

Trends and problems in the application of classification and ordination methods in plant ecology

Martin Kent & Julia Ballard

*Department of Geographical Sciences, Plymouth Polytechnic, Drake Circus, Plymouth, Devon, England
PL4 8AA*

Accepted 8.9.1988

Keywords: Ecological journal, Floristic vegetation data, Hypothesis generation, Hypothesis testing, Literature review, Multivariate analysis, Vegetation theory

Abstract

Classification and ordination methods represent the two primary groups of ordering techniques for the analysis of floristic data in plant ecology. Current problems in the use and application of the methods are introduced and through a review of 734 articles across 11 ecological journals from 1960 to 1986, the history and evolution of the methods are displayed, the extent to which different techniques have been applied in the past and up to the present is demonstrated and problems and trends are discussed. A clear and substantial increase in the application of ordination and classification methods over the survey period is shown but with this increased usage, problems have come in terms of choice and evaluation of methods, the emphasis on inductive rather than deductive approaches, possible over-emphasis on methodology and technique rather than ecological application, low levels of use in applied studies and an increased tendency to use complementary and multiple analyses.

All of the problems are related to broader aspects of the present position of vegetation description and analysis within vegetation science in general and in particular the relationship between community ecology and individualistic plant ecology.

Introduction

Over the past 25 years, the problems of handling and analysing the large amounts of data generated by the floristic description of vegetation have resulted in the development of numerous techniques for data reduction, which have usually been grouped under the two headings of classification and ordination. The methods have been used to describe and recognise patterns in vegetation distribution, define plant communities and to examine plant and community distribution in relation to environmental factors and gradients. One of the most interesting aspects of the

development of methodology has been the evolution of successive techniques, each considered, at least by its originators, to be an improvement on the last. The resulting complexity and diversity of methods has often caused confusion and difficulty for both students and more experienced workers. The aim of this article is to examine this and other aspects of the use of classification and ordination methods over the period 1960–86 through a survey of the published ecological literature and to highlight a number of current problems and debates.

Although a number of general articles on classification and ordination methods have been published

(e.g. Whittaker 1967; McIntosh 1967; Goodall 1970; Greig-Smith 1980; van der Maarel 1979, 1984a; Austin 1985; Noy-Meir and van der Maarel 1987), there has been no attempt to quantify the evolution and change in methods over time and there still remain a number of very important issues to be addressed in the theory and development of methods, their dissemination to and use by ecologists who are not specialists in quantitative plant ecology and the potential of the methods for applications in the areas of applied ecology and biological conservation.

Problems in the application of methods of classification and ordination

Following a period of relatively rapid evolution and change over the past 25 years, a number of problems in the development and application of methods can be identified:

The range of choice of methods

For both classification and ordination, a wide range of methods has been devised. However, although a number of attempts have been made to evaluate the relative performance of methods at various points over the past 25 years (e.g. Williams & Lance 1968; Gauch & Whittaker 1972b; Dale 1975; Austin 1976; Fasham 1977; Goodall 1978; Whittaker & Gauch 1978; Gauch & Whittaker 1981; Gauch *et al.* 1981; Brown *et al.* 1984; Minchin 1987a), a clear and consistent consensus over which method or methods should be recommended for general use has never emerged. Rather, as each technique or group of techniques has evolved, it has usually been assumed to represent the best available. Unfortunately, subsequent evaluation and testing through real world application and/or using simulated data has virtually always led to reappraisal of methods. Thus, exactly why a particular researcher chooses a certain method or combination of methods on a given set of data is often not very clear. Choice would often appear to be based in part on the availability of computer programs for a given method or the current feeling

on the 'goodness' of certain methods based on recent articles or textbooks. The derivation of a new method which may have widespread applicability does not automatically guarantee that wider application of that technique will be achieved (e.g. Non-Metric Multidimensional Scaling as a method of ordination, Fasham 1977; Prentice 1977; Minchin 1987a). Equally, older methods which from a careful reading of the literature may seem to have been clearly shown to have deficiencies may still have their proponents and be in relatively widespread use (e.g. Bray & Curtis or Polar Ordination, Beals 1984; Principal Components Analysis, Ezcurra 1987; Similarity Analysis and related agglomerative polythetic methods for classification, Gauch & Whittaker 1981).

It is, of course, vital that new methods of analysis are devised and that researchers should always be looking to improve on and update existing techniques. However, this problem of the diversity and apparent complexity of methods is an important one in terms of the actual application and use of methods in ecological situations. Firstly, as indicated above, at the research level, ecologists who are not specialists in the methods themselves tend to be confused by the apparent choice of methods and may as a result use methods uncritically. Secondly, in terms of teaching the potential use and value of these methods to students and undergraduates, the whole subject often appears quite bewildering because of the range of techniques. The first aim of the literature survey was to examine trends in the evolution and extent of application of different methods of classification and ordination over the 26 years, from 1960–1986.

Hypothesis generation and testing

Various authors have emphasised that most examples of the application of classification and ordination in plant ecology are inductive rather than deductive in approach and as such, the techniques are used primarily for hypothesis generation rather than testing (Orlóci 1978; Pielou 1984; Austin 1985; Keddy 1987). Keddy, in particular, makes this point very effectively. Examples where vegetation description and analysis leading to hypothesis generation

are actually followed by testing and experimental work are very few. The best and most commonly quoted example is the work of Goldsmith on sea cliffs (Goldsmith 1973a, b). However, only a relatively few articles genuinely reach even as far as the stage of hypothesis generation. A vast majority finish and are content with mere description. Whether quantitative plant ecologists should accept this situation is another important issue. As Keddy (1987) states 'perhaps community ecology would develop more rapidly if we all hung up our quadrats for a few years and instead tried to decide what questions we need to answer.' (p. 210).

This problem has led some plant ecologists to question the whole basis of quantitative plant ecology (e.g. Kellman 1980). May (1985), also quoted in Crawley (1986), states 'the wilderness of meticulous classification and ordination of plant communities, in which plant ecology has wandered for so long, began in the pursuit of answers to questions but then became an activity simply for its own sake.' (p. 33). In a book entitled 'Plant ecology' (Crawley 1986) the whole of quantitative plant ecology is then dismissed in one paragraph. While this may appear to be a rather extreme reaction, there is without doubt some basis for it.

Emphasis on techniques and methods rather than phytosociology and ecological applications

The most frequently cited papers in the literature are undoubtedly those introducing or discussing the techniques of classification and ordination themselves, rather than using the method for some ecological purpose such as phytosociology or the exploration of environmental controls or gradients. A not infrequent comment is that the multivariate techniques for analysing vegetation data have become an end in themselves. In the present survey, a further aim was therefore to assess the relative proportions of published papers which dealt primarily with philosophy and method of classification and ordination as opposed to application to some ecological situation or problem.

The role of methods of classification and ordination in applied studies, ecosystem management and biological conservation

The greatly increased awareness of the detrimental effects of man's activities in modifying and destroying vegetation and ecosystems across the globe has led to a demand for research with the specific aim of providing information for the management of vegetation and ecosystems. As a means of providing interpretable data, classification and ordination methods must have a very considerable role to play. The aim here was thus to quantify the growth in application of methods of quantitative plant ecology to applied studies and environmental management over the past 26 years. This again relates back to the previous discussion on the need for plant ecologists to ask more questions and to perhaps direct more of the application of their methods towards the demands and needs of biological conservation.

Complementary analysis using classification and ordination methods in combination

An important trend in the application of classification and ordination methods is towards 'complementary analysis'. This is where both classification and ordination techniques are employed together in an analysis of the same data set.

This strategy is usually employed where the goals of vegetation description and analysis are both the definition of vegetation types and plant communities and an appreciation of the underlying environmental gradients. This issue relates to a problem which reflected attitudes to vegetation analysis in the 1960s and early 1970s when the two groups of methods were often seen as totally separate. While there are clearly defined situations where either classification or ordination should be used on its own, there is considerable benefit to be gained in other situations from such a 'complementary' analysis using both groups of techniques.

The theoretical basis of vegetation science

Underlying all of the above points is a further, more general problem concerning the evolution of theory and a general model of vegetation and its response to environmental gradients. There are three distinct areas which deserve discussion. Firstly there is the concept of species response curves. Several researchers have discussed this issue (Austin 1976, 1979, 1980, 1985; Gauch 1982; van der Maarel, 1984a; Noy-Meir & van der Maarel 1987; Roberts 1987) and they stress that most theory is based on direct gradient analysis and the idea of Gaussian species response curves (Whittaker 1953, 1975; Gauch & Whittaker 1972a, b). Testing of the assumptions of the bell-shaped response curves has been carried out by Austin (1980), Austin & Austin (1980), Austin *et al.* (1984) and Austin (1987). Their results conclude that although bell-shaped response curves are found, they are not universal, they may be bimodal and they are often positively skewed. The patterns of species response curves along environmental gradients are also observed to be highly variable and are greatly influenced by species richness. They conclude that an adequate general model of species response does not yet exist.

Secondly, the concept of the plant community, which has been a controversial topic for the whole of this century, is still a matter of debate (Shipley & Keddy 1987). While most workers may now accept that plant communities do exist and can be recognised and described, recent concern has been expressed over the static view presented by many accounts of vegetation. Typically, vegetation is described using field methods at one point in time followed by multivariate analysis using classification and ordination to define plant communities and/or environmental gradients. The limitations of this static approach have been highlighted by van der Maarel (1984a, b), Noy-Meir & van der Maarel (1987) and Roberts (1987), who stress the dynamic nature of plant communities and the importance of successional processes and vegetational change in deriving satisfactory explanations of patterns and variations. Although the potential of both classification and ordination methods for studying vegetational change has been demonstrated (Austin 1977; Swaine &

Greig-Smith 1980), the exact role which they may be able to play in providing a more dynamic understanding of plant communities, vegetation change and related ecological processes is uncertain and still needs to be explored further.

The third difficulty in the evolution of theory in vegetation science is the relationship between community ecology and individualistic plant ecology. Since 1975, partly as a consequence of many of the problems described above, new approaches have been developed by plant ecologists, notably Harper (1977), Grime (1979) and Silvertown (1982), based on individual plants and plant species. The individual emphasis is expressed in two related concepts – plant species strategy and plant population biology. This approach has produced many valuable insights into the processes determining the ecology of individual plants and plant species. However, the extent to which it has assisted with understanding in broader scale plant community ecology is less certain. This problem is linked to the second point above concerning the importance of a dynamic view of the plant community, since it is increasingly being shown that understanding of successional processes involves appreciation of the interactions of individual plants and plant species with each other and with their environment. Thus individualistic approaches seem to many ecologists to offer more in terms of an explanation of observed patterns and a model of processes. The major problem appears to be taking the results of studies at the individualistic level and reorganising them upwards to the level of the community. Some ecologists consider this latter stage to be unnecessary and just as the Gleasonian individualistic view of the plant community, if taken to its logical conclusion, means that plant communities do not exist, they see little purpose in trying to define a higher level of organisation among plant species at the community scale. Classification methods are rendered redundant if this view is accepted, although ordination methods still have a valuable role to play in the elucidation and understanding of environmental gradients.

Whether multivariate methods have a new and relatively unexplored role in assisting with understanding at the individual plant level is yet to be proven, although a valuable indication is provided

by the work of Turkington & Harper (1979), who used multivariate analysis as a means of examining interaction and contacts between individual plants.

With these problems in mind and with the purpose of obtaining information on some of the trends in methods and their applications discussed above, a review of published papers across 11 ecological journals between 1960 and 1986 was completed. In detail, this review aimed to:

- a) show the evolution and change of methods for classification and ordination.
- b) assess the relative frequency of application of particular groups of methods.
- c) examine possible changes in emphasis in the use of methods, particularly with respect to increasing use in applied studies.
- d) show the increasing complementary use of ordination and classification.
- e) make some comments and predictions as to future directions in quantitative plant ecology in the light of current developments, applications and criticisms.

Methods

The study was based on the major ecological and biogeographical journals published since 1960 and which were readily available in the United Kingdom. The journals, the volume numbers searched and the number of articles in each journal are shown in Table 1.

The criteria used for inclusion of an article in the review were that it should be either on the methodology of classification and/or ordination or use the method in some form of ecological study. Also, the articles should be primarily on terrestrial plant ecology and not on animal, marine or aquatic ecology. A total of 734 articles were examined.

For each article which used or discussed a method of classification or ordination, the following were noted:

- author or authors
- year of publication
- journal of publication
- method or methods of classification used
- method or methods of ordination used
- nature of the article – whether primarily about

Table 1. Journals, volume numbers and numbers of articles included in the review.

| Journal title | Start date | Start volume | 1986 volume | Number of articles | % |
|-------------------------------------|------------|--------------|-------------|--------------------|-------|
| Advances in Ecological Research | 1962 | 1 | 15 | 3 | 0.4 |
| Australian Journal of Ecology | 1977 | 1 | 10 | 43 | 5.9 |
| Biological Conservation | 1968 | 1 | 37 | 14 | 1.9 |
| Ecological Monographs | 1960 | 30 | 56 | 27 | 3.7 |
| Ecology | 1960 | 41 | 67 | 107 | 14.6 |
| Environmental Management | 1977 | 1 | 10 | 5 | 0.6 |
| Journal of Applied Ecology | 1964 | 1 | 23 | 12 | 1.6 |
| Journal of Biogeography | 1974 | 1 | 13 | 39 | 5.3 |
| Journal of Ecology | 1960 | 48 | 74 | 142 | 19.4 |
| Journal of Environmental Management | 1973 | 1 | 23 | 10 | 1.4 |
| Vegetatio | 1960 | 9 | 64 | 332 | 45.2 |
| Total | | | | 734 | 100.0 |

methods (theoretical) or an application of the technique(s) to an ecological situation or problem (ecological)

- nature of the article – whether the aims of the paper were purely academic or whether they were used in some applied ecological problem or situation

These data were then coded and sorted using the cross-tabulation and contingency table analysis programs available in the SPSS-X computer package (Nie 1983).

Results

The range of journals

Of the 11 journals included in the survey (Table 1),

only four were being published in 1960, the remainder representing new journals founded after that date. Over the 26 year study period, *Vegetatio*, as the most directly relevant journal, published nearly half the papers concerning or using classification or ordination methods (45.2%). This was followed by *Journal of Ecology* (19.4%) and *Ecology* (14.6%). Of the remaining journals, *Australian Journal of Ecology* (5.9%) and *Journal of Biogeography* (5.3%) were the most significant.

Trends in the numbers of articles published are shown in Table 2. Over the whole period, there has been a steady and sustained increase in the number of articles published using ordination and classification. However, publications on or using classification or ordination methods have become concentrated markedly in *Vegetatio*, with a steady rise through the five year periods. Also, both *Ecology* and *Journal of Ecology* show fluctuating trends over the period and a relative decline overall. From a high of 27 articles between 1960–65, *Ecology* published as few as 13 between 1976–80 and only 23 between 1981–86. Similarly, *Journal of Ecology* has fallen from a peak of 39 articles between 1966–70 to only 19 between 1981–86. In both cases, the total number of articles of all types published increased substantially over the 25 year period, making the proportion concerned with classification and ordination even smaller. This may be interpreted in several ways. The

greater concentration in *Vegetatio* is undoubtedly due to the progressive upgrading of the quality and production of the journal and a substantial increase in the number of papers published each year (van der Maarel 1979; van der Maarel & van der Maarel-Versluys 1988). However, it could be argued that ecologists with an interest in quantitative plant ecology have increasingly tended to publish or have papers accepted for publication only in the most specialised journal on the subject (*Vegetatio*) and to no longer publish or have papers accepted for publication in the other broader ecological journals. Perhaps this can also be interpreted as a consequence of the difficulties which have occurred in the search for a clear model and theoretical basis for vegetation science as discussed above and the problems of integrating the community-centred approach, for which classification and ordination methods are principally (although not exclusively) appropriate and the individual plant and dynamic approach of the other current schools of thought in plant ecology.

Another finding is that the proportion of all articles published has remained remarkably constant – 1960–65: 5.9% (77/1310); 1971–75: 7.5% (137/1840); 1981–86: 5.4% (204/3763); with an overall percentage for the 26 year period of 6.5% (734/11360).

When the new journals published since 1960 are

Table 2. Number of articles treating or using classification or ordination published in each journal 1960–86.

| Journal | 1960–65 | 1966–70 | 1971–75 | 1976–80 | 1981–86 | Total |
|-------------------------------------|----------|----------|----------|----------|----------|------------|
| Advances in Ecological Research | 2 (8) | 0 (16) | 0 (12) | 0 (8) | 1 (18) | 3 (62) |
| Australian Journal of Ecology | 0 (0) | 0 (0) | 0 (0) | 20 (265) | 23 (244) | 43 (509) |
| Biological Conservation | 0 (0) | 0 (121) | 2 (131) | 4 (243) | 8 (398) | 14 (893) |
| Ecological Monographs | 6 (84) | 4 (74) | 7 (95) | 6 (98) | 4 (119) | 27 (470) |
| Ecology | 27 (780) | 25 (786) | 19 (755) | 13 (864) | 23 (966) | 107 (4151) |
| Environmental Management | 0 (0) | 0 (0) | 0 (0) | 3 (179) | 2 (340) | 5 (519) |
| Journal of Applied Ecology | 0 (58) | 1 (237) | 6 (318) | 2 (349) | 3 (450) | 12 (1412) |
| Journal of Biogeography | 0 (0) | 0 (0) | 7 (44) | 16 (149) | 16 (207) | 39 (400) |
| Journal of Ecology | 17 (306) | 39 (246) | 33 (280) | 34 (279) | 19 (399) | 142 (1510) |
| Journal of Environmental Management | 0 (0) | 0 (0) | 2 (66) | 1 (175) | 7 (316) | 10 (557) |
| Vegetatio | 25 (74) | 67 (139) | 61 (139) | 81 (219) | 98 (306) | 332 (877) |
| Total | 77 | 136 | 137 | 180 | 204 | 734 |
| Total all journals | (1310) | (1619) | (1840) | (2828) | (3763) | (11360) |

Total articles published in each journal for each time period in brackets.

examined (Table 2), two points emerge. Firstly, not surprisingly, given their broader ecological range, the number of articles using classification and ordination is comparatively low. Secondly, *Biological Conservation*, *Environmental Management*, *Journal of Biogeography* and *Journal of Environmental Management* all show a small but increasing publication rate for papers on or using ordination and classification over the 10 years to 1986. The main exception to this is the *Journal of Applied Ecology*, which has only published 12 articles over its 19 year history to 1986. This indicates a similar pattern to *Ecology* and *Journal of Ecology*, which again may reflect a relative decline in interest in the use of multivariate analysis as an effective tool for use within quantitative plant ecology particularly in Britain during the 1980s.

The other interesting journal is the *Australian Journal of Ecology*, which has made a very distinctive and individual contribution to publication since its first issue in 1976, with a total of 43 articles on or using classification and ordination in the first 11 volumes to 1986, representing 8.5% of all articles published in that journal.

A word of caution is appropriate here, however, since using simply the numbers of papers published in journals provides no information on quality and length of articles. Also a considerable number of examples of the application of multivariate methods may have occurred in unpublished research reports produced by both government and private research agencies. However, it is probable that all the trends discussed below would be similar, even if those

reports were included or an even wider range of journals surveyed.

Classification methods 1960–1986

In the 26 year period, 500 articles concerning or using classification methods for vegetation analysis were published in the 11 journals (Table 3). The numbers of papers published has remained remarkably constant, with the total staying between 99 and 115 for each five-year period since 1966. The trends in use of different approaches and methods are clear. Up to 1970, subjective continental methods were dominant, pre-dating the widespread availability of computers. Divisive monothetic methods (Association Analysis) were most significant between 1966 and 1975. Then, with the widespread availability of computers and appropriate software from the mid 1960s onwards, there was a steady rise in the use of agglomerative polythetic methods (Similarity Analysis and Information Analysis), which has continued to the present day. Divisive polythetic methods start from the early 1970s, rising to a peak with Two-Way Indicator Species Analysis – TWINSPAN (Hill 1979b) in the 1980s. Among other methods, TABORD (van der Maarel *et al.* 1978) deserves mention. The present position would seem to be that a small and decreasing number of researchers are using monothetic divisive methods, an almost equal number of papers originating primarily from Europe, America and Australia have been published using agglomerative polythetic and

Table 3. Number of articles using major approaches to classification 1960–1986.

| Year | Lifeform & structural | Subj. floristic | Divisive mono. | Agglom. poly. | Divisive poly. | Twinspan Divisive poly. | Tabord | Other & multiple | Total |
|---------|-----------------------|-----------------|----------------|---------------|----------------|-------------------------|--------|------------------|-------|
| 1960–65 | 6 | 36 | 6 | 3 | 0 | 0 | 0 | 10 | 61 |
| 1966–70 | 5 | 63 | 20 | 10 | 0 | 0 | 0 | 13 | 111 |
| 1971–75 | 6 | 40 | 18 | 21 | 2 | 0 | 0 | 12 | 99 |
| 1976–80 | 9 | 19 | 10 | 32 | 6 | 0 | 4 | 35 | 115 |
| 1981–86 | 3 | 7 | 11 | 36 | 5 | 21 | 10 | 21 | 114 |
| Total | 29 | 165 | 65 | 102 | 13 | 21 | 14 | 91 | 500 |

divisive polythetic techniques and a group centred on Scandinavia use tabular arrangement (TABORD). Although a small number of papers using subjective methods related to the various schools of European phytosociology are still produced, most of these are now published elsewhere, for example in the journal *Phytocoenologia*.

The other important trend is in the utilisation of more than one method (multiple – Table 3) for comparative purposes. The number of articles using more than one method rose over the survey period to a peak between 1976–80. The decline in multiple classification papers since 1980 is interesting and partly reflects the era of 1976–80, when agglomerative polythetic methods and the many variants of similarity analysis were being tested at the same time as the first divisive polythetic methods were coming into general use. Several papers have attempted to make evaluations of different techniques, notably Lambert & Williams (1966) and Gauch & Whittaker (1981). Since Gauch & Whittaker's 1981 paper, TWINSpan, in particular, has come into prominence. Most recently published or revised textbooks (Gauch 1982; Greig-Smith 1983; Kershaw & Looney 1985; Digby & Kempton 1987; Jongman *et al.* 1987 and Causton 1988) recommend TWINSpan as the state of the art in numerical classification and this coupled with the widespread availability of the associated computer program both on its own and in various composite packages is guaranteed to increase its usage in the next decade. However, the results of this survey show that agglomerative poly-

thetic methods are still popular and will continue to be used.

Ordination methods 1960–1986

The number of articles using the major ordination methods is shown in Table 4. Direct methods, although low in overall use, have persisted throughout the study period and have even shown a small relative rise in the 11 years from 1975–86. Indirect ordination in the 1960s was characterised throughout by Bray & Curtis/Polar methods (PO), with Principal Components Analysis (PCA) becoming significant during the second half of the decade. From 1970 to the present, the two groups of techniques have had contrasting fortunes, with PO methods going into almost complete decline but PCA remaining throughout and increasing its application. The early 1970s saw the rise of Reciprocal Averaging and Correspondence Analysis (RA/CA), particularly following the publication of Hill's paper in 1973, although several authors had published papers using it prior to this date. This was followed by Detrended Correspondence Analysis (DCA) – DECORANA in 1979 (Hill 1979a; Hill & Gauch 1980). DCA has enjoyed increasing use through the 1980s but it is interesting to note that PCA and its variants still remain very popular, with roughly equal numbers of published papers using PCA, RA/CA and DCA between 1981 and 1986.

Two other techniques are of particular interest at

Table 4. Number of articles using the major approaches to ordination.

| Year | Direct | Bray-Curtis Polar | P.C.A. | R.A./C.A. | D.C.A. | M.D.S. | Other & multiple | Total |
|---------|--------|-------------------|--------|-----------|--------|--------|------------------|-------|
| 1960–65 | 3 | 18 | 0 | 0 | 0 | 0 | 4 | 25 |
| 1966–70 | 1 | 20 | 15 | 0 | 0 | 0 | 11 | 47 |
| 1971–75 | 4 | 8 | 26 | 5 | 0 | 0 | 25 | 68 |
| 1976–80 | 12 | 1 | 33 | 21 | 1 | 1 | 44 | 113 |
| 1981–86 | 12 | 5 | 35 | 24 | 33 | 6 | 46 | 161 |
| Total | 32 | 52 | 109 | 50 | 34 | 7 | 130 | 414 |

P.C.A. – Principal Components Analysis

R.A./C.A. – Reciprocal Averaging/Correspondence Analysis

D.C.A. – Detrended Correspondence Analysis

M.D.S. – Multidimensional Scaling (Non-metric)

the present time. The first is Non-Metric Multidimensional Scaling (NM-MDS) (Fasham 1977; Prentice 1977). As Table 3 demonstrates, specific applications of NM-MDS are few. However, the table misses an important aspect of NM-MDS and its application, which is that although it has only been presented or used on its own in 7 articles, it has been used in a further 8 multiple situations. The reason behind this is that most researchers using NM-MDS have chosen to test it against other methods, notably PCA, RA/CA and DCA. In some reported results, it appears to perform well (Clymo 1980; Brown *et al.* 1984; Dargie 1984; Minchin 1987a), although others have been less impressed (Oksanen 1983).

The second recent development is that of Canonical Correspondence Analysis (CCA) (ter Braak 1986, 1987a; ter Braak & Prentice 1988). CCA is a method of correspondence analysis but one where the ordination axes are constrained to be linear combinations of environmental variables. As such CCA becomes a method of multivariate direct gradient analysis, in contrast to the majority of other techniques which are indirect in nature. The claim of CCA is that the method can be used both for detecting species-environment inter-relationships and also to study specific questions concerning species response to environmental variables. The method is so recent that it lies outside of the literature review of this paper and thus its diffusion into ecological applications will be interesting to observe over the next few years. It appears to represent an important new approach and an advance on previous techniques and clearly is the 'latest' technique which will be evaluated over the next few years alongside previous methods. Its adoption should be encouraged by the availability of a computer program CANOCO (ter Braak 1987b) with a wide range of options and good portability.

This last point clearly demonstrates the problems of the diversity and complexity of methods of ordination. As this survey shows, PCA, RA/CA and DCA are in widespread use but both NM-MDS and CCA are now present as potential improvements.

As the above discussion shows and as with classification, the final trend is the steady rise in the number of articles using several methods on the same data, presumably for comparative purposes. Numerous articles have attempted to make judgements as to the

'best' ordination method at a given time, using either simulated or field data or both, for example Austin (1976); Gauch & Whittaker (1972a, b); Gauch & Whittaker (1976); Fasham (1977); Gauch *et al.* (1977); Feoli & Feoli Chiapella (1980); Gauch *et al.* (1981); Oksanen (1983); Ezcurra (1987) and Minchin (1987a, b). Studies using simulated data have demonstrated some useful aspects of distortion attributable to different methods. However, they have not always shown how distortion manifests itself with different real-world data sets and in varying ecological situations. The whole field of interpretation of ordination diagrams and the subjectivity involved has received insufficient attention in the literature (van der Maarel 1980; Dargie 1984) despite recent suggested improvements in the construction and display of ordination diagrams, notably using the biplot method (ter Braak 1983, 1986; Oksanen 1987).

Philosophy and method versus ecological applications

One criticism which has been levelled at classification and ordination methods is that it sometimes seems as if nearly as many articles have been published on the methods themselves and their advantages and disadvantages, as using the methods for some ecological purpose. While this is clearly not true, Table 5 shows that the proportion of papers dealing primarily with philosophy and method rose from 15.6% of all articles published in 1960–65 to 35.5% in 1976–80 falling slightly to 26.0% in 1981–86. This reflects the constant evolution and testing of techniques over the study period, which itself has given rise to an increasing number of papers comparing different methods and their properties. This trend is also revealed in Tables 3 and 4 where the increase in articles referring to more than one technique (multiple) partly reflects the need for comparison.

Use of classification and ordination methods in applied studies

Although the distinction between pure and applied

Table 5. Numbers of articles on philosophy and method of classification and ordination and the numbers of articles using the methods ecologically.

| | Years | | | | | Total |
|-------------------------|---------|---------|---------|---------|---------|-------|
| | 1960–65 | 1966–70 | 1971–75 | 1976–80 | 1981–86 | |
| Philosophy and method | 12 | 25 | 48 | 64 | 53 | 202 |
| % of total | 15.6 | 18.3 | 35.0 | 35.5 | 26.0 | 27.5 |
| Ecological applications | 65 | 111 | 89 | 116 | 151 | 532 |
| % of total | 84.4 | 81.7 | 65.0 | 64.5 | 74.0 | 72.5 |
| Total | 77 | 136 | 137 | 180 | 204 | 734 |

ecology is somewhat arbitrary, it was possible to note whether an article used the methods in a situation which was related to management of vegetation and ecosystems or for biological conservation. Such an article was classified as 'applied'. Papers of a philosophical and methodological nature or only using the methods for phytosociology or gradient analysis were considered 'academic'. Table 6 shows the vast majority of papers to have been of an academic nature, which is perhaps what would be expected but is nevertheless disappointing. However, there has been a small but perceptible rise in the number of applied papers from none in 1960–65 to 18 in 1980–86.

Trends in the complementary use of classification and ordination methods

Tables 3 and 4 demonstrate that over the 26 years, rather more articles used classification than ordination (500 as opposed to 414). However, a shift in emphasis towards increasing use of ordination methods is evident, with 271 articles treating or using classifi-

cation between 1960 and 1975 and only 140 treating or using ordination. In contrast, between 1976 and 1986, the respective figures were: classification 229; ordination 274.

An important trend in the application of ordination and classification methods is towards 'complementary analysis'. This is where both classification and ordination techniques are employed together in an analysis of the same data set. Use of complementary analysis has increased over the same period, with only 9 papers in 1960–65 but 71 between 1981–86 (Table 7). These 71 articles represented 34.8% of all articles published between 1981–86. This partly reflects the greater ease of application of all methods, with the widespread availability of suitable computer packages, as well as a realisation that the two groups of methods can be used very effectively in combination.

Discussion

This survey of the literature on methods and applications of classification and ordination has produced

Table 6. Number of articles described as academic and number described as applied 1960–86.

| | Years | | | | | Total |
|----------|---------|---------|---------|---------|---------|-------|
| | 1960–65 | 1966–70 | 1971–75 | 1976–80 | 1981–86 | |
| Academic | 77 | 135 | 128 | 166 | 186 | 692 |
| Applied | 0 | 1 | 9 | 14 | 18 | 42 |

Table 7. Number of articles discussing or using both classification and ordination methods.

| | Years | | | | | Total |
|---|---------|---------|---------|---------|---------|-------|
| | 1960–65 | 1966–70 | 1971–75 | 1976–80 | 1981–86 | |
| Articles on or using both classification & ordination | 9 | 22 | 30 | 48 | 71 | 180 |
| Total articles | 77 | 136 | 137 | 180 | 204 | 734 |
| % treating or using both classification & ordination | 11.6 | 16.2 | 21.9 | 26.7 | 34.8 | 24.5 |

some useful information on the evolution and application of various techniques. The results demonstrate that over the past 26 years, there has been a steady and sustained rise in publications, new techniques have been evolved and ecological applications have generally shown a healthy increase. In the 10 years from 1977–87, eight major textbooks or revisions of major texts have appeared on the subject, including three entirely new ones in 1987–88 (Digby & Kempton 1987; Jongman *et al.* 1987; Causton 1988).

Nevertheless, at present, particularly in Britain, there is criticism of the whole approach and philosophy of quantitative plant community ecology, much of which centres on the points raised at the outset.

Range and choice of methods

The diversity and complexity of methods is a very real problem, which has important implications for both the use and application of methods for classification and ordination in ecological situations and in teaching the application of these techniques to students and undergraduates. The current plethora of methods appears both daunting and confusing to potentially interested students and is exasperating to many of their teachers and other non-mathematical ecologists.

Classification and ordination methods evolved in the 1960s, largely in response to the development and increased availability of computers. Although many techniques were originally developed to handle vegetation data (e.g. Polar Ordination, Association Analysis, TWINSpan), others such as Similarity Analysis, and most ordination techniques have their origins in other fields, such as psychology, tax-

onomy and archaeology. The improved speed, capacity and reduction in size and price of computers, together with widespread and rapid dissemination of software have all assisted with increasing the availability and diversity of methods.

The fact remains, however, that many users in the broader field of community ecology simply wish to use *a* method of classification and/or *a* method of ordination. Their prime concern is with the ecological problem and situation with which they are dealing. This survey has demonstrated that there is now as much if not more diversity and choice of methods as at any point in the history of the methods.

For classification, TWINSpan appears to be the optimal method when viewed from a British and perhaps American standpoint. However, Similarity Analysis and TABORD are still seen as useful alternatives, depending partly on the aims and objectives of a given project. The widespread availability of the TWINSpan package and its writing into other packages, e.g. VESpan (Programs for the National Vegetation Classification of Britain) are certain to guarantee its popularity and use. TWINSpan has also attracted comparatively little critical comment and re-evaluation, compared with most ordination methods and since its arrival in 1979, has not had to compete with more recent rivals. The literature survey shows that a small but nevertheless significant number of articles published in the 1980s have still used older methods, for example Association Analysis, which is now widely accepted as having important deficiencies (Gauch 1982; Greig-Smith 1983; Kershaw & Looney 1985). How referees and research supervisors should react to this is an interesting question. Should a student or an author who has used a technique such as association analysis automatically be requested by his supervisor or a referee

to rerun his or her data using a more recent method? Should the results of the many earlier papers published using such a method be re-interpreted because of more recently discovered failings in a particular technique?

With ordination methods, the problem of choice is very much more difficult. The survey results show that PCA, RA/CA and DCA have all been widely and almost equally used in the past decade but with DCA becoming increasingly popular. Many ecologists believed that after all the critical evaluations of PO, PCA and its variants and RA/CA, an effective and robust technique had been found in DCA. However, DCA, as with the other methods before it, is now being subject to rather more critical review (Beals 1984; Dargie 1986; Ezcurra 1987; Wartenberg *et al.* 1987; Minchin 1987a; Oksanen 1988). On top of this, the potential value of Non-Metric Multidimensional Scaling and Canonical Correspondence Analysis remains to be proven and yet they provide still wider choice.

Similar questions to those asked about classification methods can be asked of ordination. Is it a serious error now to have used PCA or RA as a method of analysis? As far as ecological interpretations go, how many published applications over the past 26 years have made sufficiently serious errors in interpretation because of the technique which they have used? As with all questions of this type, the answer is probably that it depends. At one level, virtually all methods will probably provide an interpretable set of results – interpretable in that the user will be able to make some useful ecological sense of them in the context of his ecological problem and using his ecological knowledge of that situation. If the user has some appreciation of the distortion of a particular method, then he should be able to improve his interpretation further, but how many people have actually done that? If the user has an appreciation of the limitations of the method then in all probability he will seek to use a better or ‘improved’ technique.

Another trend, which is again increasingly evident from the results of the survey and represents a response to this problem, is to use more than one method of analysis. This is made more feasible by the availability of a number of packages which enable the same data set to be analysed by different tech-

niques (e.g. Cornell Ecology Programs). A different problem then arises, in that the researcher is left with the decision as to which one is ‘best’. This decision can be made in one of two ways. Firstly, in the context of the ecological situation for which the analysis has been run, the researcher can decide which technique gives him the best results, although this is usually a subjective decision. One unfortunate consequence of this has been the tendency for that person then to say that that method is probably best for general use, which is not a necessary corollary. Secondly, the researcher can accept that different methods will show him different nuances of the data and interpretation can be made on the assessment of all results. However, this tends to make interpretation extremely complex.

Methods of statistical testing of the results of both classification and ordination analyses exist. Strauss (1982), for example, presented a means of testing significance of classification groups from association analysis, but most analyses would almost certainly not survive the rigour of such testing, nor would it necessarily be desirable that they should. Many sets of classification groups represent partitioning of data which are much nearer to continua than to a clearly defined group structure. In ordination, techniques for comparing ordinations from different methods have been devised (e.g. Wilson 1981; Digby & Kempton 1987). Again these can be valuable and will show limitations of particular methods but they are not widely used. In the final analysis, it can be argued that it is the ecological interpretation of the results that matter and the ecological sense which they make which is the primary criterion. The concept of user satisfaction, widely recognised in the whole field of numerical classification, is important.

Despite this extended discussion, there still appears to be no simple solution to this problem of choice and how it should be presented to the majority of non-mathematical ecologists and students who may wish to use these methods and would find them extremely valuable.

Hypothesis generation and testing

Originally, it had been one purpose of this survey to record the number of examples in the literature

where description and analysis of vegetation was followed by clear generation of hypotheses and subsequent testing. With the exception of Goldsmith (1973a, b), already mentioned, no other examples of this type were found. Austin (1985) mentions Gittins work (Gittins 1979) published outside the bounds of this survey. Clearly there is need for more research of this type to be formulated. This point also relates to aspects of the use of these approaches in applied studies and in the problems of links between community and individualistic plant ecology.

Philosophy and method rather than application

The data from the survey showed how between a quarter and a third of all papers published on or using classification and ordination have consistently been on philosophy and method rather than an example of ecological application. Whether this proportion has been and still is too high, perhaps reflecting the uncertainty over methodology, is very much an open question. The converse could be argued, that given that there are philosophical and practical problems in the application of multivariate analysis in vegetation science, then a large proportion of papers on philosophy and method at least shows there is much healthy discussion and debate, even though this once again raises problems over the range and diversity of methods. However, the high proportion of papers on philosophy and method and especially on evaluation of techniques represents one of the major sources of confusion for students, particularly if they have been encouraged to try to look into some of the deficiencies and distortions present in a chosen method.

Classification and ordination in applied studies

The figures in Table 6 for the application of methods to applied problems are smaller than was expected. While the academic emphasis of much phytosociology and gradient analysis is understandable and will quite rightly continue, equally, there must be a greater role for vegetation description and analysis using multivariate methods, within biological conserva-

tion and environmental management. Even though quite a number of applied studies may exist as unpublished research reports to government and private agencies, it would seem that further development and application in this field should be encouraged.

Complementary and multiple analyses

The trend towards both complementary and multiple analyses has been clearly demonstrated, with a third of all published articles between 1981–86 using this approach. The advantages of complementary analysis have already been discussed and are usually well justified, but the increased number of multiple uses undoubtedly reflects a response to uncertainty over which techniques are best and the problem of choice. However, as the range of techniques, particularly for ordination, becomes wider, using a multiple approach can quickly become unwieldy and problems of interpretation increase. Again a question may be asked as to why should multiple analysis be necessary, when the prime aim of most pieces of research is ecological, rather than methodological?

Conclusion – Implications for the theoretical basis of vegetation science

The problems in deriving a workable model of species response to environment and the static nature of a great deal of descriptive community ecology were discussed earlier. In the absence of a fully developed model of vegetation response to environment, perhaps it is not surprising that the various trends and problems in the evolution and application of classification and ordination methods have occurred and there seems little reason to believe that they will not continue into the near future.

At the same time, however, Minchin (1987a, b) stresses the concept of 'robustness' and the idea that many of the methods can be used in most situations to give at least satisfactory or good results. Most non-mathematical ecologists have clung onto this principle for a good number of years and probably will continue to do so. However, it is clear that while

on the one hand, most general users should look at some of the limitations of the methods more closely, on the other, specialist mathematical ecologists should do rather more to communicate the real essence of their findings to their more non-mathematical general audience and if possible try to provide clearer and less ambiguous guidelines and recommendations. There is a very definite need for this in order to assist with teaching and learning in this area of ecology. Possibly the worst reaction by the mathematical ecologists to the problems of choice raised in this article would be for them to argue that unless a student and researcher has both the time and the ability to fully unravel and comprehend the complexities and merits of different methods, then they should not use them. At the same time, any person contemplating the use of such methods must have some appreciation of the methods and their capabilities and failings. Achieving a suitable balance between these two ideas is an extremely difficult and demanding exercise but a very important one for the future.

The problems of links between community ecology and individualistic plant ecology and the exact place of much vegetation description and analysis within vegetation science as a whole also remain difficult issues. The failure of most researchers in this field to ask appropriate questions and to develop and test hypotheses, rather than always concentrating on basic description and analysis is a major problem, which although now well recognised, is not necessarily being addressed in practice. While most community ecologists seem to accept that the individualistic approach is of value and has provided a very useful way forward, the reverse is most certainly not always the case. There is a clear tendency for the individualistic plant ecologists to believe that traditional vegetation description and analysis has reached a dead end. The answer must again lie in the need for more studies to adopt the deductive approach and actually go on to detailed hypothesis testing at the individual plant level. A further link may then become possible, whereby the results of such hypothesis testing provide useful insights when reintegrated at the community scale.

Acknowledgements

The authors would like to express their thanks to the journal editors and several anonymous referees for invaluable constructive criticism during the preparation of this manuscript.

References

- Austin, M. P. 1976. Performance of four ordination techniques assuming three different non-linear species response models. *Vegetatio* 33: 43–49.
- Austin, M. P. 1977. Use of ordination and other multivariate descriptive methods to study succession. *Vegetatio* 35: 165–175.
- Austin, M. P. 1979. Current approaches to the non-linearity problem in vegetation analysis. In: Patil, G. P. & Rosenzweig, M. (eds), *Contemporary quantitative ecology and related econometrics*. pp. 197–210. Int. Coop. Publ., Fairland, Maryland.
- Austin, M. P. 1980. Searching for a model for use in vegetation analysis. *Vegetatio* 42: 11–21.
- Austin, M. P. 1985. Continuum concept, ordination methods and niche theory. *Ann. Rev. Ecol. Syst.* 16: 39–61.
- Austin, M. P. 1987. Models for the analysis of species' response to environmental gradients. *Vegetatio* 69: 35–45.
- Austin, M. P. & Austin, B. O. 1980. Behaviour of experimental plant communities along a nutrient gradient. *J. Ecol.* 68: 891–918.
- Austin, M. P., Cunningham, R. B. & Fleming, P. M. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio* 55: 11–27.
- Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Adv. Ecol. Res.* 14: 1–55.
- Brown, M. J., Ratkowsky, D. A. & Minchin, P. R. 1984. A comparison of detrended correspondence analysis and principal coordinates analysis using four sets of Tasmanian vegetation data. *Aust. J. Ecol.* 9: 273–279.
- Causton, D. 1988. *Introduction to vegetation analysis*. Unwin Hyman, London.
- Clymo, R. S. 1980. Preliminary survey of the peat-bog Hummell Knowe Moss using various numerical methods. *Vegetatio* 42: 129–148.
- Crawley, M. J. 1986. The structure of plant communities. In: Crawley, M. J. (ed.), *Plant ecology*, pp. 1–50. Blackwell, Oxford.
- Dale, M. B. 1975. On objectives of methods of ordination. *Vegetatio* 30: 15–32.
- Dargie, T. C. D. 1984. On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in southeastern Spain. *Vegetatio* 55: 37–55.

- Dargie, T. C. D. 1986. Species richness and distortion in reciprocal averaging and detrended correspondence analysis. *Vegetatio* 65: 95–98.
- Digby, P. G. N. & Kempton, R. A. 1987. *Multivariate analysis of ecological communities*. Chapman and Hall, London.
- Ezcurra, E. 1987. A comparison of reciprocal averaging and non-centred principal components analysis. *Vegetatio* 71: 41–47.
- Fasham, M. J. R. 1977. A comparison of non-metric multidimensional scaling, principal components analysis and reciprocal averaging for the ordination of simulated coenoclines and coenoplanes. *Ecology* 58: 551–561.
- Feoli, E. & Feoli Chiappella, L. 1980. Evaluation of ordination methods through simulated coenoclines: some comments. *Vegetatio* 42: 35–41.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge.
- Gauch, H. G. & Whittaker, R. H. 1972a. Coenocline simulation. *Ecology* 53: 446–451.
- Gauch, H. G. & Whittaker, R. H. 1972b. Comparison of ordination techniques. *Ecology* 53: 868–875.
- Gauch, H. G. & Whittaker, R. H. 1976. Simulation of community patterns. *Vegetatio* 33: 13–16.
- Gauch, H. G. & Whittaker, R. H. 1981. Hierarchical classification of community data. *J. Ecol.* 69: 537–558.
- Gauch, H. G., Whittaker, R. H. & Singer, S. B. 1981. A comparative study of non-metric ordinations. *J. Ecol.* 69: 135–152.
- Gauch, H. G., Whittaker, R. H. & Wentworth, T. R. 1977. A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.* 65: 157–174.
- Gittins, R. 1979. Ecological applications of canonical analysis. In: Orlóci, L., Rao, C. R. & Stiteler, W. M. (eds), *Stat. Ecol.* 7: 309–535. Int. Coop.: Fairland, Maryland.
- Goldsmith, F. B. 1973a. The vegetation of exposed sea cliffs at South Stack, Anglesey. I. The multivariate approach. *J. Ecol.* 61: 787–818.
- Goldsmith, F. B. 1973b. The vegetation of exposed sea cliffs at South Stack, Anglesey. II. Experimental studies. *J. Ecol.* 61: 819–830.
- Goodall, D. W. 1970. Statistical plant ecology. *Ann. Rev. Ecol. Syst.* 1: 99–124.
- Goodall, D. W. 1978. Numerical classification. In: Whittaker, R. H. (ed.), *Classification of plant communities*, pp. 247–286. Junk, The Hague.
- Greig-Smith, P. 1980. The development of numerical classification and ordination. *Vegetatio* 42: 1–9.
- Greig-Smith, P. 1983. *Quantitative plant ecology*. 3rd ed. Blackwell, Oxford.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Wiley, Chichester.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.
- Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61: 237–249.
- Hill, M. O. 1979a. DECORANA – A Fortran program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, NY.
- Hill, M. O. 1979b. TWINSpan – A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. Cornell University, Ithaca, NY.
- Hill, M. O. & Gauch, H. G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47–58.
- Jongman, R. G. H., ter Braak, C. J. F. & van Tongeren, O. F. R. 1987. *Data analysis in community and landscape ecology*. Pudoc, Wageningen.
- Keddy, P. A. 1987. Beyond reductionism and scholasticism in plant community ecology. *Vegetatio* 69: 209–211.
- Kellman, M. C. 1980. *Plant geography*. 2nd ed. New York.
- Kershaw, K. A. & Looney, J. H. H. 1985. *Quantitative and dynamic plant ecology*. 3rd ed. Arnold, London.
- Lambert, J. M. & Williams, W. T. 1966. *Multivariate methods in plant ecology*. IV. Comparison of information analysis and association analysis. *J. Ecol.* 54: 635–664.
- May, R. M. 1985. Evolutionary ecology and John Maynard Smith. In: Greenwood, P. J., Harvey, P. H., Slatkin, M. (eds), *Evolution: Essays in honour of John Maynard Smith*, pp. 107–116. Cambridge University Press.
- McIntosh, R. P. 1967. The continuum concept of vegetation. *Bot. Rev.* 33: 130–187.
- Minchin, P. R. 1987a. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89–107.
- Minchin, P. R. 1987b. Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* 71: 145–156.
- Nie, N. H. (ed.) 1983. *SPSSX users guide*. McGraw-Hill, New York.
- Noy-Meir, I. & van der Maarel, E. 1987. Relations between community theory and community analysis in vegetation science: some perspectives. *Vegetatio* 69: 5–15.
- Oksanen, J. 1983. Ordination of boreal heath-like vegetation with principal component analysis, correspondence analysis and multidimensional scaling. *Vegetatio* 52: 181–189.
- Oksanen, J. 1987. Problems of joint displays of species and site scores in correspondence analysis. *Vegetatio* 72: 51–57.
- Oksanen, J. 1988. A note on the occasional instability of detrending in correspondence analysis. *Vegetatio* 74: 29–32.
- Orlóci, L. 1978. *Multivariate analysis in vegetation research*. 2nd ed. Junk, The Hague.
- Pielou, E. C. 1984. *The interpretation of ecological data*. Wiley, New York.
- Prentice, I. C. 1977. Non-metric ordination models in ecology. *J. Ecol.* 65: 85–94.
- Roberts, D. W. 1987. A dynamical systems perspective on vegetation theory. *Vegetatio* 69: 27–33.
- Shipley, B. & Keddy, P. A. 1987. The individualistic and community-unit concepts as falsifiable hypotheses. *Vegetatio* 69: 47–55.
- Silvertown, J. W. 1982. *Introduction to plant population ecology*. Longman, London.
- Strauss, R. E. 1982. Statistical significance of species clusters in association analysis. *Ecology* 63: 634–639.
- Swaine, M. D. & Greig-Smith, P. 1980. An application of principal

- components analysis to vegetation change in permanent plots. *J. Ecol.* 68: 33–41.
- ter Braak, C. J. F. 1983. Principal components biplots and alpha and beta diversity. *Ecology* 64: 454–462.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- ter Braak, C. J. F. 1987a. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69–77.
- ter Braak, C. J. F. 1987b. CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis (version 2.0). TNO Institute of Applied Computer Science, Wageningen.
- ter Braak, C. J. F. & Prentice, I. C. 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18: 271–317.
- Turkington, R. & Harper, J. L. 1979. The growth distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *J. Ecol.* 67: 201–218.
- van der Maarel, E., Janssen, J. G. M. & Louppen, J. M. W. 1978. TABORD, a program for structuring phytosociological tables. *Vegetatio* 38: 143–156.
- van der Maarel, E. 1979. *Vegetatio* 1980: the past six years and the near future. *Vegetatio* 41: 129–132.
- van der Maarel, E. 1980. On the interpretability of ordination diagrams. *Vegetatio* 42: 43–45.
- van der Maarel, E. 1984a. Vegetation science in the 1980s. In: Cooley, J. H. & Golley, F. B. (eds), *Trends in ecological research for the 1980s*, pp. 89–110, Plenum Press, New York.
- van der Maarel, E. 1984b. Dynamics of plant populations from a synecological viewpoint. In: Dirzo, R. & Sarukhan, J. (eds), *Perspectives on plant ecology*, pp. 66–82. Sinauer Associates Inc., Sunderland, Mass.
- van der Maarel, E. & van der Maarel-Versluys, M. 1988. Index to *Vegetatio* volumes 51–73 and some notes on the position of the journal. *Vegetatio* 73: 123–189.
- Wartenberg, D., Ferson, S. & Rohlf, F. J. 1987. Putting things in order: a critique of detrended correspondence analysis. *Amer. Nat.* 129: 434–448.
- Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol. Monog.* 23: 41–78.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42: 207–264.
- Whittaker, R. H. 1975. *Communities and ecosystems*. 2nd ed. MacMillan, New York.
- Whittaker, R. H. & Gauch, H. G. 1978. Evaluation of ordination techniques. In: Whittaker, R. H. (ed.), *Ordination of plant communities*, pp. 277–336, Junk, The Hague.
- Williams, W. T. & Lance, G. N. 1968. Choice of strategy in the analysis of complex data. *Statistician* 18: 31–43.
- Wilson, M. V. 1981. A statistical test of the accuracy and consistency of ordinations. *Ecology* 62: 8–12.