Species richness and distortion in reciprocal averaging and detrended correspondence analysis

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Abstract

Gradients in beta diversity and species richness cause different forms of distortion in reciprocal averaging ordinations. Detrended correspondence analysis largely removes the beta diversity effect and reduces, but does not eliminate, the influence of species richness.

Introduction

Reciprocal averaging (RA) (Hill, 1973) or correspondence analysis (Hill, 1974) and detrended correspondence analysis (DCA) (Hill, 1979; Hill & Gauch, 1980) are widely used methods of indirect gradient analysis. Early use of RA revealed two problems. (1) The arch effect whereby the second and higher axes can be polynomial functions of the first. (2) Systematic distortion of inter-stand and inter-species distances such that the separations of equally-different stands are large in the centre of an axis and small at the extremes. These problems are corrected in DCA by segmenting each axis and detrending stand scores to remove any arch, and rescaling species scores on each axis, followed by stand scores, to remove any systematic distortion.

I show here that gradients in the number of species per stand (species richness or alpha diversity) creates a further form of systematic distortion in RA axes, and that DCA does not fully correct for this distortion. I use artificial vegetation data sets based only on presence/absence data, simulating various beta diversity and species richness gradients on a single stand gradient (coenocline) and two stand gradients (coenoplane) by analogy with other tests of ordination methods (e.g. Swan, 1970; Austin & Noy-Meir, 1972; Gauch, Whittaker & Wentworth, 1977). The likelihood of species richness distortion in real floristic data is discussed.

Vegetation models and ordination

Three groups of models (A, B, C) are used. The first group (A1–A4, Fig. 1) is designed to study the influence of beta diversity alone upon axis distortion in RA and the ability of DCA to correct that distortion. Alpha diversity (attributes per stand) is constant in each model but A4 is used to construct the second group (Fig. 2), taking the first twenty attributes and replicating them one (B1), two (B2) and three (B3) times. Replication produces beta diversity variation along the stand gradient in B models which therefore do not represent alpha diversity alone. They are better described more loosely as species richness models.

The third group of models (Fig. 3) involves two stand gradients arranged as a 7 × 7 coenoplane. Model C1 involves 25 attributes arranged to have constant species richness (13 attributes per stand). Model C2 replicates attributes 1–6 once and provides a species richness gradient in one direction from 19 attributes (stands 1, 8, 15, 22, 29, 36, 43) to 13 attributes (stands 7, 14, 21, 28, 35, 42, 49). Model C3 replicates attributes 1–6 and 13–18
Fig. 1. Four models of different beta diversity. Horizontal lines represent widths (presence) of attributes (Y) along a stand gradient (X) sampled at 21 regularly-spaced intervals. Alpha diversity is constant in each model and beta diversity decreases from A1 (maximum attribute width five stands) to A4 (maximum attribute width twenty stands).

Fig. 2. Three models of species richness gradients. Horizontal lines represent widths (presence) of attributes (Y) along a stand gradient (X) sampled at 21 regularly spaced intervals. Gradients in species richness steepen in the sequence 40 to 20 attributes per stand (B1), 60 to 20 (B2), 80 to 20 (B3).

once, providing two species richness gradients with extremes of 25 attributes (stand 1) and 13 attributes (stand 49).

All models were ordinated by RA and DCA using the DECORANA computer program (Hill, 1979). RA and DCA first axis coordinates for stands in A- and B-type models were rescaled to the range 0–100 and distortion was examined by plotting the rescaled values against 'correct' scores assuming no distortion.

Fig. 3. Presence distribution of attributes in 49 regularly-spaced coenoplane stands. Model C1 uses only 25 attributes; model C2 uses all C1 attributes plus a single replication of attributes 1–6; model C3 uses all C2 attributes plus a single replication of attributes 13–18.

Distortion patterns

RA coordinates (Fig. 4) characteristically underestimate stand positions between the minimum and middle axis coordinates, and overestimate them between the middle and maximum coordinates. The degree of this distortion increases with increasing beta diversity. DCA removes this distortion by rescaling (results not presented), producing coordinates which are close to 'correct' values. With low beta diversity (model A4) there is no distortion in RA results and both ordinations provide perfect results, allowing model A4 to be used as a foundation for species richness models in which the effects of beta diversity are minimized.

Distortion due to species richness (Fig. 5) is different in character. All stand coordinates are underestimated between axis extremes, especially central stands. The underestimation increases with the steepness of the species richness gradient. Ordination by DCA reduces the degree of distortion but it remains as a curvilinear pattern along the axis.