

An evaluation of the relative robustness of techniques for ecological ordination

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Abstract

Simulated vegetation data were used to assess the relative robustness of ordination techniques to variations in the model of community variation in relation to environment. The methods compared were local non-metric multidimensional scaling (LNMDS), detrended correspondence analysis (DCA), Gaussian ordination (GO), principal components analysis (PCA) and principal co-ordinates analysis (PCoA). Both LNMDS and PCoA were applied to a matrix of Bray-Curtis coefficients. The results clearly demonstrated the ineffectiveness of the linear techniques (PCA, PCoA), due to curvilinear distortion. Gaussian ordination proved very sensitive to noise and was not robust to marked departures from a symmetric, unimodal response model. The currently popular method of DCA displayed a lack of robustness to variations in the response model and the sampling pattern. Furthermore, DCA ordinations of two-dimensional models often exhibited marked distortions, even when response surfaces were unimodal and symmetric. LNMDS is recommended as a robust technique for indirect gradient analysis, which deserves more widespread use by community ecologists.

Introduction

Ordination techniques are commonly employed as research tools in the study of vegetation. A major objective of ordination in vegetation ecology is that which Whittaker (1967) termed indirect gradient analysis. When faced with the diversity of available

methodology, ecologists have sought to identify those techniques which are most appropriate for the purpose of indirect gradient analysis.

Three major approaches to the comparative evaluation of ordination techniques may be identified:

(1) The application of different ordination methods to sets of field data (e.g. Prentice, 1977; Clymo, 1980; Oksanen, 1983; Brown *et al.*, 1984).

(2) The comparison of vegetational ordinations with direct ordinations based on environmental indices (e.g. Loucks, 1962; Del Moral, 1980).

(3) The use of simulated data, derived from explicit models of community variation along environmental gradients (e.g. Swan, 1970; Austin, 1976; Fasham, 1977; review by Whittaker & Gauch, 1978; Prentice, 1980).

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The first strategy suffers from the major limitation that there is no precise statement of the underlying gradient structure which a successful ordination is expected to recover. The ordination results are assessed on the basis of preconceptions about the major environmental relationships derived from previous work. It is seldom possible to make quantitative statements about sample positions on the underlying environmental gradients which are sufficiently precise to allow a sensitive comparison of the performance of different ordination methods and independent of the biases of the formal or informal methods of vegetation analysis used in previous work.

The second approach assumes that the axes chosen for direct ordination do indeed represent the major gradients to which vegetational composition is related. There is usually no way to assess the validity of this assumption. Furthermore, it is often extremely difficult to identify an environmental variable which is susceptible to measurement and which adequately expresses the dynamic complexity of inter-related factors which characterises many environmental gradients.

The third, the simulation approach, has a number of advantages:

(1) The expected result of ordination can be specified precisely, using the known co-ordinates of sites in the simulated environment space.

(2) Various model properties may be varied independently in order to study their effects on ordination success, both alone and in combination.

(3) The degree of stochastic variation (noise) can be controlled.

The major limitation is that the models employed may not be adequate simplifications of the natural situation (Austin, 1980; Greig-Smith, 1980). Since the initial work of Swan (1970), most simulation studies have used models which assume that species responses are Gaussian, that sites are spread uniformly throughout environment space and that community properties such as alpha diversity (number of species per sample) and sample total (total abundance of all species in a sample) do not vary systematically along gradients. All these assumptions may be questioned.

The available *evidence*, from direct observations

of species' response along recognised gradients and experimental studies with mixed communities, is insufficient to develop a general model of community change along gradients (Austin, 1980). The assumptions which Gauch & Whittaker (1972a, 1976) built into their computer programs for the generation of artificial data are still only hypotheses, the critical testing of which is just beginning (Minchin, 1983; Austin, 1985, 1987). It follows that the most one can expect to achieve in simulation studies is the identification of techniques which are *robust* to variation in those features of a vegetation-gradient model which fall within the bounds of current possibilities (cf. Austin, 1976, 1980, 1985). A robust method should be capable of achieving an adequate recovery of the underlying gradients over a range of model properties. This study assesses the comparative robustness of several ordination methods.

Methods

Models

The artificial data matrices used in this comparison were generated using an early version of COENOS, a flexible computer program for the simulation of community variation along environmental gradients (Minchin, 1983, 1987), which is available upon request. The program simulates species responses using a generalised beta-function, which can produce unimodal response surfaces of differing skewness. Interaction may be introduced between species, leading to ecological responses which are shouldered, bimodal or multimodal. COENOS can produce models with up to six gradients and there are flexible options for sampling patterns and the introduction of stochastic variation (noise). In addition, the variation along gradients of community properties such as alpha diversity and sample total can be controlled.

The following model properties were examined in this study:

(1) The number of underlying gradients (1 or 2) and their beta diversities or compositional lengths.

(2) The shape of species' ecological responses (symmetric/skewed, unimodal/bimodal/multimodal).

(3) The arrangement of sites in the simulated environment space (regular/random/clumped/restricted).

Table 1. The structure of the simulation experiments designed to examine the joint effects of model properties on the performance of ordination techniques. The beta diversity of gradients is expressed in R units, where a gradient of $1R$ is equal in length to the mean range of species occurrence. Quantitative noise levels are expressed in the F units defined by Gauch & Whittaker (1972a).

Models with a single simulated gradient (coenoclines)				
Expt. no.	Model properties held constant	Model properties varied	Replicates per cell	Total no. of models
A1	Response curve shape (symmetric) Sampling pattern (regular) Trend in sample totals (not controlled)	Beta diversity (5 levels: 0.25, 0.5, 1, 2, 4 <i>R</i>) Quantitative noise (3 levels: 0.0, 0.1, 0.2 <i>F</i>) Qualitative noise (2 levels: absent, present)	1	30
A2	Beta diversity (1 <i>R</i>) Sampling pattern (regular) Quantitative noise (0.0 <i>F</i>) Qualitative noise (absent) Trend in sample totals (not controlled)	Response curve shape (6 lev.: symmetric, slight consistent skewness, <i>ibid.</i> extreme, mixed skewness, interaction between symmetric curves, <i>ibid.</i> skewed curves)	3	18
A3	Beta diversity (1 <i>R</i>) Sampling pattern (regular) Trend in sample totals (not controlled)	Response curve shape (6 lev. as in A2) Quantitative noise (3 lev.: 0.0, 0.1, 0.2 <i>F</i>) Qualitative noise (2 lev.: absent, present)	1	36
A4	Beta diversity (1 <i>R</i>) Quantitative noise (0.0 <i>F</i>) Qualitative noise (absent) Trend in sample totals (not controlled)	Response curve shape (4 lev.: symmetric, extreme consistent skewness, interaction between symmetric curves, <i>ibid.</i> skewed curves) Sampling pattern (4 lev.: regular, random, concentrated in centre, concentrated towards ends)	1	16
A5	Beta diversity (1 <i>R</i>) Sampling pattern (regular) Quantitative noise (0.0 <i>F</i>) Qualitative noise (absent)	Response curve shape (4 lev. as in A4) Trend in sample totals (3 lev.: not controlled, linear trend, parabolic trend)	1	12
Models with two simulated gradients (coenoplanes)				
B1	Response surface shape (symmetric) Sampling pattern (regular) Trend in sample totals (not controlled)	Beta diversities (3 lev.: $0.33 \times 0.33R$, $1 \times 0.33R$, $1 \times 1R$) Quantitative noise (3 lev.: 0.0, 0.1, 0.2 <i>F</i>) Qualitative noise (2 lev.: absent, present)	1	18
B2	Sampling pattern (regular) Quantitative noise (0.0 <i>F</i>) Qualitative noise (absent) Trend in sample totals (not controlled)	Beta diversities (2 lev.: $1 \times 0.33R$, $1 \times 1R$) Response surface shape (5 lev.: symmetric, slight consistent skewness, <i>ibid.</i> extreme, mixed skewness, interaction between skewed curves)	3	30
B3	Sampling pattern (regular) Qualitative noise (absent) Trend in sample totals (not controlled)	Beta diversities (2 lev.: $1 \times 0.33R$, $1 \times 1R$) Response surface shape (5 lev. as in B2) Quantitative noise (3 lev.: 0.0, 0.1, 0.2 <i>F</i>)	1	30
B4	Beta diversities ($1 \times 1R$) Quantitative noise (0.0 <i>F</i>) Qualitative noise (absent) Trend in sample totals (not controlled)	Response surface shape (3 lev.: symmetric, extreme consistent skewness, interaction between skewed curves) Sampling pattern (5 lev.: regular, random, concentrated in centre, concentrated around edges, T-shaped pattern, cross-shaped pattern)	1	18

(4) The type (quantitative/qualitative) and amount of noise.

(5) The trend of sample total along gradients (none/linear/parabolic).

A number of experiments were designed in which two or three of the properties were varied factorially while the others were held at a constant value. The structure of the experiments is summarized in Table 1. Computing limitations restricted the amount of replication. Since the robustness of ordination techniques to variation in response shape was of major interest, three replicates per treatment cell were employed in the two experiments on response shape (Table 1: A2, B2).

In all, 174 data matrices were produced, 87 with a single underlying gradient and 87 with two gradients. Some data matrices took part in more than one experiment (e.g. the noiseless, 1R data set in experiment A1 was also used as one of the symmetric response shape models in experiment A2). Each data set was subjected to ordination by each of the techniques listed below, with the exception that Gaussian ordination (GO) was applied to the unidimensional models only: the program used for GO produces only one ordination axis.

Complete details of model construction are given by Minchin (1983). In all models, the total number of species was adjusted to give an average of about 25 species per sample in the data sets created without noise. The modal abundances of species were allocated from a lograndom distribution, with limits of 1 to 100 for models with no interspecific interaction and 5 to 100 for interaction models. Species' modal positions were randomly distributed. In the models without interspecific interaction, those 15% of species with the largest response function integrals had their modes adjusted to a more even spacing (see Minchin, 1983, 1987 for more details). Ranges of occurrence on each gradient were allocated from a normal distribution, with the mean value determining the compositional length (beta diversity) of the gradient. Minchin (1987) introduced the 'R' unit to express the beta diversity of simulated gradients. A beta diversity value of 1R indicates a gradient whose length is equal to the mean range of species occurrence. There is no simple relationship between the R unit and other common measures of beta diversity, such as the half-change (Whittaker, 1960) or the *sd* unit (Hill & Gauch, 1980). However, 1R is approximately equal to 6 *sd* and 4.5 half-changes, when response functions are unimodal, fairly symmetrical and not grossly long-tailed or flat-topped. The standard deviation of species' ranges was set at 0.3 times the mean value for models without interspecific interaction and 0.5 times the mean for interaction models. The differences in the simulation parameters for interaction models, relative to those for non-interaction models, were determined after initial empirical trials. The aim was to produce interaction models with a reasonable number of complex ecological response functions but without too many 'extinctions' of species due to the interaction adjustments.

The choice of a lograndom distribution for modal abundances is based on analyses reported by Minchin (1983) and Gauch & Whittaker (1972a). No good evidence is available about

the frequency distribution of ranges of occurrence. A normal distribution was accepted as a working hypothesis on the basis of preliminary, informal analyses of Gauch & Whittaker (1972a). The use of a random distribution for species modes accords with the results of Minchin (1983). Austin (1987) suggests that the distribution of modes tends to be clumped, but his analysis was restricted to a single functional guild (canopy trees).

Techniques compared

From the range of available ordination techniques, five were selected for comparative evaluation:

1. Principal components analysis (PCA) (Hotelling, 1933).
2. Principal co-ordinates analysis (PCoA) (Gower, 1966).
3. Detrended correspondence analysis (DCA) (Hill & Gauch, 1980), using the program DECORANA (Hill, 1979).
4. Gaussian ordination (GO), (Gauch *et al.*, 1974), using Cornell Ecology Program 8B (Gauch, 1979).
5. Local non-metric multidimensional scaling (LNMDs) (Kruskal, 1964a, b; Sibson, 1972), using the program KYST (Kruskal *et al.*, unpubl.).

PCA has been shown in previous simulation studies (e.g., Noy-Meir & Austin, 1970; Austin & Noy-Meir, 1971; Gauch & Whittaker, 1972b; Fasham, 1977) to produce distorted representations of underlying gradients unless beta-diversity is low. The reason for the distortion is that the mathematical model of PCA implies a linear relationship between compositional dissimilarity (as expressed by the Euclidean metric calculated from species data) and the separation of sites along environmental gradients. In fact the relationship is non-linear: as one moves further apart in environment space, the rate of increase in compositional dissimilarity tends to decline (Swan, 1970). In order to fit its linear model, PCA must represent gradients as curved, rather than linear trends.

Despite the recognition that the linear model of PCA is inappropriate unless beta diversity is very low, the method continues to be applied to community data by plant ecologists (e.g., Bradford & Scagel, 1984; Van der Maarel *et al.*, 1985) and is apparently popular with animal ecologists (e.g., Rotenberry & Wiens, 1980). This may be partly due to a lack of acceptance of the results of simulation studies, because the Gaussian models employed therein were regarded as unrealistic. Thus PCA was included in this study to test the expectation that its linear model would lead to similar distortions with a range of alternative non-linear response models.

The performance of PCA, as a method of indirect gradient analysis, varies according to the manner in which the data are

standardized (Austin & Noy-Meir, 1971). In this study, PCA was applied with each of three standardizations: (1) centred by species mean; (2) centred by species and standardized by species standard deviation (equivalent to an R-mode PCA of the correlation matrix between species) and (3) Bray-Curtis successive double standardization (i.e. species adjusted to equal maxima, then samples standardized to equal totals), followed by centring by species. The abbreviations PCA-C, PCA-CS and PCA-BC will be used below when referring to these three variants of PCA.

PCoA is effectively a generalization of PCA which allows the use of a much wider range of measures of compositional dissimilarity. In this study it was applied to the Bray-Curtis coefficient which is also known as percentage difference (Gauch, 1982) and the Czekanowski coefficient (see, e.g., Greig-Smith, 1983). This coefficient has been widely used in ecology. Values of the Bray-Curtis coefficient have a less curvilinear relationship with environmental separation (the distance between samples in environmental space) than do values of the Euclidean distance metric (Gauch, 1973; Faith *et al.*, 1987). It was therefore expected that the use of this coefficient might increase the effectiveness of PCoA relative to PCA.

The remaining three techniques, GO, DCA and LNMDS, have been introduced to ecology as potential solutions to the problem of curvilinear distortion in linear ordinations. On the basis of simulation studies using Gaussian models (Hill & Gauch, 1980; Gauch *et al.*, 1981) DCA is now commonly regarded as the 'state of the art' method (Gauch, 1982). It is gaining broad acceptance among ecologists (e.g. Walker & Peet, 1983; Beatty, 1984; Van der Maarel *et al.*, 1985). However, the sensitivity of DCA to departures from the Gaussian model has not been assessed.

The underlying model of NMDS is relatively simple: given a matrix of resemblances (similarities or dissimilarities) between pairs of objects, NMDS constructs a configuration of points in a specified number of dimensions, such that the rank order agreement between the inter-point distances and the resemblance values is maximized. In ecological applications the objects are usually samples and the dissimilarities are calculated from the compositional data using some chosen coefficient. The epithet 'non-metric' refers to the fact that only the rank order of the input dissimilarities is utilized. This contrasts with methods of metric scaling (e.g. PCA, PCoA, correspondence analysis) where the distances between points in the derived configuration are *proportional* to the dissimilarities.

Gauch (1982; see also Gauch *et al.*, 1981), who stated that NMDS assumes 'monotonicity, which is a weaker and better assumption than linearity but is still unrealistic for handling the Gaussian curve, which is ditonic', confused the model of species' responses to gradients with the model of the relationship between ordination distance and compositional dissimilarity. The monotonicity assumption of NMDS refers to the latter. NMDS does not make a direct assumption about the form of species response functions. In theory, NMDS can accommodate any type of response function, provided that the resulting relationship between compositional dissimilarity (as expressed by some dissimilarity coefficient) and sample separation in environment space remains approximately monotonic.

The 'global' variant of NMDS derives a configuration in which the distances between all pairs of sample-points are, as far as possible, in rank order agreement with their compositional dissimilarities. Any given pair of samples which are less similar in composition than some other pair should be placed further apart than that other pair in the ordination. The 'local' variant of NMDS (Sibson, 1972) has a more relaxed criterion: for each sample, the distances from its point to each other sample-point in the ordination should be in rank order with the compositional dissimilarities between that sample and each other sample. This variant allows for the possibility that the pattern of decline in compositional dissimilarity with increasing environmental separation may differ from point to point in environment space (Prentice, 1977, 1980).

In this study, NMDS was applied in the 'local' form and DCA ordinations were used to provide starting configurations. The Bray-Curtis coefficient was used as a measure of compositional dissimilarity, thus making the NMDS ordinations directly comparable to the ordinations by PCoA. Previous work with Gaussian models (Gauch, 1973) has shown that the Bray-Curtis coefficient has an approximately monotonic relationship with sample separation along gradients. Faith *et al.* (1987) used a range of models similar to those in this study to compare the rank correlations between compositional dissimilarity and sample separation for a variety of dissimilarity coefficients. The Bray-Curtis coefficient was among the most effective and robust of the measures compared. The coefficient attains a maximum value of 1.0 for all pairs of samples which have no species in common. Values of 1.0 are indeterminate, in the sense that they indicate only a lower bound on the gradient separation of a sample pair. For this reason, all values of 1.0 were coded as 'missing' in the present LNMDS ordinations. This results in the exclusion of such sample-pairs from the monotonic regressions of distance on dissimilarity. Stress formula 1 of Kruskal (1964a) was used and the 'primary' approach to tied dissimilarities was adopted (Kruskal, 1964a): if several pairs of samples have an identical compositional dissimilarity, they need not be given equal distances in the ordination. Model data sets with a single gradient were ordinated in both one and two dimensions, while models with two gradients were subjected to LNMDS in two and three dimensions.

Gauch *et al.* (1981) compared several available programs for NMDS and recommended ALSCAL (Young & Lewycky, 1979) as the fastest and most useful. Unfortunately, ALSCAL does not perform NMDS as originally proposed by Kruskal (1964a, b). ALSCAL uses an alternating least-squares algorithm, which maximizes the monotonic fit between *squared* ordination distances and *squared* compositional dissimilarities. Consequently, the larger dissimilarities receive relatively higher weight in the fitting process. These dissimilarities, between samples with few or no species in common, are the least informative. ALSCAL ordinations therefore tend to represent local structure poorly. Comparisons based on simulated data sets (Minchin, Faith & Belbin, unpublished) have shown that NMDS ordinations by KYST consistently recover the gradient structure much more successfully than ALSCAL ordinations. All LNMDS ordinations in this study were performed using the program KYST.

Assessment of fit

For the purpose of indirect gradient analysis, a successful ordination is defined as one in which the relative positions of samples matches their relative locations in environment space. Consequently, ordination performance may be assessed by comparing ordination configurations with the configuration of samples in the simulated environmental space.

A quantitative measure of the degree of fit between an ordination and the environmental configuration was obtained using Procrustean analysis (Schönemann & Carroll, 1970; Fasham, 1977). This technique fits one configuration to another using a combination of origin translation, rigid rotation and reflection of reference axes and uniform central dilation or contraction of scaling. The combination of transformations is found analytically, so as to minimize the sum of the squared distances between each point in the fitted configuration and its corresponding point in the target configuration. The RMS average of these displacements may be used as a measure of the discrepancy between the configurations (i.e. lower values indicate better fit). In presenting the results, the Procrustean discrepancy values are denoted by the symbol D , with a subscript indicating the number of dimensions in which the fit was performed.

For LNMDS ordinations performed with one more dimension than the number of gradients in the model, Procrustean analysis was performed in the higher dimensionality. This was achieved by adding an extra dimension to the simulated configuration, upon which each sample was given a score of zero. After fitting the ordination to the environmental configuration embedded in this space, the RMS displacement (D) was computed in the subspace defined by the original model gradient(s).

A limitation of D is that it can not distinguish situations where the lack of fit is due to a *systematic* distortion of the target configuration from those in which each point has been independently perturbed. In the first case, the fit is generally much better in some regions of the configuration than in others. Because of this limitation, the assessment of ordination performance was not restricted to comparison of the D values. All configurations were plotted and examined visually.

For unidimensional models, the degree of rank-order agreement between site locations along the simulated gradient and site scores on the first ordination axis was also assessed. Kendall's rank correlation coefficient (τ) was used for this purpose.

Results

PCA and PCoA

Curvilinear distortion of the underlying gradient(s) was evident in all PCA ordinations, irrespective of response function shape or other mod-

el properties. The distortion became more severe as beta diversity increased. Of the three variants of PCA examined, PCA-CS was the most resistant to distortion and PCA-C was the least successful. These results are consistent with those of earlier studies, based on Gaussian models (e.g. Noy-Meir & Austin, 1970; Austin & Noy-Meir, 1971; Fasham, 1977). It is evident that the curvilinear distortion of gradients by PCA is not due to peculiar properties of the Gaussian model.

PCoA with the Bray-Curtis coefficient performed similarly to PCA. In general, the degree of curvilinear distortion in PCoA ordinations was somewhat greater than in those produced by PCA-CS. For unidimensional models, the sequence of sites along the simulated gradient appeared as a curved path in the space defined by the first two axes of a PCA or PCoA ordination. Even when sites were regularly spaced along the model gradient they sometimes appeared bunched in PCA or PCoA ordinations, reflecting the curvature of the gradient into the third (or higher) dimensions.

With two underlying gradients, the consequences of curvilinear distortion by PCA and PCoA were more severe (Fig. 1). The planar pattern of sites in environment space was twisted and curved into three or more dimensions, making the recognition of the two-gradient structure in the resultant ordination impossible without prior knowledge of the underlying model. If the lines joining sets of sample points with equal co-ordinates on the second simulated gradient were deleted from Fig. 1, it would be very difficult to perceive the underlying gradients in the ordinations. The distortion is not difficult to recognize for unidimensional data sets, when an arch or horse-shoe shaped configuration is usually obtained in the first two dimensions. However, the planar structure of a two-dimensional data set can be twisted and curved into more than three dimensions, so that the shape of the configuration cannot be viewed in any two or three dimensional plot.

Gaussian ordination

The only combination of model properties in which GO consistently produced better results than

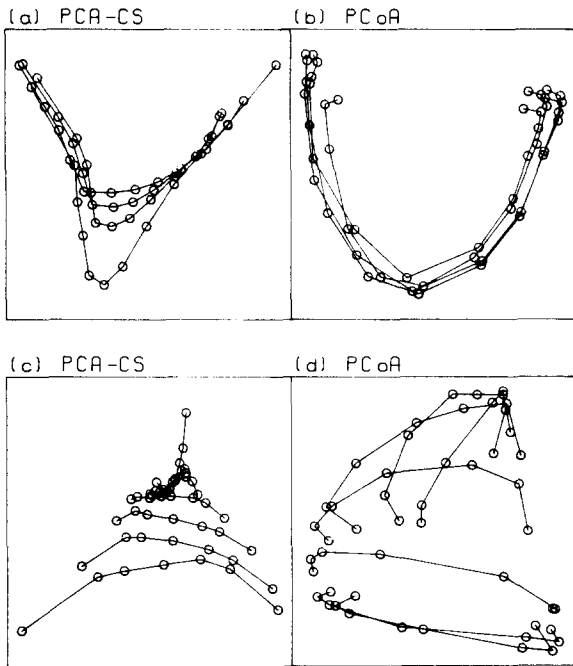


Fig. 1. PCA-CS and PCoA ordinations of a $1 \times 0.33R$ (a, b) and a $1 \times 1R$ (c, d) coenoplane. Both models had symmetric, unimodal response surfaces with no noise. Samples were arranged on regular 12×4 (a, b) and 7×7 (c, d) grids, respectively. Configurations on ordination axes 1×2 are shown, after being fitted to the simulated sampling pattern by Procrustean analysis. The lines join samples with equal co-ordinates on the second simulated gradient.

DCA and LNMDS was for data sets with a beta diversity of 1R or less, fairly symmetric response curves and either no noise or qualitative noise only. GO is relatively resistant to qualitative noise because only non-zero values are used in the fitting of Gaussian regressions, however the technique proved highly sensitive to quantitative noise.

Some performance statistics for GO in experiments A2 and A3 are given in Table 2. In the absence of noise, GO consistently recovered the correct rank order of samples only when response curves were symmetrical or of mixed skewness. The Procrustean discrepancy values in these situations were generally somewhat lower than those for DCA and LNMDS, indicating a better recovery of the inter-sample spacings.

The results in Table 2 clearly demonstrate the sensitivity of GO to the addition of quantitative

noise. For those noiseless data sets where GO achieved lower Procrustean discrepancies than DCA or LNMDS, the advantage of GO was reduced and usually reversed when noise was added. The failures of GO with noisy data sets were occasionally spectacular (e.g., Table 2, interaction model with noise level = $0.2 F$).

DCA versus LNMDS

In view of the curvilinear distortion in PCA and PCoA ordinations and the restricted utility of GO, major interest centred on the relative performance of DCA and LNMDS. The balance between these two techniques depended on model properties, in particular the number and relative beta diversities of gradients, response shape and sampling pattern.

Response function shape

Some results for unidimensional models with a beta diversity of 1R and different response function shapes are given in Table 2. In the absence of noise, DCA recovered the rank order of samples perfectly provided that all response functions were unimodal. However, DCA failed in rank order recovery on two of the interaction coenoclines, which included some species with shouldered, bimodal or multimodal responses. LNMDS proved more robust to variation in response shape: when performed in one dimension, LNMDS achieved perfect rank order recovery over all shape categories. The Procrustean discrepancy values follow a similar pattern. LNMDS had slightly worse Procrustean fits than DCA for most of the symmetrical, mixed skewness and extreme skewness models, but consistently achieved better fits than DCA for the interaction models.

The effect of variation in response shape for two-dimensional models is exemplified by the results in Table 3. For 'rectangular' coenoplanes, with a beta diversity of $1 \times 0.33R$, neither DCA nor LNMDS had a consistent advantage when response surfaces were symmetrical or of mixed skewness. Under these conditions, relative performance in terms of Procrustean fit differed between replicates. Howev-

Table 2. Ordination performance statistics for some unidimensional models in experiments A2 and A3 (see Table 1). Both Kendall rank correlations (τ) and Procrustean discrepancy values (D_1) are tabulated. The effect of quantitative noise was only studied for the first replicate in each response shape category. All models have a beta diversity of 1*R*. Larger values of τ indicate better performance. For D_1 , the opposite is true.

Ordination method	Ecological response function shape																				
	Symmetrical				Mixed skewness				Extreme skewness				Interaction (skewed)								
	Replicate		Noise level (<i>F</i>)		Replicate		Noise level (<i>F</i>)		Replicate		Noise level (<i>F</i>)		Replicate		Noise level (<i>F</i>)						
	1	2	3	0.0	0.1	0.2	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
DCA	τ	1.00	0.99	0.98	1.00	1.00	1.00	0.99	0.99	1.00	1.00	1.00	0.99	0.96	1.00	1.00	0.98	0.93	0.90	1.00	0.99
	D_1	3.1	3.1	3.7	1.5	1.7	1.2	1.5	1.7	1.4	2.8	3.1	3.3	3.9	1.8	2.1	5.2	5.9	6.7	3.6	4.3
GO	τ	1.00	0.98	0.93	1.00	1.00	1.00	0.99	0.94	1.00	1.00	0.99	0.97	0.93	0.99	1.00	0.97	0.93	0.52	1.00	1.00
	D_1	2.4	3.0	4.4	1.0	1.3	1.2	3.0	3.7	1.5	1.9	4.5	5.3	6.2	4.0	2.7	3.7	5.2	19.9	2.9	3.4
LNMDS	τ	1.00	0.99	0.97	1.00	1.00	1.00	0.99	0.99	1.00	1.00	1.00	0.99	0.96	1.00	1.00	1.00	0.98	0.93	1.00	1.00
(1D)	D_1	3.3	4.0	4.7	1.9	2.6	2.6	2.8	2.7	2.7	2.7	2.8	3.1	4.1	2.2	2.8	4.2	3.6	4.6	2.7	1.8
LNMDS	τ	0.99	0.97	0.94	0.98	1.00	1.00	0.97	0.97	0.92	1.00	1.00	0.97	0.94	1.00	1.00	0.99	0.92	0.81	0.98	0.99
(2D)	D_1	4.3	4.8	5.5	2.6	3.9	1.8	2.6	2.4	6.1	5.1	3.4	4.3	5.4	3.2	3.5	3.0	5.4	8.2	4.0	2.9

er, LNMDS consistently achieved more accurate recovery of sample positions for the $1 \times 0.33R$ coenoplanes with extremely skewed response surfaces and for the $1 \times 0.33R$ coenoplanes in which interaction between species produced more complex response shapes.

Some ordination configurations for $1 \times 0.33R$ coenoplanes are shown in Figs. 2 and 3. In each case, the samples were located on a regular 12×4 grid in the simulated environment space. Figure 2 illustrates the lack of a consistent advantage for either technique with symmetrical and mixed skewness models. When DCA gave worse fits than LNMDS (Fig. 2b, f), it was generally due to a compression of variation along the second gradient towards one end of the first gradient. For those

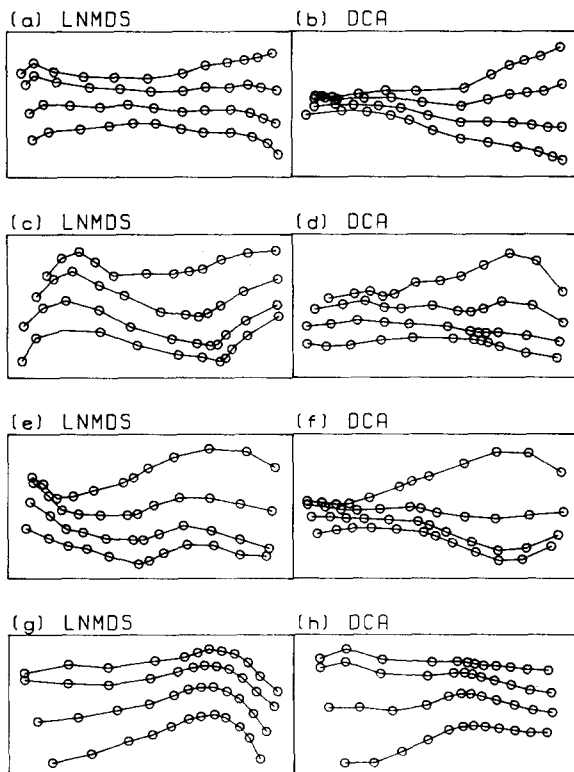


Fig. 2. LNMDS and DCA ordinations of some $1 \times 0.33R$ coenoplanes: (a) and (b) symmetric responses, replicate 1 (PCA-CS and PCoA ordinations of this model are shown in Fig. 1a, b); (c) and (d) symmetric responses, replicate 2; (e) and (f) mixed skewness, replicate 3; (g) and (h) mixed skewness, replicate 2. All models had no noise added and samples were arranged on a regular 12×4 grid.

data sets where DCA achieved better results than LNMDS (Fig. 2d, h), the LNMDS configuration generally exhibited some systematic curvilinear distortion.

Figure 3 shows two examples of the consistently superior performance of LNMDS for $1 \times 0.33R$, extreme skewness and interaction models. The DCA solution for the extreme skewness model (Fig. 3b) once again shows compression at one end of the first gradient. For the interaction model illustrated (Fig. 3c, d), the DCA ordination is marred by curvilinear distortion at the left-hand side of the configuration.

The unequivocal superiority of LNMDS over DCA for $1 \times 1R$ coenoplanes is apparent from the results presented in Table 3. Irrespective of response surface shape, LNMDS always achieved lower Procrustean discrepancies than DCA, often markedly so. Some examples of ordination results for $1 \times 1R$ coenoplanes are shown in Figs. 4 and 5. For each of the models illustrated, the samples were located on a regular 7×7 grid in the simulated environment space.

Figure 4 shows the DCA and LNMDS ordinations of all three replicates with symmetrical, unimodal response surfaces. The regular grid was recovered reasonably well by DCA for the first replicate (Fig. 4b), but the DCA configurations for the other two replicates (Fig. 4d, f) are distorted. A peculiar feature of the distortion is the displacement of the samples in one corner of the grid to

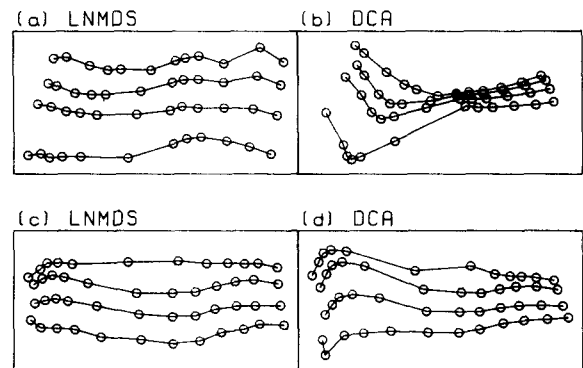


Fig. 3. LNMDS and DCA ordinations of some $1 \times 0.33R$ coenoplanes: (a) and (b) extreme skewness, replicate 1; (c) and (d) interaction model, replicate 1. In both cases, samples were arranged on a regular 12×4 grid, and no noise was included.

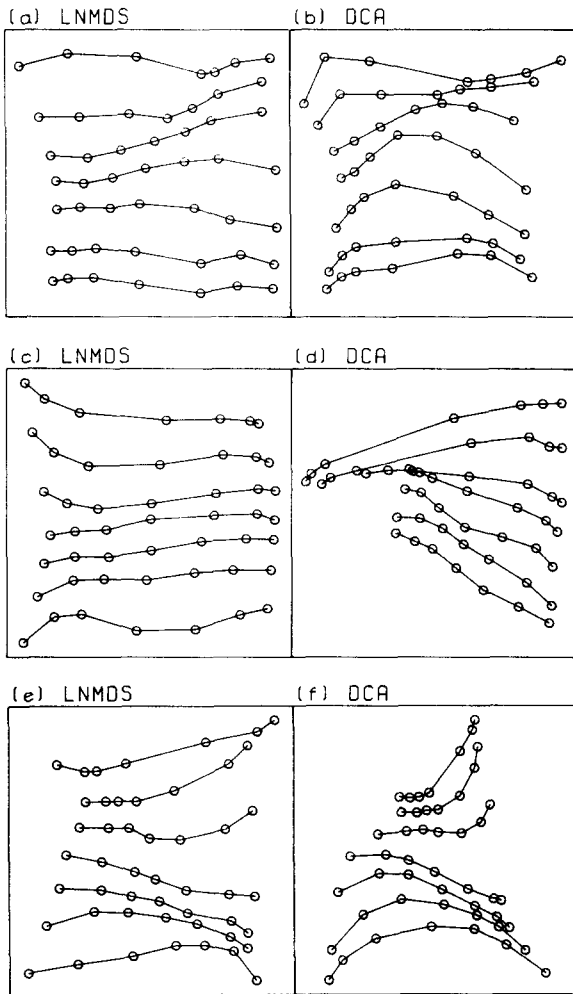


Fig. 4. LNMDS and DCA ordinations of replicate $1 \times 1R$ coenoplanes with symmetric, unimodal response surfaces: (a) and (b) replicate 1 (PCA-CS and PCoA ordinations of this model are shown in Fig. 1c, d); (c) and (d) replicate 2; (e) and (f) replicate 3. In each case, samples were arranged on a regular 7×7 grid and no noise was added.

form a narrow 'tongue' extending from one side of the configuration. The LNMDS ordinations (Fig. 4a, c, e) all display good recovery of the grid structure and there is no sign of the 'tongue' distortion produced by DCA.

Some examples of DCA and LNMDS ordinations of mixed skewness, extreme skewness and interaction coenoplanes with beta diversities of $1 \times 1R$ are shown in Fig. 5. In each case the regular 7×7 grid is recovered better by LNMDS. The DCA ordination of the extreme skewness model

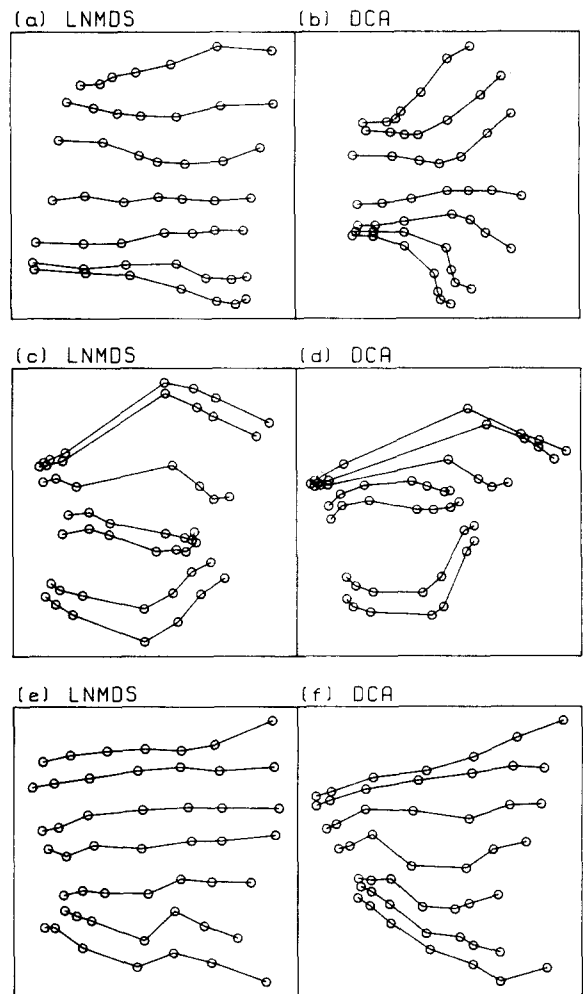


Fig. 5. LNMDS and DCA ordinations of some $1 \times 1R$ coenoplanes: (a) and (b) mixed skewness, replicate 1; (c) and (d) extreme skewness, replicate 1; (e) and (f) interaction model, replicate 1. In each case, samples were arranged on a regular 7×7 grid and no noise was included.

(Fig. 5d) shows a 'tongue' distortion similar to that observed for some of the symmetrical models. LNMDS corrects this distortion and achieves a tolerable reconstruction of the simulated grid (Fig. 5c). The performance of LNMDS on this data set was the worst for all of the regularly sampled, noiseless, $1 \times 1R$ coenoplanes examined.

LNMDS usually achieved better recovery of gradients when performed in the correct dimensionality. When offered an extra dimension, LNMDS tended to curve the gradient structure in the higher-

dimensional space, although the distortion was never as severe as that observed in linear ordinations (PCA, PCoA). Consequently, there was generally a deterioration in the accuracy with which the environmental configuration was recovered on the first one or two axes (see Tables 2, 3, 4). The problem was more severe for coenocline models and coenoplanes in which one gradient was longer than the other. For most of the $1 \times 1R$ coenoplanes studied, the first two dimensions of a three-dimensional LNMDS still represented sample positions more accurately than the corresponding DCA solution (Table 3).

Quantitative noise

Both DCA and LNMDS displayed a considerable degree of resistance to the addition of quantitative noise. The effect of noise was to introduce random displacements of points in the ordination configurations, without altering the overall form of the configurations derived for the corresponding noiseless data sets (cf. Gauch *et al.*, 1981). The introduction of noise did not alter the relative performance of DCA and LNMDS, as described in the previous section (see Tables 2, 3). Despite the addition of noise, the overall structure of the simulated environment space is recovered remarkably well.

Qualitative noise

The effect of qualitative (presence-absence) noise on ordination performance was severe, especially for models in which beta diversity was low. Both DCA and LNMDS were unable to achieve an acceptable recovery of sample positions along simulated gradients with beta diversities of less than $1R$ in the presence of qualitative noise. (It is probable that the levels of qualitative noise applied in this study were unrealistically high: many data sets contained samples with fewer than five species, against a mean of ca. 25 in the noiseless data).

Sampling pattern

Experiments A4 and B4 (Table 1) revealed marked differences between DCA and LNMDS in their sensitivity to the pattern of sampling in the simulated environmental space. For unidimensional models,

the effects of variation in sampling pattern on both DCA and LNMDS were relatively minor. The relative performance of the techniques with regularly sampled coenoclines was maintained with the other sampling patterns. The results do not agree with those of Mohler (1981), who reported better gradient recovery by DCA when samples were concentrated towards the extremes of the gradient.

The results for $1 \times 1R$ coenoplanes were quite different, illustrating the danger of assuming that phenomena observed for unidimensional models should generalize to the multidimensional case. Some performance statistics for experiment B4 are given in Table 4. DCA displayed more variation in performance between sampling patterns than did LNMDS. LNMDS achieved better recovery of sample configurations than did DCA for all data sets, with the exception of two models with cross-shaped sampling patterns. DCA performed particularly poorly when samples were randomly distributed.

Of special interest are the results for $1 \times 1R$ coenoplanes in which samples were confined to a restricted region of the simulated environmental space. Two kinds of restricted sampling pattern were studied. In the first, sites were confined to a T-shaped region (Fig. 6a), so that the second gradient was only expressed towards the lower extreme of the first gradient. The second arrangement was cross-shaped, with the second gradient being expressed only near the centre of the first (Fig. 7a). Neither DCA nor LNMDS gave satisfactory results under this type of sampling, although LNMDS was generally more successful.

Figure 6 shows the DCA and LNMDS ordinations of the symmetric response coenoplane sampled by a T-shaped pattern. In the DCA configuration (Fig. 6c), the cross-bar of the T has been bent, giving the appearance of a long gradient with a shorter side branch. In addition, variation in the direction of the second gradient among samples forming the stem of the T has been suppressed. The LNMDS ordination (Fig. 6b) represents the T-shaped pattern reasonably well, although there is some curvilinear distortion of the stem of the T. Ordinations by DCA and LNMDS of the data set derived by cross-shaped sampling of the interaction coenoplane are shown in Fig. 7. In the DCA ordi-

Table 4. Procrustean discrepancy values for ordinations of some two-dimensional models in experiment B4 (see Table 1). All models had beta diversities of $1 \times 1R$ and no noise was added. Lower values of D_2 indicate better performance.

Ordination method	Ecological response function shape																	
	Symmetrical						Extreme skewness						Interaction (skewed)					
	Sampling Pattern			Edges T			Cross			Sampling Pattern			Edges T			Cross		
	Regular	Random	Centre	Edges	T	Cross	Regular	Random	Centre	Edges	T	Cross	Regular	Random	Centre	Edges	T	Cross
DCA D_2	9.8	21.8	8.8	12.7	17.2	5.9	19.6	26.8	17.6	15.2	17.5	13.0	11.6	18.4	9.3	11.6	10.4	22.9
LNMS D_2 (2D)	6.4	6.7	7.0	8.0	9.0	8.3	12.7	14.1	12.1	14.7	12.0	11.9	6.8	7.0	6.8	7.5	8.8	22.9
LNMS D_2 (3D)	8.5	7.8	9.4	8.7	9.4	9.5	13.7	15.6	14.1	15.0	12.9	11.9	8.6	9.2	7.5	10.5	9.5	16.9

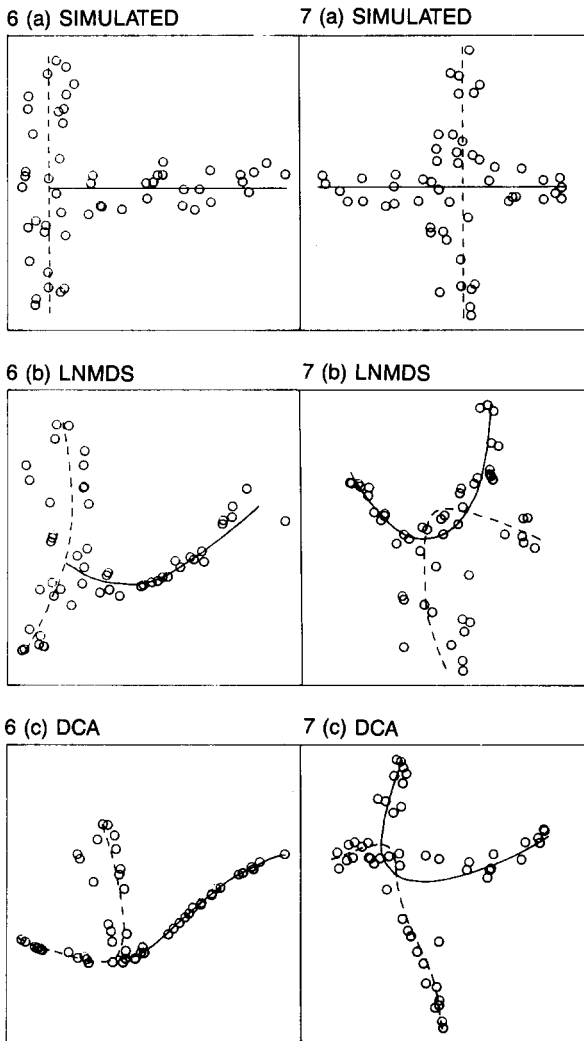


Fig. 6. Ordinations of a noiseless, $1 \times 1R$ symmetric, unimodal model (replicate 1), with samples confined to a T-shaped region in environment-space: (a) sample arrangement in model; (b) LNMDS ordination; (c) DCA ordination. The solid and dashed lines indicate the direction of the first and second simulated gradients, respectively.

Fig. 7. Ordinations of a noiseless, $1 \times 1R$ interaction model (replicate 1), with samples confined to a cross-shaped region in environment-space: (a) sample arrangement in model; (b) LNMDS ordination; (c) DCA ordination.

nation (Fig. 7c), both arms of the cross are bent through approximately 90° at their junction. One end of the arm marked by a dashed line extends into the third dimension of the ordination (not shown). The LNMDS ordination displays a similar

degree of distortion (Fig. 7b).

The poor recovery of T-shaped and cross-shaped coenoplane models by all techniques included in this study suggests the need for a greater emphasis in future studies on the implications for ordination of the shape of the underlying environmental space. In the past, it has been implicitly assumed that environmental space is completely (and often uniformly) covered by samples. However, it is often the case in nature that certain combinations of environmental conditions do not occur in a particular landscape (e.g., Austin *et al.*, 1984).

Trend in sample totals

The effect of systematic variation in sample totals was studied for unidimensional models only (Table 1, A5). Both LNMDS and DCA appeared to be relatively robust to two-fold linear and parabolic trends in sample totals. These results are preliminary and more work is required on this question, particularly with multidimensional models.

Conclusions

1. The linear ordination techniques PCA and PCoA are inappropriate for the purpose of indirect gradient analysis.
2. Gaussian ordination is very sensitive to quantitative noise and is not robust to departures from its assumed response model.
3. The currently popular DCA does not perform well with more complex response models and non-regular sampling schemes. The technique often produces distorted ordinations of $1 \times 1R$ coenoplanes, even with symmetric, unimodal response surfaces.
4. Local non-metric multidimensional scaling (LNMDS), using the Bray-Curtis dissimilarity coefficient is the most robust and effective of the methods compared.
5. None of the techniques studied achieved satisfactory recovery of coenoplane models in which samples were restricted to T-shaped or cross-shaped regions of environment space.

Discussion

Linear ordination methods

This study confirms and extends the conclusions of previous work (see above) in showing the ineffectiveness of PCA due to curvilinear distortion (the 'type A' distortion of Orlóci, 1974). PCoA with the Bray-Curtis coefficient is similarly afflicted. The distortion is not confined to models with symmetric, unimodal responses, but also occurs with the more complex models examined. Gauch *et al.* (1981) refer to the published comments of J. C. Gower on a paper by Sibson (1972). According to Gower (see Gauch *et al.*, 1981) NMDS gives very similar results to metric scaling (i.e. PCoA), but at the expense of much more computation. However, in this study the two approaches only gave similar ordinations for models with very short gradients, where the relationship between Bray-Curtis dissimilarities and environmental distances was approximately linear. In all other cases, the LNMDS ordinations recovered the gradient structure much more effectively than PCoA.

It has been argued (Greig-Smith, 1980; Feoli & Feoli Chiapella, 1980; Van der Maarel, 1980) that the curvilinear distortion in PCA does not matter, provided that interpretation of PCA ordinations takes into account its probable occurrence. However, when there is more than one underlying gradient, it is very difficult to perceive that the points in the configurations such as shown in Fig. 1 fall on a surface irregularly curved into three or more dimensions, let alone to devise a procedure for mapping the points onto a plane.

Several authors have suggested that linear ordination methods are useful for indirect gradient analysis, provided that their application is restricted to data sets with low beta diversity (e.g., Austin & Noy-Meir, 1971). Unfortunately, it is often difficult to assess *a priori* whether the beta diversity of a data set is low enough for linear techniques to be applied with negligible distortion. In any case, when beta diversity is low, good recovery of the gradients can still be obtained using a robust non-linear technique, such as LNMDS: the monotonicity assumption of LNMDS embraces linearity as a

special case. There is little justification for the continued application of linear ordination methods to community data *for the purpose of indirect gradient analysis*. That is not to say that such methods are not useful for the analysis of other types of ecological data, for which the linear model is appropriate.

Gaussian ordination and other curve-fitting methods

In this study, Gaussian ordination (GO) was shown to lack robustness to departures from its assumed symmetric, unimodal response model, thus confirming the preliminary results of Austin (1976). Furthermore, GO is very sensitive to the addition of quantitative noise, much more so than DCA and LNMDS. This result is at variance with Gauch *et al.* (1974), who imply that GO is rather resistant to noise.

The program used for GO in this work (Gauch, 1979) produces only one ordination axis and is therefore inadequate for data sets with several underlying gradients. Extensions of GO to the multidimensional case are available, but there are theoretical and computational difficulties which remain largely unresolved. The approach of Ihm & Van Groenewoud (1975) makes unacceptably stringent assumptions about the response model. Orlóci (1978, 1980) has proposed an indirect algorithm, based on the application of metric multidimensional scaling to particular measures of compositional dissimilarity and ordination distance, derived under specific assumptions about the Gaussian species response model. Some initial simulation results (Fewster & Orlóci, 1983) suggest that the performance of the method is undesirably sensitive to the assumptions made in the derivation of dissimilarities and distances.

The maximum likelihood non-linear ordination method of Johnson & Goodall (1979; Goodall & Johnson, 1982) is similar in philosophy to GO, in that it attempts to derive a sample configuration which maximizes the fit of symmetric, unimodal response functions for each species. Simulation studies of the method have been restricted to models which conform with the assumed model

and no comparison has been made with other non-linear ordination techniques, such as LNMDS.

Further simulation studies are required to assess the *robustness* of variants of GO (and other 'curve-fitting' ordination methods) to variations in the species response model and their sensitivity to noise. The excellent performance of such methods with simulated data confirming with their assumed response models is no basis upon which to predict their effectiveness with real data.

Poor performance of DCA

There are at least two factors which may contribute to the lack of robustness and erratic performance of DCA observed in this study; (1) properties of the implied dissimilarity measure, and (2) the behaviour of the detrending and rescaling processes. Hill & Gauch (1980) claim that correspondence analysis, from which DCA is derived, 'makes no use of the concept of compositional distance'. This is untrue. Correspondence analysis can be formulated as a particular variety of principal coordinates analysis, in which compositional dissimilarity is measured using the Chi-squared distance metric and samples are weighted according to their totals (Chardy *et al.*, 1976). Correspondence analysis derives an ordination in which the distances between pairs of sample points are proportional to their Chi-squared distance values.

The appropriateness of Chi-squared distance as a measure of compositional dissimilarity in ecology may be questioned (Faith *et al.*, 1987). The measure accords high weight to species whose total abundance in the data matrix is low. It thus tends to exaggerate the distinctiveness of samples containing several rare species. Unlike the Bray-Curtis coefficient and related measures, Chi-squared distance does not reach a constant, maximal value for sample pairs with no species in common, but fluctuates according to variations in the representation of species with high or low total abundances. These properties of Chi-squared distance may account for some of the distortions observed in DCA ordinations.

DCA includes two empirical procedures which

attempt *a posteriori* to rectify the curvilinear distortion of gradients: detrending and rescaling. Computational details are given by Hill (1979; see also Hill & Gauch, 1980). The procedures were apparently developed from a consideration of very simple models of species replacement along a single gradient. Both involve an arbitrary choice of the degree of segmentation of axes. From the results of this study, it appears that the effects of detrending and rescaling with non-trivial coenoplane models are not always desirable. The distortions of the underlying gradient structure in some DCA ordinations (e.g., Figs. 2b, 4d and 6c) may be attributable to the behaviour of either or both detrending and rescaling. For some of the models for which severe flattening of parts of the configuration occurred in DCA ordinations, several other DCA ordinations were performed by varying the number of detrending segments and the number of cycles of rescaling. None of these adjustments was successful in reducing the degree of distortion. In several published applications of DCA, (e.g., Robertson *et al.*, 1984; Gibson & Kirkpatrick, 1985) ordination configurations have flattened 'tongues', similar to that shown in Fig. 4d. These may be artifacts, due to the operation of detrending or rescaling.

Not all curvilinear structures which may appear in an ordination are distortions, arising from the non-linear relationship between dissimilarity and environmental distance. DCA has no way of distinguishing between 'horse-shoe' or 'arch' distortions and features of the environmental configuration which happen to be non-linear. There is a danger that DCA will introduce new distortions of its own. A good example is provided by the DCA ordination of the $1 \times 1R$ symmetric response coenoplane with a T-shaped sampling pattern, shown in Fig. 6c. The non-linear structure formed by the upright of the T and one side of the cross-bar has been flattened out, as if it were an arch distortion.

Reservations about the possible effects of the empirical adjustments in DCA have been expressed by some authors (e.g. Fewster & Orlóci, 1983). Nevertheless, DCA has become probably the most widely-used ordination technique for community data. A major contributing factor to the rapid acceptance of the method has been the distribution of

the program DECORANA (Hill, 1979), which is relatively easy to use and economical, in terms of both computing time and memory requirements. In the light of current results, the status of DCA as a satisfying solution to the problem of curvilinear distortion in ordination (cf. Gauch, 1982) must be questioned. Interpretation of DCA ordinations should take into account the possibility of artificial distortions, due to the properties of the implied dissimilarity measure or the activities of detrending or rescaling.

The current results suggest a clear preference for LNMDS over DCA. DCA consistently outperformed LNMDS only for coenoclines with simple, unimodal response curves. On the basis of very limited simulations using Gaussian models, Orłóci *et al.* (1984) have also reported rather poor recovery of simulated gradients by DCA.

Gauch *et al.* (1981) compared DCA with several variants of NMDS, including the LNMDS technique examined here. They concluded that DCA was generally more successful than NMDS. However, their study considered only a small number of Gaussian response models, all with regular sampling patterns. No replication was apparently performed within each combination of model properties. The great variation in performance by DCA among replicate models, observed in this study (e.g. Tables 2 and 3; Fig. 4), highlights the danger of arriving at misleading conclusions if comparisons are restricted to a single replicate.

The use of DCA ordinations as initial configurations for LNMDS is another major factor distinguishing the present study from that of Gauch *et al.* (1981). They employed random starting configurations for LNMDS (using the program SIBSON) and apparently used metric scaling solutions (similar to PCoA) for the other variants of NMDS examined. The choice of a poor initial configuration can reduce the likelihood of NMDS achieving a solution with the best possible monotonic fit between ordination distance and dissimilarity. The iterative procedure may become trapped in a 'local optimum', where no small change in the configuration will decrease the stress, even though different con-

figurations exist with lower stress. It is possible that many of the NMDS ordinations obtained by Gauch *et al.* (1981) were local optima, resulting from the use of random starts or metric scaling solutions which exhibited severe curvilinear distortion.

Robustness of non-metric multidimensional scaling

Published applications of non-metric multidimensional scaling (NMDS) in ecology (in either the 'global' or 'local' form) are relatively rare (e.g., Prentice, 1977; Clymo, 1980; Field *et al.*, 1982; Oksanen, 1983; Dargie, 1984), but in most cases the technique has been considered effective. Simulation studies based on Gaussian models have shown that NMDS can successfully recover gradients of high beta diversity, both in its 'global' (Fasham, 1977) and 'local' forms (Prentice, 1980). Austin's (1976) preliminary examination of some alternative response models provided an early indication of the relative robustness of 'global' NMDS.

This study has identified LNMDS, using the Bray-Curtis dissimilarity coefficient, as a robust technique for the analysis of community data when the aim is to recover the compositional dimensions associated with underlying environmental gradients. The relative merits of 'global' *versus* 'local' variants of NMDS and the possible effects of the choice of dissimilarity measure were not investigated. However, subsequent work has used a similar, but more extensive, simulation approach to compare the robustness of dissimilarity coefficients (Faith *et al.*, 1987) and several forms of NMDS (Minchin, Faith & Belbin, unpublished). The results suggest a preference for 'local' over 'global' NMDS and the Bray-Curtis measure was among the most robust of the coefficients compared, in terms of its rank correlation with simulated environmental distance.

Non-metric multidimensional scaling is recommended as a robust technique for indirect gradient analysis which deserves more widespread use by community ecologists.

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