, exhibited no significant differences in mean concentration of dissolved nitrate, nitrite, amonia, or phosphate. In general, algal species diversity was not positively correlated with nutrient concentrations.

A comment: This study was cited by ERCO as providing little support for the use of diversity in water quality monitoring.

7. GLIME, J. M. and R. M. CLEMONS. 1972.
Species diversity of stream insects on fontinalis spp. compared to diversity on artificial substrates.
Ecology, 53:458-464.

A brief review: Two types of artificial mosses (string and plastic) were compared with Fontinalis spp. for their insect inhabitants. These communities were sampled on six dates at eight stream sites and compared by community coefficients, information theory analysis, and rank correlations. The number of individuals found on artificial substrates was substantially less compared with Fontinalis, leading the investigators to conclude that these substrates provide a poor substitute for Fontinalis. However, there was a high degree of correlation of insect species among the substrates, and species diversities of the individual samples were not significantly different when comparing string and moss.

A comment: The moss sampling method was: "pulling a handful from the stream and putting it in a jar." This sampling method seems reliable according to previous work done by J. M. Glime. For the purposes of biomonitoring, there would be no information or cost benefit in substituting one of these artificial substrates for sampling purposes.

8. LLOYD, M., R. F. INGER, and F. W. KING. 1968.
On the diversity of reptile and amphibian species in a bornean rain forest.
Amer. Nat , 102:497-515.

A brief review: The diversity of a tropical reptile and amphibian community is investigated with an intensive collecting effort carried out over an entire year. "Equitability" of species is lower than expected for the tropics, which leads Lloyd et al. to re-examine the assumption that the rain forest floor environment is relatively constant and predictable. Conceivably, intense rains which cause raging floods in breeding streams might often result in catastrophic mortality to the herptiles.

A comment: This massive survey uses Pielou's recommendations for estimating the Shannon index of diversity. The investigators also partition the data heirarchially into families, genera, and species. It would have been interesting if they had published computations of diversity on the basis of biomass in addition to the number of individuals.

9. LLOYD, M., J. H. ZAR, and J. R. KARR. 1968.
On the calculation of information--theoretical measures of diversity.
Amer. Mid. Nat., 79:257-272.

A brief review: Computing formulae are given, along with an example, to show that the Shannon and Brillouin indices of diversity can be calculated with equal ease. A table is presented for rapid calculation of both indices, as well as Basharin's standard error.

<u>A comment</u>: Pocket scientific calculators and computers have eliminated computing difficulties in information-type diversity indices. Nonetheless, this paper is interesting for its discussion of the use of the indices themselves. The paper additionally gives examples of use with field data from Sander's (1936) Quaker Run Valley bird censuses.

10. <u>LONGUET-HIGGINS, M. S. 1971</u>.
On the Shannon-Weaver index of diversity, in relation to the distribution of species in bird censuses.
Theor. pop. Biol., 2:271-289.

<u>A brief review</u>: Longuet-Higgins investigates the relationship of relative abundance distributions (Dirichlet series, broken-stick, gamma) to the Shannon information measure of diversity. The log-normal distribution is also studied; it is shown that if the distribution is not truncated that the diversity H is given by:

$$H = \log S - \frac{1}{2}\sigma^2,$$

where S is the number of species in the community and σ^2 is the variance of the distribution.

<u>A comment</u>: Use of log-normal curve for large assemblages of species such as are found in diatom studies is an alternative to using a diversity index. This paper helps clarify the relationship between the two methods of representing the data.

11. <u>MacARTHUR, R. 1972</u>.
<u>Geographical Ecology</u>.
New York: Harper and Row. 269 pp.

A brief review: This is a book on patterns of distribution and abundance of species. There are chapters on climates on a rotating earth, competition and predation, economics of consumer choice (optimal feeding, geography of species classification, island patterns, species distributions, patterns of species diversity, comparisons of temperate and tropics, the role of history.

12. MacARTHUR, R. 1970.

Species packing and competitive equilibrium for many species. Theoretical Population Biology, 1:1-11.

A brief review: This is an expanded version of MacArthur (1969) with added insights and easier readability.

13. MacARTHUR, R. 1969.

Species packing, and what interspecies competition minimizes. Proc. Nat. Acad. Sci., 64:1369-1371.

A brief review: MacArthur proposes a model of many species competing for a gradient of renewing resources. Near equilibrium the model is essentially the same as the Volterra competition model. MacArthur shows that a quadratic expression of the species abundances, X_i's, is minimized at competitive equilibrium. With certain restrictions the quadratic expression can be shown to be a weighted squared deviation of available production of resources from species harvesting abilities. An environment of renewable resources will hold an additional species if by adding that species the quadratic expression is minimized further.

A comment: The concept of diversity will be of no use to ecologists interested in basic research unless it can be "explained" or "predicted" in terms of fundamental biological laws. The very definition of 'ecology' specifies this unification of life and natural laws: the definition is that ecology is the study of organisms in relation to their environment. Diversity will be unimportant to ecologists unless its dependence on environment is clarified. MacArthur's work on species packing is an important step in that direction, even though the assumptions in his models are very restrictive.

14. MAY, R. M. 1974.

Stability and complexity in model ecosystems.

Princeton: Princeton University Press.

A brief review: The relationship between complexity of interconnections in a food web and stability is examined using mathematical models of multispecies communities. The statement that increased diversity in an ecological system leads to increased stability does not appear to be a mathematical consequence in community models. Environmental fluctuations theoretically are apt to put a limit to niche overlap among competing species.

15. MAY, R. M. 1975.

Patterns of species abundance and diversity. In Diamond, J. M., and M. L. Cody (eds.) 1975.

Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Mass.

A brief review: With a theoretical argument May shows that for large assemblies of species, a lognormal pattern of relative abundance may be expected, and that Preston's canonical hypothesis is an approximate but general mathematical property of the lognormal distribution. Ecological mechanisms which would lead to the broken stick and log series distributions are also examined. It is shown that many common measures of species diversity tend not to distinguish these relative abundance distributions if the total number of species in the community is small.

A comment: R. Patrick fits lognormal curves to her diatom data; other investigators use diversity indices in biomonitoring work. This paper sheds light on the relation between diversity indices and relative abundance distributions.

16. PATRICK, R. 1963.
The structure of diatom communities under varying ecological conditions. Ann. New York Acad. Sci., 108(2):359.

A brief review: Patrick uses the technique of fitting a truncated log-normal curve to species-abundance data to compare different diatom communities.

A comment: One of her quotes from this paper is enlightening: "It is only as a result of thorough and continuous study of an environment and the species living in it that one can venture to describe the quantitative changes in the natural environment by changes in the quantitative abundance of specific kinds of species."

17. PATRICK, R. 1968.
The structure of diatom communities in similar ecological conditions. Amer. Nat., 102:173-183.

A brief review: Patrick reports results of experiments which were designed to determine the degree and kind of variability in the structure of diatom communities that one might expect under very similar ecological conditions. Species composition, Shannon diversity measure, and the structure of the truncated log-normal curves were very similar in all the communities.

A comment: This surprising lack of variability of diversity in several slide-colonizing experiments would support the use of her diatom methods in a biological monitoring program.

18. PATRICK, R., J. CAIRNS, and S. S. ROBACK. 1967. An ecosystematic study of the fauna and flora of the Savannah River. Proc. Acad. Nat. Sci. Phila., 118:109-407.

A brief review: This is a report of a program which was designed to determine the communities of aquatic organisms living in the Savannah River in the vicinity of the Savannah River Plant of the Atomic Energy Commission, and the ecological characteristics of the environment in which they are found.

A comment: This massive study contains much information on the basic ecology of the flora and fauna of a large river. The studies were designed to monitor river changes due to plant operation, but the results of value to the monitoring program were not reported in this paper.

19. PATRICK, R., B. CRUM, and J. COLES. 1969.

Temperature and manganese as determining factors in the presence of diatom or blue-green algal floras in streams.

Proc. Natn. Acad. Sci., 64:472-478.

A brief review: An average temperature of 34° to 38°C results in a shift of dominance in the algal flora from diatoms to blue-green algae. Furthermore, a blue-green and green algal flora of species typically found in organically polluted water is favored if the manganese content is a few parts per billion.

A comment: This paper contains useful information for applied workers who are studying algae in rivers or streams.

20. PIELOU, E. C. 1975.

Ecological diversity.

New York: John Wiley & Sons.

A brief review: This is a textbook on concepts and methods in ecological diversity. There are chapters on indices of diversity and evenness, species abundance distributions, testing hypotheses about species abundance, diversity and spatial pattern, diversity on environmental gradients, local and global determinants of diversity.

A comment: This is an indespensable reference for applied diversity work.

21. PIELOU, E. C. 1966.

Shannon's formula as a measure of specific diversity: Its use and misuse.

Amer. Nat., 100:463-465.

A brief review: Pielou explains the difference between the uses of Brillouin's diversity formula and Shannon's formula. Brillouin's formula gives the true diversity per individual in a finite collection; there is no sampling error. Shannon's formula is used when the community is too large for all its members to be counted. The formula must be estimated and there is a sampling variance. Pielou points out that there are pitfalls to simply plugging N_i/N values into Shannon's formula from a field sample.

A comment: It is important that field workers understand the statistical methodology of use of information diversity measures if these measures are to be a part of a biological monitoring program.

22. PIELOU, E. C. 1966.
The measurement of diversity in different types of biological collections. J. Theoret. Biol., 13:131-144.

A brief review: Information content may be used as a measure of the diversity of a many-species biological collection. The diversity of small collections all of whose members can be identified and counted, is defined by Brillouin's measure of information. With larger collections, it becomes necessary to estimate Shannon's measure of diversity. Different methods of estimation are appropriate for different types of collections.

A comment: This paper contains important statistical procedures with examples for those who use information--theoretic measures of diversity.

23. SAGER, P. E. and A. D. HASLER. 1969.

Species diversity in lacustrine phytoplankton. I. The components of the index of diversity from Shannon's formula.

Amer. Nat., 103:51-59.

A brief review: Seasonal observations on the diversity of phytoplankton communities were made in three lakes in Wisconsin. Extremes in nutrient availability and morphometry in the lakes yielded a range in diversity indices calculated from Shannon's formula. Examination of the relative importance of the two components in the index indicated that the variability of the index can in large part be attributed to the component of equitability as expressed in the 10 to 15 most abundant species.

A comment: It would seem good news to an investigator who is monitoring water quality that if many rare species are missed in a sample the computed diversity index (Shannon's) will not change much. Costs of sampling and taxonomic costs perhaps could be reduced if only the 15 most abundant species of phytoplankton need be sampled. However, this paper raises an important question about use of diversity in water quality monitoring: Do we lose too much information about the ecological community by packaging the data all up in a single number? "Species of low abundance appear to have a minor effect on the (Shannon) index of diversity" (Sager and Hasler). Yet, environmental stress of pollution is likely to have major effects on those species of low abundance.

24. WENE, G. and E. L. WICKLIFF. 1940.

Modification of a stream bottom and its effect on the insect fauna.

Can. Entomol., 72:131-135.

A brief review: This is a report on the use of the "basket method" for studying the effects of contrasting types of stream bottoms on the insect fauna. Wire baskets were constructed and filled with various types of stream bottom materials which had been previously cleaned. The insect populations reached maximum in about a month's time.

A comment: One disadvantage of artificial substrates is the colonization time. This is the time that is needed to allow the species number on the substrate to reach a maximum equilibrium value; this colonization time can be a week or two for diatoms on glass slides and a month for benthic insects in rock baskets. Such time intervals will produce delays in a monitoring program. We would also like to see any artificial substrate method tested on-location in a biomonitoring program. This paper shows the relative ease of comparing an artificial substrate with the natural stream bottom as a habitat for benthic insects.

25. WHITTAKER, R. H. 1972.
Evolution and measurement of species diversity.

A brief review: Given a resource gradient (e.g., light intensity, prey size) in a community, species evolve to use different parts of this gradient; competition between them is thereby reduced. Using this theme, niche theory and species packing is discussed. Also, several relative abundance distributions (geometric, broken stick, log normal) are discussed in terms of the way they represent manners in which resources are divided among species. Ecological and evolutionary factors which contribute to alpha, beta, and gamma diversity are discussed.

A comment: This massive paper is poorly summed up here. It is a full-scale presentation of the ecological factors behind community diversity, and an important review of the current state of diversity-related theory.

26. WILHM, J. L. 1975.
Biological indicators of pollution.
In River Ecology, B. A. Whitton, ed.
Berkeley: Univ. of Cal. Press.

A brief review: This is a thorough review of the various types of biological indicators that have been used in water quality monitoring studies. Wilhm covers biochemical indicators, cell and tissue indicators, species toxicity tests, behavior tests, species lists and species as ecological indicators, stream zones, graphic methods of view species--abundance data, and mathematical expressions including species diversity. He concludes that until biologists agree on concentrating on a thorough analysis and development of a few standard biological techniques of analyzing water quality, biological methods will not be as widely accepted in most monitoring programs as physicochemical methods.

A comment: Wilhm's conclusion serves to emphasize the importance of diversity-related work in biomonitoring.

27. WILHM, J. L. 1968.
Use of biomass units in Shannon's formula.
Ecology, 49:153-156.

A brief review: Half of the paper is a review of previous work regarding use of the Shannon-Weiner index of diversity. Wilhm then proposes use of biomass instead of numbers based on Odum's (1959) statement that the pyramid of numbers is not very fundamental or instructive as an illustrative device because of the geometrical fact that a great many small units are required to equal the mass of one large unit. Wilhm then gives data from a benthic macroinvertebrate study. Differences were noted when biomass units were used instead of numbers of individuals in computing diversities.

A comment: Seems that very little attention has been given to the question of biomass vs. number of individuals in the ecological literature. Our initial opinion is that biomass should be used more often. Ecosystems are bound by physical laws as is the rest of nature. One of the most significant physical constraints on living things is the supply of materials. Altering an organism's environment (i.e., adding nutrient, changing temperature, adding toxins or heavy metals) affects that organism's ability to uptake and assemble materials, i.e., that organism's ability to grow. In microbial organisms, a species may have exhausted the nutrient supply and maintain a constant mass through time, but continue to divide and thus vastly increase in numbers. This is possible for larger organisms also.

28. WILHM, J. L., and T. C. DORRIS. 1968.
Biological parameters for water quality criteria.
Bioscience, 18:477-481.

A brief review: Wilhm and Dorris propose the establishment of water quality criteria by the evaluation of biological conditions existing in receiving streams. Effluents produce striking changes in the structure of the benthic macroinvertebrate community. The structure of a benthic community can be summarized clearly and briefly in diversity indexes derived from information theory. Values less than 1 have been obtained in areas of heavy pollution, values from 1 to 3 in areas of moderate pollution, and values exceeding 3 in clean water areas.

A comment: The paper cites several field studies in support of using benthic macroinvertebrate diversity in a water monitoring program. It is very readable.

29. WILHM, J. L. and T. C. DORRIS. 1966.
Species diversity of benthic macroinvertebrates in a stream receiving domestic and oil refinery effluents.
Amer. Mid. Nat., 76:427-449.

A brief review: A study was made of physicochemical conditions and benthic macroinvertebrate community structure in a stream receiving domestic and oil refinery effluents. Measures derived from information theory, diversity per individual and redundancy, were found to be more precise measures of stream conditions as reflected by benthic macroinvertebrate populations than traditional methods.

A comment: This study could serve as a model stream monitoring project. The paper contains informative discussions on the use of diversity, invertebrate sampling techniques, and physicochemical monitoring.

30. WILLIAMS, L. G. 1964.
Possible relationships between plankton-diatom species numbers and water-quality estimates.
Ecology, 45:809-823.

A brief review: Semimonthly samples from 103 scattered stations on the major rivers and Great Lakes of the United States revealed differences in kinds and numbers of dominating planktonic organisms. Diatoms dominated at these stations. Eutrophic stations generally were represented by a few species composing a large portion of the diatom population, and the density level was usually high. "Clean" stations, on the other hand, had more species composing a small portion of the total live diatom population, and the overall density was low.

A comment: This is the reporting of one of the most extensive algae monitoring efforts ever undertaken in the United States, and the results generally support using diversity of diatoms in water quality monitoring. However, the familiar diversity indices were not used in this study and the data not reported to compute the indices. The paper was written before computing "diversity" came into vogue. This investigation, along with the work of R. Patrick, would indicate that diatom diversity should play a fundamental role in a biomonitoring program.

ADDENDUM

31. ALLAN, J. D. 1975.

Components of diversity.

Oecologia, 18:359-367.

A brief review: The information theory measure $H' = -\Sigma Pi \log Pi$ is partitioned into components to allow evaluation of various contributions to total diversity. If a species collection is sampled at several microhabitats within each of several sites, we may ask whether the niche breadth of a particular species, and the diversity of the entire collection, are greater with respect to microhabitats or sites. The usefulness of these measures is discussed in the context of within-habitat and between-habitat contributions to diversity.

A comment: This paper contains much of interest to the study of heirarchial classification and diversity. Of interest to monitoring: perhaps the niche-breadth of "indicator" species could be followed in addition to following trends in community diversity. In this fashion, field workers would be better able to make conclusions about what is happening in a community being exposed to pollution.

32. BUZAS, M. A. 1972.

Patterns of species diversity and their explanation.

Taxon, 21:275-286.

A brief review: Patterns of species diversity and equitability, and the hypotheses suggested to explain them are examined in the terrestrial and marine environments, and the fossil record. Although all the hypotheses are important in explaining diversity, none of them singularly or in various combinations are sufficient to explain the observed patterns.

A comment: Diversity is such a complicated function of environmental history that most ecological theories about diversity have been inadequate so far. We would caution against use of diversity in monitoring simply on theoretical grounds, and would stress that much basic research on the effects of many aquatic environmental parameters on community diversity is needed.

33. COOKE, W. B. 1956.
Colonization of artificial bare areas by microorganisms.
Bot. Rev., 22:613-638.

A brief review: This is a review (1956) of artificial substrate techniques for a variety of terrestrial or aquatic microorganisms.

34. *CORNELL, H., L. E. HURD, and V. A. LOTRICH.* 1976.
A measure of response to perturbation used to assess structural change in some polluted and unpolluted stream fish communities.
Oecologia, 23:335-342.

A brief review: A new method for measuring structural change in sets of species which have been subjected to natural or experimental perturbation is developed and is shown to be superior to static diversity and evenness measures for this purpose. Three parameters, $H\Delta'$, $J\Delta'$, and $\bar{X}\Delta$ are shown to provide necessary and sufficient information on the severity of a perturbation as well as the uniformity of its effect on all species in the set. When positive and negative changes in species abundance are considered separately, the method sensitive to compensatory changes which are not detected by static measures. The parameters are then calculated for some data sets on polluted and unpolluted fish communities in streams in Kentucky. The notion of these three parameters as the "vital signs" of a healthy ecosystem is presented.

A comment: We are studying this paper closely.

35. CUMMINS, K. W. 1962.
An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters.
Amer. Mid. Nat., 67:477-504.

A brief review: A consideration of a large number of procedures for the collection and analysis of benthic samples, with particular emphasis on stream investigations and the importance of substrate particle size as a common denominator in benthic ecology, reveals that only certain techniques are suitable.

A comment: This is a thorough study of lotic benthic sampling techniques which will be invaluable for field workers. The paper has many references.

36. CUMMINS, K. W. 1973.
Trophic relations of aquatic insects.
Ann. Rev. Entomol., 18:183-206.

A brief review: Freshwater ecosystems of the temperate zone might be generalized as having a reasonably constant biomass of macrobenthic animals, dominated by aquatic insects, which is turning over at a rate contro;;ed primarily by temperature. Food resources are partitioned on the basis of particle size and whether active, stationary, or in suspension.

A comment: This is a detailed review of the role of aquatic insects in freshwater ecosystems.

37. DICKMAN, M. 1968.
Some indices of diversity.
Ecology, 49:1191-1193.

A brief review: The Shannon-Weaver diversity formula fails to reflect significant changes in a community's structure because it is only sensitive to changes in relative abundance of a few of the trophic levels of a community. Over two-thirds of the species encountered in a typical plankton sample had no significant effect on the index of diversity (H) calculated for that sample. To overcome this, the Shannon-Weaver formula was twice altered by redefining P_i in order to give a new index of community diversity which was sensitive to changes in community structure. P_i defined in terms of relative biomass (H_b) failed to improve the index substantially and P_i was then successfully defined in terms of relative productivity (Hp). An index of community diversity sensitive to changes in relative abundance of all the trophic levels, such as the index Hp, appears to be a necessary prerequisite to comparative community studies.

A comment: This study used diversity calculated for a whole community of many phyla and several trophic levels including bacteria, phytoplankton, and zooplankton species. Obviously, when this is done, the organisms on the lower and of the "trophic pyramid" will swamp the diversity index with their relative abundance.

Diversity seems to be most effective when applied to a community of organisms that are competing along a resource gradient (or several resource gradients). When one species in such a community is eliminated, the other species may expand their resource utilization ("niche") and increase in abundance. Such changes would be reflected in a diversity index; example communities of this type would be phytoplankton (could restrict to diatoms), zooplankton, aquatic benthic insects, or fish.

This paper does not take into account the important difference between growth and reproduction in computing the diversity of productivity: P_i was defined as pr/PR where pr was the productivity of a particular species in the sample and PR the total sample productivity; productivity was calculated by multiplying a species mean sample density and biomass times the number of times a species reproduced per year. But cell growth research has indicated that there is only a loose connection between cell mass and cell division (Williams, 1971).

38. HAMILTON, M. A. 1975.

Indexes of diversity and redundancy.

J. Water Poll. Control Fed., 47:630-632.

A brief review: This is a comment on some incorrect descriptions of the Shannon formula and the "redundancy" formula that have occurred in the literature on the structure of aquatic invertebrate communities.

39. HOWELL, F. G., and J. B. GENTRY. 1974.
Effect of thermal effluents from nuclear reactors on species diversity of aquatic insects.
In Gibbons, J. W. and R. R. Sharitz (eds.). 1974. Thermal ecology. Oak Ridge: U. S. Atomic Energy Commission Technical Information Center.

A brief review: Aquatic insect populations of thermal post-thermal, and natural streams on the Savannah River Plant site were compared according to species composition and diversity. Insect communities in the natural stream had the highest diversity indexes; communities in the post-thermal stream had intermediate diversity estimates; communities in the thermal stream had the lowest diversity estimates. In the aquatic habitats sampled, species-diversity and evenness estimates were reliable indicators of thermal stress.

40. KOCHSIEK, K. A., J. L. WILHM, and R. MORRISON. 1971.
Species diversity of net zooplankton and physiochemical conditions in Keystone Reservoir, Oklahoma.
Ecology, 52:1119-1125.

A brief review: Net zooplankton collections and physiochemical measurements were made monthly in four stations at various locations in the Keystone Reservoir, Oklahoma. Shannon's formula was used to evaluate species diversity of zooplankton. Variance values of diversity indicated only a slight gain in precision by increasing the sample size to above 400 individuals. Coefficients of correlation between physicochemical parameters and species diversity unadjusted for month and station effect were compared with adjusted coefficients.

A comment: The feasibility of using zooplankton in biological monitoring has been little studied; diatoms and benthic invertebrates have received most of the attention. This paper is a useful reference on the ecology of zooplankton.

41. MacKAY, R. J., and J. KALFF. 1969.
Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream.
Ecology, 50:101-108.

A brief review: This paper contains some information on the basic ecology of benthic insects, including the importance of substrate type to insect populations. As ERCO has pointed out in its report, a stream (or other freshwater body) should be studied year-round in a monitoring program in order to gain information on natural diversity fluctuations such as those reported in this paper.

42. MUNDIE, J. H. 1971.
Sampling benthos and substrate materials, down to 50 microns in size, in shallow streams.
J. Fish. Res. Bd. Canada, 28:849-860.

A brief review: Stream bed materials, both biotic and abiotic, in the size range 50 microns - 200 millimeters can be sampled unselectively, in shallow streams, with a simple inexpensive apparatus consisting of a box provided with an adjustable upstream inlet, and, downstream, two nets, one within the other.

A comment: The paper cites quite a few other works on benthic sampling techniques.

43. PEET, R. K. 1975.

Relative diversity indices.

Ecology, 56:496-498.

A brief review: Diversity indices are frequently applied in the form of ratios of absolute diversity to the maximum diversity possible. Regardless of whether the maximum diversity is defined to be limited by the number of species or by the number of individuals present, the resultant indices can be shown to possess mathematically undesirable qualities. All such indices are inappropriate for most ecological applications.

44. WILHM, J. L. 1967.

Comparison of some diversity indices applied to populations of benthic macroinvertebrates in a stream receiving organic wastes.

J. Water Poll. Control Fed., 39:1673-1683.

A brief review: Populations of benthic macroinvertebrates can be used to assess pollution in a stream receiving organic enrichment. Sampling stations should be established at various distances below the pollution outfall. For comparative purposes, samples should be collected in clean areas either above the outfall or at a sufficient distance downstream. Sampling methods should be the same at each station. Data can be summarized clearly and briefly with a diversity index. The index selected for use must be independent of sample size.

45. WINNER, R. W. 1972.

An evaluation of certain indices of entrophy and naturity in lakes.

Hydrobiologia, 40:223-245.

A brief review: Data from five Colorado lakes were utilized to test the usefulness of net primary productivity, seston, chlorophyll a and Secchi disc transparancy as indices of eutrophy. The four were in essential agreement as to the relative degree of eutrophication in each of the five lakes. The concept of maturity is also considered by ranking the Colorado lakes according to several maturity indices: phytoplankton diversity, zooplankton diversity, Margalef's pigment ratio, P/B ratio, and assimilation number. The relative maturity of the lakes shifts considerably, according to which maturity index one utilizes.

A comment: The paper is interesting for its report of lack of correlations between phytoplankton and zooplankton diversities. Winner concludes ". . . that measurement of diversity in one community of an ecosystem does not necessarily indicate what diversities are in other communities of that ecosystem." This indicates that several aquatic "trophic levels" should be studied instead of just one in a biological monitoring program.

CLASSIFICATION OF THE ANNOTATED BIBLIOGRAPHY ACCORDING TO THE TOPICS OF PUBLICATIONS

I. Ecological theory and concepts.

10, 11, 12, 13, 14, 15, 20, 25, 32

II. Ecological applications including biomonitoring.

1, 2, 3, 4, 6, 7, 8, 16, 17, 18, 19, 20, 23, 24, 27, 28, 29, 30, 33, 35, 36, 37, 39, 40, 41, 42, 44, 45

III. Statistical methodology.

5, 9, 10, 15, 20, 21, 22, 31, 34, 38, 43

Section II

A SELECTED LIST OF PUBLICATIONS ON COMMUNITY DIVERSITY

2. AN ALPHABETICAL LIST

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APPENDIX

PROCEEDINGS OF THE NINETH INTERNATIONAL BIOMETRIC CONFERENCE

HELD AT BOSTON, AUGUST 22-27, 1976.

AN INVITED PAPER ON:

Ecological Diversity: Concepts, Indices, and Applications

By

G. P. Patil and C. Taillie

PROCEEDINGS OF THE

9th International Biometric Conference

Invited Papers

Volume II

BOSTON
AUGUST 22-27, 1976

THE BIOMETRIC SOCIETY

ECOLOGICAL DIVERSITY: CONCEPTS, INDICES AND APPLICATIONS

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SUMMARY

This paper puts forth the view that diversity is an average property of a community and attempts to identify that property. A few intuitive cases of one community being more diverse than another are formalized into a relation, "leads to". This relation generates a diversity ordering of ecological communities which is shown to be equivalent to stochastic ordering. Indices based on species ranking are discussed. Also are characterized the indices which satisfy a weighted ANOVA formula. Application of diversity to environmental monitoring requires rapid and reliable procedures. The statistical properties of one such biomonitoring procedure are developed. Finally, certain methods for estimating the number of species are discussed.

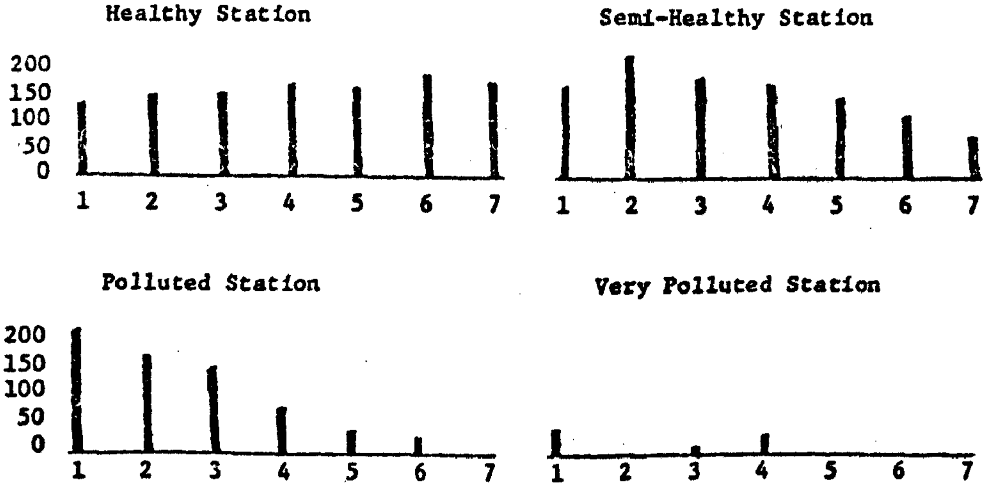
0. BACKGROUND AND INTRODUCTION

0.1 Background. "When several or many-species-populations occur together and interact with one another in a small region of space, they jointly constitute an ecological community ... The ultimate objective in studying the ecology of a community is to determine the nature and the relative importance of the factors controlling its composition; also whether, to what extent, and why, the community is changing with time. To pursue this objective it is necessary to define some measurable properties of the community as a whole. If this can be done, making it possible to write down a short list of measurements that constitute a summary description of a particular community at a particular time, it then becomes possible to make quantitative comparisons among several communities. This is a necessary first step toward an understanding of how communities function ... The diversity of natural ecological communities has never been more highly valued than they are now, as they become increasingly threatened by the environmental crisis. The purpose of measuring a community's diversity is usually to judge its relationship either to other community properties such as productivity and stability, or to the environmental conditions that the community is exposed." — E. C. Pielou [20, 21].

"Numbers alone do not make science; it is relations between numbers that are needed. Applying a formula and calculating a 'species diversity' from a census does not reveal very much; only by relating this diversity to something else — something about the environment perhaps — does it become science. Hence there is no intrinsic virtue in any particular diversity measure except insofar as it leads to clear relations." — R. H. MacArthur [16].

"For top management and general public policy development, monitoring data must be shaped into easy-to-understand indices that aggregate data into understandable forms. I am convinced that much greater effort must be placed on the development of better monitoring systems and indices than we have in the past. Failure to do so will result in sub-optimum achievement of goals at much greater expense." -- Russell E. Train [27].

"Biological monitoring plays an important role in a pollution monitoring program providing information not available through conventional physical and chemical monitoring. The structural and functional changes in aquatic communities have been used, for example, in assessing the effects of pollutants on aquatic communities. Most forms of environmental stress cause a reduction in the complexity of the system, or in other words, a simplification. From a biological point of view, this is expressed by a marked reduction in species diversity ... The most suitable means of analyzing community structure for the purposes of pollution assessment appears to be the diversity index [29]. By comparing the diversity indices between sampling stations, it is possible to determine the relative biological condition of these stations.



1. Pollution Algae 2. Tolerant Worms, etc. 3. Protozoa 4. Algae (non-pollution) 5. Clams, etc. 6. Insects, Crustacea 7. Fish

Bar graphs showing population structure of aquatic communities under different degrees of pollution. -- Cairns et al [5, 7,10].

Figure 0.1

0.2 Introduction. What is diversity? Can it be measured? If so, how? and why? This paper represents a preliminary attempt on our part to come to grips with some of these issues. Section 1 puts forth the view that diversity is an average property of a community and attempts to identify that property. Even so, diversity, like any other concept, remains elusive until it can be quantified, and so, section 2 provides some biologically realistic examples of the construction of diversity indices. Section 3 identifies the altogether too few cases in which it can be argued on intuitive grounds that one community is more diverse than another. These cases are formalized into a relation, "leads to", which in turn generates a diversity ordering of ecological communities. The ordering is shown, in section 4, to be equivalent to what is known in the statistical literature as stochastic ordering. Section 5 discusses a class of indices based on species ranking. The sampling theory for these indices poses a number of challenging and unsolved problems. For hierarchial classifications, an index which satisfies an ANOVA formula may be convenient. Section 6 characterizes the class of diversity indices which satisfy a weighted ANOVA formula. Application of diversity to environmental monitoring requires rapid and reliable procedures for estimating diversity from a sample. The statistical properties of one such procedure (Cairns sequential comparison index) are developed in section 7 with a central limit theorem of Noether as the main analytical tool. The final section 8 describes five methods for estimating the number of species in a community. The methods are applied to several data sets.

1. DIVERSITY AS AN AVERAGE PROPERTY OF A COMMUNITY

We view diversity as an average property of an ecological community. But the average of what? To an outside observer, variety is a most striking feature of a diverse community. Alfred Russell Wallace's [28] description of a tropical forest is a vivid illustration:

> If the traveller notices a particular species and wishes to find more like it, he may turn his eyes in vain in any direction. Trees of varied forms, dimensions and colours are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident. (Quotation from Hulbert [13].)

In a diverse community, such as that described by Wallace, the typical species is relatively rare and, consequently, diversity may appropriately be defined as the average rarity within the community. To make this idea precise, the concepts of "community" and "rarity" must be formalized.

For our purposes, a community may be defined as a collection of individuals grouped into species which, in turn, are ranked in order of decreasing abundance. The parameters of a community are denoted by $C = (s;\underset{\sim}{\pi})$ where s is the number of species (finite or countably infinite) and $\underset{\sim}{\pi} = (\pi_1,\pi_2,\ldots,\pi_s)$ so that $\pi_1 \geq \pi_2 \geq \ldots \geq \pi_s > 0$ are the ranked relative abundances. Necessarily $\Sigma\pi_i = 1$. Given the community, a numerical measure of rarity is to be associated with each species. Denote the rarity of the i^{th} ranked species by $R(i;\underset{\sim}{\pi})$. With these notations,

<u>Definition 1.1</u>: The <u>diversity</u> of the community $C = (s,\underset{\sim}{\pi})$ is its average rarity and is given by

$$\Delta(C) = \sum_{i=1}^{s} \pi_i R(i;\underset{\sim}{\pi})$$

where Δ is the diversity index associated with the measure of rarity R.

The concepts most fruitful for deciding upon the functional form of $R(i;\underset{\sim}{\pi})$ include:

(i) Dichotomy: $R(i;\underset{\sim}{\pi})$ depends only on the numerical value of π_i and not explicitly upon either i or the other components of $\underset{\sim}{\pi}$. For notational simplicity write $R(i;\underset{\sim}{\pi})$ as $R(\pi_i)$.

(ii) Ranking: $R(i;\underset{\sim}{\pi})$ depends only on tha rank i and not explicitly upon the numerical values of the components of $\underset{\sim}{\pi}$. Write $R(i;\underset{\sim}{\pi})$ as $R(i)$.

Before proceeding with the formal development, it may be useful to indicate how various measures of rarity can be constructed in a meaningful and interpretable way.

2. THE CONSTRUCTION AND INTERPRETATION OF DIVERSITY INDICES: EXAMPLES

Three of the more widely used indices of ecological diversity are the "species count", the Shannon-Wiener index and Simpson's (complementary index. These will be denoted as follows:

Species count: $\Delta_{-1} = s-1$

Shannon-Wiener: $\Delta_0 = -\Sigma\ \pi_i \log \pi_i$

Simpson: $\Delta_1 = 1 - \Sigma\ \pi_i^2$.

All three assign diversity zero to a single-species community.

As Simpson [25] himself has observed, Δ_1 may be interpreted as the probability that two randomly selected members of the community belong to different species. However, there is an alternative interpretation which can be fruitfully generalized. When rewritten in the form $\Delta_1 = \Sigma\ \pi_i\ (1-\pi_i) = \Sigma\ \pi_i\ R(\pi_i)$, Simpson's index expresses the average community rarity, with the understanding that species rarity is measured by $R(\pi) = 1-\pi$. Now contemplate Wallace's traveler who first comes upon a member of, say, the i^{th} species. As his journey continues, the traveler encounters other organisms, sometimes of the i^{th} species and sometimes not. The rarer species i, the more likely are interspecific encounters. $R(\pi_i) = 1-\pi_i$ is precisely the probability that a given encounter is interspecific. In what follows, this concept of inter- versus intraspecific encounters is exploited. Three different schemes are examined.

2.1 Waiting time for an intraspecific encounter. Again consider the traveler in search of the i^{th} species.

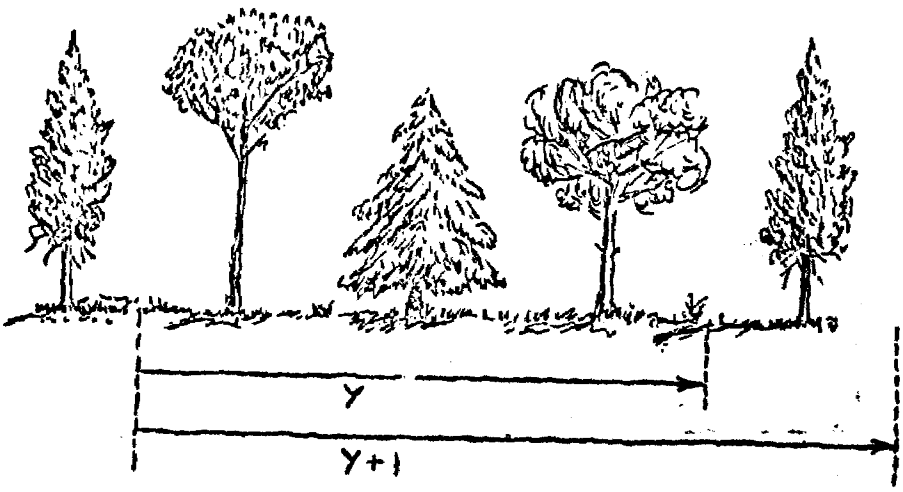


Figure 2.1

With Y+1 equal to the number of encounters upto and including the first intraspecific one, we have,

$$E[Y|\pi_i] = (1-\pi_i)/\pi_i, \qquad E[Y+1|\pi_i] = 1/\pi_i,$$
$$E[1/(Y+1)|\pi_i] = -\pi_i \log(\pi_i)/(1-\pi_i),$$

when $P(Y=y) = (1-\pi_i)^y \pi_i$, $y = 0,1,\ldots$.

Since large Y are associated with rare species, both Y and Y/(Y+1) are reasonable measures of rarity. But these are random variables and should be replaced by average quantities. There are several ways to interpret the "average" of a ratio: each gives rise to a different index.

1. Species Count:

$$R(\pi_i) = E[Y|\pi_i] = (1-\pi_i)/\pi_i, \qquad \Sigma\, \pi_i\, R(\pi_i) = \Sigma\, (1-\pi_i) = s-1.$$

2. Simpson's Index:

$$R(\pi_i) = E[Y|\pi_i]/E[Y+1|\pi_i] = 1-\pi_i, \quad \Sigma\, \pi_i\, R(\pi_i) = \Sigma\, \pi_i\, (1-\pi_i)\ .$$

3. Shannon-Wiener Index:

$$R(\pi_i) = E[\tfrac{1}{Y+1}\,|\pi_i] \cdot E[Y|\pi_i] = -\log \pi_i, \quad \Sigma\, \pi_i\, R(\pi_i) = -\Sigma\, \pi_i \log \pi_i\ .$$

4. An Unfamiliar Index:

$$R(\pi_i) = E[Y/(Y+1)|\pi_i] = 1 + \pi_i \log(\pi_i)/(1-\pi_i)$$

$$\Sigma\, \pi_i\, R(\pi_i) = 1 + \Sigma\, \pi_i^2 \log(\pi_i)/(1-\pi_i)\ .$$

2.2 Waiting time for an interspecific encounter. Here we suppose the traveler to be in search of a new species and put Z+1 equal to the number of encounters up to and including the first interspecific one.

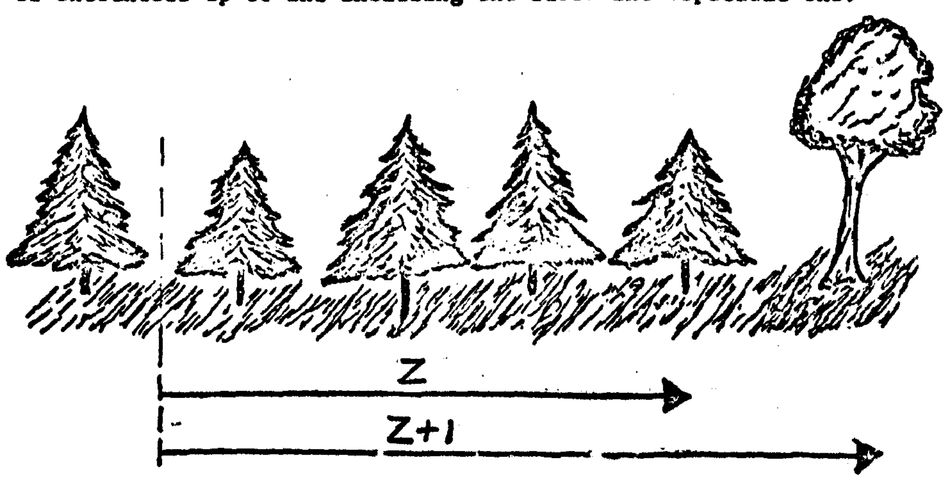


Figure 2.2

We have, $E[Z|\pi_i] = \pi_i/(1-\pi_i)$, $E[Z+1|\pi_i] = 1/(1-\pi_i)$,

$$E[1/(Z+1)|\pi_i] = \frac{-(1-\pi_i)\log(1-\pi_i)}{\pi_i} \quad .$$

Small Z are associated with rare species and the variables of interest are 1/Z and 1/(Z+1).

1. Species Count: $R(\pi_i) = 1/E[Z|\pi_i] = (1-\pi_i)/\pi_i$.

2. Simpson's Index: $R(\pi_i) = 1/E[Z+1|\pi_i] = 1-\pi_i$.

3. A Second Unfamiliar Index:

   $R(\pi_i) = E[1/(Z+1)|\pi_i] = -(1-\pi_i)\log(1-\pi_i)/\pi_i$.

   The index itself is $\Sigma\, \pi_i\, R(\pi_i) = -\Sigma\,(1-\pi_i)\log(1-\pi_i)$.

Note that $E[1/Z|\pi_i] = \infty$.

2.3 Fixed number of encounters. Here we let Y be the number of interspecific and Z the number of intraspecific encounters out of a fixed total of N encounters.

1. Species Count: $R(\pi_i) = E[Y|\pi_i] \,/\, E[Z|\pi_i] = (1-\pi_i)/\pi_i$.

2. Simpson's Index: $R(\pi_i) = E[Y|\pi_i] \,/\, E[Y+Z|\pi_i] = 1-\pi_i$.

Note that $E[Y/Z|\pi_i] = \infty$, while $E[Y/(Y+Z)|\pi_i] = 1-\pi_i$.

Remarks: 1. It is curious that the Shannon-Wiener index arises in only the first scheme.

2. For a given measure, $R(\pi)$, of species rarity, $R(0^+)$ may be finite or infinite. When it is finite, there is a dual measure. defined by $\bar{R}(\pi) = R(0^+) - R(1) - R(1-\pi)$. Three facts are easily verified,

a. $\bar{\bar{R}} = R$.

b. The two unfamiliar indices constructed above are duals of one another.

c. Simpson's index is self dual.

Some biological motivations for considering interspecific encounters have been discussed by Hulbert [13], who concluded that, if an index is to be used, Simpson's is conceptually preferable to Shannon's. His negative assessment of the Shannon-Wiener index would appear to be unduly pessimistic. In fact, additional arguments can be put forth in support of the Shannon-Wiener index. Motivated, in part, by the fact that biological growth processes are often multiplicative, Preston [22] suggests that logarithmic abundances are more useful than absolute abundances. With λ_i as the abundance of the i^{th} species, $\log(1/\lambda_i)$ becomes an intuitively reasonable measure of species rarity. Since $\lambda_i = \pi_i \cdot$ constant, the average community rarity is

$$\Sigma\, \pi_i \log(1/\lambda_i) = -\Sigma\, \pi_i \log(\pi_i) + \text{constant.}$$

We also note that it is frequently useful (in the study of contingency tables, for example) to express probabilities in the form $\pi_i = \exp(-\alpha_i)$, $\alpha_i \geq 0$. Since rare species (small π_i) correspond to large α_i, the α_i may be taken as a measure of species rarity and this leads, once again, to the Shannon-Wiener index.

3. TWO CRITERIA FOR DIVERSITY INDICES

Recalling the definition of dichotomous indices, $\Delta(C) = \sum_{i=1}^{s} \pi_i R(\pi_i)$, observe that R(0) is inherently undefined while the value R(1) is germane only to a single-species community and, in fact, equals the diversity of such a community. R(1) = 0 is a natural normalizing requirement.

What else might be required of R? On intuitive grounds, $R(\pi)$ should be a decreasing function of π (species j is rarer than species i if $\pi_i > \pi_j$).

First Criterion C1: R is a decreasing function defined on (0,1]. If the normalizing condition R(1) = 0 is also imposed, R will as a consequence, be nonnegative.

This monotonicity requirement on R, simple and intuitive though it is, has a striking implication. Consider two communities,

$$C = (s, (\pi_1,\ldots,\pi_i,\ldots,\pi_s))$$

$$C' = (s+1, (\pi_1,\ldots,\pi_i-h,\ldots,\pi_s,h))$$

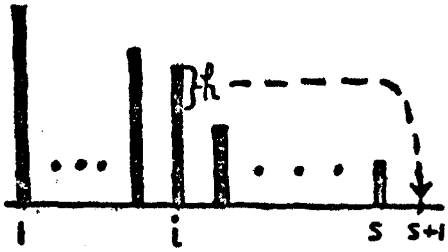


Figure 3.1

where h > 0 is sufficiently small that the species ranking is left undisturbed. (Ties are not a problem. Take i to be the highest rank within the tied set.) We say that C leads to C' by introducing a species. A possible biological interpretation is that species i shares its resources with a newly arrived competing species. Note that the relative abundances of all other species are unchanged.

Theorem 3.1: Assume R(π) is decreasing in π. Then introducing a species increases the diversity of a community. More precisely, if C leads to C' by introducing a species, then $\Delta(C) \leq \Delta(C')$.

Proof: By assumption $\pi_i > \pi_i-h \geq h > 0$ and so $R(h) \geq R(\pi_i-h) \geq R(\pi_i)$.
But

$$\Delta(C') - \Delta(C) = (\pi_i-h)\,R(\pi_i-h) + h\,R(h) - \pi_i\,R(\pi_i)$$

$$= h[R(h) - R(\pi_i-h)] + \pi_i[R(\pi_i-h) - R(\pi_i)] \geq 0.$$

Any community $C = (s, \underset{\sim}{\pi})$ with finitely many species can be constructe from a single-species community by successively introducing new species (see Figure 3.2). Theorem 3.1 asserts that the diversity increases at each step. None the less, indices satisfying Criterion C1 may have undesirable properties, as illustrated by the next example.

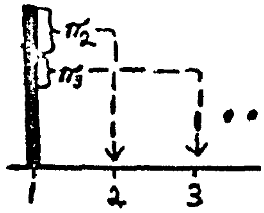


Figure 3.2

Example 3.1: Let $R(\pi) = 1/\pi^2 - 1$ and $\Delta = \sum_{i=1}^{s} 1/\pi_i - 1$. This index satisfies Criterion C1 and assigns diversity zero to a single-species community. Figure 3.3 includes a plot of the values of Δ for communities with ranked abundance vector $(1-\pi, \pi)$, $0 \leq \pi \leq 1/2$. The point A represent a single-species community, while B, C and D represent successively more even two-species communities. In accord with Theorem 3.1, B, C and D are more diverse than A. But among the three two-species communi ties, the diversity as measured by Δ decreases as the evenness increases.

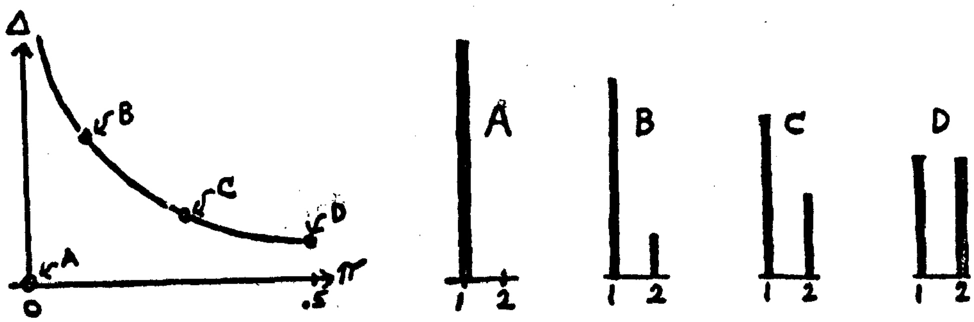


Figure 3.3

In going from B to C to D in Example 3.1, the change in community composition may be described as a transfer of abundance from one species to another less abundant species. The next definition formalizes this concept for many-species communities.

Definition 3.1: Let $C = (s,\underset{\sim}{\pi})$ and $C' = (s',\underset{\sim}{\pi}')$ be two communities. C leads to C' by a transfer of abundance if $s = s'$ and if $\underset{\sim}{\pi}$ and $\underset{\sim}{\pi}'$ have the form

$$\underset{\sim}{\pi} = (\pi_1,\ldots\ldots,\pi_i,\ldots\ldots\ldots,\pi_j,\ldots\ldots\ldots,\pi_s)$$
$$\underset{\sim}{\pi}' = (\pi_1,\ \ldots,\pi_i-h,\ \ldots,\pi_j+h,\ \ldots,\pi_s)$$

with $i < j$ and $h > 0$ small. In particular $\pi_k = \pi_k'$ for $k \neq i,j$. We write $C << C'$ when C leads to C' by either introducing a species or by transfering abundance.

Second Criterion C2: $C << C' \Rightarrow \Delta(C) \leq \Delta(C')$.

The index of example 3.1 does not satisfy Criterion C2. In fact, for this example, $\Delta(C) \leq \Delta(C')$ when C leads to C' by introducing a species while $\Delta(C) \geq \Delta(C')$ when C leads to C' by transfering abundance.

To state conditions under which the two criteria will be satisfied, it is convenient to define an auxiliary function V by

$$V(\pi) = \begin{cases} \pi R(\pi) & \pi \in (0,1] \\ 0 & \pi = 0\ . \end{cases}$$

For the index s-1, $V(\pi) = 1-\pi$ for positive π, which shows that V may be discontinuous at the origin.

Theorem 3.2: Criterion C2 is satisfied <=>

$$\frac{V(\pi_j+h)-V(\pi_j)}{h} \geq \frac{V(\pi_i)-V(\pi_i-h)}{h} \tag{3.1}$$

whenever $\pi_i > \pi_i-h \geq \pi_j+h > \pi_j \geq 0$ and $\pi_i+\pi_j \leq 1$.

Assuming differentiability of V, condition (3.1) may be replaced by

$V'(\pi_j) \geq V'(\pi_i)$ whenever $\pi_i > \pi_j \geq 0$ and $\pi_i + \pi_j \leq 1$.

Proof: Straightforward.

Example 3.2: The condition (3.1) has a simple geometric interpretation as illustrated by figure 3.4 for communities with abundance vectors (π_1, π_2, π_3). The convention $\pi_1 \geq \pi_2 \geq \pi_3$ is dropped for this example. Points on the vertices, edges, and interior of the triangle represent respectively single-species, two-species, and three-species communities. The centroid of the triangle represents the completely even three-species community. Condition (3.1) requires that the diversity increase as a point moves toward the center of the triangle along any line segment parallel to an edge. The arrows in the figure indicate the direction of increasing diversity.

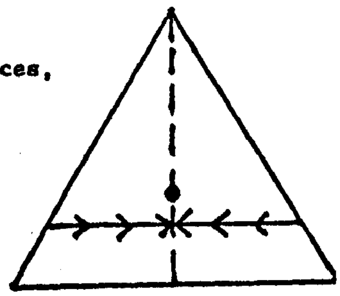


Figure 3.4

Theorem 3.3: Criterion C1 and Criterion C2 are both satisfied if V is concave on the closed unit interval [0,1].

Proof: Criterion C1: Let $0 < x < y \leq 1$. Observe that $V(x)/x$ is the slope of the line from the origin to the point $(x, V(x))$. The concavity of V implies then that $V(x)/x \geq V(y)/y$ and hence that $R(x) \geq R(y)$.
Criterion C2: Condition (3.1) requires that L should have greater slope than L' (Figure 3.6). But this is a well-known consequence of concavity.

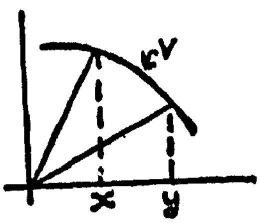


Figure 3.5

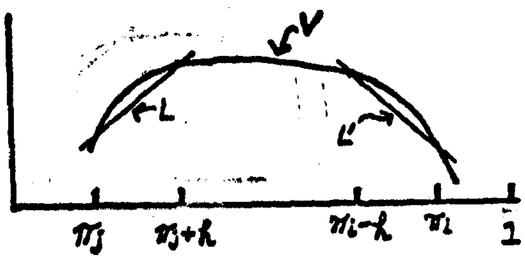


Figure 3.6

<u>Remark</u>: Because of the constraint $\pi_i + \pi_j \leq 1$, the converse of Theorem 3.3 is not quite true. For example, let $R(\pi) = 3/4 - \pi$ for $\pi \in (0,3/4)$ and $R(\pi) = 0$ for $\pi \in [3/4,1]$.

<u>Corollary 3.1</u>: The three indices $\Delta_{-1}, \Delta_0, \Delta_1$ considered in section 2 satisfy both Criterion C1 and Criterion C2.

The two criteria are invariant to positive affine transformations of form $R^* = \alpha R + \beta$, $\Delta^* = \alpha\Delta + \beta$, α, β constants, $\alpha > 0$. It is not hard to show that $R'(1)$ is strictly negative if $R(1) = 0$ and V is concave. ($R \equiv 0$ is a trivial exception.) Where available the conditions $R(1) = 0$ and $R'(1) = 0$ are convenient normalizing requirements. Δ_{-1}, Δ_0, and Δ_1 are normalized in this sense.

For concreteness, the criteria of this section were developed in terms of dichotomous indices. For the general index with rarity measure $R(i;\underset{\sim}{\pi})$, Criterion C2 requires no change and Criterion C1 is replaced by:

C1': For fixed $\underset{\sim}{\pi}$, $R(i;\underset{\sim}{\pi})$ is an increasing function of i.

4. STOCHASTIC ORDERING

Solomon [26] has proposed that diversity indices be required to preserve stochastic ordering and has stated a necessary and sufficient condition (finitely many species) which is closely related to the second condition of Theorem 3.2. Solomon actually considers the dual but equivalent notion of majorization. We would like to briefly indicate how the more primitive and intuitive concepts of the previous section relate to stochastic ordering. The main result is that stochastic order is the partial order generated by the relation $C \ll C'$.

Definition 4.1: Let $F(x)$ and $G(x)$ be two cumulative distribution functions on the real line. F is stochastically less than G ($F \overset{s}{\leq} G$) provided $1 - F(x) \leq 1 - G(x)$ for all x.

The following well-known fact is recorded for future reference. See Lehmann [15; p. 73,112].

Theorem 4.1: $F \overset{s}{\leq} G \iff \int \psi(x)\, dF(x) \leq \int \psi(x)\, dG(x)$ for all increasing functions ψ.

For a community $C = (s, \underset{\sim}{\pi})$, the ranked abundance vector $\underset{\sim}{\pi}$ may be thought of as a probability distribution on the set of positive integers. With such an interpretation, $\underset{\sim}{\pi} \overset{s}{\leq} \underset{\sim}{\pi}' \iff \sum_{j \geq k} \pi_j \leq \sum_{j \geq k} \pi'_j$ for $k = 1,2,3,\ldots$.
Notice that this says that $\underset{\sim}{\pi}'$ has uniformly greater tail weight (rarity) than $\underset{\sim}{\pi}$ and it becomes plausible that diversity indices should preserve stochastic ordering.

Theorem 4.2: Let $C = (s, \underset{\sim}{\pi})$ and $C' = (s', \underset{\sim}{\pi}')$ be two communities.

a) If $C \ll C'$ then $\underset{\sim}{\pi} \overset{s}{\leq} \underset{\sim}{\pi}'$.

b) Conversely if $\underset{\sim}{\pi} \overset{s}{\leq} \underset{\sim}{\pi}'$ and if s' is finite, then there is a finite sequence $C_0, C_1, \ldots, C_n$ of communities satisfying $C = C_0 \ll C_1 \ll \ldots \ll C_n = C'$.

Proof: By induction on s'.

Corollary 4.1: Any diversity index satisfying Criterion C2 preserves stochastic ordering on the class of communities having finitely many species. Any diversity index which preserves stochastic ordering satisfies the Criterion C2.

5. INDICES BASED ON RANKING

The indices considered thus far have been of the dichotomous type. A measure of species rarity, with a more detailed dependence upon community composition, is the number of more abundant species. For the i^{th} species, this number is $i-1$ (recall that $\underline{\pi}$ is ranked) and average community rarity becomes $\Sigma\,(i-1)\,\pi_i = \Sigma i\,\pi_i - 1$ = average rank − 1. Solomon [26], from a quite different point of view, has introduced the average rank as a diversity index. (The −1 has the effect of assigning diversity zero to a single-species community and appears to be a generally useful convention.)

A related index is Fager's [12] "Number of Moves" which is, in effect, the average rank rescaled to range between zero and one. However, Peet [19] has given persuasive arguments against rescaling diversity indices. Fager's basic idea is attractive, though. As an alternative to Fager's number of moves needed to convert a sample to an even distribution, one may consider the "work (= mass x distance)" required to construct a given community from a single species community. This "work" is seen to be average rank −1.

For the general measure of rarity based on ranks, the analogue of ... C1 is the requirement that R(i) be an increasing function of i. ... the comments at the end of section 3). Interestingly, this monotonicity turns out to be sufficient for Criterion C2.

<u>Theorem 5.1</u>: $\Delta(C) = \Sigma\, R(i) \cdot \pi_i$ preserves stochastic ordering $\Leftrightarrow$ R(i) is increasing in i.

<u>Proof</u>: $\Rightarrow$ trivial.

$\Leftarrow$ Theorem 4.1.

<u>Remark</u>: For finitely many species, a straight-forward proof may also be based on either Theorem 4.2 or, equivalently, on Solomon's [26] condition of "S-concavity".

6. PIELOU'S AXIOMS AND HIERARCHIAL CLASSIFICATION

Pielou [21,p.7] has given three axioms for a diversity index:

P1. For given s, the index should have its greatest value for a completely even community, i.e. when $\pi_i = 1/s$, $i = 1,2,\ldots,s$.

P2. Given two completely even communities, the one with more species should have the greater diversity.

P3. For hierarchial classifications, the ANOVA formula should hold.

<u>Theorem 6.1</u>: Any diversity index $\Delta(C)$ which satifies the Criterion C2 also satisfies P1 and P2.

<u>Proof</u>: For finitely many species, if Δ satisfies C2 it also preserves stochastic order.

As has been shown by Khinchin [14], the three axioms P1, P2 and P3 characterize the Shannon-Wiener index up to a constant multiple. However, <u>weighted</u> ANOVA formulas can be associated with more general indices. We restrict attention to those indices of form $\Delta = \Sigma\ \pi_i\ R(\pi_i)$ and impose the following regularity assumptions (Criteria C1 and C2 are not needed).

A1. R is continuous and not identically zero on (0,1].

A2. $R(1) = 0$.

A3. $R'(1)$ exists and is finite (one-sided derivative).

Examples: (α clarified below).

α	$R(\pi)$	Index
-1	$-(1-\pi^{-1})$	s-1
0	$-\log \pi$	Shannon-Wiener
1	$1-\pi$	Simpson

Classify the community into g categores $A_1, A_2, \ldots, A_g$ and further classify each A_i into s_i subcategories. Let π_i be the probability of A_i and $\pi_{j \cdot i}$ the conditional probability, given A_i, of the j^{th} subcategory of A_i.

π_i	A_i:	$\pi_{1 \cdot i}$	$\pi_{2 \cdot i}$	$\cdots$	$\pi_{s_i \cdot i}$

Then $\Delta(A) = \sum_{i=1}^{g} \pi_i \, R(\pi_i)$, $\quad \Delta(\text{"B"}|A_i) = \sum_{j=1}^{s_i} \pi_{j \cdot i} \, R(\pi_{j \cdot i})$,

$$\Delta(\text{total}) = \sum_{i=1}^{g} \sum_{j=1}^{s_i} \pi_i \, \pi_{j \cdot i} \, R(\pi_i \, \pi_{j \cdot i}) \text{ and}$$

$$\Delta(\text{total}) = \Delta(A) + \sum_{i=1}^{g} \pi_i \left[\sum_{j=1}^{s_i} \pi_{j \cdot i} \left(R(\pi_i \, \pi_{j \cdot i}) - R(\pi_i)\right)\right] .$$

For the above examples ($\alpha = -1,0,1$) and with $W(\pi) = \pi^{\alpha}$, this reduces to

$$\Delta(\text{total}) = \Delta(A) + \sum_{i=1}^{g} \pi_i \, W(\pi_i) \sum_{j=1}^{s_i} \pi_{j \cdot i} \, R(\pi_{j \cdot i}) \qquad (6.1)$$

or

$$\Delta(\text{total}) = \Delta(A) + E_A[W(\pi_i) \, \Delta(\text{"B"}|A_i)] \ .$$

Theorem 6.2: Assume R satisfies A1,A2, and A3. Then a weighted ANOVA formula (6.1) holds for some W <=> there exists a real number α such that $W(\pi) = \pi^{\alpha}$, and $R(\pi) = \text{constant} \cdot (1-\pi^{\alpha})$ for $\alpha \neq 0$ and $R(\pi) = \text{constant} \cdot \log(\pi)$ for $\alpha = 0$.

Proof: The proof is lengthy and will appear elsewhere.

Remark: At first glance, the theorem appears to characterize the Shannon-Wiener index using only P3 and mild regularity. But, in accord with our view that diversity is an average property of the community, there is the additional assumption that the index has form $\Sigma\pi_i\ R(\pi_i)$.

If the normalizing conditions $R(1) = 0$, $R'(1) = -1$ are imposed, the rarity measures given by the theorem assume the standardized form $R(\pi) = (1-\pi^{\alpha})/\alpha$ with diversity index $\Delta_{\alpha} = (1 - \Sigma\ \pi_i^{\alpha+1})/\alpha$. (The usual limiting convention is understood when $\alpha = 0$.)

Theorem 6.3: Criterion C1 is satisfied for all α while Criterion C2 is satisfied <=> $\alpha \geq -1$.

Proof: Apply Theorem 3.2 and Theorem 3.3.

It is worth noting that

$$\frac{-\log\ (1-\alpha\Delta_{\alpha})}{\alpha} = \frac{\log\ \Sigma\pi_i^{\alpha+1}}{-\alpha} = H_{\alpha+1}(\underset{\sim}{\pi})$$

where $H_{\alpha+1}$ is Renyi's [23] entropy of order $\alpha+1$. Since $-\log\ (1-\alpha t)/\alpha$ is an increasing function of t, it follows that $H_{\alpha+1}$ preserves stochastic ordering when $\alpha \geq -1$. The sets $\{\Delta_{\alpha}\ : \alpha \geq -1\}$, $\{H_{\alpha+1}\ : \alpha \geq -1\}$ constitute two pencils of indices having the Shannon-Wiener index as common intersectio

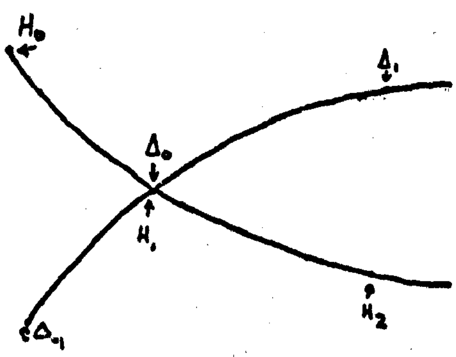


Figure 6.1

Advocates of the Shannon-Wiener index may feel equally comfortable with either family of indices (compare with Pielou [21 ,p.9]). We prefer Δ_α since it can be interpreted as an average quantity.

7. ESTIMATION OF SIMPSON'S INDEX

A problem associated with the use of diversity indices as indicators of environmental quality is the time and level of professional expertise required for a taxonomic classification of the sample. Cairns et al [6 , 8 , 9] have developed an ingenious technique to overcome this difficulty. Their approach is a nice illustration of the concept of inter- and intra-specific encounters discussed in section 2. Given a random sample $A_1, A_2, \ldots, A_N, A_{N+1}$ of specimens, define a run to be a maximal sequence of consecutive specimens of the same species. Cairns suggests the ratio, # runs/(N+1), as a measure of the diversity of the sample. In implementing the technique, the investigator need only make the successive comparisons A_1 vs A_2, A_2 vs A_3, A_3 vs A_4, etc. so that the method is rapid and does not call for sophisticated taxonomic skill. It would be possible to adapt Cairns technique to the measurement of forest diversity along a line transect. (See figures 2.1 and 2.2) .

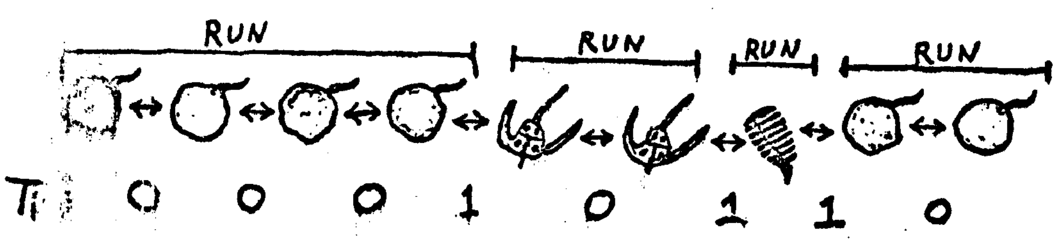


Figure 7.1

what follows, it is shown that, with a minor bias correction, Cairns' diversity measure becomes an unbiased estimator of Simpson's index Δ_1. Asymptotic normality is also established. The unbiased version is obtained as

$CL = (\#\text{ runs} - 1)/N$

and will be called Cairns linked estimator. The statistical analysis is facilitated by introducing indicator random variables T_i with the property that each occurence of $T_i = 1$ signals the start of a new run. The T_i are defined by

$$T_i = \begin{cases} 1 & \text{if } A_i \text{ and } A_{i+1} \text{ belong to different species} \\ 0 & \text{otherwise.} \end{cases}$$

Then, $T_1, T_2, \ldots, T_N$ are identical 0-1 variables, but adjacent T_i need not be independent (since the comparisons are linked). Let ρ be the correlation between T_1 and T_2.

Theorem 7.1: a) $E[T_1] = \Delta_1$, b) $Var(T_1) = \Delta_1(1-\Delta_1)$

c) $Cov(T_1,T_2) = \Sigma\, \pi_i^3 - (\Sigma\, \pi_i^2)^2$

d) $0 \le \rho \le 1/2$.

The lower bound $\rho = 0$ is achieved only for a completely even community: $\pi_1 = \pi_2 = \ldots = \pi_s$. The upper bound $\rho = 1/2$ is approached as $\pi_1 \to 1$. (ρ is undefined when $\pi_1 = 1$).

Proof: a) and b) are obvious since T_1 is a 0-1 random variable with $P(T_1=1) = \Delta_1$.

c) $Cov(T_1,T_2) = Cov\,(1-T_1, 1-T_2) = P(T_1=0, T_2=0) - (P(T_1=0))^2$

$$= \Sigma\, \pi_i^3 - (\Sigma\, \pi_i^2)^2 \; .$$

d) The covariance has the form of a variance, $\Sigma\pi_i \cdot \pi_i^2 - (\Sigma\, \pi_i \cdot \pi_i)^2$. Hence $\rho \ge 0$ with equality <=> the π_i are all equal. We employ a standard inequality to show that $\rho \le 1/2$;

$$\Sigma\, \pi_i^4 \leq (\Sigma\, \pi_i^2)^2 \quad \text{(Bechkenbach and Bellman [1,p.18]}$$

$$\leq \Sigma\, \pi_i^2\, (1-\pi_i)^2 + (\Sigma\, \pi_i^2)^2$$

$$\leq \Sigma\, \pi_i^2 - 2\, \Sigma\, \pi_i^3 + \Sigma\, \pi_i^4 + (\Sigma\, \pi_i^2)^2$$

$$2\, \Sigma\, \pi_i^3 - 2(\Sigma\, \pi_i^2)^2 \leq \Sigma\, \pi_i^2 - (\Sigma\, \pi_i^2)^2 = \Delta_1\, (1-\Delta_1)$$

Remark: The bounds $0 \leq \rho \leq 1/2$ can be improved if the value of Δ_1 is known. For given Δ_1, we have obtained sharp upper and lower bounds on ρ. These are complicated and will not be given. The upper bound confirms the intuition that ρ tends to be small for highly diverse communities.

Theorem 7.2: a) $CL = \sum_1^N T_i/N$, b) $E[CL] = \Delta_1$,

c) $Var[CL] = [1+2\rho-2\rho/N]\, \Delta_1(1-\Delta_1)/N$

$\simeq [1+2\rho]\, \Delta_1(1-\Delta_1)/N$ for large N

$\leq 2\Delta_1\, (1-\Delta_1)/N$.

d) CL is asymptotically normal as $N \to \infty$.

Proof: a) and b) are obvious and c) is a routine calculation once it is noted that nonadjacent T_i are independent. The asymptotic normality follows from Noether's central limit theorem which is stated below.

Theorem 7.3: (Noether [18]). Let $Z_1, Z_2, Z_3, \ldots$ be independent random variables. a) Let $T_1, T_2, T_3, \ldots$ be uniformly bounded random variables with T_i a function of Z_i and Z_{i+1} only. Then $S_N = \sum_{i=1}^N T_i$ is asymptotically normal provided Var $[S_N]$ is of exact order N.

b) Let T_{ij}, $i,j = 1,2,\ldots$ be uniformly bounded random variables with T_{ij} a function of Z_i and Z_j only. Then $S_N = \sum_{i,j=1}^N T_{ij}$ is asymptotically normal provided Var $[S_N]$ is of exact order N^3 .

Remark: Noether presents a proof of b). The proof of a) requires only slight modifications in his argument.

Remark: Theorem 7.2 is related to a result of Mood [17] who examined the distribution of the number of runs when a fixed sample is subjected to random permutations.

Use of the exact formula for Var [CL] requires estimation of the correlation ρ. The pairs (T_1, T_2), (T_4, T_5), (T_7, T_8) ... constitute approximately N/3 independent observations on the bivariate distribution of (T_1, T_2) from which an estimate may be obtained.

The nonnegativity of ρ indicates that linking the consecutive comparisons reduces the efficiency of the estimate and suggests an estimate based upon independent pairs of specimens. For N such pairs (2N specimens), define Cairns unlinked estimator as

CU = 1/N · (# of unlike pairs).

Then, trivially,

Theorem 7.4: a) $E[CU] = \Delta_1$, b) $Var[CU] = (1-\Delta_1)\,\Delta_1/N$,

c) CU is asymptotically normal as $N \to \infty$.

Efficiency comparisons of the linked and unlinked estimators require a common yarstick. The number of specimens in the sample is a natural yardstick if specimens are difficult to obtain. For n specimens,

$$\frac{Var[CL]}{Var[CU]} = \frac{n}{s(n-1)} + \rho\,\frac{n}{n-1}\,\frac{n-2}{n-1} \approx \frac{1}{2} \le \frac{Var[CL]}{Var[CU]} \le 1.$$

Thus CL is at least as efficient as CU in these circumstances and may be twice as efficient.

In the event that specimens are easily obtained, the number of comparisons, N, seems to be a reasonable statistical yardstick. Here the situation is reversed.

$$\frac{Var[CL]}{Var[CU]} = 1 + 2\rho\ (1-1/N) \simeq 1 + 2\rho \text{ and } 1 \le \frac{Var[CL]}{Var[CU]} \le 2 .$$

Operational considerations may give preference to the linked estimator, however, This is especially true for a highly diverse community where ρ may be expected to be small.

We now turn our attention to the case of a complete taxonomic classification of the sample, which is taken to consist of t species and n specimens with $x_1, x_2, \ldots, x_t$ as the species counts. Simpson [25] has shown that $D = \sum_1^t \frac{x_i}{n} \left(\frac{n-x_i}{n-1} \right)$ is an unbiased estimator of Δ_1. On the basis of the asymptotic behavior of the third and fourth moments, he also concluded that D was likely to be asymptotically normal (provided $\rho \neq 0$) . Bowman et al [3] have also examined the moments of D. We show how Noether's central limit theorem can be used to establish the asymptotic normality without the need for laborious moment calculations.

<u>Theorem 7.5</u>: a) $E[D] = \Delta_1$, b) $Var[D] = \frac{2\Delta_1(1-\Delta_1)}{n(n-1)} \quad [1 + 2(n-2)\rho]$,

c) If $\rho \neq 0$, D is asymptotically normal.

<u>Proof</u>: Let $S_n = \sum_{i,j=1}^{n} T_{ij}$, where

$$T_{ij} = \begin{cases} 1 & \text{if } i < j \text{ and specimens } i \text{ and } j \text{ are of different species} \\ 0 & \text{otherwise.} \end{cases}$$

It may be seen that $D = 2S_n/n(n-1)$. Using Theorem 7.1, the calculation of E[D] and Var[D] is routine after it is noted that T_{ij} and T_{km} are independent whenever $\{i,j\} \cap \{k,m\} = \phi$. Part b) implies that $Var[S_n]$ is of exact order n^3 when $\rho \neq 0$. The asymptotic normality of D now follows from Noether's theorem.

8. ESTIMATION OF SPECIES RICHNESS

Estimation of the number of species in the community is one of the more interesting and intriguing problems facing the ecologist. Usually, he is not in a position to establish sharp boundaries for the community and finds it impossible to describe his sampling scheme with any degree of statistical precision. Likewise we will not be precise about the sampling method, but shall suppose that the species are represented in the sample independently of one another and in accord with their own individual probability distributions. As usual, s is the number of species in the community and $\underset{\sim}{\pi}$ is the ranked abundance vector.

Let $p_i(x)$, $x = 0,1,2,\ldots$, $i = 1,2,\ldots,s$, be the probability that the i^{th} ranked species in the community is represented in the sample by x individuals. The probability distributions $p_1(x), p_2(x), \ldots, p_s(x)$ depend in an unknown way upon the vector $\underset{\sim}{\pi}$, the sampling intensity and the response of the various species to the sampling effort (catchability). The number of species actually present in the sample (i.e. represented by a positive number of individuals) is itself a random variable. This random variable, and sometimes its observed value, is denoted by t. We have

$$E[t] = \sum_{i=1}^{s} [1-p_i(0)] = s[1 - \frac{1}{s} \sum_{i=1}^{s} p_i(0)] = s[1-\bar{p}(0)],$$

where $\bar{p}(0) = \frac{1}{s} \sum_{i=1}^{s} p_i(0)$ is the average species absence probability. If an estimate, $\tilde{p}(0)$, of $\bar{p}(0)$ is available, then s may be estimated as $\tilde{s} = t/(1-\tilde{p}(0))$.

<u>Estimation Method 1</u>: Assume that the probability distributions $p_1(x),\ldots,p_s(x)$ are members of a known parametric family $p(s;\theta)$ with possibly different values of θ: $p_i(x) = p(x;\theta_i)$, $i = 1,\ldots,s$.

Further assume that θ is a scalar parameter and can be estimated from a single observation. Let $i_1, i_2, \ldots, i_t$ be the (unknown) ranks of the species actually present in the sample. For $j = i_1, i_2, \ldots, i_t$, estimate θ_j by, say, $\tilde{\theta}_j$ and $p(0;\theta_j)$ by $p(0;\tilde{\theta}_j)$. Take $\sum_{j=1}^{t} p(0;\tilde{\theta}_j)/t$ as the estimate of $\bar{p}(0)$. The method may be expected to underestimate $\bar{p}(0)$ and hence to underestimate s.

Estimation Method 2: Assume that the probability distributions $p_1(x), \ldots, p_s(x)$ are all identical and equal to $p(x;\underset{\sim}{\theta})$ where $p(x;\underset{\sim}{\theta})$ is a known parametric family and $\underset{\sim}{\theta}$ is a vector of parameters. Let $X_1, X_2, \ldots, X_t$ be the observed (nonzero) species counts in the sample, listed in some random order. It may be shown that, conditional on t, $X_1, X_2, \ldots, X_t$ are independent and identically distributed with common distribution $p(x;\underset{\sim}{\theta})/(1-p(x;\underset{\sim}{\theta}))$, which gives an estimate, $\tilde{\underset{\sim}{\theta}}$, of $\underset{\sim}{\theta}$. Estimate $\bar{p}(0) = p(0;\underset{\sim}{\theta})$ by $p(0;\tilde{\underset{\sim}{\theta}})$.

The above methods are standard in the literature. We suggest a third method that seems to be new and which leads to modified versions of Method 1 and Method 2.

Estimation Method 3: Let the sample consist of n individuals of which n_1 are singletons. Assume the sample is representative of the community in the sense that the 'rare' species (i.e. singletons) in the sample correspond to the 'rare' (i.e. unobserved) species in the community. The singletons taken together comprise a fraction n_1/n of the sample and they divide this fraction among themselves into n_1 equal parts. Extrapolating (not interpolating!) to the community, conclude that the unobserved species comprise a fraction n_1/n of the community and that they divide this fraction among themselves into n_1 equal parts. In particular, estimate the number of unobserved species as n_1 and the total number of species as $t+n_1$. To correct for any bias of this estimator, note that

$$E[t] = s[1-\bar{p}(0)], \quad E[n_1] = \sum_{i=1}^{s} p_i(1) = s\bar{p}(1),$$

$$E[t+n_1] = s[1-\bar{p}(0) + \bar{p}(1)] .$$

Under the assumptions of either Method 1 or Method 2, both $\bar{p}(0)$ and $\bar{p}(1)$ may be estimated by, say, $\tilde{p}(0)$ and $\tilde{p}(1)$. Take $\tilde{s} = (t+n_1)/(1-\tilde{p}(0) + \tilde{p}(1))$ as a modified estimate of s.

Example 8.1: The five methods were applied to the Rothamsted light trap data reported by Bliss [2]. The underlying distribution for Method 1 and Method 2 was assumed to be Poisson. The last column of the table gives the estimate of s which Bliss obtained by fitting the lognormal distribution (Method 2). All figures are rounded to the nearest integer. Standard errors are being computed.

Year	t	n_1	Method 1	Modified Method 1	Method 2	Modified Method 2	Method 3	Lognormal
1933	183	32	232	250	183	215	215	208
1934	176	34	226	251	176	210	210	199*
1935	202	39	260	289	202	241	241	239
1936	157	51	243	295	157	208	208	222

*Bulmer [4] has obtained the estimate $s = 226$ by fitting the Poisson-Lognormal distribution.

Remark: In a different context and with a different viewpoint, Robbins [24] has suggested an estimator similar to n_1/n for estimating the proportion of unobserved outcomes.

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