

MEASURES OF NATURAL DIVERSITY

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ABSTRACT

Diversity measures have been developed for a variety of ecological applications. These include within community, among habitat, and landscape measures. Each of these measures is affected by sampling techniques and efficiency. Furthermore, indices vary in their sensitivity to diversity components (richness, evenness, and pattern). Applications and limitations of each diversity measure are discussed. Research directions are identified that will provide measures of diversity consistent with the needs of forest managers.

INTRODUCTION

Diversity is defined in the rules to implement the National Forest Management Act (NFMA) of 1976 as "the distribution and abundance of different plant and animal communities and species within the area covered by a land and resource management plan" (U.S. Department of Agriculture 1979). This definition differs little from some textbook definitions of the entire field of ecology (e.g., Krebs 1978). It is clear from the report of the Committee of Scientists (1979) on Section 6(h) of the NFMA that no single definition of diversity presently used by ecologists is adequate to meet the needs of the diversity provisions of the NFMA. The Committee suggested that Congress intended the "term diversity to refer to biological variety rather than any of the quantitative expressions now found in the biological literature." Concern for at least three levels of such biological variety is implicit in that report: (1) "the variety of endemic and desirable naturalized plant and animal species," (2) the relative abundances of various species within communities (the Committee noted that no reference to species abundances appears in the NFMA or its legislative history), and (3) the variety of natural communities or landscape variety. These levels of concern span the range of diversity measures in the biological literature.

The concept of species diversity has played a central role in the development of ecological theory. However, it is generally agreed that operational definitions of diversity (i.e., the way we actually measure it) have not always matched our theoretical conceptions. This situation led Hurlbert (1971) to call species diversity a non-concept. Recent reviews of diversity

measures (Whittaker 1972, Peet 1974, Pielou 1975) have clarified not only the application of various diversity measures, but also their properties and limitations.

As suggested in the report of the Committee of Scientists, diversity is a generic concept, encompassing several levels of ecological complexity. Whittaker (1965) divided diversity into alpha (within habitat diversity), beta (among habitat diversity or, more specifically, species change along important environmental gradients), and gamma (landscape diversity). Alpha diversity generally is agreed to include measures of species richness (the number of species in an area), species evenness or equitability (the distribution of abundances among constituent species in a community), and heterogeneity (synthetic measures that are sensitive to both richness and equitability) (Hurlbert 1971, Peet 1974). We shall structure our discussion around these categories.

Although this multiplicity of measures may seem confusing at first (if not annoying), it is not unlike the multiplicity of possible management objectives for natural diversity. We feel that an understanding of the diversity of such measures can help to focus more precise attention on specific management problems. However, we also feel that many of the most important issues in the diversity provisions of the NFMA defy simple quantification.

Our goals in this paper are five-fold:

- 1) to identify and classify the most widely used diversity measures,
- 2) to describe the characteristics and sensitivities of each measure to variations in diversity components and sampling techniques,
- 3) to describe the application of these measures to specific problems in diversity management,
- 4) to define the limitations of each diversity measure,
- 5) to identify research directions that will provide measures of diversity more consistent with the needs of the forest manager.

WITHIN COMMUNITY DIVERSITY MEASURES

Species Richness

If we were concerned only about diversity (richness, equitability, or heterogeneity) within a specified sample area (e.g., a 0.1 ha plot) in which all organisms were tallied, measuring diversity would be rather straightforward. Such simplicity would be the case if we were comparing changes in diversity in permanent plots monitored through time. It is when we wish to use our sample data to estimate diversity in a somewhat larger universe (e.g., an entire forest stand, a watershed, or deciduous forests in general) that significant problems arise. When a sample is used to estimate species richness in an entire community, we must assume that there is some predictable

relationship between the number of species in our sample (s) and the actual total number of species (S). For example, if we assume, as Gleason (1922, 1925) did, that species number increases in direct proportion to the logarithm of the area sampled, then a prediction can be made. Unfortunately, no such single relationship has been found to hold regularly and species area curves display a remarkable diversity of shapes (Fig. 1).

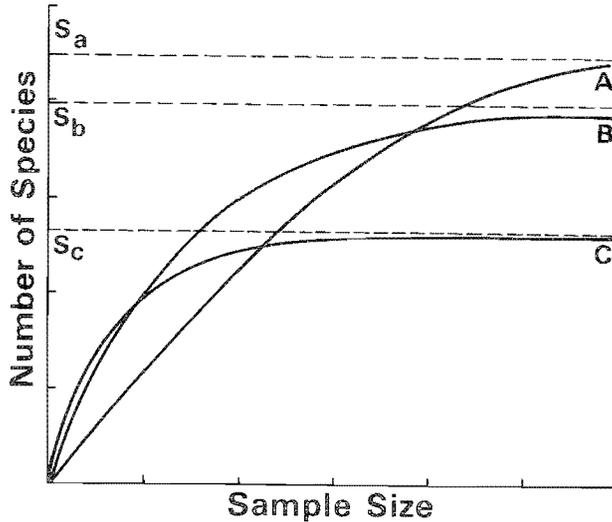


Figure 1. Species-area curves for three hypothetical communities.

Let us assume that we wish to compare richness between two areas that represent different management regimes. Because our estimate of species richness in each area is affected by sample size, we know that comparisons of estimated richness are only valid if we sample equivalent areas or numbers of individuals. But even with that precaution, we are making an additional assumption that equivalent areas sample equivalent proportions of the total species within each area. A comparison of the two hypothetical species-area curves in Fig. 1 demonstrates that this is not necessarily true.

In general, the rate of increase in species number with increasing sample size is affected by two other components of diversity, evenness and spatial pattern. Both of these factors are discussed below. Thus, given equally rich communities, species numbers will increase toward an asymptote most rapidly in those communities in which the constituent species are most equally abundant and randomly intermingled in space. As community equitability decreases or species become segregated spatially, more samples are required to observe a particular proportion of the total species present. Prediction of species area relations *a priori* requires more information about a community or sample area than is usually known.

Species richness also may be affected greatly by the scale of the universe we choose to consider. For example, mean plant species richness per 0.1 ha in 75 loblolly pine forests on the North Carolina Piedmont is 51.0 and in 72 deciduous hardwood stands is 53.9. At the scale of 0.1 ha, we can conclude that there is no significant difference in richness between pine forests and hardwoods. However, 347 species were encountered in all of the hardwood stands taken together, whereas only 260 were sampled in the pines. If preservation of regional richness is a management goal, then information on richness at smaller scales may be misleading.

It is well known that abundance is rarely distributed among species in a statistically normal fashion. Preston (1948, 1962) and May (1975) suggested that a log normal distribution provides the best fit for species abundance data. Such a distribution of herbaceous species among logarithmically increasing abundance classes is illustrated in Fig. 2. Based on this relation-

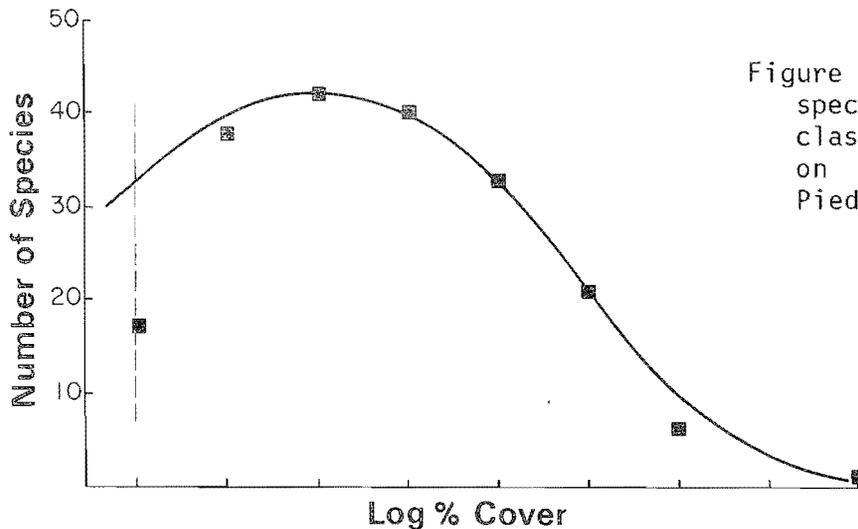


Figure 2. Number of herb species in log % cover classes in hardwood forests on the North Carolina Piedmont.

ship, Preston suggested that total species number in a sampling universe could be predicted as

$$S = Y_0 \sigma (2\pi)^{\frac{1}{2}}$$

where Y_0 is the modal octave or abundance class and σ is the logarithmic standard deviation. Two difficulties exist with this approach. First, the index depends on accurate estimates of population parameters that require a large sample. Second and more critically, the index assumes a log normal distribution of species abundance, which is often not the case.

The recognition that species number usually changes in a non-linear fashion as sample size increases has led to indices such as Margalef's (1957)

$R_1 = (s-1)/\log n$ or Menhinick's (1964) $R_2 = s/(n)^{\frac{1}{2}}$. However, such adjustments do little to cure the sampling problems identified earlier. Whittaker (1972) and Peet (1974), among others, have suggested that average number of species per sample, "while lacking theoretical elegance, provides one of the simplest, most practical, and most objective measures of species richness."

Heterogeneity Indices

Richness is only one of several factors that can affect our perception of community diversity. Species relative abundance can be just as important. Consider two stands of trees with five species each. In the first, the species are equally abundant whereas, in the second, one species comprises 90

percent of the individuals. To the casual observer, the first stand "appears" to have more species. A more quantitative statement is that if two trees are taken at random from each stand, the probability that the two belong to the same species is higher for the second stand. It is to measure this "apparent richness" that ecologists have developed indices that are sensitive to both richness and equitability. Indeed, several authors have suggested that diversity can be defined only by such measures (Margalef 1957, Pielou 1975). Here we compare two such measures.

Undoubtedly, the most widely used indices are those based on information theory (Margalef 1957). Some of the early applications of these measurements were related to a partially successful attempt to integrate information theory into general theories for community development and structure (Margalef 1968, Odum 1969). Community heterogeneity can be "equated with the uncertainty that exists regarding the species of an individual selected at random from a population" (Pielou 1966a). That uncertainty increases with either increased richness or equitability. Because information content is a measure of uncertainty, it is also a measure of heterogeneity (Pielou 1966a, Peet 1974).

Information content per individual (H') is given most commonly by the Shannon-Weaver (1949) formula:

$$H' = - \sum p_i \log p_i$$

where p_i is the percent importance of the i th species. The units depend on the log base used: \log^2 gives bits, \log^{10} gives decits, and \log^n gives "nits" per individual. In practice, p_i is estimated by n_i/N , where n_i is the number of individuals of species i and N is the number of individuals sampled. For small samples, n_i/N is a biased estimate of p_i ; however, this effect is inconsequential for most ecological applications (Peet 1974). The exponent of H' ($e^{H'}$ in nits, or $\text{Exp } H'$) is equal to the number of equally common species that would provide the same heterogeneity or H' as the sample. Thus, $\text{Exp } H'$ is a more intuitively meaningful expression than H' . (Pielou [1967] suggested the use of the Brillouin formula in preference to the Shannon-Weaver formula for finite samples; however, Peet [1974] demonstrated that its results may be misleading.)

Simpson (1949) proposed that diversity (heterogeneity) is inversely related to the probability that two individuals selected at random from a community will belong to the same species. This probability is mathematically expressed as

$$\lambda = \sum p_i^2$$

for finite sample sizes

$$L = \sum (N_i[N_i - 1]) / (N[N - 1])$$

As indicated, L varies inversely with heterogeneity, with a maximum value of 1 and a minimum approaching zero. Thus, $D = 1 - L$ (Gini 1912) or $1/L$ (Williams 1964) is directly proportional to heterogeneity. Like $\text{Exp } H'$, $1/L$ can be interpreted as the number of equally common species required to produce

the same heterogeneity as that observed in the sample. Related indices include Hurlbert's (1971) probability of interspecific encounter (PIE) and McIntosh's (1967) index of diversity. Numerous other indices also have the property of being sensitive to both richness and evenness, but they are not as commonly used as these indices and are therefore less valuable for comparisons.

Peet (1974) compared these indices and found that their mathematical characteristics vary in their relative sensitivity to richness and evenness. Comparatively, the information indices are more sensitive to changes in the importance of rare species, whereas the various forms of Simpson's index are more sensitive to changes in common species. We found that the ratio of $\text{Exp } H'$ to $1/L$ (Hill's $R1:2$, 1973a) for tree species varied between 1.3 and 2.0 among various hardwood community types and was as low as 1.1 in some pine stands (Fig. 3). These variations are due largely to complex differences in species abundance patterns (see below).

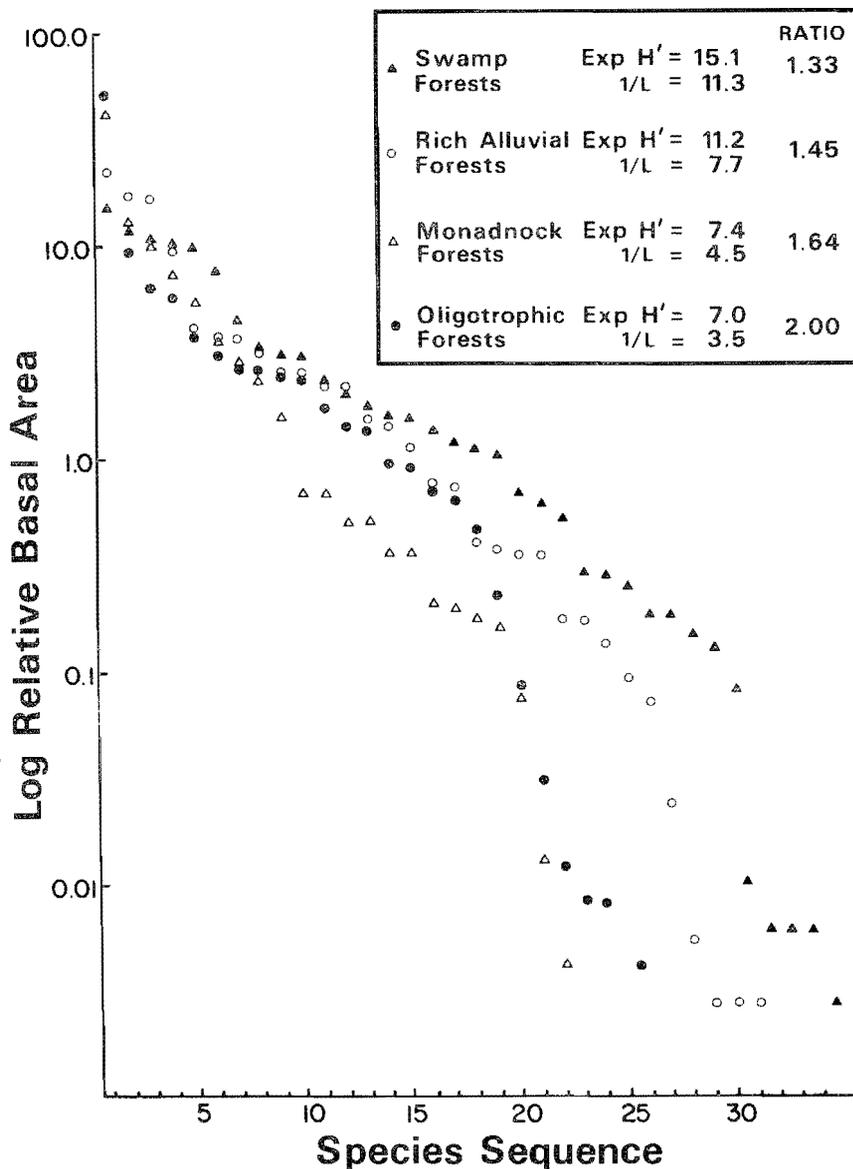


Figure 3. Dominance diversity curves for the tree species in four hardwood forest types on the North Carolina Piedmont.

Peet (1974) suggested that either $\text{Exp } H'$ or $1/L$ is sufficient to answer most questions that a heterogeneity index can answer. Given the diversity provisions of the NFMA, we might well ask what these questions are. Two communities obviously can share the same $\text{Exp } H'$ or $1/L$ and yet be quite different in the diversity considerations mandated in the NFMA. Most information of interest to the forest manager is submerged from view in a single number which can be arrived at in an infinite number of ways.

Equitability Indices

A concern for relative species abundances is implicit in the Committee of Scientists' report (1979), as well as in the NFMA regulations. Several indices have been developed from heterogeneity measures by standardizing against the maximum possible value, given the number of species (S) in the community. The most common of these is $J' = H'/H'_{\text{max}}$ (Pielou 1975). However, Peet (1974, 1975) raised serious questions regarding use of such indices. In practice, the number of species sampled (s) is usually substituted for the number of species actually present in the sampling universe (S). Thus, S is always underestimated and equitability overestimated. Given the difficulties identified earlier with estimates of richness, we can hardly expect this bias in the estimate of equitability to be the same from community to community. Obviously, variations in sample size, random variations in s , or variations in the distributions of abundances among species affect these measures (Peet 1975).

Where species abundance relations are known to be log normal, the logarithmic standard deviation of species abundances (σ) is a reasonable measure of population dispersion or equitability (Peet 1974). However, this measure also assumes a knowledge of S . Under most circumstances it is best to avoid using these equitability indices.

Dominance Diversity Curves

For many applications, comparison of dominance diversity curves proposed by Whittaker (1965, 1972, 1975) may be more informative than calculation of any particular diversity index. Such curves are constructed by ranking species from most to least important along the abscissa (thus x-axis length = richness) and plotting log of relative importance (basal area, density, production, etc.) on the ordinate. Whittaker (1972, 1977) viewed the average slope of the graph as a measure of heterogeneity. Four examples of dominance diversity curves for tree species in different hardwood communities in the North Carolina Piedmont are shown in Fig. 3. The shapes of the curves can be interpreted in terms of their similarity to those produced by various models of species abundance, and it is this application that has received the greatest use. Typically, a spectrum of shapes can be found varying from nearly a straight line in communities dominated by a few species to a sigmoid shape for communities with little biotic dominance (Whittaker 1965, May 1975).

Pattern Diversity

As mentioned previously, the spatial patterning of species will affect the estimates of richness, heterogeneity, and equitability. Pielou (1966b)

proposed a diversity index that is sensitive to richness, equitability, and spatial pattern based on nearest neighbor analysis. This value measures the probability that the n -nearest neighbors to an individual taken at random will be different species. Because it requires specific and time consuming sampling, this measure is of little practical value to the forest manager. Nonetheless, it is essential to remember that differences in the values of species diversity measures can arise because of the spatial pattern of species within a community.

AMONG HABITAT AND LANDSCAPE MEASUREMENTS

The Problem of Identifying Habitat Types

Concern for the variety of plant and animal communities, as opposed to species, within management areas is explicit in the language of the NFMA and the report of the Committee of Scientists. Ecologists have given considerably less attention to the measurement of diversity *per se* at this level.

An interesting and potentially useful application of H' to landscape variation was proposed by Pielou (1975) and recently applied by Romme (1982) to examine fire effects on landscape diversity in Yellowstone National Park. Community types, rather than species, are used to calculate a community level H' as

$$H' = -\sum a_i/A_t \log a_i/A_t$$

where a_i is the spatial area occupied by the i th community and A_t is the total area considered. Obviously, an analogous measure could be calculated using Simpson's index. As in within community heterogeneity indices, a considerable amount of information may be submerged (for better and worse) in a single number. There are infinite landscape patterns that can have the same H'_C . The problems of comparing such values among regions where the criteria for defining habitat units are different are obvious.

Measurement of diversity at the landscape scale clearly requires an extensive survey that identifies both the kinds of habitats (habitat richness) and their relative aerial extent (habitat equitability). Despite differences among taxonomists, species are rather easily defined taxonomic units and obtaining an accurate species count is largely a sampling problem. After years of debate, community ecologists now agree that defining communities is arbitrary by necessity. Furthermore, the criteria for defining communities in one region or biome are quite different from those in another. Given this necessary subjectivity, the definition of community types will be influenced more by political, social, and economic considerations. Community ecology offers no remedy to this problem other than several procedures for identifying and quantifying community variation.

Community Ordination and Classification

In many regions, rather detailed community inventories and classifications have been accomplished. In regions where environmental gradients are obvious and steep, a more or less subjective approach to community classification may be adequate (e.g., Daubenmire 1965). However, where alpha diversity

is high and environmental gradients subtle (such as in the eastern deciduous forests), detailed subjective classification may not be possible.

Oosting (1942), based on limited sampling, recognized three upland forest types on the North Carolina Piedmont: pre-climax (post oak-blackjack oak), climax (mixed oak-hickory), and post-climax (beech-red maple). He acknowledged, however, considerable variation within each of those forest types. Over several years, we have sampled herbaceous and woody vegetation in 106 hardwood dominated stands in the eastern Piedmont region. We also measured important site variables in each stand, including topographic location, moisture conditions, and soil chemical characteristics. Details of vegetational and environmental sampling and measurements are described in Peet (1980) and Peet and Christensen (1980).

The vegetation data were analyzed using several ordination techniques, most especially reciprocal averaging (RA) (Hill 1973b) and detrended correspondence analysis (DCA) (Hill 1979, Hill and Gauch 1980). Rigorous description of these multivariate analyses is beyond the scope of this paper. More intuitively, these methods compare the assemblage of stands in a multidimensional space. One such space is an "s-dimensional space," where s is the total number of species present and the importance of each s species defines a stand's position in that space. Many of the axes in that hyper space will be correlated; that is, some species will occur together frequently and others very rarely. Ordination methods, then, identify some smaller number of dimensions which contain most of the information present in the original space. The first axis is a line in the multidimensional space accounting for the greatest possible variation in species composition. The second axis contains the second most information with the constraint that the axis be perpendicular to the first. Theoretically, as many new lines can be drawn as there are species, but in most vegetational comparisons, axes beyond the third account for small variations. Thus, variations in numerous variables (species) can be limited to a small number of axes. Each stand is assigned a position along each of these statistically derived axes. Reciprocal averaging and DCA are superior to many other ordination techniques in that the axes are likely to correspond to important underlying environmental gradients, and there is no need to select end point stands (see Gauch et al. 1977 for a more thorough comparison of such techniques).

Stand positions along ordination axes are often correlated with environmental variables. In our example (Fig. 4A), stands with low first axis scores are primarily alluvial or riparian forests with well defined drainages and abundant moisture and nutrients. Stands with intermediate first axis but low second axis scores are more swamp-like, with frequently saturated (often gleyed) soils and poorly defined drainages. Stands with high first axis but low second axis scores are on upland sites but have shallow montmorillonitic subsoils which impede drainage. They vary between extremes of wet and dry. There is an obvious cluster of stands in the upper right portion of this graph, representing a mixture of upland types. Note that the lines on these graphs were drawn subjectively.

We removed the alluvial, swamp, and montmorillonate forests from this data set and then re-ordinated the residual stands, a process we refer to as progressive fragmentation (Peet 1980). By so doing, we allowed more subtle trends of variation in the data to become evident. Repeated application of

this process disclosed and "explained" habitat variation not immediately obvious in the raw data (Fig. 4B,C,D). Eventually, we identified eleven community types. Furthermore, this manipulation provided a measure of the relationship of those types to important environmental variables (Table 1). The composition and characteristics of each of these types are described in Peet and Christensen (1980). We have done similar analyses on 136 pine stands (Christensen and Peet 1981).

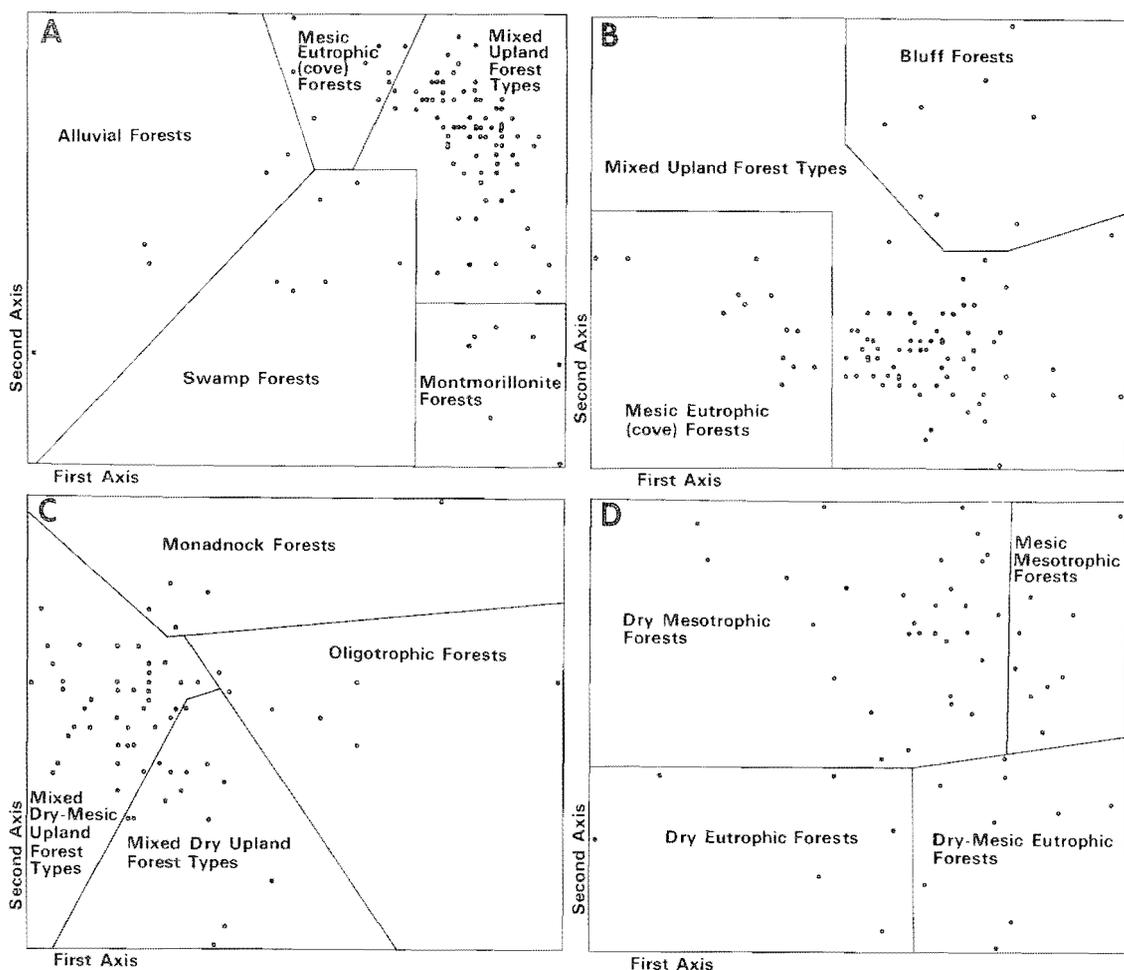


Figure 4. Four iterations of ordinations (first and second axes) of hardwood forest stands using the progressive fragmentation technique of Peet (1980).

Several clustering techniques are available that group samples based on relative similarity (see Goodall 1978, Orloci 1978) or on ordination results (e.g., TWINSpan) (Hill 1979, Gauch 1982). Clearly, the number of possible clusters in such an analysis is equal to the number of samples. The ecologist must decide on the relative level of within versus among cluster variation necessary to define habitat types.

Table 1. Spearman rank correlations of soil variables with ordination axes (from Peet and Christensen 1980).

	pH	Total cations ^a	Ca	Mg	K	Organic matter	PO ₄	AWI ^b	PWP ^c
Ordination 1									
Axis 1	-0.717 ^d	-0.768 ^d	-0.743 ^d	-0.792 ^d	-0.285 ^d	0.031	-0.091	0.353 ^d	0.111
Axis 2	0.380 ^d	0.275 ^d	0.255 ^d	0.267 ^d	0.346 ^d	0.185	0.201	-0.129	-0.092
Ordination 2									
Axis 1	-0.744 ^d	-0.763 ^d	-0.734 ^d	-0.753 ^d	-0.425 ^d	-0.103	-0.300	0.540 ^d	0.193
Axis 2	-0.095	-0.215	-0.196	-0.241	0.041	0.055	0.023	-0.012	0.036
Ordination 3									
Axis 1	-0.628 ^d	-0.509 ^d	-0.472 ^d	-0.549 ^d	-0.231	-0.093	-0.132	0.440 ^d	-0.250
Axis 2	-0.074	-0.378 ^d	-0.353 ^d	-0.374 ^d	-0.072	0.034	-0.258	0.208	-0.254
Ordination 4									
Axis 1	0.418 ^d	0.140	0.124 ^d	0.176 ^d	0.137	0.019	-0.181	-0.111 ^d	-0.088
Axis 2	-0.493 ^d	-0.599 ^d	-0.581 ^d	-0.542 ^d	-0.093	0.013	-0.336	0.603 ^d	0.123

^a Total cations = sum of Ca, K, and Mg in milliequivalents.

^b AWI = available water index = -1 bar water retention minus -15 bar water retention.

^c PWP = permanent wilting point = -15 bar water retention.

^d Significant at 0.01 level.

Such quantitative approaches to classifying habitats have two virtues compared to more subjective approaches in management of natural diversity: (1) they avoid pre-conceptions of what site variables are regulating diversity (indeed they can be used to identify such site variables); and (2) they require thorough and systematic sampling, reducing the likelihood that rare community types will be missed.

Beta Diversity

Whittaker (1972) defined beta diversity as the extent of differentiation in species turnover along habitat gradients. He suggested that beta diversity in its simplest form could be measured as

$$B = S/\bar{s}$$

where S equals the total richness of all samples taken together and \bar{s} the mean sample richness.

Other approaches to quantifying beta diversity are based on measurements of relative similarity among samples. Several similarity measures are available (see Whittaker 1972, 1975, Gauch 1982); however, percent similarity (PS) is most commonly used in calculations of beta diversity (Bray and Curtis 1957).

$$PS = 2 \sum \min(s_{ij}, s_{ik}) / S_j + S_k$$

where s_{ij} and s_{ik} are abundance of the i th species and S_j and S_k total abundance of all species in stands j and k , respectively.

Samples may then be arranged by differences in a particular environmental variable (e.g., elevation) and gradient distance plotted against PS. A

hypothetical example is shown in Fig. 5, along with the equation for beta diversity in species half changes. In a more general sense, beta diversity is the slope of this relationship.

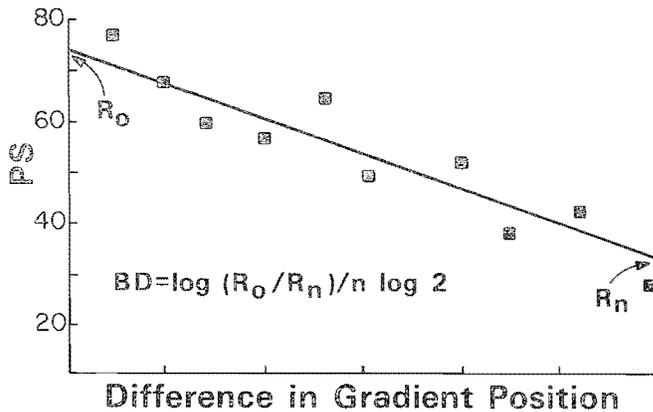


Figure 5. Example of calculation of beta diversity using Whittaker's (1972) method. PS = percent similarity. Gradient position refers to a particular environmental gradient, such as elevation or fertility.

In practice, a sample representing an extreme on the gradient (e.g., lowest elevation or soil fertility) is chosen as an endpoint and other samples are plotted relative to it (Whittaker 1960, Whittaker and Niering 1965, 1968). Wilson and Mohler (*in press*) recently have proposed a gradient re-scaling technique which alleviates some of these problems inherent in the method. Nonetheless, accurate calculation of beta diversity for a particular environmental gradient is rather difficult where multiple factors affect composition.

One of the virtues of DCA is that its axes are scaled to standard deviations (SD) of species change (Hill 1979, Hill and Gauch 1982). One such SD is roughly equivalent to 1.2 half changes. Thus, beta diversity may be measured as axis length in such ordinations.

LIMITATIONS IN SIMPLE DIVERSITY MEASURES

Calculation of diversity indices can be seductively simple. Numerous pitfalls await the unwary user. Here we wish to point out only two. First, community composition cannot be assumed to be at equilibrium; diversity could be changing. Second, simply maintaining diversity does not ensure maintenance of quality. We have to be sure we save the right species and the right communities.

Perhaps the most important development in theoretical considerations of diversity in the past two decades is the recognition that diversity is an equilibrium process; that is, diversity of a habitat or landscape is maintained by the balance between the processes bringing species to the area--immigration and speciation--and the processes causing them to disappear--emigration and extinction (MacArthur and Wilson 1967). Considerable disagreement still exists over the application of these equilibrium principles, first developed for islands, to landscape management (Sullivan and Schaffer 1975, Simberloff and Abele 1976a, 1976b, Terborgh 1975, 1976, Diamond 1976, Whitcomb et al. 1976). There is, however, no question that landscape patterns greatly affect species diversity of the individual communities on that landscape (Ranney et al. 1981, Pickett and Thompson 1978, Peet et al. *in press*, Scanlan 1981, Whitcomb et al. 1981). An understanding of how specific

landscape features (e.g., community size, separation, and the presence of corridors) affect the processes that determine diversity should be a primary research goal. Such an understanding will allow us to identify landscape diversity measures that are most relevant to management needs.

Management and development of the landscape for man's use typically involves fragmentation of the original continuous natural vegetation into island-like pieces. Recent studies with such artificial islands have shown that equilibrium is not immediately realized. Instead, the species number slowly drops, or "relaxes" toward the new equilibrium values. It is likely that most natural and semi-natural vegetation in eastern North America is currently undergoing such relaxation. Research is needed in the strategies most likely to minimize this species loss.

It is well known that the forests of eastern North America often have their highest richness a few years after clearcutting. This richness occurs because the low levels of competition allow not only many of the original species to grow, but also weedy species and species usually restricted to other habitats. However, extensive clearcutting ultimately leads to a decrease in the number of species on the landscape because those species that are intolerant of disturbance are lost. Similarly, island equilibrium theory suggests that the maximum number of species is maintained by having many small preserves rather than a few big ones. The problem is that this strategy saves those species we are least interested in saving and those that are most likely to survive on the managed landscape--mainly the weeds. Many of the species of special interest are rare and often isolated on unusual sites with little unnatural disturbance. Detection and management of each species' population require a rather specific understanding of their life history and habitat requirements.

CONCLUSION

Based on the preceding discussion, there obviously is no shortage of diversity measures. Unfortunately, community ecology cannot offer the forest manager a single index with which to measure natural diversity management goals or accomplishments. There are an infinite number of ways to configure a community to arrive at a particular value of H' or Simpson's index; some may be desirable and others disastrous. The same is true of landscape diversity measures. Clearly, communities should not be managed to maintain H' and landscapes should not be managed to maintain a particular beta or gamma diversity value. Rather, proper management at each of these levels depends on the identification and understanding of the structural and functional features of the constituents at each level.

It would, however, be a mistake to discard these measures altogether. Each index is sensitive to particular components of diversity. Used with a clear understanding of their characteristics and sensitivities, these indices may be helpful in pinpointing particular problems. Comparison of such indices in permanent plots or in areas that are continuously monitored may allow detection of diversity changes that might otherwise go unnoticed given the complexity of such data sets. Nevertheless, specific diagnosis of the causes of such changes will require a more thorough understanding of the system being measured than a single index can give.

There can be no question that any assessment of diversity depends on adequate classification and census. Taxonomists have provided a relatively clear system of species classification and the central problems in assessment of richness are those of sampling. At the landscape level, on-the-ground mapping techniques, aerial photography, and satellite imaging have simplified sampling problems. In some regions, detailed community classification models have been constructed; in others, very little is known about the nature of among community variations. Regardless, measurement of diversity at this level is certainly going to be most affected by our subjective choice of landscape classification methods.

Theoretical ecology has not released the forest manager from the onus of deciding what actually constitutes diversity. As Gleason (1926) suggested, every individual forest stand is unique and, theoretically, we can create as many categories as we have stands to categorize. The reproductive isolation of species provides a reasonable natural rule for their definition. No such rule exists for communities of organisms. Disputes regarding the enforcement of the landscape diversity provisions of the NFMA will likely focus on details of landscape classification rather than diversity measurement techniques.

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