

## CANOCO – an extension of DECORANA to analyze species-environment relationships

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A common problem in community ecology and ecotoxicology is to discover how a multitude of species respond to external factors such as environmental variables, pollutants and management regime. Data are collected on species composition and the external variables at a number of points in space and time. Statistical methods available so far to analyze such data either assumed linear relationships or were restricted to regression analysis of the response of each species separately. To analyze the generally non-linear, non-monotone response of a community of species, one had to resort to the data-analytic methods of ordination and cluster analysis – ‘indirect’ methods that are generally less powerful than the ‘direct’ statistical method of regression analysis. Recently, regression and ordination have been integrated into techniques of *multi-variate* direct gradient analysis, called canonical ordination (Jongman *et al.*, 1987; ter Braak & Prentice, 1988). The use of canonical ordination greatly improves the power to detect the specific effects one is interested in. One of these techniques, canonical correspondence analysis, escapes the assumption of linearity and is able to detect unimodal relationships between species and external variables (ter Braak, 1986, 1987a). The computer program CANOCO is designed to make these techniques available to ecologists studying community responses.

CANOCO is a genuine extension of DECORANA (Hill, 1979). It includes the indirect techniques of principal components analysis (PCA), (detrended) correspondence analysis and principal coordinates analysis and also the direct

techniques of weighted averaging, canonical correspondence analysis, canonical variates analysis (= linear discriminant analysis) and redundancy analysis. In PCA, there are options for centring/standardization by species and by samples and for producing biplots (ter Braak, 1983). CANOCO can also carry out ‘partial’ ordination, in which the effects of particular environmental ‘background’ variables are eliminated. A partial ordination allows one to display the residual variation in the species data (see for a simple example Swaine & Greig-Smith, 1980) and to relate the residual variation to the variables one is specifically interested in.

CANOCO allows one to test statistically whether the species are related to supplied environmental variables. The test provided is a Monte Carlo permutation test. This facility of CANOCO makes it attractive for environmental impact assessment, as an alternative for MANOVA (Green, 1979; Morrison, 1976; Stroup & Stubbendieck, 1983) and for Pielou’s method of random skewers (Pielou, 1984; Schaeffer & Perry, 1986).

CANOCO allows interactive data analysis: results of an analysis can be displayed at the terminal and after inspection the analysis can be pursued, for example.

- by changing from an indirect gradient analysis to a direct gradient analysis,
- by dropping environmental variables,
- by reading other environmental variables to be related to the current ordination axes or to be used in further canonical analyses.

CANOCO is available on mainframes and on

personal computers. It is written in standard FORTRAN 77 and can be supplied on 5.25 inch diskette for IBM-compatible PC's, on 3.5 inch diskette for Apple MacIntosh and ATARI-ST PC's, on magnetic tape (1600 bpi, ASCII-code) or via BITNET/EARN. On an IBM-compatible PC with 640 Kb, CANOCO can analyse ca. 750 samples, 600 species, 60 environmental variables and 100 covariables. An order form is sent on request. The one-time costs are at present ca. \$150 for educational institutions and ca. \$300 for others. A comprehensive manual (ter Braak, 1988) and a collection of relevant papers (ter Braak, 1987b) will be sent with the program. Researchers from countries with valuta problems may send in a request for a free copy.

## References

- Green, R. H., 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York, 257 pp.
- Hill, M. O., 1979. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, Ithaca, New York, 52 pp.
- Jongman, R. H. G., C. J. F. ter Braak, O. F. R. van Tongeren, 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen, 299 pp.
- Morrison, D. F., 1976. Multivariate statistical methods. McGraw-Hill, Tokyo, 415 pp.
- Pielou, E. C., 1984. Probing multivariate data with random skewers: a preliminary to direct gradient analysis. *Oikos* 42: 161–165.
- Schaeffer, D. J. & J. A. Perry, 1986. Gradients in the distribution of riverine benthos. *Freshwat. Biol.* 16: 745–757.
- Stroup, W. W. & J. Stubbendieck, 1983. Multivariate statistical methods to determine changes in botanical composition. *J. Range Mgmt* 36: 208–212.
- Swaine, M. D. & P. Greig-Smith, 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 method 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. Unimodal models to relate species to environment. Agricultural Mathematics Group, Wageningen, 151 pp.
- ter Braak, C. J. F., 1988. CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Report LWA-88-02. Agricultural Mathematics Group, Wageningen, 95 pp.
- ter Braak, C. J. F. & I. C. Prentice, 1988. A theory of gradient analysis. *Advances in ecological research* 18: 271–317.