Journal of Ecology (1984), **72,** 1055–1064

MEASURING BETA DIVERSITY WITH PRESENCE–ABSENCE DATA

M. V. WILSON* AND A. SHMIDA

Environmental Studies Program, University of California, Santa Barbara, California 93106, U.S.A. and Department of Botany, Hebrew University, Jerusalem, Israel.

SUMMARY

(1) Six measures of beta diversity (five from the literature, one proposed here) were compared and evaluated. Application was limited to measures suited for species presence–absence data along environmental gradients.

(2) Four ecological criteria of 'good' performance of beta diversity measures were developed: (i) conformity with the notion of community turnover ensures that the magnitude of a measure is meaningful; (ii) additivity is the property that the sum of beta diversities between contiguous segments equals the beta diversity of the entire gradient; (iii) independence from alpha diversity ensures useful application of a measure to systems with different alpha diversities; (iv) independence from excessive sample size obviates any spurious effects of oversampling.

(3) Two measures of beta diversity (one proposed by Whittaker (1960) and one proposed in the present paper) came closest to fulfilling all four criteria and should be of most use in ecological applications.

(4) Field data from Mt Hermon in Israel were used to compare the usefulness of the six measures.

(5) Current problems and issues, including the relationship between species-area curves and beta diversity, and future applications in measuring beta diversity are discussed.

INTRODUCTION

Beta diversity can be defined as the 'extent of species replacement or biotic change along environmental gradients' (Whittaker 1972). The studies of Whittaker (1960, 1972, 1977), MacArthur (1965, 1972) and others have established the importance of identifying beta diversity and alpha diversity (the number or diversity of species within community samples) as components of overall diversity. Accurate measurement of beta diversity is important in at least three ways: (i) it indicates the degree to which habitats have been partitioned by species; (ii) values of beta diversity can be used to compare the habitat diversity of different study systems; (iii) beta diversity and alpha diversity together measure the overall diversity or biotic heterogeneity of an area.

The purpose of this paper is to compare the different measures of beta diversity used in the ecological literature. Also proposed is a new and possibly superior measure. Each measure is described with a common algebraic notation, and evaluated using explicit criteria. Attention is limited to the measurement of beta diversity along single environmental gradients, although possible extensions are also considered. Only those measures suitable for presence and absence data are discussed. Wilson & Mohler (1983) have discussed guidelines for measuring beta diversity with quantitative data. To our knowledge, the present paper is the first comparative evaluation of beta diversity measures.

---

* Present address: Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331–2902, U.S.A.

MEASURES OF BETA DIVERSITY

This section presents six measures of beta diversity. Five have been discussed in detail elsewhere, and only the definition of these and a few worked examples are given here. For consistent presentation, the symbol for each measure, and in some cases its formulation, have been changed slightly from those in the original.

One necessary change has been the adjustment of units, which can be interpreted in two ways. The first is that beta diversity is the amount of change or turnover in species composition from one location to another; in examinations of species and communities arranged along a gradient, beta diversity is the biological length of the gradient (cf. Wilson & Mohler 1983). The second is that beta diversity represents the number of communities present. Since communities in nature are seldom discrete and countable, a given value, say c, of beta diversity in this interpretation is actually equivalent to the amount of heterogeneity that would obtain if there were exactly c distinct communities present. In practice, the two formulations are nearly the same, because changes in community composition, as measured by the equivalent number of communities present, are simply a function of the degree of species turnover. A convenient term for changes in species composition is 'community turnover'; the amount of complete community turnover is simply one less than c, the number of communities.

Measure 1: β_W

Whittaker (1960) established a straightforward measure of beta diversity, which will here be called β_w:

$$\beta_W = s/\bar{\alpha} - 1,$$

where s is the total number of species recorded in the study system, and $\bar{\alpha}$ is the average number of species found within the community samples. (Community samples differ in size, shape and definition from one investigation to another. For the purposes of this paper, a community sample is any species inventory acquired from a consistently applied vegetation measurement plot.) The measure β_W is simple to calculate and explicitly relates the components of diversity, α and β, to overall diversity, s.

Measure 2: β_C

In his discussion of bird species distributions on three continents, Cody (1975) defines beta diversity as 'the rate at which ... species are being replaced in censuses ... at each point on the habitat gradient'. Measures such as Cody's (see also Bratton 1975; Pielou 1975) of rates of biotic change or rates of species turnover at various stations on a gradient can be used to define ecotones between community types (Whittaker 1960; Beals 1969). As a measure of the range of habitats present and as a useful component of overall diversity, however, beta diversity should be considered an amount of differentiation, not a rate of change. For these reasons and to be consistent we define a measure of amount of biotic change, β_C, by integration of Cody's rate measure with respect to the habitat gradient. Thus,

$$\beta_C = [g(\mathrm{H}) + l(\mathrm{H})]/2,$$

where $g(\mathrm{H})$ is the number of species gained (i.e., newly encountered) along the habitat gradient, H, and l (H) is the number of species lost along H. The measure β_C is appealing because its use of gain and loss of species matches well the intuitive sense of species turnover. It is defined explicitly for samples arranged along gradients of environmental change.

Measure 3: β_R

Routledge (1977), in his examination of how diversity measures can be partitioned into components of alpha and beta, gave two measures of beta diversity suitable for use with presence and absence data. His first, which we call β_R, is:

$$\beta_R = s^2/(2r + s) - 1,$$

where s is the total number of species found in the study system, and r is the number of species pairs whose distributions overlap.

Measures 4 and 5: β_I and β_E

Another measure discussed by Routledge (1977), simplified here for presence and absence data and equal sample sizes, is:

$$\beta_I = \log(T) - [(1/T)\sum_i e_i \log(e_i)] - [(1/T)\sum_j \alpha_j \log(\alpha_j)],$$

where e_i is the number of samples along the gradient in which species i is found, α_j is the richness or alpha diversity of sample j, and $T = \sum_i e_i = \sum_j \alpha$. The measure β_I is appealing for its symmetry and its basis in information theory.

A closely-related measure results from the exponentiation of the entropy measure, β_I. This transformation is analogous to the derivation of diversity number measures by Hill (1973) and produces components of diversity that, when multiplied together, yield the total diversity (Routledge 1977). In terms of community turnover, however, the exponentiation is simply,

$$\beta_E = \exp(\beta_I) - 1$$

Measure 6: β_T.

Our field research on the distribution of species along environmental gradients has led us to a sixth measure of beta diversity. This measure, β_T ('beta turnover'), combines the idea of species turnover reflected by the gain (g) and loss (l) of species along the gradient, as used in β_C, with a standardization by average sample richness, $\bar{\alpha}$, inherent in β_W. Thus,

$$\beta_T = [g(H) + l(H)]/2\bar{\alpha}.$$

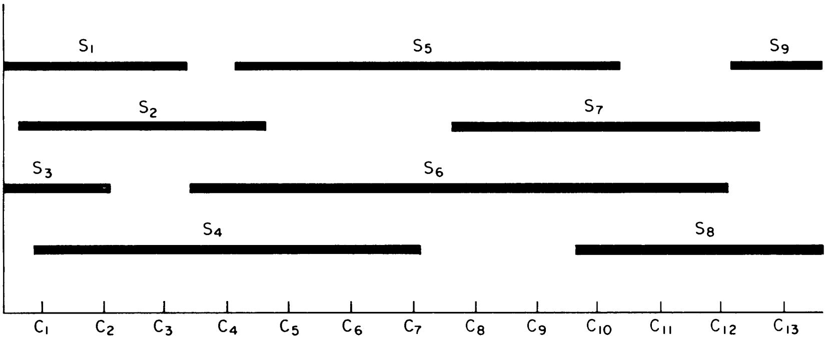

FIG. 1. An hypothetical environmental gradient with nine species (S_1–S_9) and their distribution at thirteen community sample stations (C_1–C_{13}).

The calculations of these measures of beta diversity are best seen with a simple example. Figure 1 is a schematic representation of nine species (S_1–S_9) distributed along an hypothetical environmental gradient. Lines indicate the distribution of each species. Species presence or absence is recorded within thirteen community samples (C_1–C_{13}) located as shown along the horizontal axis. For example, only species 2, 4 and 6 are present within sample 4. From these presence and absence data can be calculated the values of the six beta diversity measures. The appendix shows the computational details of the formulae presented in this section. Values vary considerably, from β_I, the smallest at 0·89, to β_C, the largest at 6·00.

EVALUATIONS OF MEASURES

Any measure of beta diversity should be ecologically meaningful and logically consistent. In this section the six measures are set against four criteria of 'good' performance: (1) conformity with an intuitive notion of community turnover; (2) possession of the property of additivity; (3) independence from alpha diversity; and (4) independence from over-sampling. These criteria are explained below. The results of this section are shown in Table 1. A field example illustrates the general results.

TABLE 1. Six measures of beta diversity rated by four ecological criteria of 'good' performance. Y = criterion fulfilled, N = criterion not fulfilled.

	Measures					
Criterion	β_W	β_C	β_R	β_I	β_E	β_T
Number of community changes	Y	N	Y*	N	Y*	y†
Additivity	Y*	Y	N	N	N	Y*
Independence from alpha diversity	Y	N	Y	Y	Y	Y
Independence from excessive sampling	Y	Y	Y	N	N	Y

* If $\alpha_j = \bar{\alpha}$ for all samples j.
† If $(\alpha_l + \alpha_n)/2 = \bar{\alpha}$.

Criteria of performance

(1) *Conformity with the notion of community turnover*

The utility of a measure of beta diversity depends, to a great extent, on its ability to reflect accurately the range of community composition contained within an area, that is, the degree of community turnover. To test this ability (see Routledge 1977), consider two extreme conditions which can be well-defined: (i), a system composed of a single unit with each species present throughout the gradient; and (ii), a system of c completely distinct units, each of which contains species that are completely co-extensive within the unit but whose distributions along the gradient do not overlap with the distributions of species from other units. In case (i) there is exactly one community, with no community turnover; in case (ii) there are exactly c distinct communities and $c - 1$ complete turnovers in community composition. A beta diversity measure that fulfills criterion (1) has the following property: for a given study system, the value (β) of the measure is equivalent in magnitude to the value that would be obtained in a system of exactly β complete community changes, or of exactly $\beta + 1$ completely distinct community units.

Four measures (β_W, β_R, β_E and β_T) at least partially fulfil criterion (1) (Table 1). One β_W, accurately reflects extremes of community turnover under all special conditions; β_T does so only if the average alpha diversity of the end samples equals the average alpha diversity over all the samples; β_R and β_E only do so under the more restrictive condition that each community sample contains the same number of species. The remaining two (β_C and β_I) do not reflect the notion of community turnover.

(2) *Additivity*

A measure of beta diversity should have the property of additivity. For example, with three sampling stations (a, b, c) along a gradient, the sum of β from a to b and β from b to c should equal β from a to c:

$$\beta(a, c) = \beta(a, b) + \beta(b, c).$$

Without the property of additivity, β will depend on the particular location of samples along the gradient, and will not be solely a reflection of the community turnover along the gradient.

Only one measure, β_C, is additive under all conditions (Table 1); β_W and β_T are strictly additive only if each sample along the gradient contains the same number of species; β_R, β_I and β_E are not additive. Degrees of additivity for the six measures are illustrated later with field data.

(3) *Independence from alpha diversity*

Within a given data set, measures of alpha and beta diversity should be independent for three reasons: (i) levels of alpha and beta diversity are established by different suites of ecological mechanisms (Shmida & Wilson 1983) and the measures α and β should reflect this; (ii) without independence, the comparison of species-rich and species-poor systems would be impossible; (iii) the interpretation of α and β as components of overall system diversity is facilitated by their independence.

One test of the property of independence is the comparison of values of β for two similar systems, in which each species of one system is duplicated by a pair of species in the other system with the original and the duplicating pair having identical distributional limits. In this test case, alpha diversity at every point along the gradient in the second system is double that of the alpha diversity of the first, but the set of species ranges, hence the degree of community turnover, remains the same. A measure of beta diversity that is independent of alpha diversity should have identical values in the two systems. Five of the six measures (β_W, β_R, β_I, β_E and β_T) are independent of alpha diversity under these conditions (Table 1); β_C will increase with increases in alpha diversity, and thus is not independent of alpha diversity.

(4) *Independence from sample size*

A measure of beta diversity should be independent of sample size, except for very small sample sizes. (Hume & Day (1974) present a statistical method for determining optimal sampling intensity.) A test for this criterion is the examination of the stability of β with an increase in the number of samples but with no change in information about species distribution. In the present study this is tested by taking several identical samples at each point so that sampling intensity is increased without adding any other information.

Four measures (β_W, β_R, β_C and β_T) are independent of sampling intensity (Table 1); β_I and β_E change values with the addition of samples that contain no further information on species distributions. Both β_I and β_E are derived from measures of niche width and overlap presented by Pielou (1972, 1975) for the study of insects on discrete host plants, wherein the number of samples (hence habitats) does convey information. In the analysis of species distribution data along continuous gradients, however, habitats are often not discrete and the use of β_I or β_E is less appropriate.

Comparisons of measures

Of the measures of beta diversity considered, only two (β_W and β_T) fulfil, at least in part, all four of the criteria of good performance; β_R performed nearly as well as β_W and β_T, but failed the test for additivity. The relative advantages of these three measures are discussed below. The failure of β_C, β_I and β_E to meet several of the test criteria suggest that they are unsuitable for general use in ecological analyses of beta diversity with presence and absence data.

FIELD EXAMPLE

In this section we apply the six measures of beta diversity discussed above to species range data collected from the western flanks of Mt Hermon, in north-eastern Israel (33°25′N, 35°48′E). The vegetation of Mt Hermon ranges from evergreen maquis at low altitudes in the west, through an open deciduous scrub-forest, to an alpine tragacanth (*Astragalus*) belt. This altitudinal zonation is similar to that on other mediterranean mountains, except that at middle and high altitudes the vegetation is more xeromorphic than that typically found on European mediterranean mountains (Shmida 1977). Species presence or absence was noted within survey samples at 100 m intervals of altitude. A total of 936 vascular

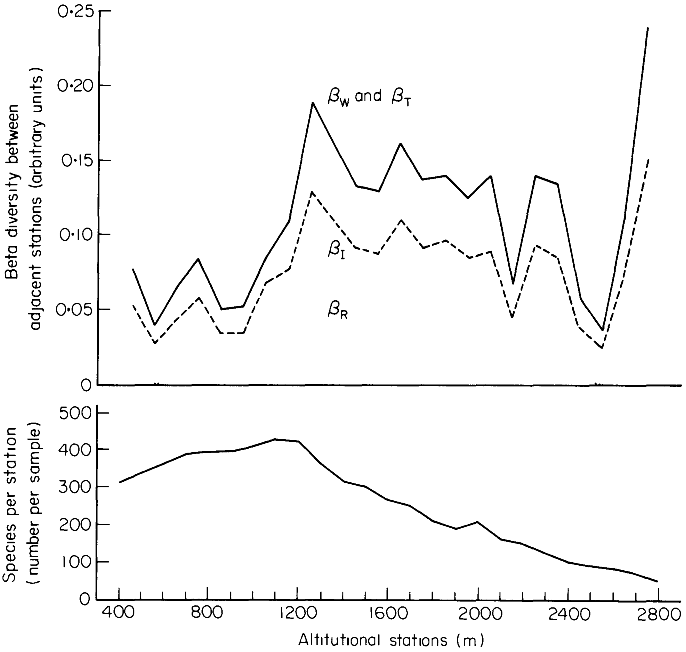

FIG. 2. Values for four beta diversity measures for adjacent stations along an altitudinal gradient of Mt Hermon, Israel, (——), β_W and β_T; (– – –), β_I; (· · · · ·), β_R. (Values for $\beta_E \approx \beta_I$.) The shapes of the curves are similar but their magnitudes are quite different.

plant species was recorded. The distribution of a species is considered to be continuous between the lowest and highest stations within which the species is present, even though the species may have been absent from intermediate stations.

Total beta diversity values for the gradient between 400 m and 2800 m vary greatly, and in decreasing order of magnitude are: $\beta_C = 679$, $\beta_T = 2{\cdot}6$, $\beta_E = 2{\cdot}5$, $\beta_W = 2{\cdot}3$, $\beta_R = 1{\cdot}7$ and $\beta_I = 0{\cdot}9$. These differences in magnitude are also present in values between adjacent stations (Fig. 2). Three curves of beta diversity between adjacent stations are plotted. Since $\beta_T = \beta_W$ whenever the measures are calculated for only two samples, the curves for these measures are identical. Also, for the range of values found on the Mt Hermon gradient $\beta_E \approx \beta_I$, so only the curve for β_I is shown. The curve for β_C has been excluded because its unstandardized values are not directly comparable to those of the other units.

Since the interval of altitude for each pair of adjacent stations is always 100 m, the shapes of the curves in Fig. 2 represent the changing *rates* of compositional turnover along the gradient. The shapes of the four curves are similar even though the derivations of the associated beta diversity measures are quite different. The peak in beta diversity occurring between 1200 m and 1300 m corresponds to the transition between a maquis and montane flora; the large values between adjacent stations above 2600 m may reflect rapid and ecologically significant changes in the alpine environment. Therefore, for the purpose of revealing the relative rates of compositional turnover along gradients, any of the measures is suitable.

The comparison of the sum of beta diversity values between adjacent stations with the value of beta diversity for the gradient as a whole indicates the degree of additivity of each measure. Specifically, percentage error in additivity is defined as:

$$\frac{(\beta_{\text{entire}} - \beta_{\text{adjacent}})}{\beta_{\text{entire}}} \times 100$$

The only completely additive measure is β_C (0% error), but, with the Mt Hermon data, β_T (4%), β_W (18%), and β_E (24%) are nearly additive; β_R (66%) and β_I (100%) are far from additive.

DISCUSSION

Six measures of beta diversity suitable for the analysis of presence and absence data along ecological gradients have been evaluated: β_W, Whittaker's (1960) original measure; β_C (Cody 1975); β_R, β_I and β_E (modified from Routledge 1977); and β_T, introduced in this paper. Judging these measures by the four criteria described above, along with the test of their performances with field data, two measures (β_T and β_W) appear most suitable for the ecological analysis of community data. Both work well under all the theoretical conditions here examined and both were helpful in interpreting the field data. One (β_T) has a direct, intuitive meaning of degree of species turnover along gradients; it is recommended when sample data can be arranged along a single overriding environmental gradient. The other (β_W) is perhaps the most widely used measure of beta diversity. Because its formulation does not assume a gradient structure, β_W is the measure of choice when samples cannot be arranged along a single gradient. The interpretation of values of β_W (or of any other measure) is, however, more difficult when data do not fit within a gradient structure.

Two other issues may be addressed. First, should the area of a community affect the measure of beta diversity of a system? The idea of the number of communities, irrespective of the relative abundance of community types, is reflected by β_T and β_W. Other measures, such as β_I and β_E, reflect both the notion of the number of communities and the evenness with which the communities are represented within the system. In this way β_W, as a measure of beta diversity, is analogous to richness measures of species diversity, and β_I and β_E are analogous to heterogeneity measures (*sensu* Peet 1974). Secondly, how should alpha diversity be measured? Four of the six measures of beta diversity considered (β_W, β_T, β_I, β_E) rely on explicit values for alpha diversity. It is well known that species richness is an increasing function of sample area. One solution to this problem of dependence of measures on sample area is the use of standardized sample areas. Collecting data along an ecological gradient is an alternative solution because, with such data, it is the presence of a species under the environmental conditions corresponding to points along the gradient that is important, not the presence of the species within any arbitrarily delimited sample plot.

The rate at which species richness increases with increasing sample area (the slope of a species-area curve) has sometimes been used as an index of habitat heterogeneity (Williams 1964; Whittaker, Niering & Crisp 1979) or of beta diversity (Connor & McCoy 1979). This interpretation is hindered by three problems. First, species-abundance relations alone result in increases in species richness with increasing sample area (May 1975; Pielou 1977)—the area *per se* hypothesis of Connor & McCoy (1979). The extent to which habitat heterogeneity contributes to the rate of species accumulation cannot be determined without a complete knowledge of the species-abundance relations. Secondly, most species-area curves in island studies are not nested. Samples, such as islands, are geographically separated and may be quite dissimilar in species composition for reasons of history. Without nesting samples, slope parameters of species-area curves cannot be used as indices of community turnover. Thirdly, it is difficult statistically (May 1975; Connor & McCoy 1979) and inappropriate ecologically (Shmida & Wilson 1983) to choose among competing mathematical models for representation of species-area curves. Species-area curves can have great value for the interpretation of species-abundance relations or immigration and extinction rates in individual field studies, but the use of estimates of slope parameters of mathematical models for the measurement of beta diversity is inappropriate.

The study of beta diversity is moving beyond the traditional description of the ecological length of environmental gradients in several directions. (i) Measurements of beta diversity will be instrumental as a point of reference for comparative studies of competition of both plant and animal species along environmental gradients. Such comparisons will be particularly useful if beta diversity is measured uniformly (say with β_T or β_W) and with consistent sampling methods. (ii) Wilson & Mohler (1983) use units of beta diversity as an ecologically meaningful basis for rescaling environmental gradients; rescaled gradients permit clearer interpretations of the width and overlap of species distribution curves. (iii) Beta diversity can also be applied to other spatial scales. As noted by Whittaker (1977), beta diversity on the community level is one realization of the general concept of what he called 'differentiation diversity' and has analogues on different scales; for example, pattern diversity within communities (Whittaker, Gilbert & Connell 1979; Whittaker, Niering & Crisp 1979; Wilson 1982). Beta diversity can also be extended to gradients of time, for measuring the ecological length of successional or phenological sequences (Shugart & Hett 1973; Jassby & Goldman 1974). (iv) A major unanswered question in the analysis of beta diversity is how its measurements from single, but perhaps interacting, environmental gradients with an area can be combined into a value for overall beta diversity for the multigradient system.

ACKNOWLEDGMENTS

We thank S. A. Levin, P. L. Marks, C. L. Mohler, R. K. Peet, the late R. H. Whittaker, and K. D. Woods for their helpful comments. This research was supported, in part, by a grant from the National Science Foundation of the United States to the late Robert H. Whittaker.

REFERENCES

Beals, E. W. (1969). Vegetation change along altitudinal gradients. *Science, New York*, **165,** 981–985.

Bratton, S. P. (1975). A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. *Bulletin of the Torrey Botanical Club*, **102,** 55–60.

Cody, M. L. (1975). Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and Evolution of Communities* (Ed. by M. L. Cody and J. M. Diamond), pp. 214–257. Harvard University Press, Cambridge.

Connor, E. F. & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *American Naturalist*, **113,** 791–833.

Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54,** 427–432.

Hume, L. & Day, J. C. (1974). The determination of an efficient sampling intensity for studying beta diversity in plant communities. *Canadian Journal of Botany*, **52,** 189–199.

Jassby, A. D. & Goldman, C. R. (1974). A quantitative measure of succession rate and its application to the phytoplankton of lakes. *American Naturalist*, **108,** 688–693.

MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews*, **40,** 510–533.

MacArthur, R. H. (1972). *Geographical Ecology*. Harper & Row, New York.

May, R. M. (1975). Patterns of species abundance and diversity *Ecology and Evolution of Communities* (Ed. by M. L. Cody and J. M. Diamond), pp. 81–120. Harvard University Press, Cambridge.

Peet, R. K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5,** 285–307.

Pielou, E. C. (1972). Niche width and niche overlap: a method for measuring them. *Ecology*, **53,** 687–692.

Pielou, E. C. (1975). *Ecological Diversity*. Wiley, New York.

Pielou, E. C. (1977). *Mathematical Ecology*. Wiley, New York.

Routledge, R. D. (1977). On Whittaker's components of diversity. *Ecology*, **58,** 1120–1127.

Shmida, A. (1977). *A quantitative analysis of Tragacanthic vegetation of Mt. Hermon*. Ph.D. thesis, Hebrew University of Jerusalem, Israel [in Hebrew, with English summary].

Shmida, A. & Wilson, M. V. (1983). Biological determinants of species diversity. *Journal of Biogeography*, **4.**

Shugart, H. H. & Hett, J. M. (1973). Succession: similarities of species turnover rates. *Science, New York*, **180,** 1379–1381.

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

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, **21,** 213–251.

Whittaker, R. H. (1977). Evolution of species diversity in land communities. *Evolutionary Biology*, **10,** 1–67.

Whittaker, R. H. Gilbert, L. E. & Connell, J. H. (1979). Analysis of two-phase pattern in a mesquite grassland, Texas. *Journal of Ecology*, **67,** 935–952.

Whittaker, R. H., Niering, W. A. & Crisp, M. D. (1979). Structure, pattern, and diversity of a mallee community in New South Wales. *Vegetatio*, **39,** 65–76.

Williams, C. B. (1964). *Patterns in the Balance of Nature*. Academic Press, New York.

Wilson, M. V. (1982). *Microhabitat influences of species distributions and community dynamics in the conifer woodland of the Siskiyou Mountains, Oregon*. Ph.D. thesis, Cornell University.

Wilson, M. V. & Mohler, C. L. (1983). Measuring compositional change along gradients. *Vegetatio*, **54,** 129–141.

(*Received 26 November 1983*)

APPENDIX

This Appendix describes how the six beta diversity measures described in the text are calculated, using the hypothetical system presented in Fig. 1. In this presentation, several basic characteristics of the system are first calculated, then the value for each beta diversity measure is derived.

The simple system shown in Fig. 1 has nine species depicted, so $s = 9$. There are thirteen sample stations (seen along the horizontal axis). The alpha diversity, or number of species in each of the samples, is 4, 4, 3, 3, 3, 3, 3, 3, 3, 4, 3, 3 and 2, respectively from left to right. Thus,

$$\sum_j \alpha_j = 41 \quad \text{and} \quad \bar{\alpha} = 3{\cdot}15.$$

Similarly for the number of samples in which each species is found,

$$\sum_j e_i = 3 + 4 + 2 + 7 + 6 + 9 + 5 + 4 + 1 = 41.$$

Going from left to right in Fig. 1, the number of species gained (or newly encountered) after the first sample, is

$$g = 5 \text{ (species 5, 6, 7, 8, 9);}$$

and the number of species lost after the first sample is

$$e = 7 \text{ (species 1, 2, 3, 4, 5, 6, 7).}$$

In this system of nine species, there are forty-five possible pairs of species. Of the forty-five pairs, $r = 16$ pairs have overlapping distributions, as observed by joint occurrence in a sample. These pairs are {(1, 2), (1, 3), (1, 4), (2, 3), (2, 4), (2, 6), (3, 4), (4, 5), (4, 6), (5, 6), (5, 7), (5, 8), (6, 7), (6, 8), (7, 8), (8, 9)}.

Each beta diversity measure can now be calculated. Refer to the text for additional details on each measure.

(1) $\beta_W = s/\alpha - 1 = (9/3{\cdot}15) - 1 = 1{\cdot}85$

(2) $\beta_C = [g(H) + l(H)]/2 = (5 + 7)/2 = 6{\cdot}00$

(3) $\beta_R = s^2/(2r + s) - 1 = 81\ (32 + 9) - 1 = 0{\cdot}98$

(4) $\beta_I = \log (T) - [(1/T) \sum_i e_i \log (e_i)] - [(1/T) \sum_j \alpha_j \log (\alpha_j)]$
$= 3{\cdot}71 - 1{\cdot}66 - 1{\cdot}16 = 0{\cdot}89$

(5) $\beta_E = \exp (\beta_I) - 1 = \exp (0{\cdot}89) - 1 = 1{\cdot}44$

(6) $\beta_T = [g(H) + l(H)]/2\bar{\alpha} = (5 + 7)/(2)\,(3{\cdot}15) = 1{\cdot}90$