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FORUM

Are ordination and constrained ordination alternative or complementary strategies in general ecological studies?

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Introduction

General-purpose ecological studies are performed in order to summarize the main structure in a species-by-sample data matrix, to relate structure in vegetation to external factors, and to generate hypotheses about vegetation-environment relationships (Økland 1990a). Two main multivariate gradient-analysis techniques are currently used in such studies (ter Braak & Prentice 1988; Palmer 1993): Ordination or Indirect Gradient Analysis, and Constrained Ordination or Direct Gradient analysis. While Ordination has been used in vegetation ecology for more than 30 yr (Kent & Ballard 1988), Constrained Ordination (CO) has become popular in recent years (Birks et al. 1994) due to (1) easy access via the program package CANOCO (ter Braak 1987b, 1990); (2) growing awareness of defects in all available ordination techniques (e.g. Minchin 1987); (3) its intuitive appeal, by relating vegetational variation directly to environmental factors; (4) circumvention of the tedious interpretation process necessary with ordination; (5) easy access to joint plots (with species and/or samples *and* vectors representing the direction of maximum change in each external variable) in CANODRAW (Smilauer 1992), a plotting program issued with CANOCO.

Ordination and Constrained Ordination may appear similar as both give rise to the characteristic diagrams often referred to as 'ordinations': plots of species and/or samples with respect to axes (e.g., Palmer 1993). The two approaches are presently used side by side for general-purpose ecological studies; most authors do not even motivate their choice. Authors using both have often expressed preference for CO (e.g. Odland et al. 1990; del Moral et al. 1995). Complementarity, but with superiority of CO is also indicated in more theoretically minded studies: "Often, community-environment relationships have been explored by ... ordination, followed by interpretation of axes in terms of environmental variables. But if environmental data are to hand, constrained ordination ... provides a more powerful means to the same end." (ter Braak & Prentice 1988, p. 308). And: "... CCA [Canonical Correspondence Analysis; ter Braak 1986, 1987a] is a direct gradient analysis [constrained ordination] technique that is an elegant extension of the indirect gradient analysis [ordination] technique, Correspondence Analysis. CCA has all of the advantages and none of the disadvantages of [the ordination method] DCA [Detrended Correspondence Analysis; Hill 1979; Hill & Gauch 1980]." (Palmer 1993, p. 2228).

The aim of this note is to show that Ordination and Constrained Ordination suit different purposes in ecological analysis.

Ordination and Constrained Ordination: conceptual similarities and differences

Ordination aims at ordering samples and/or species along (a few) axes that represent the main compositional gradients in the data set, using abundance data for the m species in the n sample plots only. Because most species respond to the same set of complex-gradients (single environmental gradients that vary more or less parallel in time or space; Whittaker 1956), relationships in the data set can be adequately represented in a low-dimensional subspace of the data matrix space (cf. Gauch 1982; Økland 1990a). Geometrically, all ordination methods perform multidimensional scaling because they aim at representing samples and/or species in a

low-dimensional ordination space by optimizing the correspondence between original dissimilarities (between samples or species) and distances in the ordination (Prentice 1977). Ordination methods can be characterized (1) by a combination of dissimilarity measure and stress function (measure of goodness-of-fit between original dissimilarities and distances in the ordination), and also in some cases (2) statistically; "ordination axes [are] considered as latent variables, or hypothetical environmental variables, constructed in such a way as to optimize the fit of the species [abundance] data to a particular (linear or unimodal) statistical model of how species abundance varies along gradients." (ter Braak & Prentice 1988). Ordination axes are computed by iteration. They are interpreted *a posteriori*, by relating the axes to supplied environmental variables and other external information (see R. Økland 1990a for a survey of techniques).

Constrained Ordination is ordination with an additional (usually linear) multiple regression step (trial ordination scores are regressed onto a set of external variables, and fitted values are used as new trial scores) inserted into the iteration procedure. The CO axes optimize the fit of samples and/or species relative to a set of explanatory variables (ter Braak & Prentice 1988). This extra step makes ordination and CO conceptually different: while ordination axes are gradients in the composition of vegetation, the final sample scores in CO are (linear) combinations of explanatory variables (chosen so that the highest possible fraction of variation in species abundances is 'explained' by the axis).

Choice of strategy for general ecological studies

In my opinion, the general-purpose ecological study with its focus on *generation* of hypotheses about vegetation-environment relationships, raises an ordination problem. At the start of a study, the ecologist uses his or her ideas of complex-gradients that may impact the vegetation for selection of environmental (and other explanatory) variables to be recorded. CO axes are dependent on this set of explanatory variables. For general-purpose studies, this is problematic for three reasons:

1. Different sets of explanatory variables used with one species-by sample matrix (and one CO method) are likely to give rise to different axes. Ordination axes are invariant of data on external factors; these only influence the interpretability of axes.
2. Regardless of the ecologist's skills, no guarantee can be given that all relevant (independent) factors associated with each major compositional gradient have been measured. In CO, *all* variation in vegetation that is not related to the supplied variables is discarded. The efficiency of the CO method CCA in discarding compositional variation that are not represented by explanatory variables is demonstrated by Palmer (1993). CO thus ensures that the ecologist is not even notified about compositional gradients he or she was not initially aware of, whereby the potential for generation of *new* hypotheses is lost! Examples of appearance of unexpected vegetational gradients in ordination are many (e.g. Kantvilas & Minchin 1989; Økland 1990b). Important environmental factors that are difficult to quantify (and hence, not often included among explanatory variables) include historical factors (e.g. associated with previous disturbance; Jonsson & Esseen 1990; Hörnberg et al. 1995), turnover rates for essential nutrients (such as N; Robertson et al. 1988), soil moisture (Andersson 1970), herbivory (Ericson 1977) and extreme values for climatic factors (e.g. a 100-yr drought; Økland & Eilertsen 1993).
3. In CO, only variation in vegetation with a specified statistical relationship (in CCA: linear) to one of the supplied variables will be extracted by the axes. Adequacy of results thus also depends on proper transformation of variables (in CCA: to a scale approximately linear with compositional variation).

Current usage of CO as an alternative to ordination for general-purpose ecological studies is partly theoretically, partly practically motivated. CO methods (those available in CANOCO, and potential methods based on the principle of Non-metric Multi-Dimensional Scaling are extensions of currently used and frequently criticized ordination methods. Shortcomings of these ordination methods will, therefore, to some degree also be inherent in the corresponding CO techniques. Furthermore, excellent recovery of compositional gradients by CO as demonstrated by Palmer (1993) is restricted to the unrealistic. In the context of general-purpose studies, uninteresting cases where all relevant environmental factors are known and appropriately scaled *before* the start of the study. In real situations, however, the environmental structure is not initially known and the appropriateness of a set of explanatory variables cannot be assessed.

Interpretation of unconstrained axes in hybrid ordination (initial extraction of s^* constrained axes, followed by $s^\wedge$ unconstrained axes; ter Braak 1987b) has been proposed as a means of expanding the potential of CO to hypothesis-generating situations (Machena 1987; Økland 1990a,b). Low eigenvalues of unconstrained axes relative to constrained axes should indicate that the most impor-

tant explanatory variables have been included in the analysis. However, there are reasons to believe that the subjective choice of explanatory variables (and transformations of them) strongly influences the way variation associated with each compositional gradient is partitioned on constrained and unconstrained axes. Hybrid analysis is therefore no alternative to ordination for the general-purpose study.

Practical arguments, e.g. relating to the advanced plotting options frequently used with CO (including bi- and triplots), are irrelevant as these are equally available for the interpretation of ordination results.

Appropriate use of ordination and constrained ordination

Appropriateness of ordination for general-purpose ecological studies requires availability of reliable techniques. All ordination methods in current use are, however, burdened with defects such as the potential appearance of artifact or distorted axes (Kenkel & Orlóci 1986; Minchin 1987; Økland 1990a). The potential for methodological improvements in ordination is unknown. At present, I consider the best way to circumvent this serious problem to be *parallel* application of two principally different ordination methods (Økland 1990a; Økland & Eilertsen 1993). Congruent configurations can be used as an indication (but not proof) that a near-optimal solution has been found. Cases of incongruence generally cannot conclusively resolved, although knowledge about the cause and appearance of distortions may be helpful (see e.g. Minchin 1987; Oksanen 1988; Økland 1990a, b; Jackson & Somers 1991; Økland & Eilertsen 1993). Suggested methods (see Økland 1990a; Økland & Eilertsen 1993) are (L)NMDS variants (e.g. Minchin 1987; Belbin 1991) and DCA.

Constrained ordination is a powerful tool for the hypothesis-testing stage of ecological analysis:

1. The significance of the influence of (sets of) explanatory variables on vegetation can be tested by use of a Monte Carlo approach with permutation procedures appropriate for data sets and hypotheses (e.g. Odland et al. 1991; ter Braak & Wiertz 1994 and Lepš et al. 1995). In particular, the significance of minor environmental factors of particular interest can be tested (Cramer & Hytteborn 1987).

2. By partialling out the (uninteresting or undesirable) effect of covariables, the variation in the species-by-sample matrix can be partitioned on different sets of explanatory (e.g. environmental and spatial) variables (Borcard et al. 1992; Økland & Eilertsen 1994).

3. Significance of single ordination axes can be tested by using sample scores as constraining variables (Økland 1995).

I conclude that Ordination and Constrained Ordination are fundamentally different gradient analysis techniques serving different purposes in ecological analysis.

References

Andersson, F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. I. Vegetational and environmental structure. *Opera Bot.* 27: 1-190.

Belbin, L. 1991. Semi-strong hybrid scaling, a new ordination algorithm. *J. Veg. Sci.* 2: 491-496.

Birks, H.J.B., Peglar, S.M. & Austin, H.A. 1994. *An annotated bibliography of canonical correspondence analysis and related constrained ordination methods 1986-1993.* Report Botanical Institute, University of Bergen, Bergen.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.

Cramer, W. & Hytteborn, H. 1987. The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore. *Vegetatio* 69: 157-167.

del Moral, R., Titus, J.H. & Cook, A.M. 1995. Early primary succession on Mount St. Helens, Washington, USA. *J. Veg. Sci.* 6: 107-120.

Ericson, L. 1977. The influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. *Wahlenbergia* 4: 1-114.

Gauch, H.G. 1982. Noise reduction by eigenvector ordinations. *Ecology* 63: 1643-1649.

Hill, M.O. 1979. *DECORANA - A Fortran program for detrended correspondence analysis and reciprocal averaging.* Cornell Univ., Ithaca, NY.

Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.

Hörnberg, G., Ohlson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth *Picea abies* swamp-forests. *J. Veg. Sci.* 6: 291-298.

Jackson, D.A. & Somers, K.M. 1991. Putting things in order: the ups and downs of detrended correspondence analysis. *Am. Nat.* 137: 704-712.

Jonsson, B.G. & Esseen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J. Ecol.* 78: 924-936.

Kantvilas, G. & Minchin, P.R. 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. *Vegetatio* 84: 99-112.

Kenkel, N.C. & Orlóci, L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* 67: 919-928.

Kent, M. & Ballard, J. 1988. Trends and problems in the application of classification and ordination methods in

plant ecology. *Vegetatio* 78: 109-124.

Lepš, J., Michálek, J., Kulisek, P. & Uhlík, P. 1995. Use of paired plots and multivariate analysis for the determination of goat grazing preference. *J. Veg. Sci.* 6: 37-42.

Machena, C. 1987. Zonation of submerged macrophyte vegetation in Lake Kariba, Zimbabwe and its ecological interpretation. *Vegetatio* 73: 111-119.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89-107.

Odland, A., Birks, H.H., Botnen, A., Tønsberg, T. & Vevle, O. 1991. Vegetation change in the spray zone of a waterfall following river regulation in Aurland, Western Norway. *Regul. Rivers Res. Manage.* 6: 147-162.

Odland, A., Birks, H.J.B. & Line, J.M. 1990. Quantitative vegetation-environment relationships in west Norwegian tall-fern vegetation. *Nord. J. Bot.* 10: 511-533.

Økland, R.H. 1990a. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. *Sommerfeltia Suppl.* 1: 1-233.

Økland, R.H. 1990b. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. *Nord. J. Bot.* 10: 79-108.

Økland, R.H. 1995. Persistence of vascular plants in a Norwegian boreal coniferous forest. *Ecography* 18: 3-14.

Økland, R.H. & Eilertsen, O. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. *Sommerfeltia* 16: 1-254.

Økland, R.H. & Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. *J. Veg. Sci.* 5: 117-126.

Oksanen, J. 1988. A note on the occasional instability of detrending in correspondence analysis. *Vegetatio* 74: 29-32.

Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.

Prentice, I.C. 1977. Non-metric ordination methods in ecology. *J. Ecol.* 65: 85-94.

Robertson, G.P., Huston, M.A., Evans, F.C. & Tiedje, J.M. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69: 1517-1524.

Smilauer, P. 1992. *CANODRAW: user's guide. v. 3.0.* - Microcomputer Power, Ithaca, NY.

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, principal components analysis and redundancy analysis (version 2.1).* TNO Inst. appl. Comp. Sci., Stat. Dept. Wageningen, Wageningen.

ter Braak, C.J.F. 1990. *Update notes: CANOCO version 3.10.* Agricultural Mathematics Group, Wageningen.

ter Braak, C.J.F. & Prentice, I.C. 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18: 271-317.

ter Braak, C.J.F. & Wiertz, J. 1994. On the statistical analysis of vegetation change: a wetland affected by water extraction and soil acidification. *J. Veg. Sci.* 5: 361-372.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1-80.