COENOSES 7(2): 91-101, 1992

ON THE USE OF MANTEL'S STATISTIC AND FLEXIBLE SHORTEST PATH ADJUSTMENT IN THE ANALYSIS OF ECOLOGICAL GRADIENTS

O. Wildi

Swiss Federal Institute for Forest, Snow and Landscape Research, Department of Landscape Ecology,
CH-8903 Birmensdorf, Switzerland

Keywords: Flexible shortest path adjustment, Gradient analysis, Non-linearity, Ordination, Site factors, Spatial analysis

Abstract. The ecological interpretation of ordinations is easiest when there is a linear relationship between the site variables and the ordination axes. There are methods, such as detrending, which were claimed to remedy the horseshoe- or arc effect in ordinations. "Flexible shortest path adjustment" (FSPA) is a possible alternative. It is suspected that this method may improve the interpretability of ordinations, by reduction of the non-linearity between vegetation and environment in the ordination projection. The efficiency of this is measured by computing the stress between the ordination and the original resemblance matrices. Ecological interpretability is evaluated first by correlating the ordination axes with environmental data. Alternatively, Mantel-correlograms are computed for the vegetation and environmental data. In one example, using 63 relevés of a statistical sample from a transition bog gradient, principal coordinates analysis combined with FSPA yielded an extremely efficient ordination and improved considerably the linearity. The results were further improved when noise was removed from the data by secondary analyses. The efficiency of FSPA is confirmed in a second example, where 71 centroid records of Swiss forest types with very high species turnover rate were ordinated. The problem of interpretation in the application of the Mantel-statistics in non-stationary systems is discussed. It is concluded that FSPA and Mantel-statistics, when used with care, are very helpful to interpret biological and environmental relationships.

Introduction

The resemblance pattern of plant community data sampled along a straight gradient is affected by the so-called horseshoe effect (Swan 1970, Kendall 1971). This renders interpretation of ordinations difficult. In response terms, the horseshoe effect is the consequence of the non-linear relationship between biological and environmental variables which was discussed in detail by Orlóci (1978). The horseshoe effect is typical where the response type of species performance to site factors is Gaussian as has been shown by Jongman *et al.* (1987). In this case, a species will only grow well in the vicinity of its ecological optimum. Outside that range it will be largely lacking, which introduces zeros in the data. Such zeros cause distortions which are difficult to handle in the mathematical functions of species correlations and in the usual methods of ordination.

Various attempts to correct for non-linearity in ordinations have used intervention in different stages of the mathematical analysis. For example, Fewster and Orlóci (1983) use manipulations at the level of the resemblance function, while others, such as correspondence analysis (CA, Hill 1984), applied force to straighten the clouds of points to appear less a horseshoe and more an oval solid. As mentioned by Ter Braak (1986), correspondence analysis operates optimally when species response is Gaussian. But this is doubtful in the light of findings by Kenkel and Orlóci (1986). Gaussian ordination may deserve further attention in this connection (Minchin 1987).

When measuring joint resemblance of relevés, the methods that handle joint presence differently from the joint absence of species can remove some of the non-linearity effect (Legendre and Legendre 1984, Faith *et al.* 1987). Adjustments of the types Orlóci (1978) described and other corrections that involve the resemblance space as in Bradfield and Kenkel (1987), are more effective. Recently, the justification of detrending as used in detrended correspondence analysis has been criticized by several authors (Oksanen 1987, Wartenberg *et al.* 1987, Knox and Peet 1989).

Returning to the idea of manipulations with the original resemblance space, *i.e.* the resemblance matrix, attention was drawn in Bradfield and Kenkel (1987) to work by Williamson (1978). Williamson's idea is to recalculate resemblances between relevés that have almost no species in common, by additionally considering relevés with intermediate species composition. Even though his "step-across" method has lost attention in favour of DCA, Bradfiled and Kenkel (1987) demonstrated the outstanding performance of this idea, which they named "flexible shortest path adjustment" (FSPA), and used in ordination of artificial data with very high species turnover. The aim of the present paper is to investigate the further potentials of FSPA in the face of non-linear species responses which generate the horseshoe effect.

The way correlation is measured is important. The Mantel statistic (Mantel 1967), commonly used for the determination of spatial autocorrelation, is one possibility. The reason for considering it is the known property that it can detect correlation even if it is linear only within a small range of the ecological spectrum (Legendre and Fortin 1989). But, it must be noted that the consequences of any type of "correction" depends on the resemblance structure of the analysed data and is affected by noise. After testing the biological data for dependence on spatial location, the analysis will turn to actually measuring the efficiency of FSPA, in my first example. The second example investigates the effect of FSPA applied to vegetation data with very high species turnover which is indicative of a resemblance pattern with low coherence.

Methods

Correcting the resemblance pattern has promising consequences when the species turnover-rate along the dominating gradient is high. In the examples presented below the length of the gradients is calculated in sd-units as described by Hill and Gauch (1980). DECORANA is used for this calculation.

The algorithm applied for flexible shortest path adjustment has been proposed by Minieka (1978). This requires a decision for recalculating long distances. Williamson's (1978) and Bradfield and Kenkel's (1987) criterion is the overlap occurring in species composition. If two relevés have only few species in common, then it is suspected that their distance requires a correction. This assumes incidence (presence-absence) data. I suggest to base the decision for recalculating distances on a statistic of the resemblance matrix. In this case, any kind of distance measure can be used and the data type may be qualitative or quantitative. Considering Williamson's (1978) matrix

$$\mathbf{A} = \begin{array}{ccccccccccccccc}
1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1
\end{array}$$

the matrix of squared Euclidean distances among the rows is

$$\mathbf{D}^2 = \begin{array}{cccccc}
0 & & & & & \\
4 & 0 & & & & \\
8 & 4 & 0 & & & \\
10 & 8 & 4 & 0 & & \\
10 & 10 & 8 & 4 & 0 & \\
10 & 10 & 10 & 8 & 4 & 0
\end{array}$$

In this specific case, the elements in $\mathbf{D}^2$ are identical to the number of mismatches in the list of species. Excluding the diagonal elements, the distribution of squared distances in the matrix is found in the following histogram automatically, generated in program FSPA (Wildi and Orlóci 1990):

Distance class no.	from	to	frequency
1	3.994	4.595	5
2	4.595	5.196	0
3	5.196	5.798	0
4	5.798	6.399	0
5	6.399	7.000	0
6	7.000	7.601	0
7	7.601	8.202	4
8	8.202	8.804	0
9	8.804	9.405	0
10	9.405	10.006	6

Eliminating and recalculating the class of the longest distances ($d^2 = 10$) yields the new corrected matrix

$$\mathbf{U} = \begin{array}{cccccc}
0 & & & & & \\
4 & 0 & & & & \\
8 & 4 & 0 & & & \\
12 & 8 & 4 & 0 & & \\
16 & 12 & 8 & 4 & 0 & \\
20 & 16 & 12 & 8 & 4 & 0
\end{array}$$

The three new distances 12 result from summations of distances 4 and 8, 16 is the sum of elements of length 4 and 12 or 8 and 8, etc.

The program we are using allows to apply FSPA in conjunction with similarity measures, provided that their transformation to distances is considered tolerable. In the examples below, any similarity s_i is transformed to dissimilarity d_i according to

$$d_i = \min(s) - s_i.$$

The points are mapped into the reduced ordination space by Gower's (1967) principal coordinates analysis (PCoA). Unlike nonmetric multidimensional scaling, this avoids iteration and yields a unique solution directly through an eigenanalysis.

In order to relate the floristic matrix **F** to the site matrix **S**, autocorrelation is used as in Legendre and Fortin (1989) and Wildi (1990). The Mantel statistic correlates the spaces,

$$r = \frac{\sum_i f_i s_i - \frac{1}{k}\sum_i f_i \sum_i s_i}{\sqrt{[\sum_i f_i^2 - \frac{1}{k}(\sum_i f_i)^2][\sum_i s_i^2 - \frac{1}{k}(\sum_i s_i)^2]}}, \quad i = 1,...,k,$$

where $k = (n(n-1))/2$ and n is the number of data points. While this is a measure of agreement between **F** and **S**, information on the linearity of this relationship is available from correlograms. Legendre and Fortin (1989) show that if the correlation is linear over the entire ecological range (*e.g.*, for small as well as for large differences in pH or any other site factor), then the correlogram forms a straight line. If non-linearity occurs, it forms a curve which levels off near $r = 0$.

In case of spatial analysis, the site matrix **S** is replaced by physical distances **D**. Since in the present context, spatial trends rather than autocorrelation is of interest, specific directions have to be considered in the projection of the distances in **D**. Projection yields the new distance matrix **D'**. The overall Mantel statistic r and the correlograms are then computed based on **D'** (Wildi 1990).

To apply Mantel's statistic, the dimensionality of the data does not need to be reduced as for ordinations. This allows to correlate space or site versus floristic compostion either directly on the basis of resemblance matrices, or on ordinations of any dimension. For meaningful comparisons, the definition of the resemblance space should be commensurable with the ordination methods considered. It is hence assumed that a correlation matrix corresponds best to the pattern found in a PCA-ordination. The same applies to PCoA ordination derived from a correlation matrix. Considering now the case of a corrected resemblance pattern, analysis of a correlation matrix processed by FSPA, can be an equivalent to PCoA ordination corrected by FSPA.

It is known that a correcting effect is inherent in correspondence analysis (CA, Hill 1974) via data adjustments (Orlóci 1978) inherent in CA. To perform comparisons between CA and a full resemblance matrix, we decided to subject the data to transformation prior to computing the resemblance matrix. The adjustment is calculated according to

$$q_{hj} = \frac{f_{hj}}{\sqrt{f_{h.}f_{.j}}} - \frac{\sqrt{f_{h.}f_{.j}}}{f_{..}}$$

where f_{hj} is an original score and q_{hj} is an element of the transformed matrix. The similarity Matrix **C** used is the non-centred cross product of **Q**,

$$\mathbf{C} = \mathbf{QQ'}.$$

The fit of any 2-dimensional ordination space D2 and the n-dimensional resemblance space Dn can be measured as a stress function $\sigma(\rho)$, where

$$\sigma(\rho) = 1 - \rho^2(Dn;D2)$$

(Orlóci 1978). In this, ρ is the correlation coefficient of all off-diagonal elements in the distance matrices of these spaces. Statistical analysis in general and ordinations in particular, can be severely affected by outliers (Goodall 1969). To identify these, a nearest neighbour criterion is used (Wildi 1989). This is not done in a statistical nor in a phytosociological sense but simply as a filter to remove the low density phases. The question is how many relevés should be eliminated. Since there exist no a priori criteria for this, Podani's (1984) concept of continuous processes is followed. In the present case, the most isolated observation is eliminated first, then the entire analysis is repeated. This process of elimination and analysis is continued a number of times and a series of results is obtained.

Floristic and environmental connections

The first example draws on data from an oligotrophic wetland near Rothenthurm, Switzerland (Wildi 1977). Sixty three relevés describe a gradient from *Sphagnum* type transition bog to a marshy sedge meadow (*Carex davalliana* type). Table 1 presents the data after cluster analysis. The total number of species is 119 of which the 15 most discriminating are given. The plots are circular (2 m diameter), abundances are estimated on the Braun-Blanquet scale. A systematic sampling design is used with a grid width of 10 m (Figure 1). The data includes also18 site variables, mostly describing soil chemistry and the physics of ground-water and peat. For the present example, 6 of them were chosen to demonstrate typical cases. They are listed in Table 2 where their mean and standard deviation is given. Where necessary, logarithmic transformation is applied to reduce skewness. A detailed description of the chemical analysis is given in Wildi (1977) where the relevés are referenced under labels 501 through 563.

The floristic relevés summarized in Table 1 are classified using minimum variance clustering. A dominating coenocline emerges after rearrangement of groups by concentration anlysis (Feoli and Orlóci 1979). By applying DECORANA, we determined 3.121 sd-units for the length of the first and 1.866 sd-units for the second ordination axis. In an ordinary PCoA ordination based on a correlation matrix, the coenocline with groups 2 and 3 at one and 6 and 7 at the other end is horseshoe shaped (Fig. 2, a). As expected, CA produces an arc-shaped point pattern, a direct consequence of species responses (and correlations) being strongly non-linear (Fig. 2, b). The modification of the correlation matrix by FSPA is based on the following statistics of distances:

Table 1. Classification of a transition bog vegetation. Group 7 is a vegetation type dominated by small sedges, group 2 is transition bog vegetation proper. Out of a total of 119, the 15 species with maximum discriminating power are shown. The entries in the matrix are percentages of species presence within relevé groups. Group size is measured in relevé numbers.

	Relevé group no.	7	6	4	5	1	3	2
	Group size	10	7	9	6	8	11	12
11	Carex hostiana	80	71		16			
106	Stachys officinalis	20	100				9	
45	Carex pulicaris	90	100	33	33			
86	Galium uliginosum	60	100		66		9	
10	Carex davalliana	100	100	44	33	12	9	
23	Parnassia palustris	100	71	77	50			
21	Tofieldia calyculata	100	85	66	16	12	9	
110	Ranunculus nemorosus	80	85	11	100		27	
13	Carex echinata	30		100	100	100	91	91
54	Sphagnum recurvum			55	83	87	100	91
37	Sphagnum medium			44	66	75	91	100
55	Sphagnum rubellum			33	16	100	81	100
26	Arnica montana			11	16	100	81	100
4	Oxycoccus quadripetalus			11		37	100	91
29	Polytrichum strictum				16	12	81	100

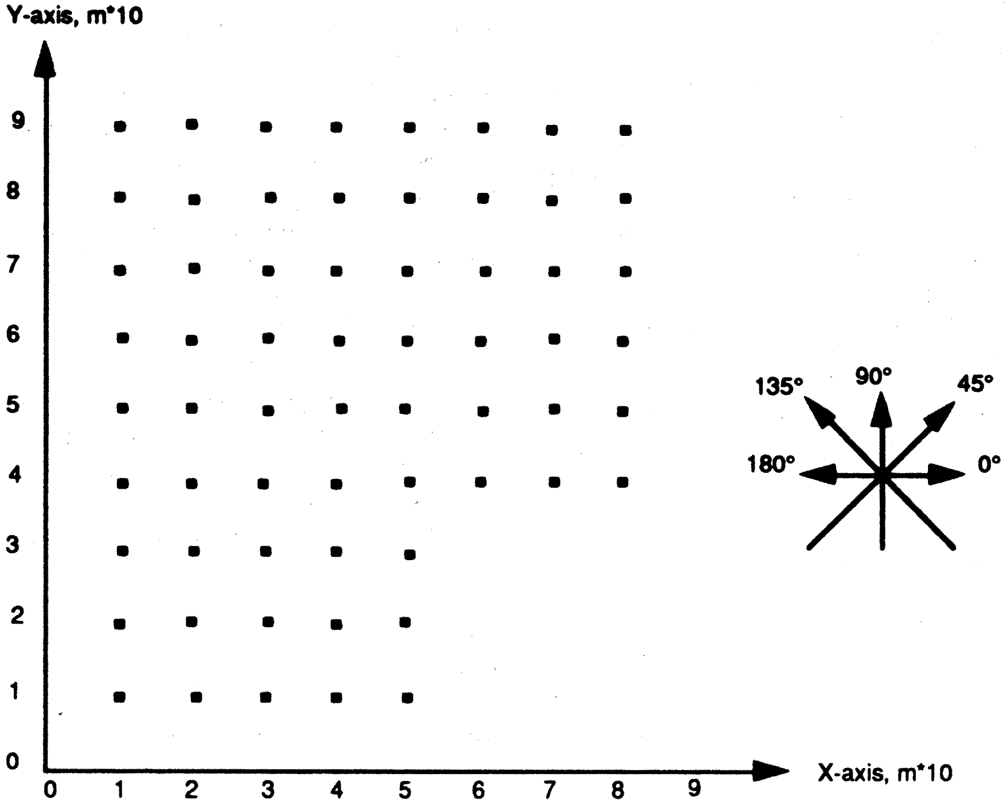

Figure 1. Sampling design and directions in space of the investigated site considered in the first example.

Distance class no.	from	to	frequency
1	.144	.259	33
2	.259	.374	145
3	.374	.489	274
4	.489	.604	305
5	.604	.718	282
6	.718	.833	250
7	.833	.948	262
8	.948	1.063	267
9	1.063	1.178	126
10	1.178	1.292	9

The threshold for recalculating the distances is set to 0.718. Consequently, about half of the elements in the distance matrix are re-calculated. This causes the point cloud to appear completely stretched (Fig. 2, c). The main gradient now corresponds to the first axis. The second axis explains additional variation, mainly in groups 4, 6 and 7. The usefulness of applying PCoA combined with FSPA is supported by the high proportion of variation accounted for by the first axis (Table 3). There is an extremely high coincidence between the resemblance space and the ordination space of corrected PCoA as can be seen from the $\sigma(\rho)$-values. Surprisingly, stress between the non-adjusted correlation matrix and the adjusted 2-dimensional ordination yields $\sigma(\rho) = 0.116$, while stress between the ordinary correlation matrix and PCA ordination with $\sigma(\rho) = 0.159$

Table 2. Site factors of bog data.

Site factor	mean (n=63)	standard deviation
(1) pH of peat	5.15	0.807
(2) log ash content, %	1.75	0.169
(3) acidity (mval/100g peat),	25.1	10.7
(4) average ground water table (cm)	13.2	4.41
(5) pH ground water	5.52	1.20
(6) log conductivity ($\Omega^{-1}cm^{-1}$ at 20 °C)	1.52	0.262

Table 3. Percentage contribution of the 3 largest eigenvalues λ of the ordinations in Fig. 2 and stress $\sigma(\rho)$ between the 2-dimensional ordination and the n-dimensional resemblance space. See main text for explanations.

Method	λ_1	λ_2	λ_3	$\sigma(\rho)$
PCA	27.96	9.43	5.99	0.159
CA	19.38	7.84	5.93	0.457
PCoA, FSPA	60.36	11.15	6.48	0.059

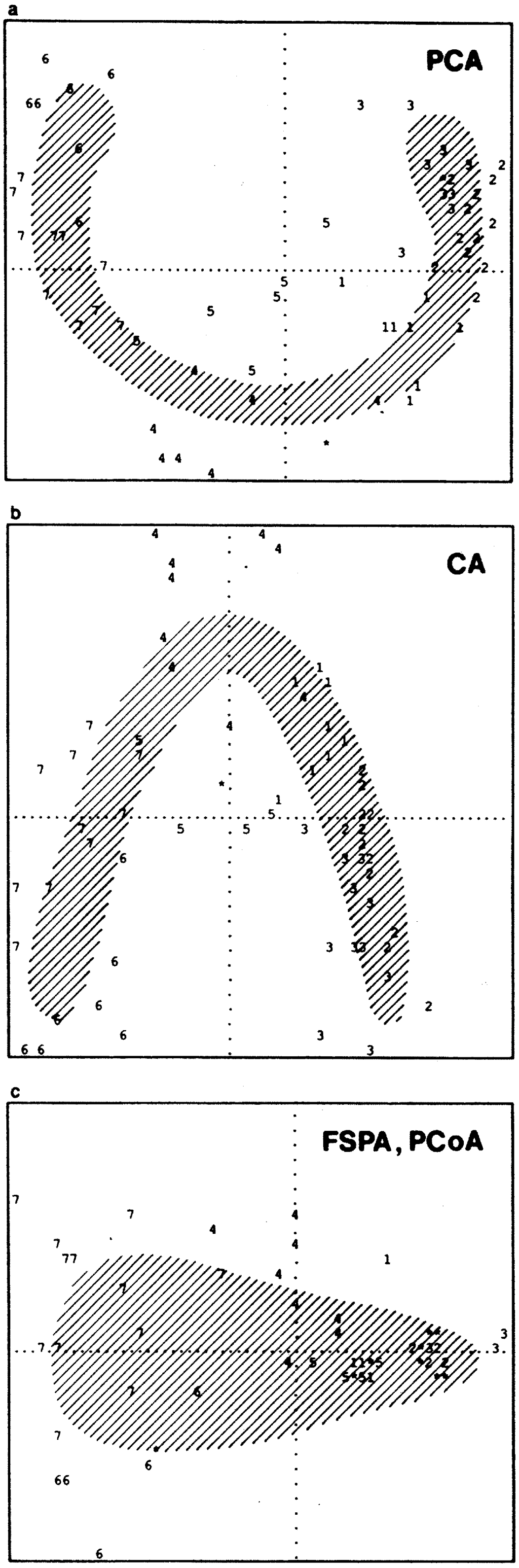

Figure 2. Ordinations of the wetland data (n=63) by (a) PCA, (b) CA, and (c) PCoA adjusted by FSPA. Asterisks mark two or more coinciding data points.

Table 4. Linear correlations of 6 site factors with the first two axes of the ordinations in Fig. 2.

Site factor	Axis no.	r(PCA)	r(CA)	r(PCoA, FSPA)
(1) pH of peat	1 2	-.877 -.154	-.896 .152	-.892 .148
(2) log ash content,%	1 2	-.427 -.016	-.482 .067	-.456 -.079
(3) acidity (mval/100g peat)	1 2	.687 -.152	.723 .105	.733 .099
(4) average ground water table (cm)	1 2	-.264 .654	-.264 -.659	-.323 -.619
(5) pH ground water	1 2	-.951 .088	-.951 -.100	-.940 -.029
(6) log conductivity ($\Omega^{-1}cm^{-1}$ at 20°C).	1 2	-.661 .490	-.659 -.466	-.724 -.255

Table 5. Mantel's r computed for 6 site factors using three diffent resemblance measures for the vegetation data. r - correlation; c - covariance of data transformed to deviation from expectation; u - correlation adjusted by FSPA. The size of the original data set (o) is n=63. The reduced data set (f) has size n=42.

Site factor	Data set	r matrix	c matrix	u matrix
(1) pH of peat	o f	.650 706	.635 .595	.678 .726
(2) log ash content,%	o f	.075 .001	.083 .029	.088 .007
(3) acidity (mval/100g peat)	o f	.408 .243	.363 .195	.447 .278
(4) average ground water table (cm)	o f	.355 .218	.188 .122	.359 .204
(5) pH ground water	o f	.808 .804	.731 .623	.826 .846
(6) log conductivity ($\Omega^{-1}cm^{-1}$ at 20°C).	o f	.600 .552	.360 .253	.625 .618

is higher. This supports the findings of Williamson (1978), and Bradfield and Kenkel (1987) that FSPA, with respect to linear criteria like the $\sigma(\rho)$ values, may yield extremely efficient ordinations. On the other hand the C-Matrix does not sufficiently reproduce the patterns generated by CA (Table 3). Computing stress based on this definition of ρ is meaningful in the context of spaces that are related to the euclidean geometry, but other definitions would have to be used for ρ in the case of CA.

The ecological interpretation of ordinations is easiest when there is a direct relationship between site variables and ordination axes. In Table 4 the linear correlations between site measurements and the first two axes of the ordinations in Fig. 2 are shown. When comparing PCA and CA, the results are either almost identical with respect to the first axis or CA is superior (variables 2 and 3). This confirms that CA can be somewhat more efficient than PCA in linearly explaining ecological data. PCoA combined with FSPA is superior to PCA in 5, and to CA in 3 out of 6 cases. Generally, PCoA combined with FSPA concentrates more correlation on the first axis than the other two methods.

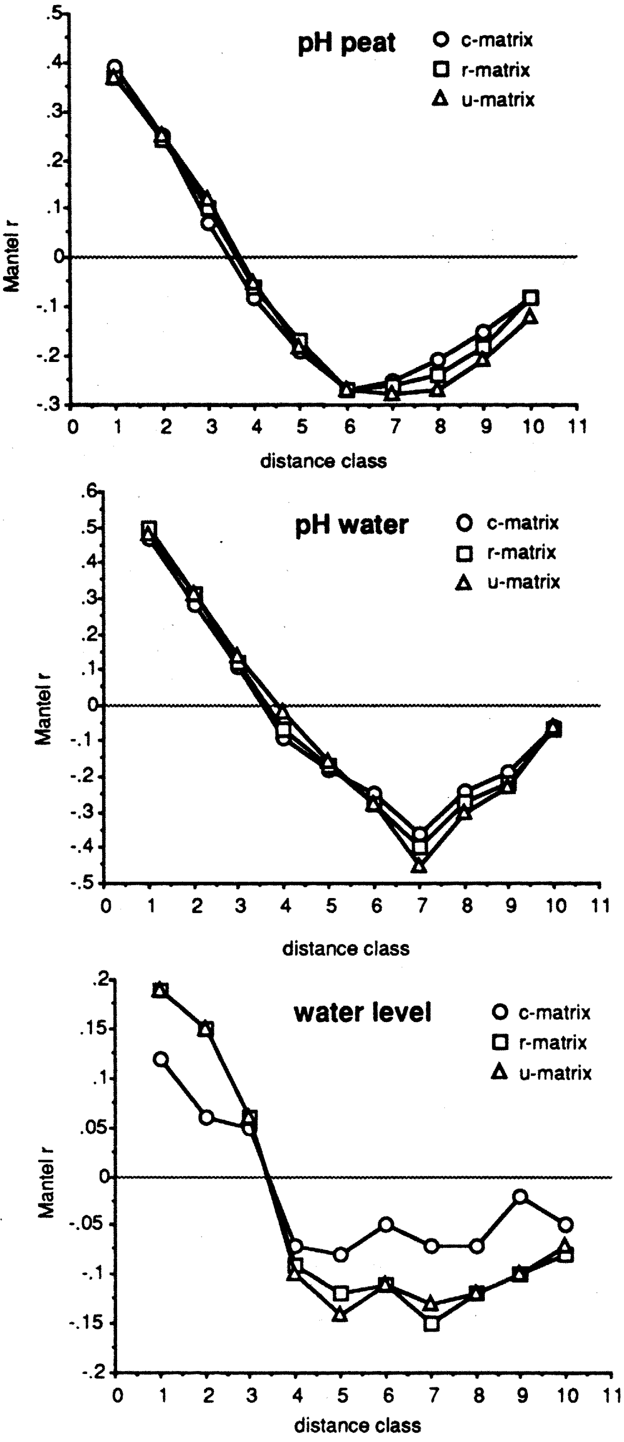

Figure 3. Correlograms of site variables pH peat, pH water and water level applied to different resemblance matrices of the same floristic data. Complete data set used (n=63).

The Mantel statistics is an indication of fit between vegetation and environmental data which is not constrained by dimensionality or the orientation of the axes. In Table 5 Mantel's r is used as a measure of fit between the 6 site variables selected and three different floristic resemblance matrices. In all cases, overall correlation is higher when using the adjusted correlation matrix instead of the non-adjusted one.

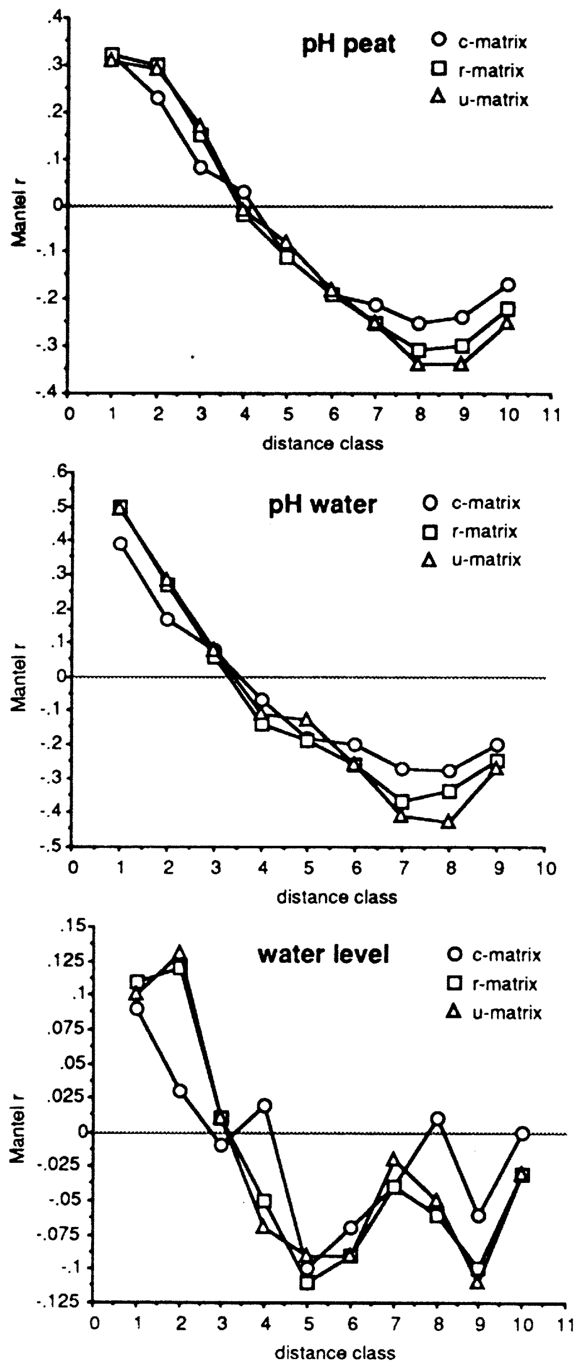

Figure 4. Correlograms of 3 site variables pH peat, pH water and water level applied to different resemblance matrices of the same floristic data. Reduced data set used (n=42).

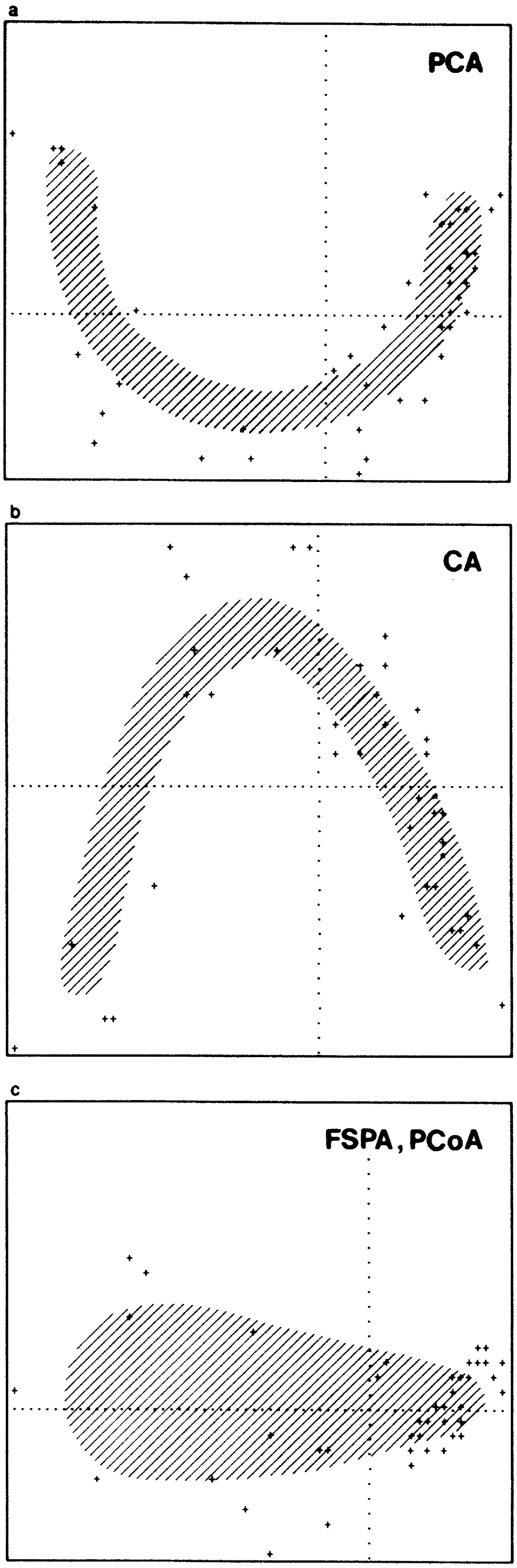

Figure 5. Ordinations of the classified and reduced wetland data (n=42) by (a) PCA, (b) CA, and (c) PCoA adjusted by FSPA. Asterisks mark two or more coinciding data points.

Modification by FSPA also leads to correlograms with the most extreme deviations of Mantel's r values from zero (Fig. 3). This can also be attributed to improved linearity.

In all correlograms of Fig. 3, correlation breaks down when the differences of the site conditions become too big, and, with respect to the floristic data, at big compositional distances. Several potential reasons are known for this phenomenon (Orlóci 1978, Legendre and Fortin 1989). Firstly, it happens that the relation becomes non-linear. FSPA should correct for this. Secondly, noise in the data disturbs the function. To reduce the latter, isolated observations have to be removed.

During the continuous process of noise elimination described in the previous section, all the linear correlations between the ordination axes and the site measurements decrease, which indicates that the interpretability of the individual axes decreases also. On the other hand, Mantel's r remaines stable. When the filtering process reaches the point where the most isolated relevés have a similarity ratio of s = 0.6 to their nearest neighbour, 42 out of 63 relevés are left in the data set. Here, the Mantel-r reaches a maximum for those site factors which initially had already the highest correlation with the vegetation, *i.e.* site factors 1 and 5 (pH in water and peat, Table 5). The correlograms in Fig. 4 show that the range of linear correlation for pH in water and peat is extended and the linearizing effect of FSPA is even more pronounced than with the unfiltered data set. By contrast, the correlogram of the average water table looses distinctness. It seems that the filtering process removes relevés representing this trend. The ordinations derived from the reduced data also show improved interpretability (Fig. 5). PCA-ordination generates an almost perfect horseshoe, CA an arc and PCoA combined with FSPA stretches the point cloud entirely. It is concluded that the reduced data describe a vegetation gradient which is almost exclusively determined by pH. The water table has no considerable influence.

Spatial relationships

The data in the first example describe a gradient. It is evident then that the sampling units, *i.e.* the relevés, are not really statistically independent as would be required for applying methods of parameter estimation. Knowing this, it may be quantified. An application of the Mantel statistics represents one approach of autocorrelation analysis, that allows to determine the spatial relations of biological and environmental data. In a first attempt, correlograms are constructed for different directions in space (Fig. 6). The most pronounced dependence occurs at directions near 100 degrees (upper graph), upon higher resolution of angles, at 85 degrees (lower graph). In the direction of 140 degrees, the change in biological compostion is almost independent of spatial interplot distance.

A more precise estimation of this direction is attempted in a further step. There, overall Mantel statictics is determined as a function of direction in space. As can be seen from Figure 7, this relationship forms a smooth curve with a maximum at 85 and a minimum at 140 degrees. These are the directions of maximum spatial dependence, where the most pronounced gradient occurs, and zero dependence, at which the system is stationary.

The efficiency of ordinations

Linear ordination is becoming unefficient when the species turnover-rate along gradients is high (Gauch 1982). For the second example, focussed on this property, I use a data set describing 71 Swiss forest types (Ellenberg and Klötzli 1972). The sampling units are group centroids of relevés, collected by several authors at different times. Due to the wide ecological range covered by the data, a high turnover-rate (and consequently a high beta diversity) exists. With DECORANA I found 5.636 sd-units for the length of the first and 3.954 sd-units for the second ordination axis. Even so no appropriate site parameters are available, the efficiency of the different ordination methods in representing the original resemblance pattern can be determined. Table 6 lists the stress values calculated between the original resemblance spaces and the ordinations with dimensions 1 through 3. In all cases, PCoA is used as a projecting method. The advantage of FSPA as a linearizing method is striking. Unlike in the first example, the second axis is essential in order to explain the resemblance pattern. In the second part of Table 6, the analysis is repeated with a reduced data set with 3 extreme outliers removed (similarity to the nearest neighbour $s \leq 0.3$). After this process, the efficiency of FSPA is yet increased, especially for the three-dimensional ordination, where stress drops to $\sigma(\rho) = 0.075$.

Table 6. Ordinations of Swiss forest types. Stress values $\sigma(\rho)$ between the original resemblance spaces and ordinations of dimension 1 through 3 are given. PCoA is used as a projecting method. The complete data set has size n=71. After reducing, n=68.

Resemblance space	1-dimensional ordination	2-dimensional ordination	3-dimensional ordination
PCoA, n=71	0.717	0.449	0.274
PCoA, FSPA, n=71	0.520	0.183	0.139
PCoA, n=68	0.711	0.415	0.252
PCoA, FSPA, n=68	0.483	0.161	0.075

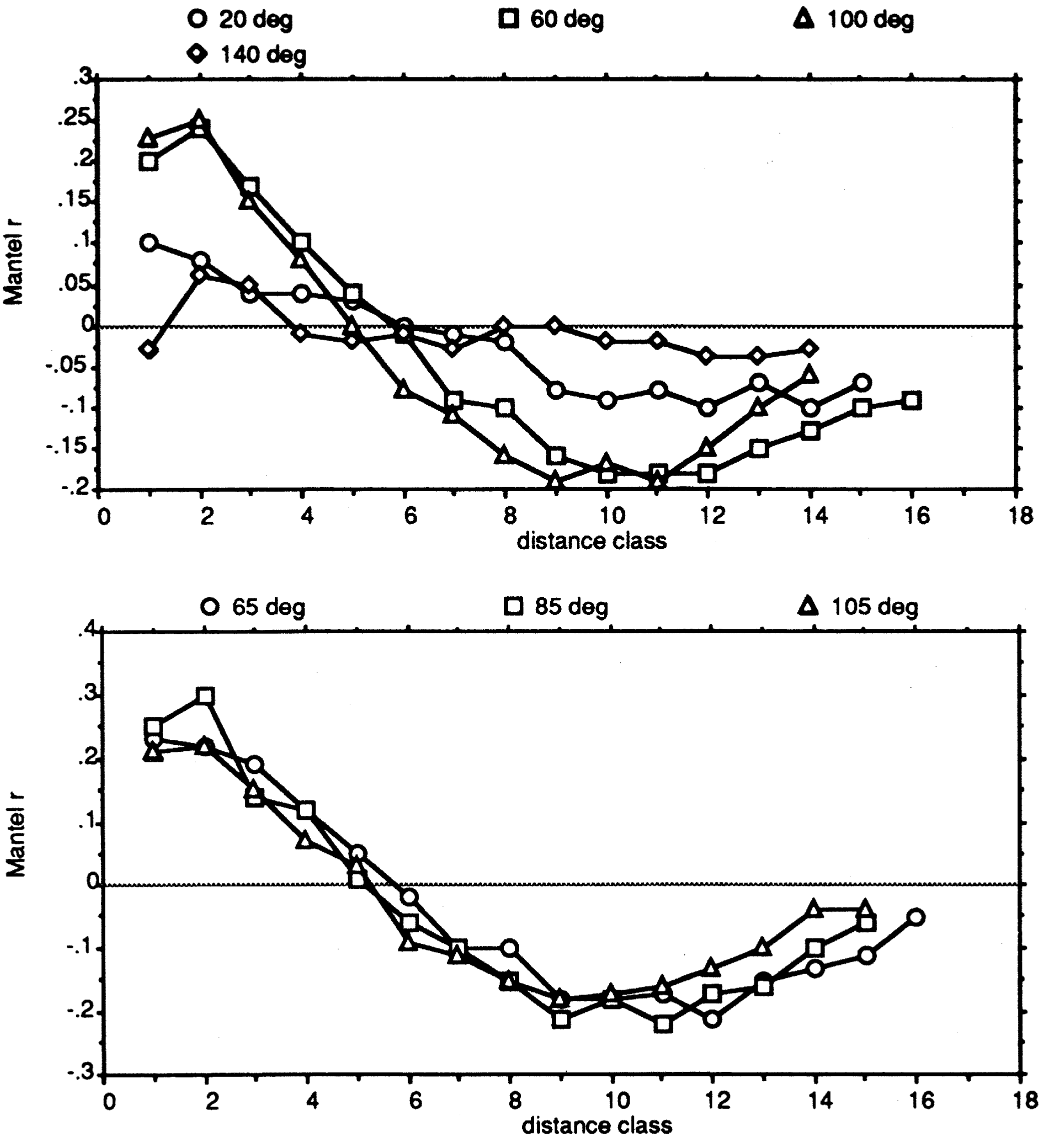

Figure 6. Correlograms for selected directions in space (upper graph). Spatial dependence is most pronounced near 85 degrees (lower graph).

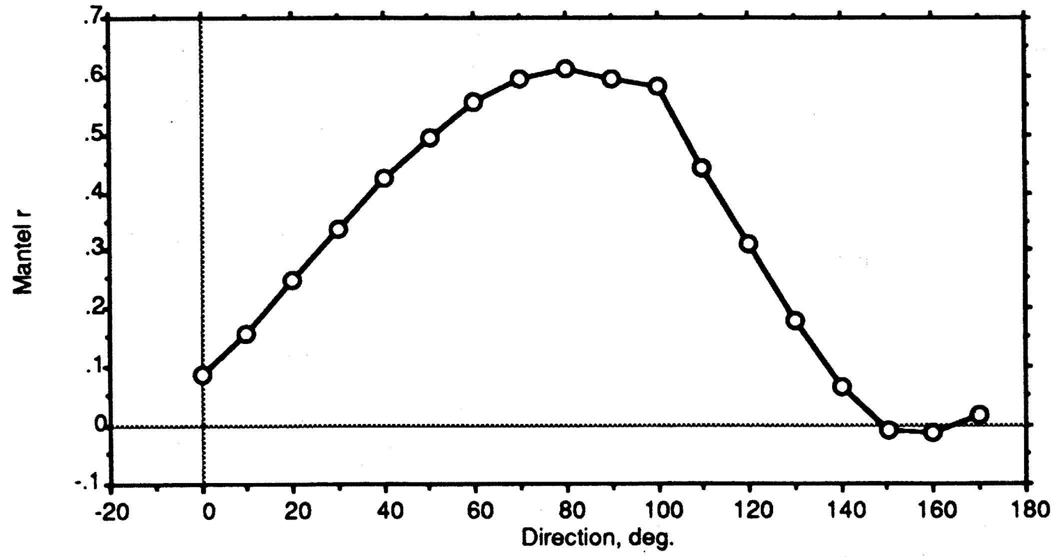

Figure 7. Overall autocorrelation as a function of spatial orientation. See Figure 1 for directions.

Discussion

In the present paper, flexible shortest path adjustment (FSPA) is investigated for its performance in linearizing ecological relationships. In the context of detrended correspondence analysis, several authors have expressed their concern about the value of detrending. Irrespective of the method, modifying the resemblance pattern of observations is a risky task. At least four conditions should be fulfilled to avoid misinterpretations: (1) gradients should be expected in the data, (2) there should be a high species turnover-rate along the axes, (3) extreme outliers should not be present and (4) obvious discontinuities should be absent. I also agree with Kenkel and Orlóci (1986) that modifications of the sort should be verified by checking the result with the corresponding non-adjusting method.

This discussion about FSPA may stipulate a comparison with DCA, still one of the most widely used ordination methods in ecology. However, I do not consider this an essential aspect. The two methods differ clearly. Some of the advantages of detrended correspondence analysis are the ease of computation, the availability of a scale for the axis that measures the species turnover rate and its ability to handle discontinuities reasonably (Hill and Gauch 1980). But as criticized by Wartenberg *et al.* (1987) it cannot improve the rank order of the points along the first axis. FSPA, on the other hand, does this, as it operates in all dimensions of the resemblance space simultaneously. Furthermore, it can be applied to any kind of distance space and is not restricted to CA. It can even handle involute point patterns as demonstrated by Bradfield and Kenkel (1987). The danger of miscalculating discontinuities, mentioned by Hill and Gauch (1980), is minor: the algorithm yields no solution if a gap occurs that is larger than the threshold chosen for recalculating the distances.

Apart from theoretical considerations, the present paper investigates the ability of FSPA to linearize the relationships of biological and environmental data in a special case. Example 1, analyzed with a gradient of length sd ≈ 3 (about three species half-changes), confirms that CA is superior to PCA, at least as correlations with the first ordination axis are concerned. As soon as the correlation matrix is corrected by FSPA, the results from PCA are equal or sometimes better than those of CA. In Example 2, where the main gradient has length sd $= 5.6$, principal coordinates analysis (PCoA) combined with FSPA also increases the efficiency of the second and third axis of the ordination in projecting the resemblance space. It is in the case, where beta diversity is very high, that the use of FSPA is strongly recommended.

The ordinations, when corrected by FSPA change dramatically in their shape. On the other hand, the gain in linear relationship to ecological measurements is moderate. The use of the Mantel statistics indicates that there is some increase in the range where linearity occurs. The interpretation of the Mantel statistics is a problem by itself. Legendre and Fortin (1989) use it for measuring autocorrelation. All examples shown here come from systems that are non-stationary, so that autocorrelation in its proper sense cannot be analysed (Upton and Fingleton 1985). This is why significance tests applied to mantel correlograms as shown by Legendre and Fortin (1989) have no meaning in the present context.

It is interesting to note that many methods which attempt to overcome non-linearity are heuristic, like DCA and nonmetric multidimensional scaling (NMDS Kruskal 1964a, b). FSPA is not an exception in that a threshold for recalculating distances has to be chosen. Based on experience I recommend to set this limit as low as possible. This decision is of course arbitrary. But the result then comes close to the minimum spanning tree method for calculating distances among relevés, proposed by Lagonegro (1986). Unlike this, however, FSPA is not affected by local noise in the data and the solution gains in stability when the sample size becomes sufficiently large. The same considerations may hold as for the stress function used here to measure the fit of resemblance spaces of different dimensionality and also for the application of the Mantel statistic. For the latter, Legendre and Fortin (1989) suggest to use a sample of size $n \geq 30$.

The results presented in this paper encourage further applications of FSPA and the Mantel statistics. Both can help in the interpretation of data in cases of non-linearity. Ecological examples using data with high beta diversity are of major interest. Unlike in some other methods, the improved interpretability of the second and the following axes of the ordinations appears to be an added advantage of this particular method. Other combinations with ecologically relevant methods, like NMDS, canonical analysis or spatial autocorrelation analysis, are of interest. Finally, FSPA should be tested in combination with many other resemblance concepts which proved to be successful in ecology (Faith *et al.* 1987), but could not be combined with previous linearizing methods.

Acknowledgments. I thank M. Frech, B. O. Krüsi, L. Orlóci and two unknown referees for many suggestions and critical discussions and N. C. Kenkel for lending an efficient algorithm for programming FSPA.

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Manuscript received: September 1991