Promoting the Science of Ecology

A Quantitative Evaluation of the Bray-Curtis Ordination
Author(s): Hugh G. Gauch, Jr.
Source: *Ecology*, Vol. 54, No. 4 (Jul., 1973), pp. 829-836
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1935677
Accessed: 10/11/2010 08:09

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=esa.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

http://www.jstor.org

A QUANTITATIVE EVALUATION OF THE BRAY-CURTIS ORDINATION[1]

HUGH G. GAUCH, JR.
Ecology and Systematics, Cornell University Ithaca, New York 14850

Abstract. The Bray-Curtis ordination provides position values (x) along an ordination axis and distances (e) from the axis for samples of communities. Upon ordination, samples are displaced from their true positions on the coenocline axis into an arch the height of which increases as beta (between-habitat) diversity increases. The cause of this displacement is the fact that the similarity measure is not a linear estimator of ecological separation. The shape of this arch and the consequent effects on the x and e values are shown for various beta diversities. Refinements are suggested for the Bray-Curtis ordination.

INTRODUCTION

Since its introduction, the Bray and Curtis (1957) ordination technique has found extensive use. During the past decade, more sophisticated ordination techniques (such as principal components and factor analysis) have been applied to community samples, and there has been some feeling that these techniques ought to be more effective for ecological research (Orloci 1966, Austin and Orloci 1966, Anderson 1971). However, when the purpose of ordination in ecology is not primarily a mathematically efficient arrangement of entities but the clarification of ecological relationships, the judgment on ordination techniques must be based on ecological function and not solely on mathematical elegance or efficiency. Apparently all ordination techniques (except, perhaps, those of direct gradient analysis) produce some distortion in their representation of relationships of samples and species to environmental gradients. That is, there are two distances, the original distances along environmental gradients and the distances computed in an ordination; and these two generally will not bear a perfect relationship to each other; there is distortion.

One of the techniques most widely used is principal components ordination. Given samples from a fairly wide range of community variation, principal components ordination produces severe curvilinear distortions of the linear environmental gradients relating those samples, and yields axes that may consequently be ecologically uninterpretable (Noy-Meir and Austin 1970, Austin and Noy-Meir 1971, Jeglum et al. 1971, Westman 1971, Gauch and Whittaker 1972*a*, *b*). Principal components analysis is not mathematically appropriate to the complex, curvilinear relations of species to one another and environmental gradients. Despite this fact, principal components analysis can be useful when applied with care to sample sets representing a limited range of community variation, and with the support of environmental measurements or direct gradient analysis to check interpretation of the resulting axes. For larger ranges of community variation, and for sample sets without supporting information, principal components ordination (as any other linear model) in ecology may be a precarious technique, potentially more misleading than informative. These points are supported by results from Noy-Meir (*personal communication*), who has recently done an excellent analysis of principal components ordination.

The other most widely used technique, the Wisconson comparative or polar ordination of Bray and Curtis, has its own limitations; but in general it is subject to less distortion and is able to handle a wider range of community variation, especially when used with certain types of distance functions; it is also simpler as a research tool in ecology (Gauch and Whittaker 1972*b*). While principal components ordination will no doubt continue to have a useful role in ecology, direct gradient analysis and the Bray-Curtis technique appear to have much utility. This article seeks to strengthen the usefulness of the Bray-Curtis technique by inquiry into the sources of distortions affecting it, and suggesting means for reducing these distortions.

DISTORTIONS IN ORDINATION

Austin and Orloci (1966, Orloci 1966) were perhaps the first to attempt objective evaluation of some ordination techniques. Although their results indicated superior qualities of ordinations by techniques other than the Bray and Curtis method, subsequent investigations have often led other authors to contrary conclusions (Bannister 1968, Austin and Noy-Meir 1971, Gauch and Whittaker 1972*b*, Whittaker and Gauch 1972). Bannister's (1968) evaluation of ordination techniques was particularly noteworthy. He perceived several problems of the Bray and Curtis technique: that minimum similarity of samples with

[1] This research was supported by a grant from the National Science Foundation. Valuable insights and comments on the manuscript from R. H. Whittaker are gratefully acknowledged. Manuscript received May 26, 1972; accepted December 5, 1972.

other samples may be a poor basis for choosing endpoint samples, since often several samples have similar minimum similarity values; that "in general, stands that are poorly related to all other stands are best avoided"; and that interstand distances within the ordination can be poorly related to the original interstand distances. Nevertheless, he realized, "general experience" has shown that "most published ordinations of this type . . . have been successful in demonstrating correlations between vegetation and habitat."

Westman (1971) ordinated forest communities from the coastal terraces of Mendocino County, California, and noted that the Bray-Curtis ordinations frequently produced a pronounced arch (Fig. 1). Swan (1970) observed that similarity measures can be poor estimators of ecological distance. Swan stressed problems resulting from the bell-shaped (rather than linear or monotonic) response of species importance values along a gradient of community composition (or "coenocline"), and from zero values in a sample similarities matrix. Using simulated data, he showed the consequent distortions. Austin and Noy-Meir (1971) observed that "A survey of published PCA and stand-defined ordinations of vegetation shows that in more than half of them there is at least one major axis which shows a clear curvilinear relationship with another axis, as in Swan's (1970) one-gradient models." They concluded the crux of the problem was distortion due to the incompatibility of the linear mathematical model and the non-linear ecological model of species response

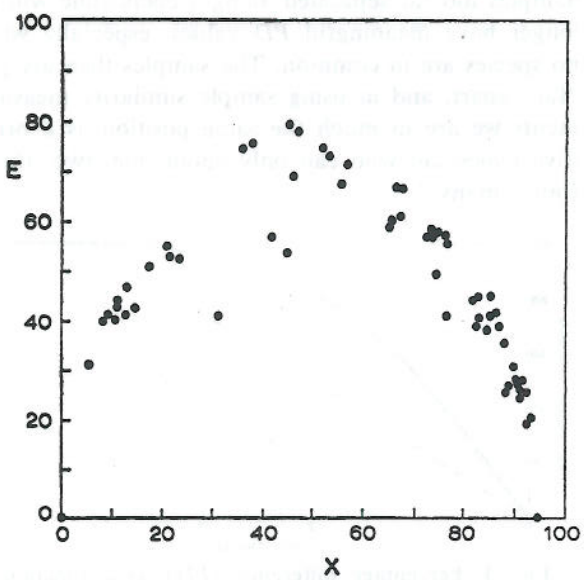

FIG. 1. A typical Bray-Curtis ordination with x and e values showing a pronounced arch, from a study of a vegetation gradient from *Sequoia sempervirens* forest to *Cupressus pygmaea* pygmy forest in Mendocino County, northern California. (Adapted with permission from Westman 1971.)

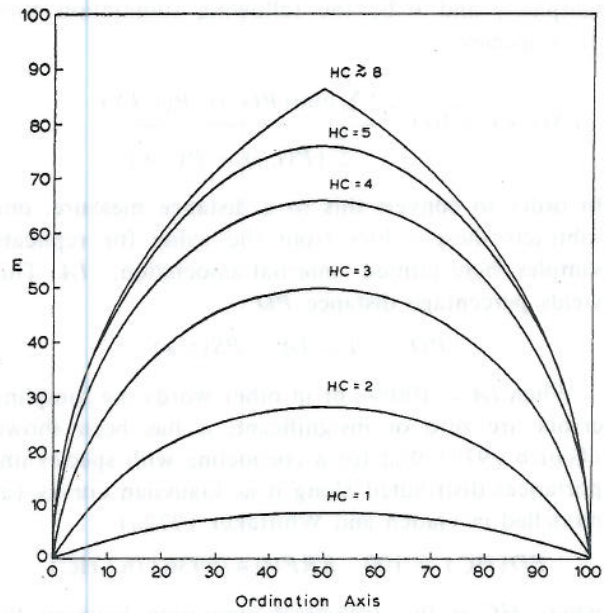

FIG. 2. Shape of the Bray-Curtis arch for six representative levels of beta diversity.

to environment. The introduction by Swan in 1970 of simulated vegetational data may have been necessary to clarify these problems before their effective study could begin.

I shall examine here the source of the arch, its consequences for ordination, and its relation to the similarity measures employed in ecology, using the model of species response along a coenocline developed in a preceding article (Gauch and Whittaker 1972*a*). Although the arch often had been observed, its exact shape or its meaning could not easily be clarified with field data including sample error and sample variation along more than one environmental gradient. The form of the arch, as it appears more clearly from theory (developed in a later section), is shown in Fig. 2.

The distortion in the Bray-Curtis ordination (because of the arch) is different in character from the distortion in principal components ordination. In principal components ordination, all axes are the final products of the ordination. In Bray-Curtis ordination, only the placement of samples along an ordination axis is of primary interest, and not the distance above this axis. Hence displacement of sample positions up onto the arch is of only secondary concern; while the attendant effect on spacing of samples along the ordination axis is of central importance.

THE PERCENTAGE DIFFERENCE MEASURE

The measure of similarity used by Bray and Curtis (1957) was percentage similarity, *PS*, computed from the importance values of species i in samples j, denoted here as $P(i, j)$, defined between pairs of

samples j and k by the following summation over the I species:

$$PS(j, k) = 100 \cdot \frac{2 \sum^{I} \min(P(i, j), P(i, k))}{\sum^{I} (P(i, j) + P(i, k))} .$$

In order to convert this to a distance measure, one subtracts these values from the value for replicate samples; here termed "internal association," IA. This yields percentage distance PD:

$$PD(j, k) = IA - PS(j, k) .$$

When $IA = 100\%$, or in other words the sampling errors are zero or insignificant, it has been shown (Gauch 1973) that for a coenocline with species importances distributed along it as Gaussian curves (as modelled in Gauch and Whittaker 1972*a*)

$$PD(HC) = 100 \cdot ERF(0.4769362762\ \mathrm{HC}) ,$$

where HC is the ecological separation between the two samples along the coenocline axis measured in units of half-changes. Here ERF is the error function defined as

$$ERF(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-u^2}\, du .$$

Its values may be obtained from standard books of mathematical tables; also many computers include the error function as a supplied subprogram. (Unfortunately, ERF is sometimes defined as above but with the argument of the exponent divided by two; this ambiguity can cause confusion if not recognized.) One half-change is simply the amount of ecological separation at which the percentage similarity between two samples equals 50% of the IA (Whittaker 1960). The value at which $ERF(x)$ equals 0.5 is 0.4769362762.

The "half-life" of radioactive decay expresses the coefficient in a negative exponential; hence, for example, after 2 half-lives ¼ of the radioactive material remains. Half-changes, which are defined here by a point on an error function curve, do not possess this characteristic. Thus, though at one HC percentage similarity is 50% of IA, at two HC the value is not the 25% implied by a simple negative exponential, but is approximately 18%. Change in sample similarity along an environmental gradient is neither linear, nor simply a negative exponential. Nevertheless, despite these complexities (or perhaps because of them), half-changes are useful for expressing ecological separation in a form that has some concrete meaning. Another concrete expression of the meaning of half-changes is that half-changes are related to the average width σ of the species curves along a coenocline by a simple relation: one half-change corresponds to that portion of a coenocline axis for which an average of 1.34898 σ is included.

The form of the $PD(HC)$ curve is shown in Fig. 3. Also a dotted straight line is given from the origin through the point at $HC = 1$, to show that the $PD(HC)$ function is very nearly linear up to slightly more than 1 HC. This is a trivial consequence from the fact that the Maclaurin expansion of the error function is

$$ERF(x) = \frac{2}{\sqrt{\pi}} \sum_{n=0}^{\infty} \frac{(-1)^n x^{2n+1}}{n!(2n+1)} ;$$

thus, for small values, $ERF(x) \approx x \cdot c$ (the first term of the expansion times a constant). Hence, PD is a good, almost linear estimator of ecological separation as long as one remains within the range of approximately one half-change. Also, shown as a dashed line are the values of an inverse function of the $PD(HC)$ function which I denote as $PDINV(x)$. The purpose of $PDINV(x)$ is to transform PD values into a linear variable; that is, $PDINV(PD(HC)) = HC \cdot c$, where c is a constant. (I evaluate $PDINV(x)$ by 10 logarithmic searches of $ERF(x)$ values followed by linear interpolation, which is adequate for approximately six significant digits; doubtless other procedures are possible.) That $PD(HC)$ has an asymptote of 100% for large values of HC means that for these HC values this inverse function is not defined; we have chosen $HC = 4$ as a value beyond which $PDINV$ may as well be considered to have the value 100 (in fact, it is between 99.3 and 100). Samples too far separated along a coenocline will no longer have meaningful PD values, especially when no species are in common. The samples then are just "far" apart, and in using sample similarity measurements we are in much the same position as a primitive tribesman who can only count one, two, three, four, "many."

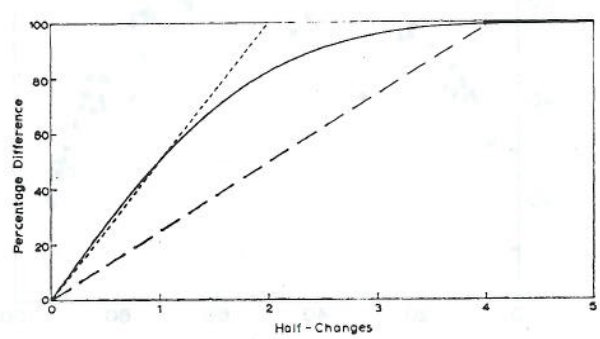

FIG. 3. Percentage difference (PD) as a function of beta diversity, shown by the solid line. The dotted line is a straight line through the origin and the point on the $PD(HC)$ curve at $HC = 1$, showing that for small values $PD(HC)$ is very nearly linear. The dashed line represents a linear estimator of ecological distance, as explained more fully in the text.

The Bray-Curtis Arch

We have noted that the Bray-Curtis ordination tends to distort sample locations into an arch, as in Fig. 1 and 2. Consider in Fig. 3 the dashed line representing a linear estimator of ecological distance. By comparison with a linear estimator, the corresponding *PD* values are too large. It is the fact that these distances are too large that causes the arch.

"Beta" (between-habitat) diversity may be defined as the extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment or a pattern of environments (Whittaker 1960). The height of the arch, relative to the length of the ordination axis, increases with beta diversity and may be computed as follows. In the extreme case of very high beta diversity, the two end points are at a distance of $PD = 100$ from each other, and there will also be samples with $PD = 100$ with respect to both end points, thus placing them at the top of an equilateral triangle with the two end points at the two ends of the base of the triangle. At this extreme, the height becomes simply $100 \cdot (\sqrt{3}/2) = 86.60$, and since the ordination axis length is 100, the height of the arch relative to the axis length obtains this maximum value of 86.60%.

For other beta diversities, the relative height of the arch as a function of *HC* can be computed as follows. For a beta diversity of *HC*, the length of the base line (or ordination axis) L is $L = PD(HC)$. Beals' (1960) equations are

$$x = \frac{L^2 + D_1^2 - D_2^2}{2L}$$

and

$$e = \sqrt{D_2^2 - x^2}$$

where x is the ordination value, e the distance off the axis, and D_1 and D_2 the distances from the first and second end points respectively. But since at the midpoint, or apex of the arch, $D_1 = D_2$, these equations at the apex simplify to

$$x = \tfrac{1}{2}\, PD(HC)$$

and

$$e = \sqrt{[PD(HC/2)]^2 - [PD(HC)/2]^2}\,.$$

Dividing e by the length of the ordination axis yields the desired equation for relative height *RH*:

$$RH(HC) = \frac{100}{PD(HC)} \cdot \sqrt{[PD(HC/2)]^2 - [PD(HC)/2]^2}\,.$$

This function's values are graphed in Fig. 4.

The arch itself may be computed as follows. Let a given coenocline axis have a total beta diversity between its end points of X, which will give an ordination base line length of $L = PD(X)$. Then a plot located x from the first end point has $D_1 = PD(x)$; and distance $X - x$ from the second end point, so that $D_2 = PD(X - x)$. Beals' (1960) equations may then be used to compute the coordinates of points along this arch. The arches for $X = 1, 2, 3, 4, 5$, and $\gtrsim 8$ have been given in Fig. 2, where all arches have been scaled to have the same base line length; this facilitates comparison of the relevant matter, the shape of the arches.

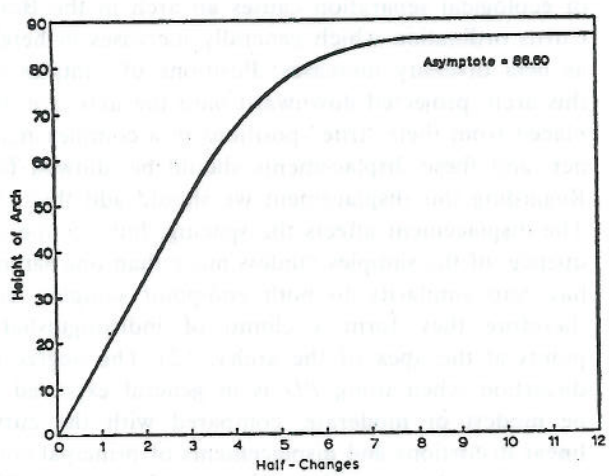

Fig. 4. Height of the arch relative to the length of the ordination axis as a function of beta diversity.

Distortion on the Ordination Axis

For the Bray-Curtis ordination, the primary concern is the arrangement of the samples on the ordination axis itself with their x values being the coordinates; the distances e off the axis are not an essential result in this ordination, and therefore are of only secondary concern. I here examine the effect of beta diversity on the x values.

Consider first the two extremes of beta diversity. If the beta diversity is $HC = 0$, there will be no distortion and consequently the ordinated x values will not be displaced from their original positions on the gradient. But if $HC = \infty$, all samples will be ordinated to the midpoint of the axis, 50, except the end points located at 0 and 100. Thus for a large number of uniformly placed samples along this axis, the average displacement after Bray-Curtis ordination will be 25 (out of an axis length of 100). Such an ordination is entirely uninformative. Thus an average x displacement of 25 may be viewed as complete distortion, and the average x displacements multiplied by 4 may be used as a percentage distortion by the ordination.

Average x displacement, relative to the length of the ordination axis, has been computed using 1,000 sample points placed uniformly along the coenocline

axis. The results are presented in Fig. 5. Distortion climbs to a peak of 6.0 (or 24% distortion) at $HC \approx 3.8$, decreases to a local minimum of 2.2 (or 8.8% distortion) at $HC \approx 6.0$, and thereafter increases monotonically toward an asymptote of 25 (or 100% distortion). The nature of the x value displacements as a function of beta diversity is shown for 10 representative levels of beta diversity in Fig. 6, showing the left half of the ordination axis (the right half is symmetric). The positions on the lowermost x axis represent the undistorted sample locations (for no distorting effect of beta diversity). The top line represents the sample locations with infinite beta diversity; here the left end point is in its correct position, and all other points have been shifted to the midpoint (50). In between these extremes are shown the results of the Bray-Curtis ordination for eight intermediate levels of beta diversity; and the positions taken by each sample point as beta diversities increase are connected, so the direction and amount of displacement will be apparent. The endpoint and the midpoint retain their original positions, never experiencing distortion. For the other points, it is seen that up to $HC \approx 6$ the sample points are being displaced outward. After $HC \approx 6$, the sample points begin drifting inward towards the center, and at $HC \approx 6$–7 many points have drifted back to near their original locations; as HC increases further, the sample points begin to clump into the center. Thus as beta diversity increases, there is at first a general tendency towards dispersal near the ends of the ordination axis; then this trend is reversed and replaced by a clumping into the middle of the ordination axis. Note that as shifting inward begins to replace shifting outward, there is a zone around 6 HC where these two opposite phenomena nearly cancel out each other and many points have drifted back to near their original positions. Thereafter, shifting inward replaces almost entirely shifting outward, so distortion increases. This provides an explanation for the local maximum and minimum that occur in Fig. 5, and the ordination improvement from 3.8 to 6.0 HC that this involves.

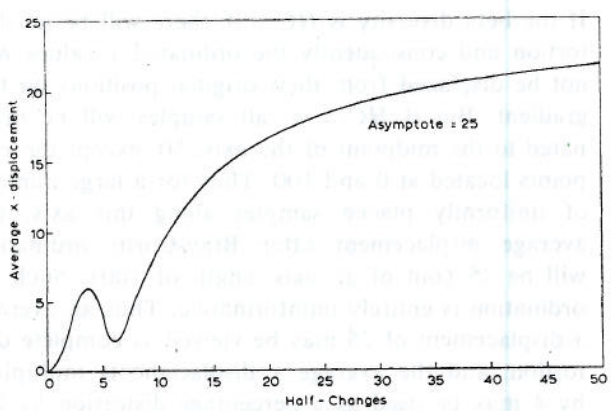

FIG. 5. Average x displacement relative to the length of the ordination axis resulting from distortions in the Bray-Curtis ordination, as a function of beta diversity, using 1,000 uniformly placed samples along the original coenocline axis.

In Fig. 6 it may be noted that at any given level of beta diversity, there is a single point on the ordination axis (left-half) to the left of which all sample points are shifted outwards, and to the right of which all samples are shifted inwards. For example, from Fig. 6, at a beta diversity of 7.5 HC, sample points to the left of approximately 15 are shifted outwards, and those to the right of approximately 15 are all shifted inwards. The position of this transition can be found by a logarithmic search algorithm. The results summarize where sample points are shifted inward or outward, and are presented in Fig. 7. The ordinate is a coenocline axis (in arbitrary units of 0 to 100, relativizing all axes to this same length), and the abscissa represents beta diversity increasing from 0 to 15 HC. The line shows the transition line between shifting outwards and inwards as a consequence of the distortions in the Bray-Curtis ordination; sample points on this line experience no displacement. Sample points above the line are displaced toward the middle, and below the line toward the ends. Note in particular that below approximately 5.92 HC only displacement toward the ends occurs, that at 6.25 HC approximately half the points are shifted outwards and half shifted inwards (causing clumping of sample points both at the center and at the ends), and that for higher beta diversities there is a rapidly increasing dominance of shifting inwards. The rapid replacement of shifting outwards by shifting inwards is striking; only 0.4 HC after shifting inwards begins, it has overtaken half the ordination axis.

SUGGESTED REFINEMENTS

The fact that PD values exceed a linear estimator of ecological separation causes an arch in the Bray-Curtis ordination which generally increases in height as beta diversity increases. Positions of samples on this arch, projected downward onto the axis, are displaced from their "true" positions in a complex manner, and these displacements should be allowed for. Regarding this displacement we should add that (1) The displacement affects the spacing, but not the sequence, of the samples (unless more than one sample has zero similarity to both end-point samples, and therefore they form a clump of indistinguishable points at the apex of the arch). (2) The degree of distortion when using PD is in general expected to be modest or moderate, compared with the curvilinear distortions and displacements of principal components analysis based on the covariance. (3) Displacements of the same kind are obtained in the

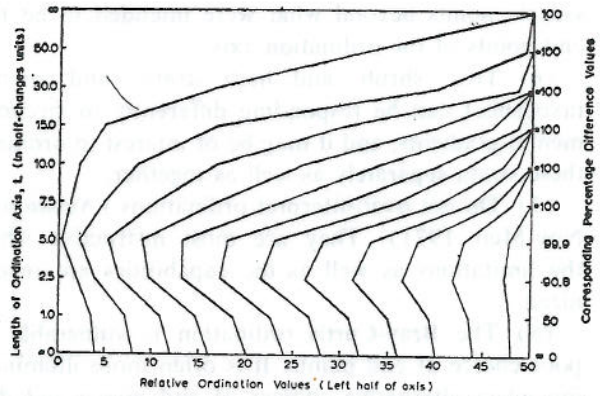

FIG. 6. The Bray-Curtis ordinations (left half of axis; the right half is symmetric) showing nature of displacement of sample points on the ordination axis, with true positions as indicated on the lowermost x axis, for 10 levels of increasing beta diversity (Y axis, L values expressed in half-changes, with corresponding percentage difference values on right margin). To determine expected displacements in a given application of Bray-Curtis ordination, locate L, the length of the ordination axis, on the Y axis; and trace a horizontal line from this across the chart. The positions of samples where intersected by this line, compared with their true positions on the lowermost X axis, indicates direction and degree of displacement. Note that up to $HC \approx 5$ the sample positions are displaced toward the ends of the ordination axis, and thereafter the trend reverses and by $HC \approx 8$ most sample positions are clumping in toward the midpoint of the ordination axis.

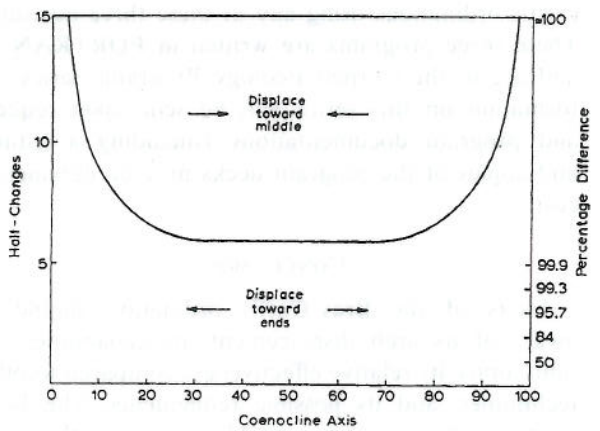

FIG. 7. The transition upon the Bray-Curtis ordination of displacement of sample points from their true position on the coenocline axis toward the middle or ends of the axis, as a function of increasing beta diversity (corresponding percentage distance is shown on the right margin). Points inside the curve are displaced towards the middle, those outside towards the ends. Note the rapid reversal of tendency around 6 HC.

Bray-Curtis technique with the use of such other sample similarity measures as coefficient of community (Sørensen 1948) and Euclidean distance because they are also curvilinear in relation to sample separation on the gradient (Gauch 1973). Euclidean distance in particular is more strongly curvilinear than is percentage similarity, and produces a greater distortion of the ordination (Gauch and Whittaker 1972*b*). And, (4) the Beals (1960) equations for x and e implicitly assume Euclidean metric properties, whereas PD may not have this property (Orloci 1972, *personal communication*). Alternatives avoiding this problem should be investigated.

Besides the fact that PD is a nonlinear measure of ecological separation, the Bray-Curtis algorithm has two other problems. One is that the Bray-Curtis technique (as originally presented) selects end points by searching for the lowest similarity index, and this step can fail entirely if there is no unique lowest value. The other is that vegetation generally has several gradients, not one; and although the Bray-Curtis technique provides reasonably effectively for extraction of further axes, the effects of the several gradients are sometimes intermixed in a more complicated manner than Bray-Curtis ordination can sort out satisfactorily.

Beyond recognition of the above problems, several specific recommendations may be made:

(1) Limit beta diversity (Swan 1970, Austin and Noy-Meir 1971, Gauch and Whittaker 1972*b*). The Bray-Curtis ordination cannot be expected to perform well with a beta diversity over several half-changes. Subdivision of the total data set into subsets with reasonable beta diversities is often desirable (Jeglum et al. 1971, Westman 1971, Cottam et al. 1972). Samples too widely different from all other samples should be avoided, especially in choice of end points (Bannister 1968).

(2) Grouping of similar samples into composite samples is sometimes advantageous (Whittaker 1956, Cottam et al. 1972). Use of composite end-point samples (Whittaker 1960), as these are compared with the remaining individual samples, may improve ordination by reducing the effects on ordination resulting from error and irregularity in the composition of individual end-point samples. Grouping of all samples of the set into composite samples for ordination (Frydman and Whittaker 1968, Maarel 1969) requires some kind of classification, but sometimes clarifies results by reducing the effects of sample error and population irregularity in individual samples. Such grouping may also make possible ordination of large sample sets. Decisions on optimal number of samples for a given ordination (to represent adequately the variability of communities under study, without excessive field and computational effort) are not easy. Use of composite samples may aid in ordination when the purposes of field research have resulted in sample sets that are otherwise unwieldy, or unduly expensive even for computer ordination. By the same reasoning, grouping of sets of

species with similar distributions is sometimes useful (Frydman and Whittaker 1968, Maarel 1969). Grouping of either samples or species, by decreasing sample irregularity and increasing similarity measurements, may extend somewhat the range of beta diversity that can be included in a set without making ordination ineffective. In effect, the grouping reduces false beta diversity resulting from sample irregularity.

(3) Bray and Curtis (1957) had the smallest similarity index objectively determine the end-point pair to use. I find that in practice this method can fail because there are several zeros, or can be meaningless because other candidate samples are near enough to the smallest index to be statistically indistinguishable, or can lead to a choice without evident ecological meaning. For many research purposes, deliberate end-point pair selection based upon ecological knowledge of the data at hand may be best.

(4) Bray and Curtis used percentage difference, but other measures such as coefficient of community or Euclidean distance can also be used and may emphasize different aspects of community composition (Bannister 1968, Westman 1971, Gauch and Whittaker 1972*b*, Whittaker and Gauch 1972). Also Bray and Curtis applied a double standardization to the original data matrix prior to computation of the *PS* secondary matrix. I have found that in some applications this causes more difficulty than advantage, and do not recommend its universal use (also see Austin and Greig-Smith 1968). However, in situations where the totals of importance values in samples are variable, simple relativization of these importance values (to total 100 percent in each sample) may aid ordination. Also, use of the *PDINV* function as a linearizing transform improves Bray-Curtis ordination with moderate beta diversity, and slightly extends the range of beta diversity that can be handled by this ordination (Gauch 1973; also see Austin and Noy-Meir 1971, Cottam et al. 1972). In addition, use of this transform restores metric properties (because $D_1 + D_2 = L$, so there is no upward extension into a triangle anyway).

(5) Percentage similarity and coefficient of community must be subtracted from 100% or an internal association to obtain distance measures. Bray and Curtis (1957) used 85% as an average internal association. Happily, Bannister (1968) has shown that the *IA* value makes relatively little difference, and there is usually little profit from using anything other than 100%. To this it may be added that overestimating *IA* causes less distortion than underestimating it, so it is safer to use an overestimate when in doubt. If *IA* is too small, then too short a base line, or negative distance values, or both, can result. This produces strong distortion, particularly around the ends of the ordination axis, including placement of sample points beyond what were intended to be the end points of the ordination axis.

(6) Tree, shrub, and herb strata (and animal taxocenes) can be responding differently to environmental gradients, and it may be of interest to ordinate these strata separately as well as together.

(7) Do not over-interpret ordinations (Austin and Noy-Meir 1971). They are most instructive when the limitations as well as the capabilities are recognized.

(8) The Bray-Curtis ordination is vulnerable to poor choice of end points. It is often more illuminating when alternative choices of end points and distance measures are compared, or when Bray-Curtis is compared with other ordinations in treatment of a given sample set (Bannister 1968, Swan 1970, Gauch and Whittaker 1972*b*, Cottam et al. 1972). More generally, the Bray-Curtis ordination may be most successful when supported by other means of interpretation, such as direct gradient analysis, classification, and knowledge from the field of the communities, environmental gradients, and species characteristics (Gauch and Whittaker 1972*b*).

We have written computer programs to doubly standardize or relativize a data matrix; to compute percentage similarity, coefficient of community, and Euclidean distances as secondary matrices from the original species importances matrix; and to do Bray-Curtis ordinations using any of these three measures. These three programs are written in FORTRAN IV and are in the Cornell Ecology Programs series. Information on this series will be sent upon request, and program documentations (including a listing) and copies of the program decks may be obtained at cost.

Conclusion

Users of the Bray-Curtis ordination should be aware of its arch displacement, its capabilities and limitations, its relative effectiveness compared to other techniques, and its possible refinements. The Bray-Curtis arch is an interpretable aspect of this technique. For beta diversities of more than several half-changes, the Bray-Curtis ordination is not effective and other tactics must be used, such as subdivision of the data set, direct environmental gradient analysis, or weighted-average ordination (Whittaker 1967). Within these limits, the Bray-Curtis ordination is useful, with advantages of both relative simplicity and relative freedom from distortion as compared with many other and more complex ordination techniques (Gauch and Whittaker 1972*b*). The Bray-Curtis ordination has been a popular and useful technique; I hope that a more critical appreciation of its errors and possible refinements will add to its usefulness as a tool in ecological research.

LITERATURE CITED

Anderson, A. J. B. 1971. Ordination methods in ecology. J. Ecol. **59**: 713–726.

Austin, M. P., and P. Greig-Smith. 1968. The application of quantitative methods to vegetation survey. II. Some methodological problems of data from rain forests. J. Ecol. **56**: 827–844.

Austin, M. P., and I. Noy-Meir. 1971. The problem of non-linearity in ordination: experiments with two-gradient models. J. Ecol. **59**: 763–773.

Austin, M. P., and L. Orloci. 1966. Geometric models in ecology. II. An evaluation of some ordination techniques. J. Ecol. **54**: 217–227.

Bannister, P. 1968. An evaluation of some procedures used in simple ordinations. J. Ecol. **56**: 27–34.

Beals, E. W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. **72**: 156–181.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. **27**: 325–349.

Cottam, G., F. G. Goff, and R. H. Whittaker. 1972. Wisconsin comparative ordination [German summary] *In* R. Tüxen [ed.] Handbook of Vegetation Science, Part V, Ordination and classification of communities, R. H. Whittaker [ed.] Junk, The Hague. (*In press*).

Frydman, I., and R. H. Whittaker. 1968. Forest associations of southeast Lubin Province, Poland. Ecology **49**: 896–908.

Gauch, H. G. 1973. The relationship between sample similarity and ecological distance. Ecology (*In press*).

Gauch, H. G., and R. H. Whittaker. 1972*a*. Coenocline simulation. Ecology **53**: 446–451.

———. 1972*b*. Comparison of ordination techniques. Ecology **53**: 868–875.

Jeglum, J. K., C. F. Wehrhann, and J. M. A. Swan. 1971. Comparisons of environmental ordinations with principal component vegetation ordinations for sets of data having different degrees of complexity. Can. J. For. Res. **1**: 99–112.

Maarel, E. van der. 1969. On the use of ordination models in phytosociology. Vegetatio **19**: 21–46.

Noy-Meir, I., and M. P. Austin. 1970. Principal component ordination and simulated vegetation data. Ecology **51**: 551–552.

Orloci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecol. **54**: 193–215.

Sørensen, T. A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Biol. Skr. K. Dan. Vidensk. Selsk. **5**(4): 1–34.

Swan, J. M. A. 1970. An examination of some ordination problems by use of simulated vegetational data. Ecology **51**: 89–102.

Westman, W. E. 1971. Production, nutrient circulation, and vegetation-soil relations of the pygmy forest region of northern California. Ph.D. Thesis. Cornell Univ., Ithaca, N.Y.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. **26**: 1–80.

———. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. **30**: 279–338.

———. 1967. Gradient analysis of vegetation. Biol. Rev. **42**: 207–264.

Whittaker, R. H., and H. G. Gauch. 1972. Evaluation of ordination techniques [German summary] *In* R. Tüxen [ed.] Handbook of vegetation science, Part V, Ordination and classification of communities, R. H. Whittaker [ed.] Junk, The Hague. (*In press*).