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APPLYING METRIC AND NONMETRIC MULTIDIMENSIONAL SCALING TO ECOLOGICAL STUDIES: SOME NEW RESULTS[1]

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Abstract. Metric (eigenanalysis) and nonmetric multidimensional scaling strategies for ecological ordination were compared. The results, based on simulated coenoplane data showing varying degrees of species turnover on two independent environmental axes, suggested some strong differences between metric and nonmetric scaling methods in their ability to recover underlying nonlinear data structures. Prior data standardization had important effects on the results of both metric and nonmetric scaling, though the effect varied with the ordination method used. Nonmetric multidimensional scaling based on Euclidean distance following stand norm standardization proved to be the best strategy for recovering simulated coenoplane data. Of the metric strategies compared, correspondence analysis and the detrended form were the most successful. While detrending improved ordination configurations in some cases, in others it led to a distortion of results. It is suggested that none of the currently available ordination strategies is appropriate under all circumstances, and that future research in ordination methodology should emphasize a statistical rather than empirical approach.

Key words: coenoplane; data standardization; eigenanalysis; nonmetric multidimensional scaling; principal components analysis; principal coordinates analysis.

INTRODUCTION

Methods of multidimensional scaling or ordination seek a parsimonious representation of individuals in a space of low dimensionality. Parsimony in this context implies that the distances between individuals in ordination space optimally represent their dissimilarities in variable space, in some defined sense. Techniques differ in their definition of optimality, but a minimal requirement of most methods is a rank order agreement between distances and dissimilarities (Shepard and Carroll 1966, Orlóci 1978). Factor revelation is achieved when the ordination is interpretable in terms of environmental gradients which impose structure on the data. Ideally these gradients should bear a linear relationship to the ordination axes (Hill and Gauch 1980). This is not always necessary for successful interpretation (Phillips 1978, Feoli and Feoli-Chiapella 1980), but a linear relationship is to be preferred since otherwise the ordination may be difficult to interpret, particularly if the data are noisy (Austin 1976*a*, Gauch 1982*a*) and there is more than one major gradient.

Dale (1975) distinguished three major objectives of ordination: the direct arrangement of stands along one or more environmental gradients, factor revelation or path (trend) seeking, and dimensionality reduction. There is normally some convergence of the latter two objectives (Nichols 1977), and according to Austin (1976*a*) the two are necessarily linked. To differentiate between objectives is nonetheless useful, as it clarifies the distinction between dimensionality reduction as a statistical objective and factor revelation as an ecological objective. Any method which leads to factor revelation implicitly reduces the dimensionality of a complex data set (though with differing degrees of information loss; Orlóci 1974), but a method which is efficient in dimensionality reduction does not necessarily meet the ecological objective of factor revelation. An efficient redescription is achieved only when both objectives are met.

A large number of ordination algorithms have been described (see Orlóci 1978). Of these, the geometric projective methods (reviewed by Noy-Meir and Whittaker 1977) were developed by ecologists. These require the selection of gradient endpoints and are therefore suitable only for the arrangement of stands along strong environmental gradients where endpoints are known a priori. While they have sometimes been recommended for factor revelation (Gauch and Whittaker 1972*b*), it is doubtful that external endpoints alone can offer an adequate summarization of multidimensional data (Anderson 1971, Dale 1975). A second group of methods involves the eigenanalysis of a sum of squares and cross-products (SSCP) matrix. Of this group, principal components analysis (PCA; Hotelling 1933) is the most familiar method. A variant known as principal coordinates analysis (P-Co-A; Gower 1966) or metric multidimensional scaling (Torgerson 1952) will handle other matrices provided that they are related to the general SSCP form. Another variant known as correspondence analysis (CA; Benzécri 1969, Hill 1974) has been shown to have some advantages over PCA in summarizing nonlinear trends in artificial data sets (Gauch et al. 1977), and is useful in the analysis of

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concentration tables (Feoli and Orlóci 1979). A third method, derived from the psychometric literature, is known as nonmetric multidimensional scaling (NMDS; Kruskal 1964 *a, b*). It was originally developed to allow for the analysis of matrices resulting from experiments in which subjects are asked to make pairwise judgements of similarity or preference (Schiffman et al. 1981).

Comparisons of ordination techniques have generally involved the use of artificial data sets showing underlying Gaussian species responses to a single environmental gradient (coenocline), or two or more independent gradients (coenoplanes or coenocubes). The model described by Gauch and Whittaker (1972*a,* 1976) has generally been applied. Austin (1976*a,* 1980) has questioned the realism of this model, pointing out that skewed and even bimodal species responses can often be expected in field data. Despite these limitations the model is at least a crude approximation of the underlying structure of ecological data, and can therefore serve as a general, simple model for assessing the robustness of ordination methods. But as Dale (1975) has pointed out, any conclusions regarding the utility of ordination techniques must consider the limitations of the model. This implies that the conclusions made are relevant only to the model specified.

Studies which have compared ordination techniques have found that PCA shows serious involution of gradients, attributable to the use of a linear model to attempt to summarize trends related to nonlinear and nonmonotonic species responses (Gauch and Whittaker 1972*b,* Kessell and Whittaker 1976, Fasham 1977, Gauch et al. 1977). This observation had been anticipated by Goodall (1954) and van Groenewoud (1965). More recent papers have utilized the same general strategy in comparing CA, NMDS, and some lesser known ordination techniques. Gauch et al. (1977) found CA to be superior to PCA, assuming coenocline and coenoplane recovery to be of principal importance. However, Greig-Smith (1983) has suggested that this superiority may be attributable to differences in data standardization. In practice the double standardization implicit in the CA algorithm may lead to an undue emphasis on outliers (Hill and Gauch 1980), though this is not apparent from the analysis of artificial simulated data which show a smooth, continuous structure.

NMDS has invariably performed well in comparative tests. Dale (1975) and Noy-Meir and Whittaker (1977) recommend its use, notwithstanding the computational burden. Some workers (Anderson 1971, Gower cited in Sibson 1972, Gauch et al. 1981) have noted that NMDS may produce results similar to metric scaling strategies, and have questioned the worth of a computationally less efficient algorithm in achieving the same end. Fasham (1977) and Orlóci et al. (1984) have stressed the importance of coefficient choice in NMDS, while Prentice (1977, 1980) suggested the use of Sibson's (1972) local variant version of NMDS in conjunction with a coefficient suggested by Kendall (1971). He found that such a strategy gave results which were superior to metric scaling methods when applied to both real and artificial data sets. Gauch et al. (1981) concluded that NMDS was often superior to metric methods, though this depended on the data set analyzed.

Comparisons of ordination techniques have tended to confound three factors: the methodological algorithm, the resemblance measure employed, and the standardization used (Orlóci 1974, 1978). Objective comparisons are made more difficult by the fact that many techniques permit only certain coefficients to be used, and that certain standardizations are implicit in these.

The importance of standardization on PCA was examined in detail by Austin and Noy-Meir (1971; also see Noy-Meir et al. 1975). They concluded that standardization can have some influence on ordination results, and in some situations can considerably lessen the degree of distortion attributable to underlying nonlinear species response. Corresponding studies involving NMDS are less complete. Fasham (1977) tested NMDS using a number of resemblance coefficients, and found that the cos-theta similarity function (Anderberg 1973) gave good results when applied to coenoplane data. Most other workers (e.g., Anderson 1971, Austin 1976*b,* Prentice 1977, 1980, Gauch et al. 1981) have been satisfied with using a single resemblance measure in conjunction with NMDS, comparing the results obtained with standard metric ordination methods.

The purpose of this study was to assess the possible utility of metric and nonmetric multidimensional scaling in ecological investigations. Specifically we addressed: (a) the behavior of these ordination methods when algorithm, resemblance measure, and standardization are not confounded, (b) the effect of data standardization on the results of metric and nonmetric scaling, and (c) the utility and possible advantages of nonmetric scaling in examining ecological data.

Metric Multidimensional Scaling

Principal components analysis is a widely-used ordination method first suggested by Goodall (1954) as being of potential use in ecology. It offers an efficient redescription of a complex data set, and is recommended for use in dimensionality reduction whenever certain basic assumptions are met (Dale 1975). The method examines a sum of squares and cross-products (SSCP) matrix, and working in this Euclidean space performs eigenanalysis to summarize linear trends of variation. This implies that nonlinear trends will be distorted into higher dimensions. Axes are orthogonal, the first depicting the main direction of linear variation, the second the main residual variation after removal of the trended linear variation accounted for by the first, and so forth (Pielou 1984). Thus the method does

TABLE 1. Characterization of three different methods of metric multidimensional scaling (eigenanalysis). **X** is a $p \times n$ matrix, where p = number of variables and n = number of individuals. Values of b are eigenvector elements (adjusted to unit length) associated with an eigenvalue λ, and t is the number of axes extracted.

Method	Definition of sum of squares and cross products matrix (**S**)	Definition of component scores (Y_{mk}; $m = 1, \ldots, t$)
Principal components analysis (PCA; covariance)	**S** $(p \times p)$; $S_{ij} = \frac{1}{n-1}\left[\sum (X_{ik} - \bar{X}_i)(X_{jk} - \bar{X}_j)\right]$; $k = 1, \ldots, n$	$Y_{mk} = \sum [b_{im}A_{ik}]$; $i = 1, \ldots, p$ where $A_{ik} = (X_{ik} - \bar{X}_i)/(n-1)^{1/2}$
Principal coordinates analysis (P-Co-A; Euclidean)	**S** $(n \times n)$; $S_{kh} = e_{kh} - \bar{e}_{k.} - \bar{e}_{.h} + \bar{e}_{..}$ where $e_{kh} = -\frac{1}{2}\left[\sum (X_{ik} - X_{ih})^2\right]$; $i = 1, \ldots, p$	$Y_{mk} = \lambda_m^{1/2} b_{km}$
Correspondence analysis (CA)	**S** $= \mathbf{U}'\mathbf{U}$ $(n \times n)$; $U_{ik} = \frac{X_{ik}}{(X_{i.}X_{.k})^{1/2}} - \frac{(X_{i.}X_{.k})^{1/2}}{X_{..}}$	$Y_{mk} = \frac{(b_{km} - \bar{b}_m)}{\left[\sum (b_{km} - \bar{b}_m)^2\right]^{1/2}} \left(\frac{X_{..}}{X_{.k}}\right)^{1/2}$; $k = 1, \ldots, n$

not produce a reduction in dimensionality per se, but merely rotates axes rigidly to produce a more parsimonious representation. Dimensionality reduction only occurs when lesser axes are subsequently discarded (Orlóci 1974).

PCA as described above will operate only on a product moment SSCP matrix. Torgerson (1952) considered a strategy to handle more general cases of the SSCP form. He showed that a meaningful eigenanalysis can be based on any resemblance measure which shows an underlying correspondence to a metric Euclidean distance. Gower (1966) investigated this further, suggesting the name principal coordinates analysis for the steps involved. The method has the same basic restrictions (linearity and additivity) as PCA, but does permit a wider choice of resemblance measures. This is important since some inherent nonlinearity in the data structure may be straightened out by an appropriately chosen coefficient (Dale 1975).

Correspondence analysis (Benzécri 1969, Ihm and van Groenewoud 1984) can be thought of as a variant of component analysis in which eigenvalues are extracted from a cross-products matrix derived from doubly standardized (normalized by taking the square root of the row and column totals) data (Gittins 1985). Component scores are obtained through a rescaling of the eigenvector elements (Orlóci 1978). Hill (1973) developed a computationally efficient iterative algorithm which avoids an eigenanalysis. In the formulation of Williams (1952), the method treats the raw data as a contingency table, producing a factorial partitioning of the contingency chi-squared statistic, and therefore implicitly assumes discrete data (Hill 1974, Nishisato 1980). It is also instructive to note that CA is closely related to canonical correlation analysis (Hill 1974, Gittins 1985).

CA has been shown to be efficient with highly heterogeneous nonlinear data (Hill 1974, Gauch et al. 1977), but has the disadvantage that higher axes, while linearly independent (i.e., having zero covariance), show higher order correlations. Furthermore, tests with artificial coenoplane data have indicated that the ends of ordination axes are compressed relative to the middle (Gauch 1982*b*). To overcome these problems, Hill and Gauch (1980) suggested a method to "detrend" a CA ordination. Detrended correspondence analysis (DCA) incorporates two important modifications to the CA algorithm: (a) axis orthogonality is replaced by the requirement that axes be independent in a nonlinear sense (though higher order interactions may remain) and (b) axes are rescaled by standardizing species scores within sets of stands. Being an empirically based strategy, DCA manipulates the data to reflect specific preconceived notions and expectations, implying a systematic modification of the underlying data structure (Pielou 1984). However, preliminary tests involving both real and artificial data have suggested that detrending may result in a more readily interpretable ordination (Gauch 1982*b*, Pielou 1984), particularly when the data contain strong discontinuities.

There are major differences among the three metric methods (Table 1), but it is important to realize that they all analyze a cross-products matrix by extracting latent roots and vectors. In this respect the methods are restricted by an underlying linearity assumption. However, suitable data transformations can be defined to allow for the summarization of nonlinear trends under specific conditions (Hill 1974).

NONMETRIC MULTIDIMENSIONAL SCALING

This method, which is based on the rankings of distances between points, was first suggested by Shepard

TABLE 2. Description of the eight ordination strategies compared. Euclidean distance matrices were used for both P-Co-A and NMDS.

Method	Standardization or version
Principal coordinates analysis (P-Co-A)	unstandardized (PCAE) simultaneous double standardization (PCAD) stand norm standardization (PCAC)
Nonmetric multidimensional scaling (NMDS)	unstandardized (MDSE) simultaneous double standardization (MDSD) stand norm standardization (MDSC)
Correspondence analysis (CA)	unmodified (CA) detrended (DCA)

(1962), while Kruskal (1964*a*, *b*) developed a more stringent algorithm with an objective optimization criterion. The method is of considerable theoretical interest since it circumvents the linearity assumption of metric ordination methods. Lucid accounts of NMDS in an ecological context can be found in Fasham (1977) and Prentice (1977).

The basic idea is intuitively appealing. An arrangement of individuals is sought in a reduced metric space such that the distances **d** in this reduced space are as closely monotonic as possible to the dissimilarities δ calculated in variable space. The monotonicity requirement originally suggested was the tetrad inequality: that $d_{ij} \geq d_{kl}$ whenever $\delta_{ij} > \delta_{kl}$. Sibson (1972) termed this global order equivalence, and suggested as an alternative the triad inequality (or local order equivalence): that $d_{ij} \geq d_{ik}$ whenever $\delta_{ij} > \delta_{ik}$.

The algorithm, while simple in theory, is difficult and computationally demanding to implement in practice. A method of successive approximation is involved, and although the algorithm normally converges to an optimal solution, local (nonoptimal) solutions are also possible, particularly when the data are poorly structured (Shepard 1974). In practice, a number of different starting configurations may have to be tried, and the solution minimizing stress (a measure of deviation from monotonicity; Kruskal 1964*a*) chosen. Random starting configurations will likely circumvent local minima problems (Fasham 1977), while input configurations based on metric scaling often constrain the solution.

The method requires the user to specify the number of dimensions of the final solution. Early workers followed Kruskal's (1964*a*) guidelines, choosing a dimension which reduced stress to a sufficiently small value. However, Shepard (1974) has argued strongly for solutions in two, or at most three, dimensions, as these are more readily interpretable. It should be noted that the k-dimensional solution obtained in NMDS is not a projection of a solution in higher dimensions as in the metric ordination methods.

Kendall (1971) has argued that nonmetric scaling is superior to metric methods since it is based on fewer assumptions. Gower (in Sibson 1972) has questioned this, arguing that computational expense is a more important consideration, particularly if metric and nonmetric methods tend to converge to a similar solution. Nonmetric scaling has the advantage that, because only rank order is used, it can accept as input a large variety of resemblance measures.

METHODS

Metric and nonmetric scaling ordination methods were compared using data derived from a coenoplane model. While the limitations of such a model are considerable, the strategy was felt appropriate in that it rendered the study comparable to previous work. Furthermore, tests involving artificial data of known structure provide information about the behavior of ordination methods under fixed conditions, permitting an objective comparison of results.

To minimize the confounding of algorithm, resemblance measure, and standardization, only Euclidean distance measures were used, in each case utilizing the raw data, data standardized by stand normalization (the chord distance of Orlóci 1967), and simultaneous double standardization (Austin and Noy-Meir 1971). Euclidean distance measures were utilized since they have certain desirable axiomatic properties (Anderberg 1973) not held by so-called semimetric measures such as percent difference, which was used by Gauch et al. (1981). Furthermore, while semimetric measures can be handled by NMDS, their suitability as input to P-Co-A is questionable since they violate the assumed underlying SSCP form (Orlóci 1974, Dale 1975). Table 2 summarizes the eight strategies which were contrasted. The emphasis was on comparing metric and nonmetric scaling methods in the absence of confounding: thus, for example, P-Co-A using Euclidean distance after stand normalization was compared to NMDS using the same distance measure and standardization. CA and DCA, which incorporate a simultaneous double standardization of data, were also performed. They are in some ways comparable to P-Co-A ordinations of doubly standardized data, but there are some differences, particularly in the definition of component scores, which point against a direct comparison (Table 1).

TABLE 3. Description of the 11 coenoplane data sets used in the study, and corresponding Procrustes analysis sum of squares values for the ordination strategies outlined in Table 2.

Species turnover rate (HC)*	H'†	Procrustes analysis sum of squares residual values‡							
		PCAE	PCAD	PCAC	MDSE	MDSD	MDSC	CA	DCA
2.65 × 2.65	2.75	1.47	0.47	0.71	1.14	0.24	0.06	0.18	0.14
2.65 × 3.05	2.69	1.76	0.64	0.83	1.71	0.26	0.12	0.25	0.23
2.65 × 3.75	2.59	3.01	1.56	1.29	3.04	1.08	0.64	1.45	0.98
2.65 × 5.30	2.31	8.55	8.06	8.63	7.97	1.73	1.45	6.64	2.35
3.05 × 3.05	2.62	1.94	0.45	0.78	2.17	0.34	0.02	0.20	0.12
3.05 × 3.75	2.55	2.52	0.68	1.16	3.08	0.68	0.21	0.47	0.44
3.05 × 5.30	2.24	3.89	0.77	1.63	3.08	1.09	0.76	1.38	1.23
3.75 × 3.75	2.17	2.67	0.83	1.41	2.96	0.97	0.04	0.34	0.19
3.75 × 5.30	2.13	5.87	0.95	2.13	4.59	1.33	0.26	0.72	1.29
5.30 × 5.30	1.81	5.64	1.98	1.97	7.59	9.16	0.15	0.95	1.76
7.50 × 7.50	1.23	9.23	8.99	4.66	10.57	10.74	0.27	1.71	7.52

* HC = half-change units = the measure of species turnover rate on each of the two independent environmental gradients of the coenoplane.

† Averaged Shannon-Wiener stand alpha diversity.

‡ The sum of squares measures goodness of fit: the smaller the sum of squares, the more successful the ordination has been in recovering the original data structure (which is known for each of these test data sets).

P-Co-A analyses were performed using the Wildi and Orlóci (1983) package, while the DECORANA program (Hill 1979) was used to produce the CA and DCA ordinations. Scores on the first two ordination axes were used in each case to produce scattergrams. Two-dimensional global order equivalence NMDS ordinations were obtained using a version of the Brambilla and Salzano (1981) program described by Orlóci and Kenkel (1985). Random starting configurations were specified, and three runs were performed on each data set. Replicate ordination configurations were very similar, except for two runs in which the iterative procedure did not converge (as indicated by a very high stress value).

To produce the simulated data, a program was written based on the model presented by Gauch and Whittaker (1976). It is similar to the program CEP-21 published by Gauch (1977), but differs in that (a) the distribution of species surface heights is normal, not lograndom or lognormal and (b) species modes are positioned in a stratified random manner. The program was initially tested by producing three data sets similar to those used by Gauch et al. (1977, 1981), Fasham (1977), and Prentice (1980). Each consisted of 40 stands, positioned at regular intervals on a 5 × 8 grid (representing two independent environmental gradients), and 30 species each showing a Gaussian distribution. Whereas in the original data sets species modal positions were located systematically, the data generated here utilized a stratified random procedure in locating species modes. This involved subdividing the coenoplane into 30 equal-sized strata, and randomly locating one modal position within each. Species surface heights were normally distributed within the 60–100 range. The three data sets showed different levels of species turnover on the two gradients, measured in half-change (HC) units (Gauch and Whittaker 1972*a*). The values were: 1.5 × 1.5 HC; 1.5 × 4.5 HC; and 4.5 × 4.5 HC. The resultant CA ordinations were very similar to those presented by Fasham (1977), but with somewhat greater displacement of sample positions. This is likely attributable to the stratification of species modal positions. Interestingly, displacement was also observed by Gauch et al. (1981) when they added "noise" to their data. DCA improved the results of the 1.5 × 4.5 HC coenoplane (Hill and Gauch 1980). The results of NMDS using Euclidean distance following stand normalization (chord distance) were very similar to those obtained by Fasham (1977), who used the cos-theta similarity function. This was expected since these resemblance measures are inversely monotonically related (Orlóci 1967).

The methods outlined in Table 2 were applied to 11 simulated coenoplane data sets. In all cases two independent environmental gradients were assumed, and 36 stands were placed at regular intervals on a 6 × 6 grid. Each data set consisted of 36 species, with four species modal positions located randomly within each of nine equal-sized strata. Heights of species surfaces were normally distributed within the 60–100 range. The 11 data sets differed in the amount of species turnover on the two gradients (Table 3). Stand alpha diversity decreases as species turnover increases, but species richness of the data sets was constant (Table 3).

The results of the analyses were assessed by visual inspection (plotting the ordinations obtained), and compared using Procrustes analysis (Schönemann and Carroll 1970). This method uses the 6 × 6 regular spacing of stands on the coenoplane as a target configuration, minimizing the sum of squares residuals in a rigid rotation of the resultant ordination configuration with respect to the target. The sum of squares quantity thus measures goodness of fit: the smaller the value, the more successful the ordination has been in recovering the original data structure (Fasham 1977).

Results

Salient features are apparent upon visual inspection of selected ordination scattergrams with grid lines connecting the 36 points (Fig. 1), and from the Procrustes analysis residual values presented in Table 3. We summarize and discuss the results as a series of observations.

1) Regardless of the method used, the ability to recover underlying data structure decreased as species turnover increased. This is in keeping with the well-known fact that as the proportion of zeros in the data increases, the data become less coherent (Swan 1970, Kendall 1971). Note that complete species turnover (when at least some stands have no species in common) occurs at ≈4.5 HC (Gauch 1982*b*). Beyond this point the relationship between stands with no species in common is definable only in terms of pathways which link stands showing a common floristic component. The robustness of these ordination strategies to increasing coenoplane beta diversity was quite variable. NMDS of stand-normalized data proved to be the most robust strategy. CA and DCA were the most robust of the metric strategies tested, but results were more dependent on the data set analyzed than were those of NMDS following stand norm standardization. Of the other strategies tested, P-Co-A and NMDS analyses of raw data were the most susceptible to distortion with increasing species turnover.

2) Standardization had important effects on ordination results. Both stand normalization and simultaneous double standardization were far superior to the analysis of raw data when P-Co-A was applied, though substantial distortion was nonetheless present at moderate levels of species turnover (Austin and Noy-Meir 1971, Gauch et al. 1977). NMDS and P-Co-A ordinations were similar when unstandardized data were analyzed directly. Conversely, NMDS following stand norm standardization (MDSC) produced results which were consistently superior to the other strategies, and far superior to P-Co-A using the same standardization. NMDS following simultaneous double standardization (MDSD), by contrast, was somewhat sensitive to outliers and anomalies in the data structure, though the ordinations were generally superior to those obtained using unstandardized data.

3) CA and DCA ordinations were similar except when considerable differences in species turnover on the two gradients occurred, in which case DCA performed notably better. At low to moderate species turnover, CA and DCA results were similar though slightly inferior to NMDS results based on stand-normalized data, while at high species turnover NMDS was clearly superior. Note also that detrending (DCA) collapsed and distorted CA results at high levels of species turnover and low alpha diversity.

4) The distinction between the results of P-Co-A following simultaneous double standardization and CA underlies the differences between these methods in the definition of the cross-products form and the eigenvector elements (Table 1). Thus the simultaneous double standardization implicit in CA is not the sole reason for the superiority of correspondence analysis over component analysis in the recovery of simulated coenoplane structure, though it is important: compare the P-Co-A ordinations based on raw data with those following simultaneous double standardization.

Discussion

Our results suggest that considerable variation exists in the ability of different ordination strategies to recover simulated coenoplane data. In particular, the evidence indicates that the success and robustness of both metric and nonmetric scaling methods in the summarization of nonlinear data is strongly dependent upon prior standardization. The results also suggest that the same standardization can have very different effects, depending upon whether metric or nonmetric scaling is performed. For example, while the results of metric and nonmetric scaling using raw data were very similar, standardization by stand norm, while it improved P-Co-A results to some extent, resulted in very efficient NMDS ordinations. Why should the effect of data standardization be dependent upon the ordination method used? We suggest two possible reasons. First, the linear constraints of eigenanalysis may restrict the ability of many metric methods to recover nonlinear data structure. NMDS, by contrast, involves a simple mapping of resemblance structure into a space of specified dimensionality. Thus, inherent nonlinearity can be provided for through the appropriate definition of resemblance structure. Secondly, the manner by which dimensionality is reduced may be important. In eigenanalysis, dimensionality reduction is achieved only when higher axes are discarded. This may lead to substantial information loss, and can result in misleading interpretations, if an inherently k-dimensional solution (real or the result of curvilinear distortion) is presented in fewer dimensions. Nonmetric scaling differs in that the solution in k dimensions is optimal for that number of dimensions, by a well-defined optimality criterion.

The results also confirm previous studies which have indicated that correspondence analysis is more successful in coenoplane recovery than are other metric ordination methods. However, the results also suggest that detrending a correspondence analysis ordination can, at least in some situations, distort underlying data structure (see also Wilson 1981). While additional heuristic investigations are clearly required, our results do indicate that conclusions recognizing DCA as the most efficient of the available ordination techniques (Hill and Gauch 1980, Gauch 1982*b*) were perhaps premature. In utilizing an empirically based strategy such as DCA, we suggest that users should also perform a CA ordination to objectively assess the effect of detrending on their particular data set.

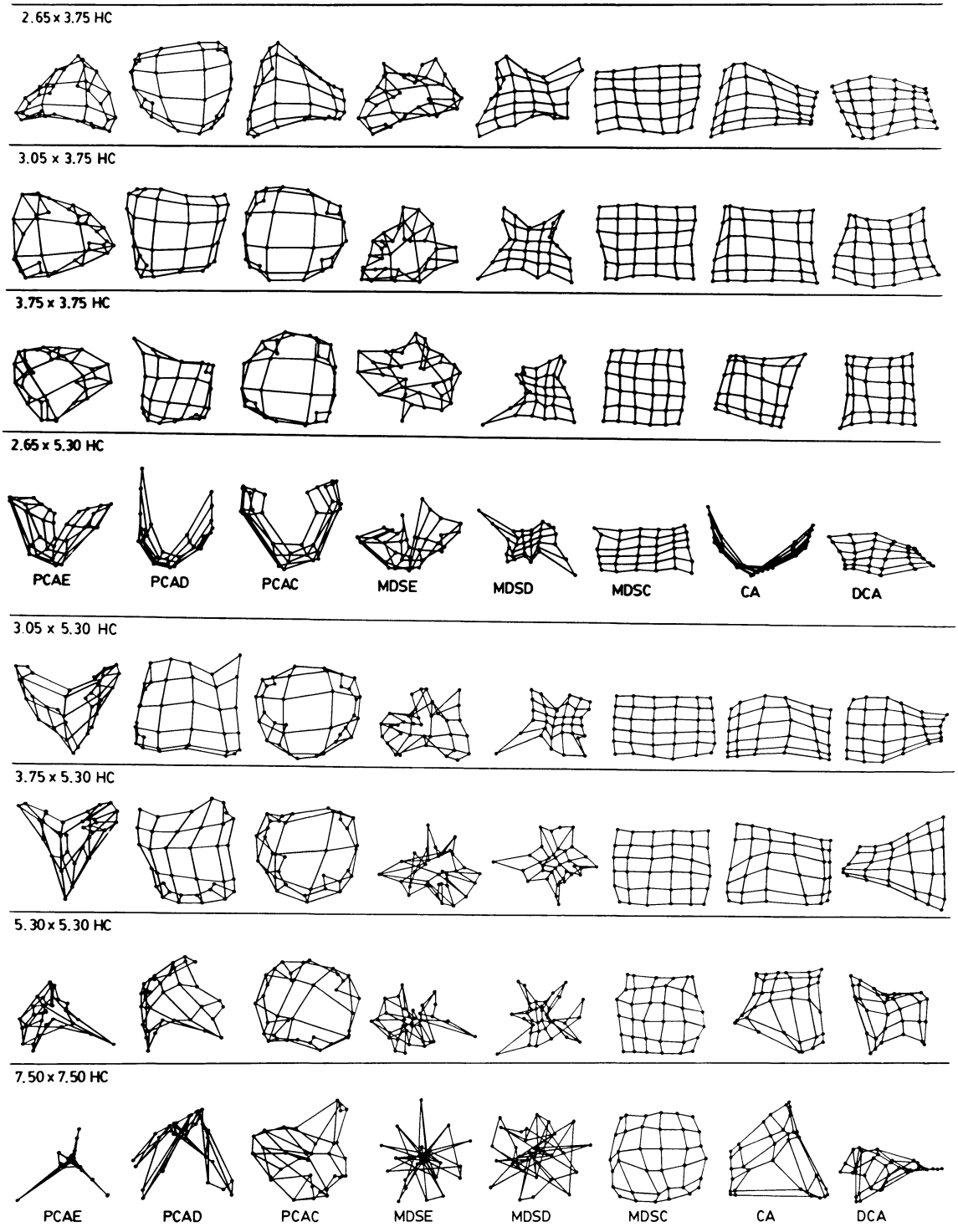

FIG. 1. Scattergrams of eight ordination strategies (see Table 2), each applied to 8 of the 11 artificial coenoplane data sets described in Table 3. In each case the 36 stands on the 6 × 6 grid are connected by lines. HC = half-change units = the measure of species turnover rate on each of the two independent environmental gradients of the coenoplane.

The limited number of comparisons made in this study indicate the importance of the definition of resemblance structure when applying NMDS. Further research should therefore be devoted to the theoretical derivation of resemblance measures suitable for the recovery of strongly nonlinear data (Austin 1976*a*). Considerations of the relationship between sample similarity and "ecological distance" (the physical distance between stands along an environmental gradient; Gauch 1973) may be a useful first approach. Orlóci (1980) used this approach to show that the calculation of Euclidean distance following stand norm standardization (chord distance; Orlóci 1967) leads to an appropriate definition of resemblance structure when nonlinear species responses are anticipated. The present study and an earlier one by Fasham (1977), who used a similarity function which is inversely monotonic to the chord distance, offer strong empirical evidence for the utility of this strategy. Other resemblance measures which appear to be useful in accommodating nonlinear data structure include the percent difference coefficient (Gauch et al. 1981) and a coefficient suggested by Kendall (1971) and used by Prentice (1977, 1980). Resemblance coefficients which cannot be accommodated by metric ordination methods, such as the Calhoun ordinal distance (Bartels et al. 1970) and probabilistic measures (Goodall 1966), may also prove useful.

In applying NMDS one must select the dimensionality of the final solution. Austin (1976*b*) has shown, using simulated data, that NMDS may distort structure if the dimensionality specified is greater than that underlying the data. However, it seems unlikely that this situation would arise in practice, particularly if two- or three-dimensional solutions are selected (Shepard 1974). Using the stress value to determine dimensionality, as originally suggested by Kruskal (1964*a*), is made difficult by the fact that stress is a function of the number of individuals, the distribution of resemblance quantities, and the noise level of the data (Gauch 1982*a*). Wish and Carroll (1982) concluded that goodness of fit, interpretability, and parsimony of data representation must all be considered in selecting the appropriate dimensionality.

Objectives should always be considered when selecting an ordination technique. If the principal objective is the recognition of distinct noda (Noy-Meir 1973, Hill et al. 1975, Peet 1980), an eigenanalysis strategy may be preferred, since data clusters and outliers tend to attract metric ordination axes (Anderson 1971, Gauch et al. 1977). However, this may result in the separation of strongly divergent clusters at the expense of obscuring trends within the remaining individuals, at least on the first few axes (Hill and Gauch 1980). If the objective is to summarize overall interspecific relationships, NMDS may be preferred, since it will optimize and preserve relative distances between all individuals irrespective of the presence of distinct noda (Anderson 1971). Prentice (1977, 1980) has suggested that the model underlying NMDS is more in keeping with our current understanding of vegetation than the models using metric methods, which make more stringent assumptions regarding data structure. In ordinating species, Matthews (1978) has pointed out that the theory underlying NMDS represents an implicit statement of the objectives of a species plexus. This argument can be readily extended to the examination of relationships among individuals.

Greig-Smith (1980, 1983) has indicated that there exists no objective method to assess ordination efficiency. While the ability to recover artificial data structures does give some indication of ordination efficiency and robustness, the large number of possible models of vegetation structure implies that inductive inferences regarding ordination utility cannot be made from such studies (Dale 1975, Austin 1976*a*, 1980, Wilson 1981). Further work in ordination methodology should therefore be directed toward the development of statistically derived nonlinear methods rather than deterministic, empirically derived ones (Orlóci 1979). In the interim, there is much to be said for the analysis of a given data set using a number of ordination methods (Orlóci 1978, Green 1979, Greig-Smith 1983). Because different methods emphasize different aspects of the data, such a strategy may be more revealing of data structure than the automatic application of any single method.

While the results of this study should be regarded as preliminary, they do offer some insight into the possible utility and limitations of a number of ordination strategies. Further work is clearly desirable, both in the heuristic testing of methods and in the statistical development of a general theory for the ordination of nonlinear ecological data.

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