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A COMPARATIVE STUDY OF CLASSIFICATION AND ORDINATION METHODS ON SUCCESSIONAL DATA

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Abstract. The paper analyzes succession from *Calluna vulgaris* - dominated heathland to woodland dominated by *Betula pubescens* and *B. pendula* in Scotland and Northern England. Seven methods were used, classical phytosociological analysis, three ordination methods (Principal Component Analysis, PCA, Detrended Correspondence Analysis, DCA, Bray and Curtis Ordination, BCO) and three classification methods (Cluster Analysis, Indicator Species Analysis, Two Way Indicator Species Analysis). Phytosociological analysis well categorized distinct vegetation types, but failed to classify transitional stages. DCA, BCO using Euclidean distance and in particular PCA clearly displayed the successional trends. Numerical classification did not perform well on the raw data, but ordination complemented by classification (e.g., clustering of the component scores from PCA) gave the best insight into vegetation patterns. The suitability of different methods according to the nature of the data to be analyzed is discussed.

Introduction

Classification and ordination are two different ways of looking at variability in vegetation data. The former seeks compositional discontinuities in sets of relevés, while the latter emphasizes trends of variations and highlights continuities. Many methods of classification and ordination have been proposed (for an introduction see Clifford and Stephenson 1975; Orlóci 1978; Greig-Smith 1980; Gauch 1982; Ludwig and Reynolds 1989; for a review see Kent and Ballard 1988; Mucina and van der Maarel 1989). Different approaches can extract different information from the same data set (Campbell 1978) and, in many cases, a complementary use of both classification and ordination can be opportune (Komarkova 1980). Kent and Ballard (1988) have reviewed the use in the literature of methods of data analysis in vegetation science and discuss this point further.

It is possible to distinguish three main groups of papers in the ecological literature comparing different methods. In the first group, classical phytosociological classification has been compared to different numerical methods. There are examples of comparisons to other classification techniques (Ivimey-Cook and Proctor 1966; More *et al.* 1970; Stanek 1973; Werger 1973; Coetzee and Werger 1973; Campbell 1978; Gauch 1982) and ordination methods (Moore *et al.* 1970; Werger 1973; Van der Maarel 1966). These comparisons generally showed consistent agreement between the results of phytosociological classifications and of numerical methods, which has been considered as confirming the validity of the former.

In the second group, different techniques of numerical clustering were compared to observe the effects of changing resemblance measures (Campbell 1978; Hubalek 1982; Jackson *et al.* 1989) or agglomeration criteria (Robertson 1978; Gauch and Whittaker 1981). In a few cases, the applications used simulated data sets (Robertson 1979).

The third group examined the results of applying various ordination techniques to different data sets, both real (Robertson 1978; Clymo 1980; Del Moral 1980; Oksanen 1983; Casado *et al.* 1989) and simulated (Swan 1970; Gauch and Whittaker 1972; Austin 1976; Kessel and Whittaker 1976; Fasham 1977; Gauch *et al.* 1977, 1981; Feoli and Feoli Chiapella 1980; Mohler 1981; Kenkel and Orlóci 1986), to compare their relative performance. For example, when applied to data sets generated by simulation algorithms, Principal Components Analysis (PCA) has been reported to be affected by problems of curvilinear distortion compared to other techniques, e.g., Reciprocal Averaging or Detrended Correspondence Analysis (DCA) (Austin 1976; Fasham 1977; Gauch *et al.* 1977; Whittaker and Gauch 1982). However, Austin (1985) and Minchin (1987) have pointed out how such artificial data sets can contain intrinsic biases when used in this way. On the other hand, PCA has been used with good results in many studies on real data (e.g., Austin 1968; Werger 1973; Bouxin 1976; Oksanen 1983; Oliver and Webster 1987), and also on complex simulated data sets (Allen and Shugart 1983). Further, Casado *et al.* (1989) reported that PCA performed better than DCA in detecting small scale patterns along a transect.

Despite the large debate found in the literature on which method is "best", clearly the suitability of

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Table 1. Study sites and vegetation characters.

Site	Sample area	Predominant species	Tree age	Phytosociological classification
● Delnalyne	1	C. vulgaris	-	C
	2	B.pubescens	20	P
■ Tulchan	3	C. vulgaris	-	V
	4	B. pendula	18	*
	5	B. pendula	26	*
	6	B. pendula	38	T
	7	B. pendula	90	T
○ Craggan	8	C. vulgaris	-	V
	9	B.pubescens	18	*
	10	B.pubescens	27	T
	11	B.pubescens	53	T
△ Spinningdale	12	C. vulgaris	-	V
	13	B.pubescens	26	T
□ Kerrow	14	C. vulgaris	-	N
	15	B. pendula	17	
	16	B. pendula	25	P
	17	B. pendula	69	P
⊘ Dulsie Wood	18	C. vulgaris	-	V
	19	B. pendula	27	B
✱ Kill Burn	20	C. vulgaris	-	E
	21	B. pendula	24	B
▲ Silpho (a)	22	C. vulgaris	-	*
	23	B.pubescens	15	*
(b)	24	C. vulgaris	-	*
	25	B.pubescens	51	G
	26	B.pubescens	67	G
(c)	27	B.pubescens	29	G
	28	B.pubescens	60	G
◕ Cambus o'May	29	C. vulgaris	-	*
	30	B. pendula	25	B
⧄ Dunalaistair	31	C. vulgaris	-	C
	32	B. pendula	25	B
▼ Easter Bohespic	33	B. pendula	11	*
⊞ New Kinord	34	C. vulgaris	-	C
	35	B. pendula	31	T
# Lochhead	36	C. vulgaris	-	*
	37	B. pendula	18	T

* - unclassifiable
C - Carici binervis-Ericetum cinereae Br.-Bl. et Tx. (1950) em. Birse
V - Vaccinio-Ericetum cinereae Birse et Robertson 1976 em. Birse
E - Vaccinio-Ericetum tetralicis J.J. Moore 1962
N - Narthecio-Ericetum tetralicis J.J. Moore (1964) 1968
T - Trientali-Betuletum pendulae Birse 1982
G - Galio saxatilis-Quercetum Birse et Robertson 1976
P - Primulo Quercetum Birse et Robertson 1976
B - Blechno Quercetum Br.-Bl. et Tx. (1950) 1952

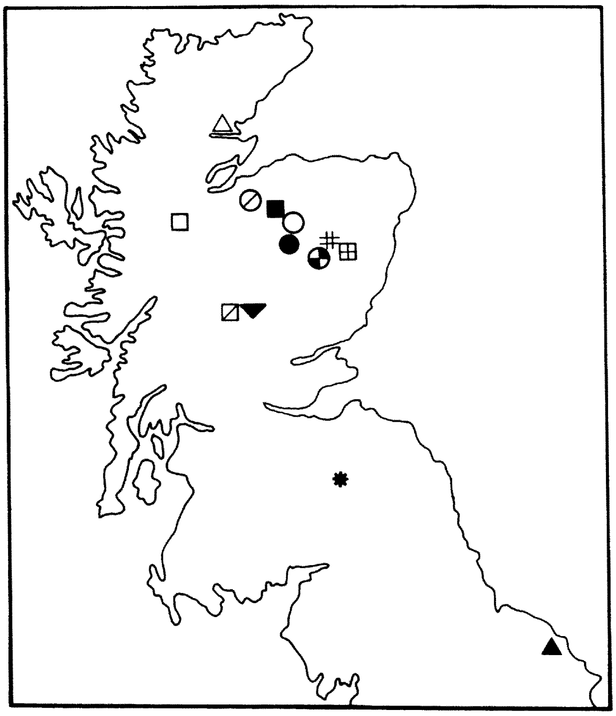

Figure 1. Location of study sites. Symbols are reported in Table 1.

different methods may vary according to the nature of the data to be analyzed and the aim of the study. In this paper we have tried to break new ground, firstly by taking a very wide approach which includes the aims of all three groups of studies noted earlier and, secondly, by analyzing a set of mainly successional data, a category which has been little studied by photosociologists because of the difficulties of making well-structured tables and defining vegetation types in very dynamic conditions. Specifically, we used classical phytosociological analysis and six numerical methods, three of ordination and three of classification, to analyze data on the succession from *Calluna vulgaris*-dominant heathland to woodland dominated by birch (*Betula pubescens* and *B. pendula*) in northern England and Scotland.

Materials and Methods

Floristic data were collected from 13 sites in Britain located from northern Scotland to northern England (Fig. 1 and Table 1). The criterion for the selection of these sites was the presence of birch colonizing an area of heather moorland with relatively uniform topography, vegetation and soil. Single effectively even-aged stands were present on nine sites. The other four sites bore three or more adjacent stands of different ages, thus allowing time sequences to be constructed with the moorland representing time zero (Table 1).

The vegetation composition and structure was recorded in nine random quadrats (each 1m × 1m) within each sampling area, i.e., each birch age class at each site. Thus sites with only a single birch stand gave two sampling areas, one in the birch stand and the second in the adjacent moorland type. If more stands of different ages were present each of them was sampled plus the adjacent moorland. A total of 333 quadrats (37 sample areas) was described and 120 different species were recorded. Cover-abundance was assessed by the Domin scale. Analyses were done both on Domin scores and on % cover, the latter being derived from Domin scores as follows:

Domin:	0	1	2	3	4	5	6	7	8	9	10
% Cover:	0	0.5	1	3	8	18	30	45	65	85	95

The data were analyzed at two levels, by quadrats

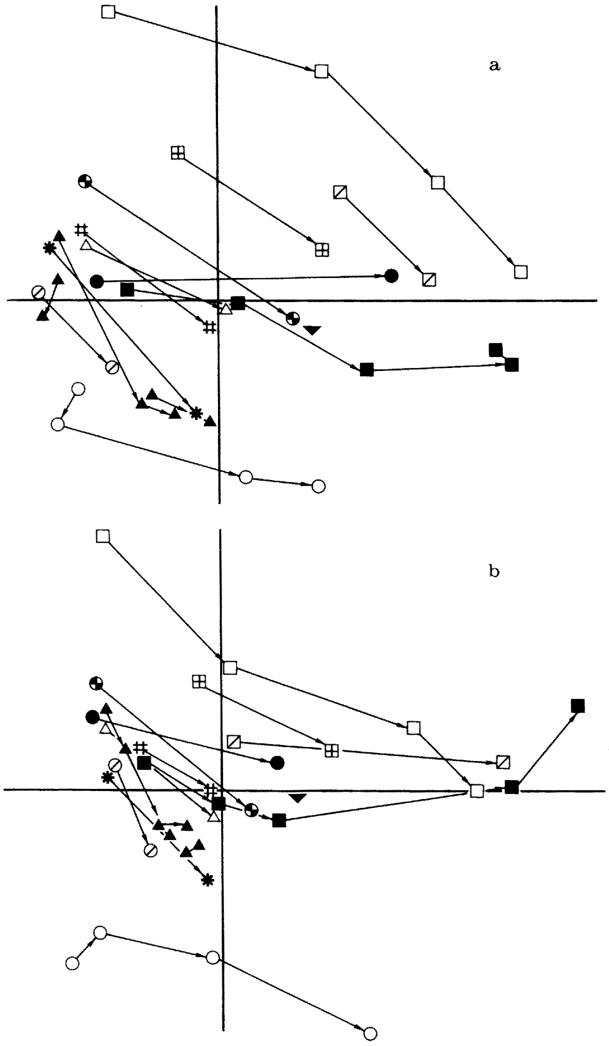

Figure 2. Ordination of the sample areas given in Table 1 by the first and second axes from Principal Component Analysis of (a) Domin values and (b) % cover of species. Symbols as in Table 1; arrows denote increasing age of birch stands at the same site.

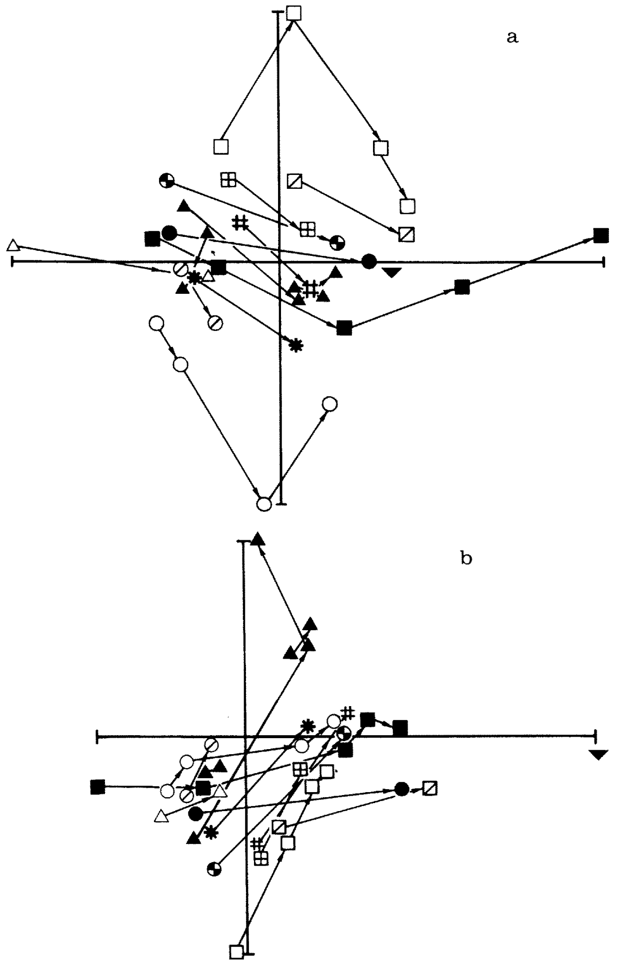

Figure 3. Bray and Curtis ordination of the sample areas given in Table 1 by the first and second axes using (a) Domin values and (b) % cover of species. Symbols as in Table 1; arrows denote increasing age of birch stands at the same site.

and by sample areas. Cover values for sample areas were simple means of the quadrat values. Average Domin scores for sample areas were calculated by back-transforming the mean cover values.

The following methods of analysis were used:

Phytosociological method according to the Braun-Blanquet system (Braun-Blanquet 1928).

Ordinations:

1) Principal Component Analysis (Orlóci 1966).

2) Bray and Curtis ordination on *(i)* Euclidean distance and *(ii)* a Bray and Curtis (1957) similarity coefficient resemblance matrices.

3) Detrended Correspondance Analysis (Hill and Gauch 1980).

Classification:

1) Cluster analysis by a centroid agglomeration criterion (Orlóci 1978) on Euclidean distance resemblance matrix of *(i)* the original data and *(ii)* the first 3 principal components from principal component analysis.

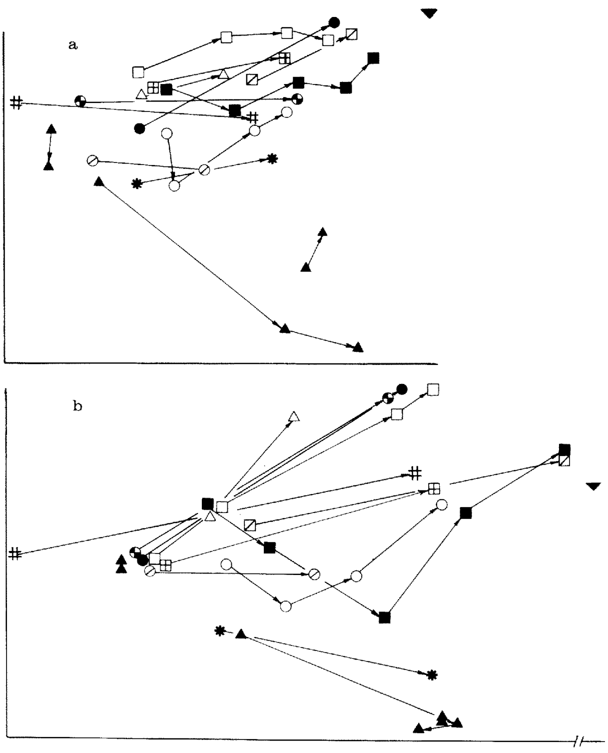

Figure 4. DECORANA ordination of the sample areas given in Table 1 by the first and second axes using (a) Domin values and (b) % cover of species. Symbols as in Table 1; arrows denote increasing age of birch stands at the same site.

2) Indicator Species Analysis (Hill *et al.* 1975).

3) Two-way Indicator Species Analysis (Hill 1979).

Two separate vegetation tables, for the *Calluna* and birch stands, were analyzed by the Braun-Blanquet phytosociological method. The tables were structured in the traditional way by subjective re-arrangements of species and relevés in the tables (Mueller-Dombois and Ellenberg 1974). Each vegetation type was either referred to published phytosociological syntaxa or considered unclassifiable.

Because of computing limitations, the size of the data matrix had to be reduced in applying the numerical methods. This way done by excluding all the species present in less than 5% of the quadrats unless they also had a mean cover greater than 10%. This reduced the number of species to 33, which however included all the species with a differential value in the phytosociological classification.

Results

Phytosociology

The syntaxonomical definition of the sample area was not straightforward because most quadrats had many species in common. A clear pattern of differentiation was lacking in the structured tables (not

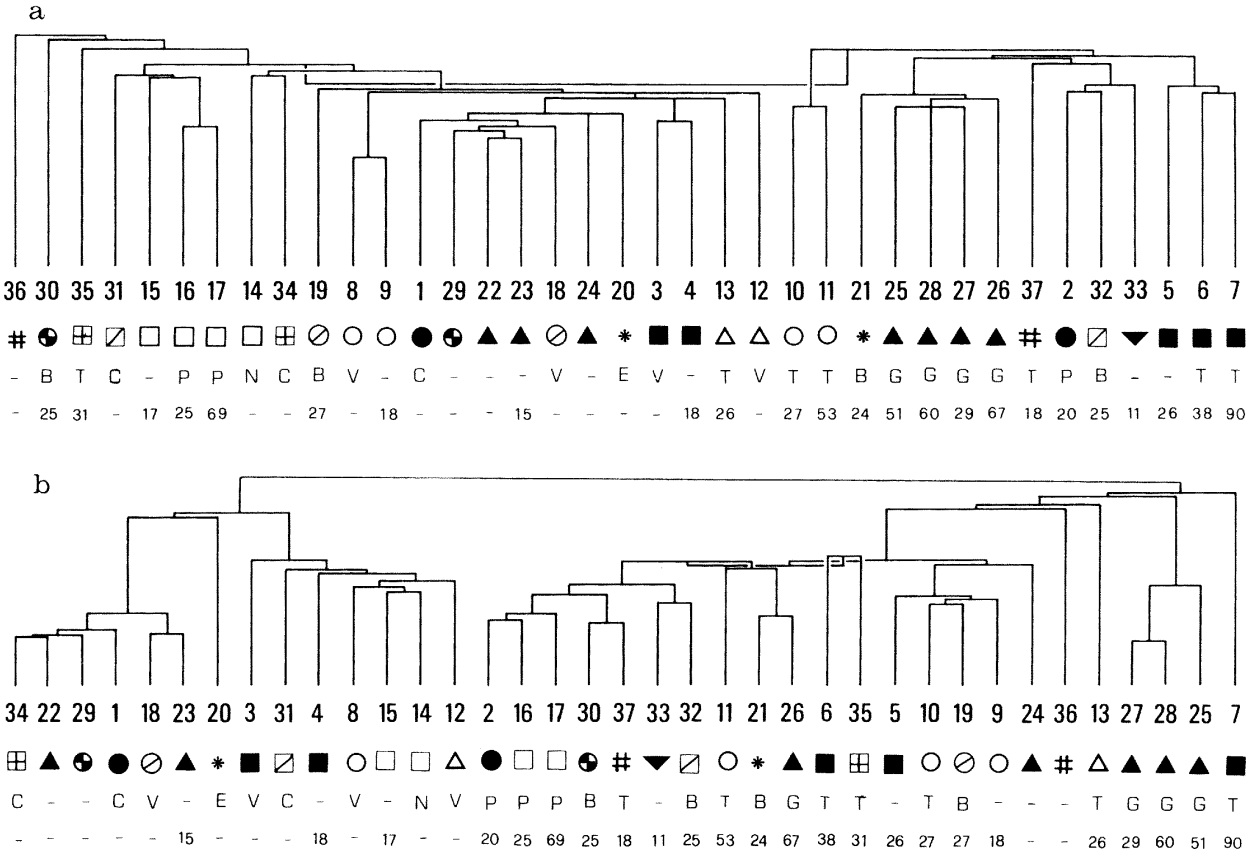

Figure 5. Dendrograms from cluster analysis by centroid linkage agglomeration procedures on raw data using Domin values (a) and % cover of species (b). Large numbers are sample area, small are birch age. Symbols and letters as in Table 1.

shown here) with no distinctively outstanding groups of relevés. Ten stands were considered unclassifiable in phytosociological terms, but all the others were referrable to published syntaxa (Table 1).

Four associations (Carici binervis-Ericetum cinereae Br.-Bl. et Tx (1950) 1952 em. Birse, Vaccinio-Ericetum cinereae Birse te Robertson 1976 em. Birse, Vaccinio-Ericetum tetralicis J.J. Moore 1962 and Narthecio-Ericetum tetralicis J.J. Moore (1964) 1968) were recognized in the Calluna stands; these are in two different classes, the first two Nardo-Callunetea PRSG. 1949 and the latter two Oxycocco-Sphagnetea Br.-Bl. et Tx. 1943. Nardo-Callunetea includes acid grassland and heather moor, while Oxycocco-Sphagnetea includes wet moors. In the birch stands four different associations (Primulo-Quercetum Birse et Robertson 1976, Galio saxatilis-Quercetum Birse et Robertson 1976, Trientali-Betuletum pendulae Birse 1982 and Blechno-Quercetum Br.-Bl. et Tx. (1950) 1952) were recognized; the first referred to Querco-Fagetea Br.-Bl. et Vl. 1937 and the other three to Quercetea robori-petreae Br.-Bl. et Tx. 1943, including base-rich broadleaved forests and acid oak woodland vegetation respectively.

Principal Component Analysis (PCA)

PCA performed very well in detecting successional trends (Fig. 2). The first axis represented the change from dwarf shrubs to herbaceous ground vegetation, reflecting increasing birch age and related soil changes (Miles and Young 1980), whereas the second axis separated the different sites. The data scale used did not change the resulting pattern of successional gradients within sites, but Domin ratings (Fig. 2a) did relatively better than % cover (Fig. 2b). When % cover was used, the increased weight of dominant species in the calculations compressed the variability both among sites and in the early successional stages. Whereas Domin scores, weighting in favour of the subdominant and rarer species enhanced the stands differences especially in the middle of the successional range (Fig. 2a vs. 2b).

Bray and Curtis ordination (BCO)

This method showed a similar pattern to PCA when Euclidean distance was used as the resemblance measure (Fig. 3), but applying the ordination to the matrix of similarity coefficients gave no clear patterns

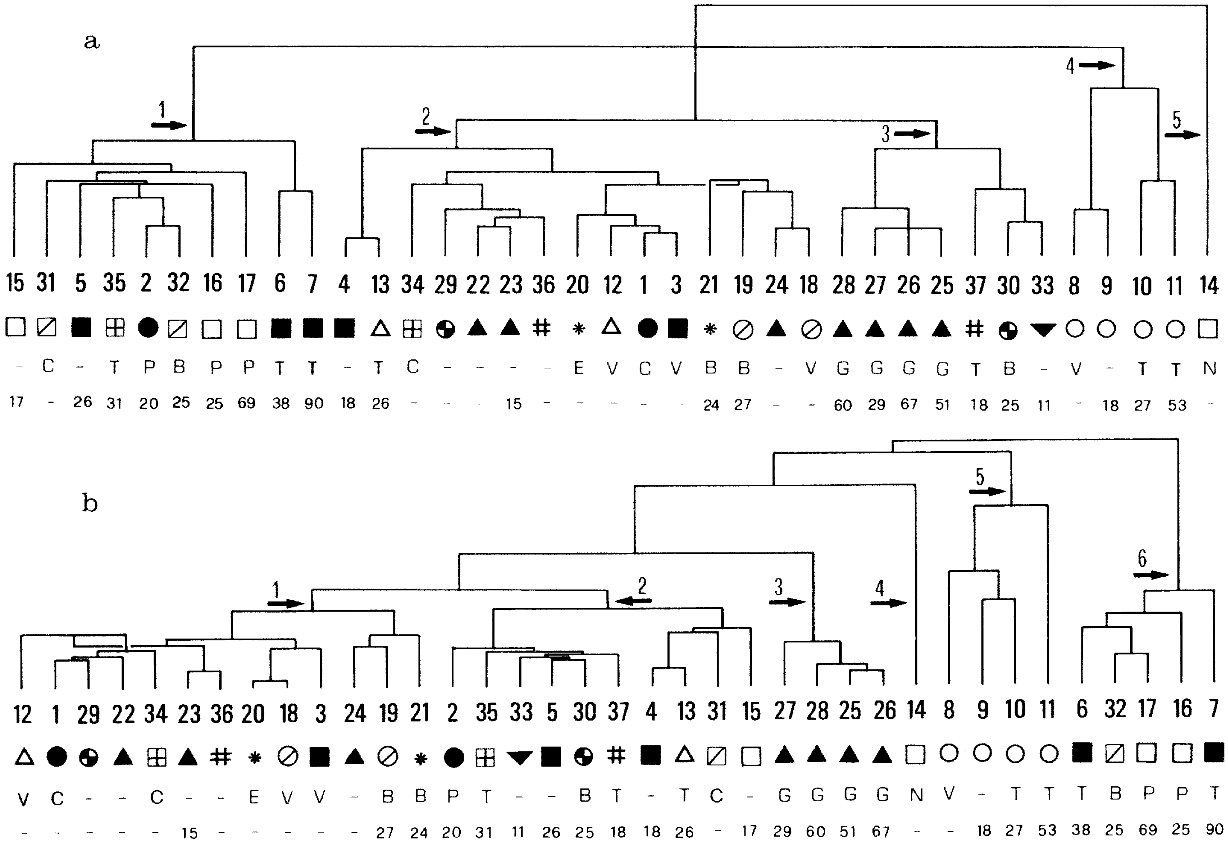

Figure 6. Dendrograms from cluster analysis by centroid linkage agglomeration procedure on first three components from PCA, using Domin value (a) and % cover of species (b). Numbered arrows indicate clusters reported in Fig. 8c and 8d. Legend as in Fig. 5.

(not shown here). The successional trends and site differences were clear with Domin scores (Fig. 3a), whereas % cover produced less obvious trends and badly separated the different sites (Fig. 3b).

Detrended Correspondance Analysis (DCA)

DCA produced a broadly similar pattern of ordination to PCA and BCO (Fig. 3). However, it did not distinguish as well as PCA either between sites or the moorland vegetation types, and also showed a greater variation in successional trends. There were little differences in the results from Domin scores or % cover (Fig. 4a and 4b respectively), though this method performed rather better with % cover than did PCA and BCO.

Cluster analysis (CA)

None of the cluster analyses produced groups comparable with those derived from phytosociological analysis, with the exception of Silpho sample areas 25, 26, 27 and 28 (Galio saxatilis-Quercetum) which were always separated out as a distinct group. All the procedures intermingled pioneer birch stands with *Calluna* stands.

When clustering raw data using Domin scores (Fig. 5a), no clear groups or patterns were obtained. In fact, this analysis did not even clearly separate *Calluna* and birch stands. Clustering of % cover estimates (Fig. 5b) separated most *Calluna* and birch stands, presumably because of the greater weight given to the dominant species, but the groups were broad and not very meaningful phytosociologically, except for the older birch stand at Silpho as noted earlier.

Clustering of components from PCA, using both Domin scores (Fig. 6a) and cover estimates (Fig. 6b), gave reasonable separation of *Calluna* and birch vegetation and also picked out the old Silpho stands, all areas at Craggan (sample areas 8, 9, 10, 11) and the wet *Calluna* site at Kerrow (area 14). Interestingly, younger birch stands on poorest soils were combined to most heather stands (groups 2 and 1 in Figures 6a and 6b respectively) and, viceversa, successionally younger sites with relatively richer soils were grouped with late succession stands (group 1 in Fig. 6a).

Indicator Species Analysis (ISA)

The way ISA splits every class dichotomously at every level of the classification gave an obvious separation between heather and birch stands, but each

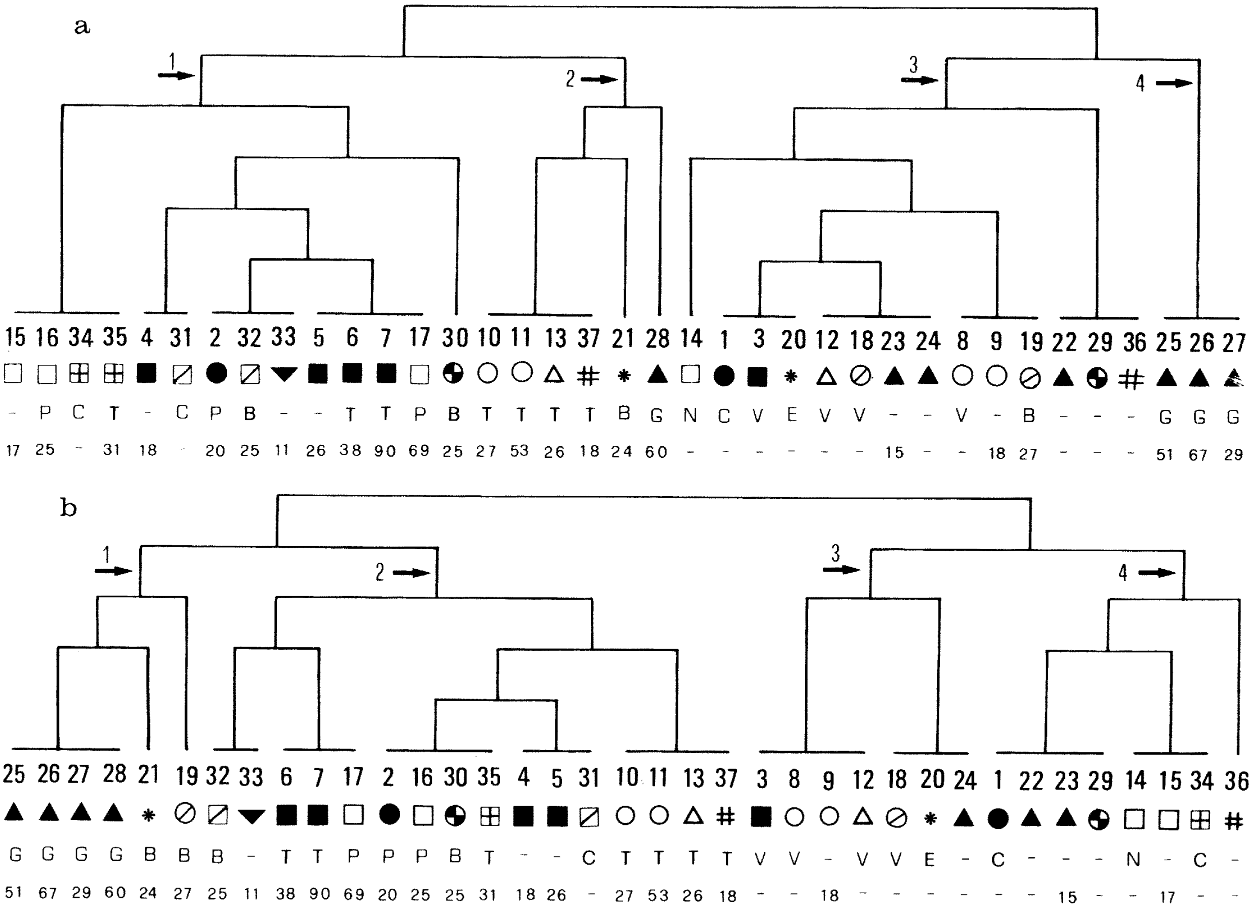

Figure 7. Classification of the sample areas given in Table 1 by Two-way indicator species analysis, on Domin scores (a) and % cover of species (b). Numbered arrows indicate clusters reported in Fig. 8e and 8f. Legend as in Fig. 5.

succeeding split gave progressively more meaningless divisions, especially among the heather stands (not shown here). It thus neither showed clear successional patterns, nor gave interpretable phytosociological categories.

Two-way Indicator Species Analysis (TWINSPAN)

Whether Domin scores or % cover estimates were used, this method produced groups with larger correspondence to the phytosociological classification than the CA (Fig. 7). Not only Silpho birch stands were separated, but also the Trientali-Betuletum pendulae was picked out in a satisfactory way. As in the CA, the *Calluna* stands were grouped with some pioneer birch stages, but these were nearly all in sites with very poor soils, where there was little change in the ground flora during early succession. With Domin scores, two *Calluna* stands (31 and 34) were displaced from the main heather group, while with % cover only one site was separated (31). However, this may reflect the occurrence of these stands on soils of relatively high base status.

Discussion

The complementary analysis of the results from classification and ordination provided good insights into the data structure. Fig. 8 shows the results of overlapping the groups obtained by the classification techniques to the scatter plot by PCA.

Age classes form a clear pattern along the diagonal between the first and second axes (Fig. 7a). The phytosociological classification reflected this pattern and provided some information on vegetation and site differences; classes and associations were well separated and marked overlapping occurred only between Trientali-Betuletum pendulae and Blechno-Quercetum within the Quercetea robori-petreae class.

The numerical clustering on components (Figures 8c and 8d) gave a very good reflection of soil conditions and changes especially when used on cover estimates (Fig. 8d): the first axis separated the clusters of podzolic sites (groups 1, 4 and 5) and the sites with soils not much altered from original podzols during succession (group 3) from the groups of sites with 'transitional' brown podzolic soils (cluster 2) and those with 'richer' brown

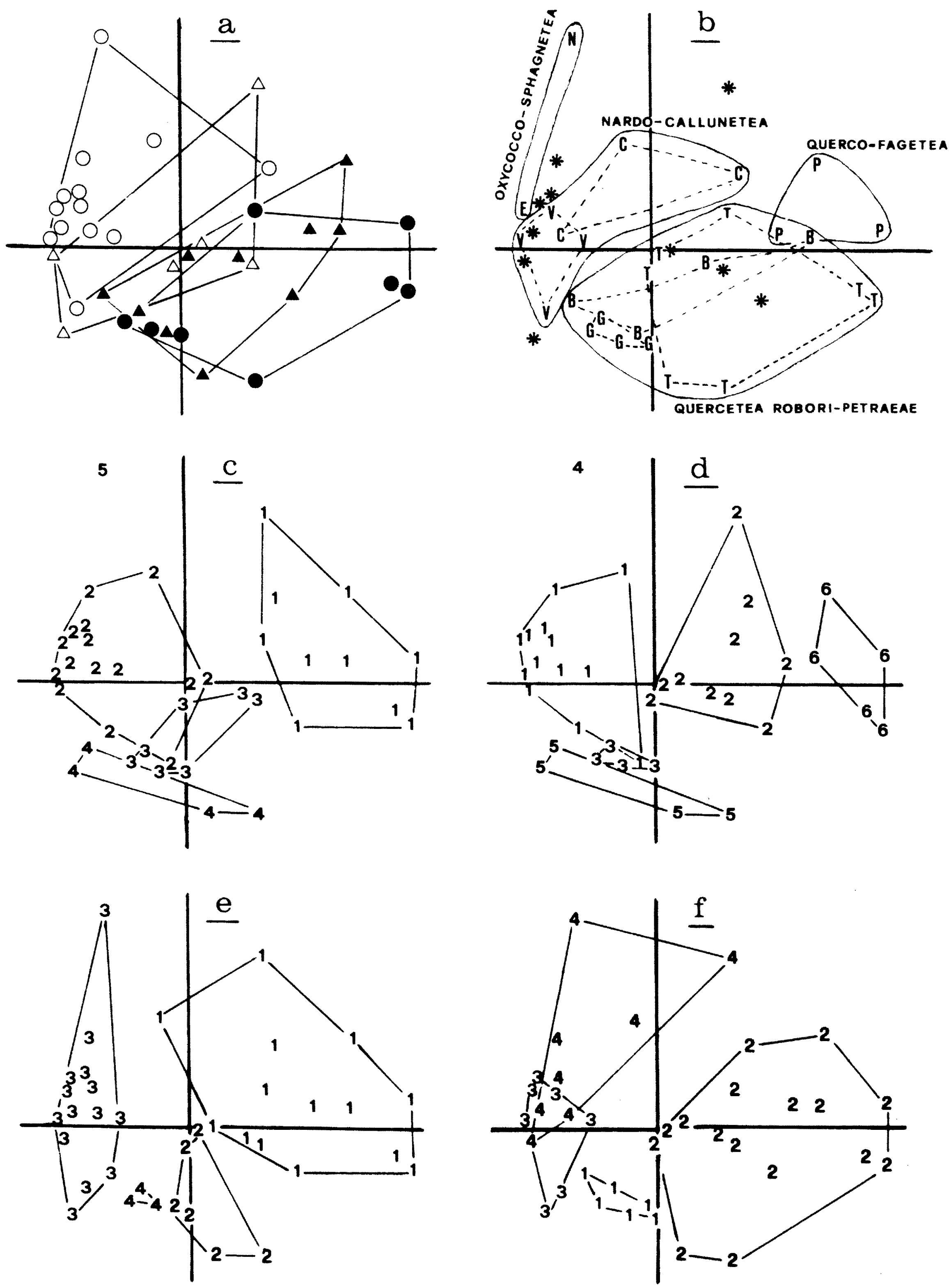

Fig. 8. Comparison between ordination by PCA as shown in Fig. 3a and stand age classes (a), phytosociological syntaxa (b) and numerical clustering on component scores from PCA and TWINSPAN using (respectively c and e) Domin ratings and (d and f) % cover values. Lines encircle the same age class (a), syntaxonomical unit (b) or clusters (c) (d) (e) (f) of the respective classifications. Symbols in a: Calluna stands (open circles), Betula spp stands aged < 20 years (open triangles), 20-30 (filled triangles), > 30 (filled circles). Letters and asterisks in b as in Table 1. Numbers in c, d, e and f refer to groups in Figures 6a, 6b, 7a and 7b respectively.

podzols and brown earths (group 6). The second axis reflected differences between kinds of moorland soils.

TWINSPAN (figures 8e and 8f) produced reasonable separation of main classes, but little indication of successional processes; the patterns obtained by this method intermingled the groups by CA with those by the phytosociological classification.

When different types of clustering procedures have been applied to data matrices describing well defined vegetation types, a very good correspondence has generally been found between them and traditional phytosociological classification (Ivimey-Cook and Proctor 1966; More *et al.* 1970; Stanek 1973; Werger 1973; Coetzee and Werger 1973; Campbell 1978; Gauch 1982). In this study, there was no such a great correspondance in all the procedures, except for the four oldest birch stands at Silpho (Galio saxatilis-Quercetum). These four stands were relatively species-poor and showed little floristic development with increasing age compared with the other three multi-aged sites (Tulchan, Craggan and Kerrow). Further, most floristic changes from heather dominance occurred early in the succession.

Phytosociology is not well suited for analyzing very dynamic successional vegetation. Essentially, it is based on detecting patterns of presence-absence of species which characterize the vegetation types. In cases where presence-absence is more important than species abundance in defining the vegetation, numerical clustering procedures will show more correspondance to 'associations' or other phytosociological syntaxa (e.g., Silpho in this study and most cases reported in the literature). However, if the compositional gradient is 'short', quantitative variations become more important as phytosociology loses efficency (increasing number of unclassifiable relevés). Although two quadrats with the same species presence are defined as part of the same syntaxonomic unit, they invariably have differences in the species relative dominance which can be sorted out better by numerical analysis. Lower level syntaxa should be separated by quantitative similarity coefficients, while qualitative coefficients can be used in ranking the higher-level phytosociological syntaxa (Campbell 1978).

Interestingly, while the large amount of overlapping in composition of the seral stands made structuring of the phytosociological tables difficult, the results were substantially consistent with the ordination plots from PCA. On the other hand, numerical clustering on the raw data was effectively useless whereas clustering on the component scores again produced interpretable results and TWINSPAN also performed well. Thus, the subjectivity of phytosociological analysis produced interpretable patterns of a similar scale, but different to those from the ordination, while numerical clustering only produced readily interpretable groups to any extent after previous ordination, either PCA in the CA or factorial analysis implicit in the TWINSPAN procedure (Hill 1979).

Most published studies on comparing ordination methods judged their performance in terms of their ability to recover an original known sequence and not to displace points along that sequence. However, these usually compared the ordinations in one dimension only, whereas the trends may be better displayed by using two or more dimensions. Displacement along any one axis, as when an "arch" is formed in a PCA, does not matter as long as the trend displayed can readily be interpreted in a biological sensible way. Also, arches need not be merely artefacts of the ordination methods (Orlóci 1978, 1979). French and Smith (1985) give a good example of this in an ordination of a "long" environmental/vegetational gradient which produced several marked archs, but where both the linear axes and the arches all had real ecological meaning.

Hill and Gauch (1980) stated that DCA will usually give better results than any other ordination techniques (i.e., will better reflect the underlying environmental or successional gradients). Whittaker and Gauch (1982) affirmed, based on simulated data, that PCA would produce distortions in the ordination if beta diversity is above 2-3 half changes. Our data had beta-diversity slightly above 4, yet PCA consistently outperformed DCA in showing both the successional trends and the initial differences between sites. Casado *et al.* (1989) similarly reported that PCA reflected floristic and structural variations along a transect in an oakwood clearing better than DCA. Therefore, despite the adverse comments about PCA and in favour of DCA in the literature, it seems clear that PCA is sometimes the more appropriate method. A discussion of the relative merits and disadvantages of the two methods is beyond the scope of this paper. However, it should not be surprising that no one method proves the best for all types of data and aims of analysis.

Austin and Orlóci (1966) showed that BCO could produce problems of interpretation because it was based on a non-Euclidean measure of similarity. Our study supported this view. When the similarity coefficient was used, no interpretable patterns were generated, but substitution of Euclidean distances in the method yielded similar patterns to PCA.

Figure 9 summarizes diagramatically the limit of applicability of the different approaches. When the vegetation types have few species in common (Ia), the data matrix shows a clear distinction of phytosociological groups (Ic). In this case, clustering of the raw data by any numerical technique (Ib) will be effective and can be used as an helpful tool in defining a structured phytosociological table (e.g., the package by Wildi and Orlóci 1983). In these cases PCA, which depends on linear relationships, can be expected to

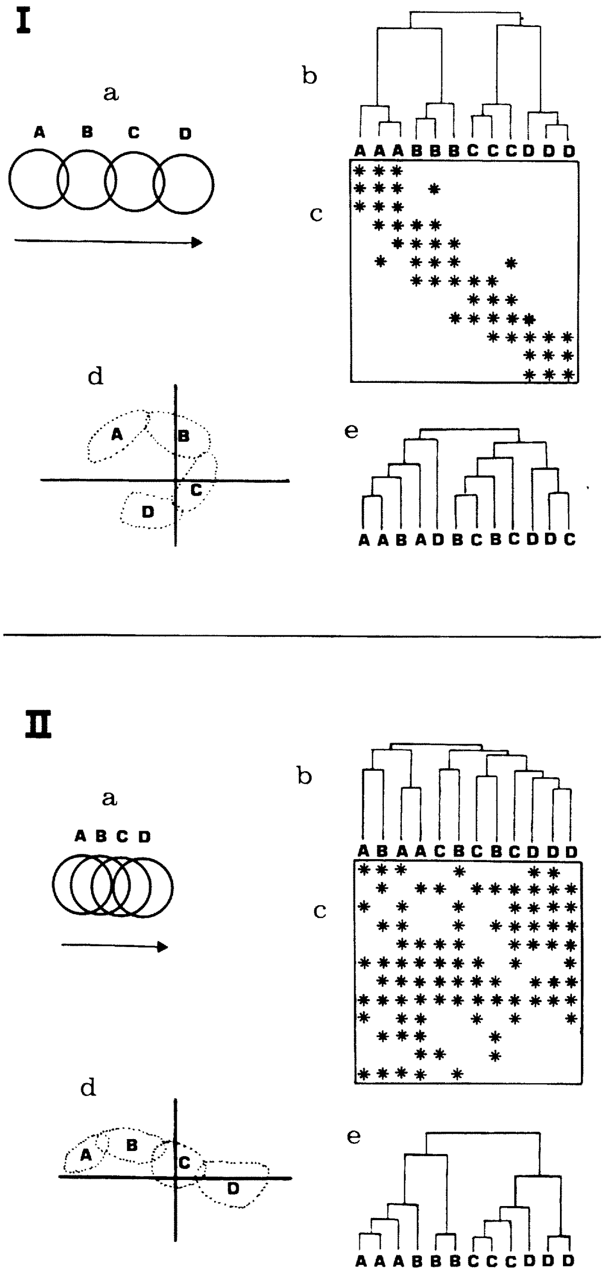

Figure 9. Diagrammatic representation of the use of phytosociological and numerical classification and ordination methods on data sets representing for vegetation types with few (I) and many (II) species in common. In (a) A, B, C and D denote vegetation types and arrows, temporal or environmental gradients; (b) Numerical clustering of relevés on raw data (dendrograms of species classification not shown); (c) structured phytosociological table; (d) Principal Component Analysis; (e) numerical clustering of ordination's scores.

show distortion problems such as the well-documented 'arch effect' (Id), due to the presence of the large number of zeros in the data matrix (Swan 1970). Clustering based on the component scores (Ie) is not expected to be efficient, since the ordination is not clear. Other ordination methods such as DCA handle this situation better, but when classification by the traditional phytosociological method clarifies the pattern, subsequent ordination is arguably unnecessary!

When the vegetation types have many species in common (Fig. 9 IIa), the data matrix presents badly separated phytosociological groups (IIc). In this case, the clustering procedures on raw data will not be efficient (IIb), but an ordination can clarify the main trends in the changes of relative abundance of the species (IId). In this latter case, the application of cluster analysis to the ordination scores (IIe) helps in detecting the transitional stages of this 'short' sere.

Many real data sets, including those reported here, have to some extent both sets of contrasting attributes shown in Fig. 9 I and II.

In our data there is a continuity related to the age of the birch stands, but also a series of breaks because of the gaps in the observed age distributions of the stands. For such data sets, which are "intermediate" in terms of Fig. 9, ordination complemented by classification is likely to give the best insights of the vegetation patterns, as did PCA and phytosociological/CA/TWINSPAN analysis in our study as well as in other published examples (e.g., Van der Maarel 1966; Werger 1973; Komarkova 1980).

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