A METHOD FOR RECIPROCAL SCALING OF SPECIES TOLERANCE AND SAMPLE DIVERSITY[1]

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Abstract. The method and the associated graphical representations proposed in this paper facilitate the interpretation of the correspondence analysis (CA) of a samples/species data table. By using the "reciprocal discrimination" model of CA, this method introduces directly and on the same graph the notions of niche width and within-sample diversity. We propose two Macintosh programs for computing conditional means, variances, and covariances of factor scores for species and samples, and for drawing ellipses and Gaussian curves from these values. Two examples of ecological interest show how resulting graphics help in understanding the results of multivariate analyses.

Key words: biplots; correspondence analysis; diversity; dual scaling; ellipses; Gaussian curves; GraphMu; Macintosh; MacMul; niche width; ordination; statistical graphics.

INTRODUCTION

Reciprocal ordination of species and sampling units, response curves of species, and α (within) or β (between) diversity of samples are three problems very intimately linked. This point was introduced by Gauch (1973): "Concern with such spaces (abstract spaces of ordination) now interrelates two major areas of research: gradient analysis including sample ordinations, and diversity studies including habitat and niche relations," and emphasized in the paper of Gauch et al. (1977): "Analogous to the effects of species width or amplitude are those of sample equitability—relative similarity of adjacent values in the importance value sequence—or its inverse, relative concentration of dominance."

Here we propose a statistical technique, called reciprocal scaling (from "reciprocal averaging" [Hill 1973] and "dual scaling" [Nishisato 1980]), which, after the correspondence analysis (CA) of a data set, takes into account the three following points of view: reciprocal averaging, measure of sample diversity, and measure of species tolerance. It leads to graphical display and provides a new insight for these notions.

SAMPLE ORDINATION AND SPECIES RESPONSE CURVES

Species niche width: sample averaging

According to Noy-Meir and Whittaker (1977), the term ordination has two meanings: (a) "the process of arranging sites (or species) in relation to one or more

environmental (or successional) gradients," and (b) "continuous multivariate techniques which arrange sites (or species) along axes, regardless of the interpretation of axes."

When samples are ordered, "both direct (obverse) and indirect (reverse) gradient analyses, to use Whittaker's (1967) terminology, choose one set of information and search for patterns in it and impose these patterns on the other set" (Dale 1975). We are then concerned by the indicator value of a species (Persson 1981), linked to the position of the species on the gradient, and to its amplitude, or tolerance (niche width, or variance).

A set of papers by ter Braak (1983, 1985, 1986, 1987, 1988) shows how weighted averages play a prominent part in the modelling of species response curves.

Let A be a table having s sampling units (or sites) and t species (or taxa). Let a_{ij}, for $1 \le i \le s$ and $1 \le j \le t$, be the abundance of species j in sampling unit i. Moreover, let

$$a_{i.} = \sum_{j=1}^{t} a_{ij} \qquad \text{(total for sample } i\text{)}$$

$$a_{.j} = \sum_{i=1}^{s} a_{ij} \qquad \text{(total for species } j\text{)}$$

and

$$a_{..} = \sum_{i=1}^{s} \sum_{j=1}^{t} a_{ij} \qquad \text{(matrix total)}$$

be the abundance by sample, by species, and the total abundance. We define also

$$p_{i.} = \frac{a_{i.}}{a_{..}} \qquad \text{(sample } i\text{'s proportion of } a_{..}\text{)}$$

$$p_{.j} = \frac{a_{.j}}{a_{..}} \qquad \text{(species } j\text{'s proportion of } a_{..}),$$

which are the marginal relative frequencies, and

$$p_{j|i} = \frac{a_{ij}}{a_{i.}}$$

$$p_{i|j} = \frac{a_{ij}}{a_{.j}},$$

which are the conditional relative frequencies of species j in sample i, and of sample i for species j, and which verify

$$\sum_{i=1}^{s} p_{i|j} = \sum_{j=1}^{t} p_{j|i} = 1.$$

If samples are ordered on g gradients by the values $L_k(i)$, with $1 \leq i \leq s$ and $1 \leq k \leq g$, then species have the following positions on gradient number k by weighted averaging:

$$C_k^{(L)}(j) = \sum_{i=1}^{s} p_{i|j} L_k(i) \qquad (1)$$

(the taxon's optimum, abundance-weighted mean), and their conditional variances are equal to

$$W_k^{(L)}(j) = \sum_{i=1}^{s} p_{i|j} |L_k(i) - C_k^{(L)}(j)|^2, \qquad (2)$$

which corresponds to the niche width of McNaughton and Wolf (1970), and has been used as the breadth of historical presence of species by Usseglio-Polaterra and Bournaud (1989). It may also be compared to the taxon's tolerance, or the weighted, squared standard deviation (Birks et al. 1990), and to the geometric mean of niche breadth (Sabo and Whittaker 1979).

This is the well-known, simplest ordination of species by samples, which may be used with the three kinds of environmental gradients, as stated by Austin (1980): "indirect environmental gradients where the environmental factors have no direct physiological influence on plant growth, e.g., elevation; direct environmental gradients where the factor has a direct physiological effect on growth but is not an essential resource, e.g., pH; resource gradients, where the factor is an essential resource for plant growth."

Sample diversity: species averaging

Starting from an ordination of species on g gradients by $C_k(j)$, with $1 \leq j \leq t$ and $1 \leq k \leq g$, we obtain an ordination of samples by averaging

$$L_k^{(C)}(i) = \sum_{j=1}^{t} p_{j|i} C_k(j). \qquad (3)$$

If we suppose that

$$\sum_{j=1}^{t} p_{.j} C_k(j) = 0, \qquad (4)$$

then we have

$$\sum_{i=1}^{s} p_{i.} L_k(i) = 0. \qquad (5)$$

The variance of the positions of samples on the gradient summarizes the differences between samples and measures β diversity:

$$B_k^{(C)} = \sum_{i=1}^{s} p_{i.} \left[L_k^{(C)}(i) \right]^2. \qquad (6)$$

The conditional within-sample variance measures α diversity relative to the gradient:

$$W_k^{(C)}(i) = \sum_{j=1}^{t} p_{j|i} \left[C_k(j) - L_k^{(C)}(i) \right]^2. \qquad (7)$$

The total α diversity is then equal to

$$W_k^{(C)} = \sum_{i=1}^{s} p_{i.} W_k^{(C)}(i), \qquad (8)$$

and we have the following "analysis of variance" equation:

$$\sum_{j=1}^{t} p_{.j} C_k^2(j) = W_k^{(C)} + B_k^{(C)}. \qquad (9)$$

These approaches to α and β diversity are implicit in the simulation models of Gauch and Whittaker (1972a, b) and LaFrance (1972), but they do not take into account the total species abundance $(a_{.j})$. Hill and Gauch (1980) define β diversity as the length of an axis, which is directly linked to the variance of the positions of the elements on this axis. When the ordination is defined by correspondence analysis of the table, this variance is equal to the eigenvalue λ_k, which may be compared to the half-change (Gauch 1973) by the empirical relationship (Gauch and Stone 1979)

$$HC = \sqrt{12\lambda/(1-\lambda)}/1.349. \qquad (10)$$

Gauch et al. (1977) have emphasized the duality between species width and sample equitability. It is sound to compute both in the same way, and to expect the same properties from reciprocal ordination methods (Gauch et al. 1977: 166).

Hill and Gauch (1980) invented detrended correspondence analysis because the β diversity is badly represented near both ends of the gradient. This has been thoroughly discussed by Van Der Maarel (1980) and Feoli and Feoli-Chiapella (1980). Wartenberg et al. (1987) has shown how the notion of diversity is important in an ordination technique.

The above-mentioned definitions are illustrated by Fig. 1, which emphasizes the symmetry of the computation of species tolerance (α-type) and niche separation (β-type) for a given sample ordination, and of between-samples (α-type) and within-sample (β-type) diversity. Here, Gaussian curves are only a graphical
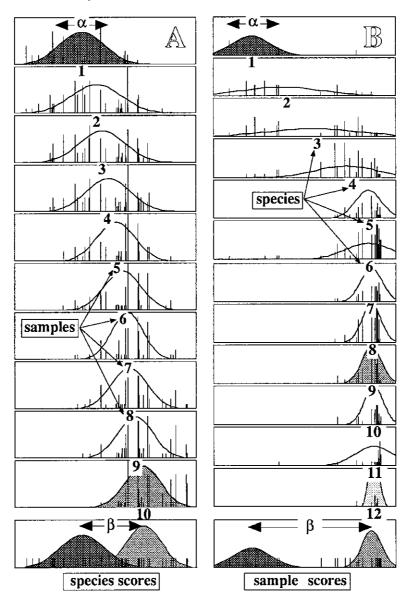
FIG. 1. (A) Ordination by reciprocal averaging (RA) of the data table from Whittaker et al. (1979: 67). Vertical sticks position the 44 mallee species on the first axis, with their heights corresponding to the species' abundances. Gaussian curves represent the mean and variance of the 10 quadrats. Total inertia = 0.866, λ_1 = 0.432 (49.9%). (B) Ordination by RA of a table crossing 28 sites and 12 hunting spider species (Van Der Aart and Smeek-Enserik 1975, cited in ter Braak 1986: 1173). Total inertia = 1.211, λ_1 = 0.590 (48.7%). "α" and "β" symbolize α-type diversity (within species and within sample) and β-type diversity (between species and between samples). The collection of curves has been drawn automatically by GraphMu, and superimposed on the collections of vertical sticks. The figure was finished with MacDraw by adding labels (A, B, Samples, Species, α, β, etc.) and arrows.

way to represent means and variances, and not the Gaussian ordination of Gauch et al. (1974). The last graphic in columns A and B shows the maximum β diversity, whereas α diversity is represented by the width of Gaussian curves in each graphic.

Scaling of species by samples and reciprocal

Let us consider now that gradients are obtained from a multivariate analysis of a hypothetical table A. It is

well known that any inertia analysis of table A with two sets of weights (for rows and columns) leads to two dual analyses and two coordinate systems (Austin and Orloci 1966, Austin and Greig-Smith 1968, Noy-Meir et al. 1975, Laurec et al. 1979). But few methods have optimal properties from the point of view of weighted averaging. Moreover, the standardization of coordinates to 1 or to λ (the eigenvalue), and the habit of "convenience rescaling" (for instance between 0 and

100) create a lot of difficulties. One may obtain a biplot by averaging in one of the following ways:

1) noncentered principal components analysis (PCA) of table $[p_{j|i}]$ (averaging species per sample);

2) noncentered PCA of table $[p_{i|j}]$ (averaging samples per species) (Ezcurra 1987, with use of biplot of Gabriel 1971, see Gordon 1982);

3) centered PCA of table $[p_{j|i}]$ with the biplot distance of ter Braak (1983) (translated averaging species per sample);

4) centered PCA of table $[p_{i|j}]$ with the biplot distance of ter Braak (1983) (translated averaging samples per species);

5) Reciprocal averaging (RA) (Hill 1973, 1974), or correspondence analysis (Benzecri 1973): double dilated averaging species per sample and samples per species. This is why, when a joint display of species and sites is needed, reciprocal averaging takes a fundamental place (Oksanen 1987).

We can have only one averaging with a PCA (Gower 1967), and ter Braak (1983) introduces the relation between ordination and diversity with centered PCA. But we need another PCA to introduce the relation between ordination and niche width. ter Braak (1985) and Hill (1977) then use RA. We may have two averagings with RA, which has been largely explained by Greenacre (Greenacre 1984, Greenacre and Vrba 1984, Greenacre and Hastie 1987). Chessel et al. (1982) use both averagings of CA to introduce a double measure of niche breadth and β diversity (see Oksanen 1987). This is summarized in Fig. 2.

So, the question is, is it possible to keep a double reciprocal averaging and a double reciprocal scaling of niche breadth and α diversity? We propose here a very straightforward answer to this question.

CORRESPONDENCE TABLE

A solution to the problem is known by statisticians but does not seem to have been used until now. It is found in Lebart et al. (1977), translated into English in Lebart et al. (1984). Let c be the total number of nonempty cells in table A. These cells are called "correspondences," from the name of "correspondence analysis." This point of view corresponds to the field ecologist's notebook, such as:

sample i

species j_1	abundance n_{ij_1}
species j_2	abundance n_{ij_2}
$\vdots$	
species $j_{c(i)}$	abundance $n_{ij_{c(i)}}$

sample $i + 1$

$\vdots$

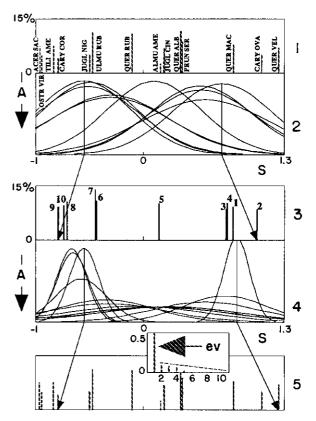There are $c(i)$ correspondences for sample i, and c

FIG. 2. Reciprocal averaging and symmetrical scaling of niche breadth and α diversity. The data table (Gauch 1982: 122) crosses 14 species and 10 composite forest samples. ev = eigenvalues ($\lambda_1 = 0.479$; 61.8% of inertia, and there is only one gradient structure). (1) Ordination of species on the first axis. (2) Conditional means and variances of each sample. (3) Ordination of samples on the first axis. (4) Conditional means and variances of each species. (5) Same as 1. "A" means "Averaging." "S" means "Scaling" (multiplication by $1/\sqrt{\lambda_1}$). What we need is to be able to draw these four figures with the same scale.

correspondences as a whole. It is therefore possible to construct two correspondence tables (X and Y), as explained in Fig. 3. Lebart et al. (1984: 79–80 and 84–88) show how it is possible to perform simultaneously the canonical correlation analysis of X and Y, or the double discriminant analysis of X by Y and of Y by X. The mathematical proofs are in Lebart's book, and we are emphasizing here their practical consequences.

Hill (1977) uses the discriminant analysis of X by Y to maximize the (within-species variance)/(between-species variance) ratio, and Chessel et al. (1982) use the discriminant analysis of X by Y to maximize the within-species variance or the between-species variance under the constraint that the total variance is equal to 1.

To maximize both variances simultaneously, we have to order the correspondence table, and to postulate that the position of a sample is given by the mean of the positions of correspondences that belong to this sam-

Thioulouse, J., and D. Chessel. 1992. A method for reciprocal scaling of species tolerance and sample diversity. Ecology 73:670-680.
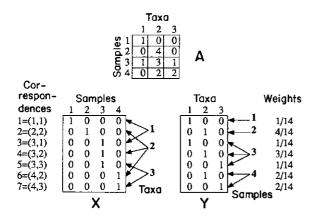http://pbil.univ-lyon1.fr/R/articles/arti071.pdf

FIG. 3. Diagram of the double discriminant analysis of Lebart et al. 1984. Table A is a samples/species table. We can define two tables: the correspondences–samples table (X) and the correspondences–species table (Y). Both tables must be weighted by $a_{ij}/a_{..}$. Each table defines the categories of the discriminant analysis of the other. Reciprocal averaging, RA (or correspondence analysis, CA), performs both discriminant analyses, so the coordinates of the rows of tables X and Y can be computed from the coordinates of rows and columns in the CA of table A with Eq. 11.

ple, and that the position of a species is given by the mean of the positions of correspondences in which this species appears. It is then possible to use the following equations.

The cell (i, j) of table A is given the coordinate $H_k(i, j)$ on the kth axis:

$$H_k(i, j) = \left(\frac{L_k(i) + C_k(j)}{\sqrt{2\lambda_k \mu_k}} \right)$$
$$\mu_k = 1 + \sqrt{\lambda_k}. \tag{11}$$

Here, $L_k(i)$ and $C_k(j)$ are the coordinates of samples and species on axis k of the CA of table A. The total variance for all cells is equal to 1.

The values $H_k(i, j)$ are also the coordinates of the rows in the weighted canonical correlation analysis of tables X and Y (Fig. 3). Using these formulas, we can express the conditional means and variances of sample scores:

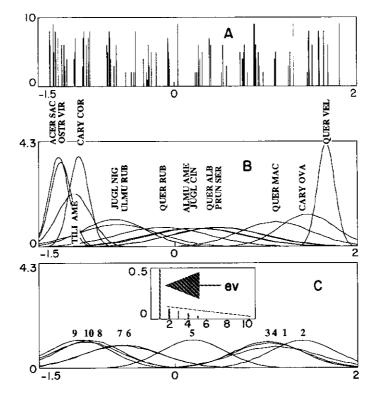$$m_k(i) = \frac{1}{a_i} \sum_{j=1}^{t} a_{ij} H_k(i, j) \tag{12}$$

FIG. 4. Reciprocal scaling of species tolerance and sample diversity, using the same data table as in Fig. 2, and calculating the score of each cell of the table with Eq. 11. The conditional means and variances are computed with Eqs. 14 and 15. Hence, parts A, B, and C share the same scales and may be superimposed (except for the y-axis scale of part A, which is related to the abundance of species). Part A shows the positions of "correspondences" (i.e., the presence of one species in one sample) on the first axis of correspondence analysis. Bar lengths are proportional to species abundance (see Gauch 1982: legend of Table 4.4). Graph B is the "Gaussian curves" representation of conditional means and variances of correspondences for each species, and part C is the same for samples, plus the graph of eigenvalues (identical to the one in Fig. 2).

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$$s_k^2(i) = \frac{1}{a_{i\cdot}} \sum_{j=1}^{t} a_{ij} H_k^2(i, j) - m_k^2(i). \qquad (13)$$

These values can be more easily computed from CA factor scores:

$$m_k(i) = \frac{\sqrt{\mu_k}}{\sqrt{2\lambda_k}} L_k(i) \qquad (14)$$

$$s_k^2(i) = \frac{1}{\sqrt{2\lambda_k\mu_k}} \left[\frac{1}{a_{i\cdot}} \sum_{j=1}^{t} a_{ij} C_k^2(j) - \lambda_k L_k^2(i) \right]. \qquad (15)$$

Symmetrically, one can obtain the conditional means and variances of species scores. A good graphical representation of these conditional means and variances of species and sample scores may be the Gaussian curves having similar means and variances. The collection or superimposition of these Gaussian curves makes easier the study of species and samples relationships (as in Fig. 2).

Fig. 4 shows the results obtained with the data table from Gauch (1982: 122), and should be compared to Fig. 2. The scales of Fig. 4A–C are the same, and so they can be compared directly, which is not true in Fig. 2. The major feature revealed by Fig. 4 is the difference between the shape of species and sample Gaussian curves. While Fig. 4C suggests an ordination of samples (Gaussian curves are all alike and flat), Fig. 4B seems to indicate a classification of species, with particular species at both ends of the pioneer–climax gradient (acute Gaussian curves).

When two factors are concerned, one can define the conditional covariance of sample scores for factors k and l:

$$c_{kl}(i) = \frac{1}{a_{i\cdot}} \sum_{j=1}^{t} a_{ij} H_k(i, j) H_l(i, j) - m_k(i) m_l(i), \qquad (16)$$

which can be computed from CA factor scores as

$$c_{kl}(i) = \frac{1}{2\sqrt{\lambda_k\lambda_l}\sqrt{\mu_k\mu_l}}$$

$$\cdot \left[\frac{1}{a_{i\cdot}} \sum_{j=1}^{t} a_{ij} C_k(j) C_l(j) - \sqrt{\lambda_k\lambda_l} L_k(i) L_l(i) \right]. \qquad (17)$$

By combining these means, variances, and covariances of sample and species scores, it is possible to draw *simultaneous* representations where each sample and each species is represented by an ellipse. The center of an ellipse is given by the mean of each factor score (on axes k and l), the ellipse axes correspond to the variance of scores, and the covariance gives the slope of the ellipse (Fig. 5).

SOFTWARE

The above statistical method is of no use to ecologists without support by an easy-to-use software: ellipses
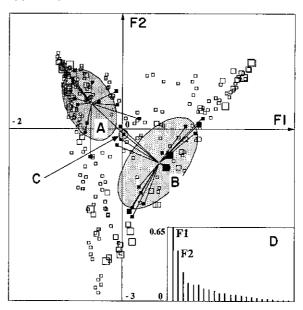

FIG. 5. Correspondence analysis (CA) seen as a double discriminant analysis. The data set (Table 1) crosses 23 forest samples and 43 tree species. Each square represents one cell of the table, i.e., one sample–species "correspondence." The size of each square is proportional to the abundance of the species, and its coordinates are computed from CA factor scores using Eq. 11. Ellipse A represents one of the samples of the table (sample number three, from Neuhoff), and ellipse B represents one of the species (*Fraxinus excelsior*). The bar chart D shows the decrease of successive eigenvalues, and indicates that two or three factors may be of interest. GraphMu can draw automatically the collections of ellipses for species and samples, and the maps with squares. Lines connecting squares to the centers of ellipses may be drawn with the "Digitized maps" option. Labels (A, B, C, D, F1, F2) and arrows have been added with MacDraw. The bar chart of eigenvalues has been drawn separately with GraphMu and pasted over the figure.

and Gaussian curves are difficult to draw by hand, and there is no commercial software to produce such representations. Two programs for the Apple Macintosh micro-computer, named MacMul and GraphMu (Thioulouse 1989, 1990), can achieve this. These programs have an English language interface and are available on diskettes,[2] or directly by downloading through Internet (THIOULOU@FRCISM51.BITNET).

ECOLOGICAL APPLICATIONS

Classification vs. ordination: species and samples

Fig. 5 shows only the ellipses of one species and of one sample of the data set from Hasnaoui (1979). Fig. 6 shows with the same scale the ellipses of the 23 samples (top) and 43 species (bottom) for the same

[2] See ESA Supplementary Publication Service Document No. 9101 for a full description of the software and instructions for obtaining the software. Order from the first author or The Ecological Society of America, 328 East State Street, Ithaca, NY 14850-4318 USA.

Thioulouse, J., and D. Chessel. 1992. A method for reciprocal scaling of species tolerance and sample diversity. Ecology 73:670–680.
http://pbil.univ-lyon1.fr/R/articles/arti071.pdf

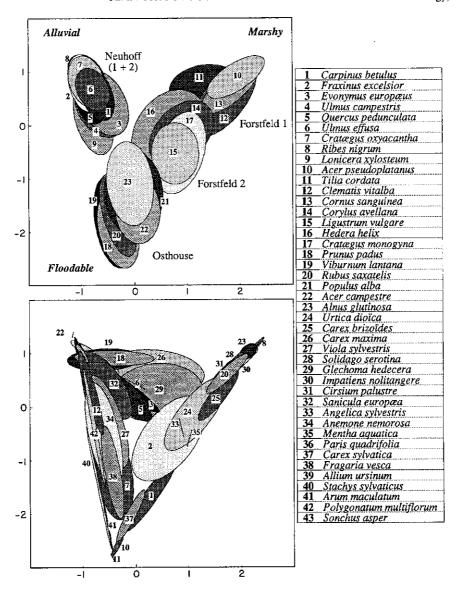| 1	Carpinus betulus
2	Fraxinus excelsior
3	Evonymus europæus
4	Ulmus campestris
5	Quercus pedunculata
6	Ulmus effusa
7	Cratægus oxyacantha
8	Ribes nigrum
9	Lonicera xylosteum
10	Acer pseudoplatanus
11	Tilia cordata
12	Clematis vitalba
13	Cornus sanguinea
14	Corylus avellana
15	Ligustrum vulgare
16	Hedera helix
17	Cratægus monogyna
18	Prunus padus
19	Viburnum lantana
20	Rubus saxatelis
21	Populus alba
22	Acer campestre
23	Alnus glutinosa
24	Urtica dioica
25	Carex brizoides
26	Carex maxima
27	Viola sylvestris
28	Solidago serotina
29	Glechoma hedecera
30	Impatiens nolitangere
31	Cirsium palustre
32	Sanicula europæa
33	Angelica sylvestris
34	Anemone nemorosa
35	Mentha aquatica
36	Paris quadrifolia
37	Carex sylvatica
38	Fragaria vesca
39	Allium ursinum
40	Stachys sylvaticus
41	Arum maculatum
42	Polygonatum multiflorum
43	Sonchus asper

FIG. 6. Reciprocal scaling of tree species tolerance and sample diversity: results obtained for the data set from Hasnaoui 1979 (see legend to Fig. 5). Top: each of the 23 samples from three types of forests (alluvial, marshy, and floodable) is represented by an ellipse. Bottom: ellipses of the 43 tree species (may be superimposed to figure at top). The list of species names is given at right. Differences between the two figures are interpreted in the text (see *Ecological applications: Classification vs. ordination: species and samples*).

data set. The underlying biological problem is to determine whether the list of tree species in regeneration clearings (tree fall gaps or clearing cuttings) is due mainly to the type of surrounding forest, or if allochthonous species characteristic of pioneer stage are present. The 23 samples come from three types of forest in the east of France: alluvial (Neuhoff), marshy (Forstfeld), and floodable (Osthouse) forests. In Neuhoff and Forstfeld forests, two sampling sites were studied, with five (Neuhoff) and four (Forstfeld) samples taken at each site. Only one site is studied in Osthouse, with six samples. The data set is given in Table 1, with the origin of each sample; species names are given in Fig. 6.

In Fig. 5, ellipse B represents the second species (*Fraxinus excelsior*); the center, axes and slope of this ellipse are computed from CA factor scores of the data table using Eqs. 14, 15, and 17. Squares representing the 18 correspondences in which this species is present are filled with black, and lines connect the center of each square with the center of the ellipse. This procedure provides a graphical representation of the within (α-type) diversity, while β-type (between) diversity can be assessed by looking at the collection of ellipses for all species (Fig. 6, bottom). Symmetrically, ellipse A in Fig. 5 represents the third sample of the table (from Neuhoff, alluvial forest). The 17 correspon-

dences for this sample are represented with black squares, one of which (C) is the correspondence with *Fraxinus excelsior.*

The interpretation of this figure is very clear: the composition of samples and their diversity is entirely dictated by the forest from which they come. Ellipses on top are grouped according to the forest from which comes the corresponding sample (the two Forstfeld sites are well separated, whereas those at Neuhoff are not), and for different forests, ellipses hardly overlap. This pattern is characteristic of a classification process, i.e., it is possible to discriminate samples from the abundance of the species they contain, because the between-sample diversity is larger than the within-sample diversity.

Reciprocally, species ellipses do not show clusters. On the contrary, many ellipses overlap, and they are typically stretched between two vertices of the triangle defined by the three types of forests (alluvial, marshy, and floodable). This means that only a few species are specific to each kind of forest, and that most species may be ordinated along the three gradients. Therefore the discrimination between forests is not due to the presence or absence of particular species, but to characteristic combinations of species. The species list of regeneration clearings is characteristic of the forest from which they come rather than characteristic of the pioneer stage.

Species diversity and environmental changes: the ecotone

The second example presented here is from Tatibouet and Broyer (1980) and concerns the study of bird species diversity in rural and urban environments. McDonnell and Pickett (1990) have recently emphasized the interest in such studies. The data set consists of 51 sampling units that are aligned on an urban–rural transect. In each sampling unit, the abundance of bird species is estimated by listening to songs. Fig. 7 shows the results of the reciprocal scaling method, with species (top) and sampling units (bottom) ellipses, and species names.

Here again, there is a difference of structure between the plane of sampling units and that of species: sampling unit ellipses show a discontinuity between urban (on the left) and rural (on the right) units. On the left are units located at the city center, with a gradient to less urbanized sites. The break (vertical bar) separates urban from rural sampling units, which also have larger ellipses because of a higher β diversity.

The species plane (top) shows that the maximum species diversity corresponds to the maximum change in environmental conditions (urban–rural frontier), this being characteristic of an ecotone. Both planes may be superimposed, and it is easy to see that a large number of ellipses are grouped near the vertical bar corresponding to the break. Moreover, these ellipses are bigger,

TABLE 1. Abundance (Braun-Blanquet notation) of trees of each species in each sample in the forest data set of Hasnaoui (1979). The columns correspond to 23 samples taken in three types of forest: Neu1 and Neu2 are sites in Neuhoff (alluvial forest), For1 and For2 are sites in Forstfeld (marshy forest), and Osth is Osthouse (floodable forest). The rows correspond to the 43 tree species listed in Fig. 6.

Neu1	Neu2	For1	For2	Osth
00000	0000	0020	1333	533443
00120	0101	1223	4422	131222
11201	0100	0000	1210	000000
14010	1040	0000	0020	000000
00003	0240	0000	0221	000001
00000	0300	0000	1000	000000
00102	0002	0000	1000	131111
00000	0000	4013	1000	000000
00002	1011	0000	0000	100000
00000	0000	0000	0000	121100
00000	0000	0000	0000	120000
01023	1000	0000	0000	020000
10002	0133	0000	0000	000100
34133	2333	0000	0000	000000
31211	1100	0000	0000	000000
32213	0111	0000	0000	020000
12201	1110	0000	0000	000000
11212	1310	0210	0000	000000
10002	1001	0100	0000	000000
00000	0000	1100	0000	000100
32000	3101	0000	0000	000000
01001	2211	0000	0000	000000
00000	0000	4343	0000	000000
00100	0000	2312	3321	000211
00000	0000	1242	1223	000000
21112	2010	2202	2022	000000
20121	2222	0000	0020	002231
00000	0000	3333	1030	000000
02110	0112	2021	1230	000002
00000	0000	2022	0020	000000
00000	0000	1111	1010	000000
11100	0010	0000	0010	000001
00000	0000	0000	0120	000000
22232	2223	0000	1010	342212
00000	0000	0000	2300	000000
11101	0000	0000	0000	000000
00000	0000	0000	0020	043223
00100	0100	0000	0000	011101
44231	3333	0000	0000	012202
10000	0000	0000	0000	110000
00000	0001	0000	0000	110000
01010	0000	0000	0000	100000
11000	0000	0000	0000	000000

which means that the tolerance of these species is wider.

CONCLUSIONS

Both examples and several other uses (see, for example, Balocco-Castella 1988 for a comparison of the floristic structures in two hydrosystems) show that this method leads to a good representation and understanding of the global organization of floro-faunistic data tables. An accurate evaluation of possible structure models (gradients, breaks, mixings) may therefore be carried out. Moreover, the underlying principle is general enough to be introduced into constrained ordination methods: canonical correspondence analysis of ter Braak (1986), correspondence analysis with respect
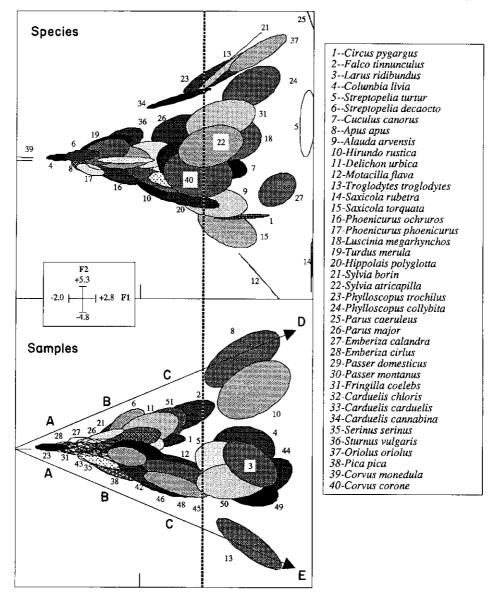
FIG. 7. Reciprocal scaling of bird species tolerance and sample diversity in rural and urban environments. Top: the 43 bird species ellipses (species names are given at right). Bottom: the 51 sampling sites ellipses. Letters indicate the type of environment: A = city center, B = city districts, C = suburbs, D = rural closed, E = rural opened. The scale (valid for both figures) is given by the diagram in the middle of the figure.

to "instrumental variables" of Chessel et al. (1987), partial canonical correspondence analysis of ter Braak (1988), within-class and between-class correspondence analysis of Doledec and Chessel (1990), within-species groups and within-sample groups correspondence analysis of Cazes et al. (1988).

LITERATURE CITED

Austin, M. P. 1980. Searching for a model for use in veg-
etation analysis. Vegetatio 42:11–21.
Austin, M. P., and P. Greig-Smith. 1968. The application
of quantitative methods to vegetation survey. II Some
methodological problems of data from rain forest. Journal
of Ecology 56:827–844.

Austin, M. P., and L. Orloci. 1966. Geometric models in
ecology. II An evaluation of some ordination techniques.
Journal of Ecology 54:217–227.
Balocco-Castella, C. 1988. Les macrophytes aquatiques des
milieux abandonnés par le Haut-Rhône et l'Ain: diagnos-
tique phyto-écologique sur l'évolution et le fonctionnement
de ces écosystèmes. Thesis. University of Lyon, Lyon,
France.
Benzecri, J. P. 1973. L'analyse des données. Tome 2: L'ana-
lyse des correspondances. Dunod, Paris, France.
Birks, H. J. B., J. M. Line, S. Juggins, A. C. Stevenson, and
C. J. F. ter Braak. 1990. Diatoms and pH reconstruction.
Philosophical Transactions of the Royal Society of London
B 327:263–278.
Cazes, P., D. Chessel, and S. Doledec. 1988. L'analyse des

correspondances interne d'un tableau partitionné: son usage en hydrobiologie. Revue de Statistique Appliquée 36:39–54.

Chessel, D., J. D. Lebreton, and R. Prodon. 1982. Mesures symétriques d'amplitude d'habitat et de diversité intra-échantillon dans un tableau espèces-relevés: cas d'un gradient simple. Comptes Rendus de l'Académie des Sciences de Paris D 295:83–88.

Chessel, D., J. D. Lebreton, and N. Yoccoz. 1987. Propriétés de l'analyse canonique des correspondances: une illustration en hydrobiologie. Revue de Statistique Appliquée 35:55–72.

Dale, H. B. 1975. On objectives of methods of ordination. Vegetatio 1:15–32.

Doledec, S., and D. Chessel. 1990. Rythmes saisionniers et composantes stationnelles en milieu aquatique. II. Prise en compte et élimination d'effets dans un tableau faunistique. Acta Oecologica, Oecologia Generalis 10:207–232

Ezcurra, E. 1987. A comparison of reciprocal averaging and non-centered principal component analysis. Vegetatio 71:41–47.

Feoli, E., and L. Feoli-Chiapella. 1980. Evaluation of ordination methods through simulated coenoclines: some comments. Vegetatio 42:35–41.

Gabriel, K. R. 1971. The biplot graphical display of matrices with application to principal component analysis. Biometrika 58:453–467.

Gauch, H. G., Jr. 1973. The relationship between sample similarity and ecological distance. Ecology 54:618–622.

———. 1982. Multivariate analysis is community ecology. Cambridge University Press, Cambridge, England.

Gauch, H. G., Jr., G. B. Chase, and R. H. Whittaker. 1974. Ordination of vegetation samples by Gaussian species distributions. Ecology 55:1382–1390.

Gauch, H. G., Jr., and E. L. Stone. 1979. Vegetation and soil pattern in a mesophytic forest at Ithaca, New York. American Midland Naturalist 102:332–345.

Gauch, H. G., Jr., and R. H. Whittaker. 1972a. Coenocline simulation. Ecology 53:446–451.

Gauch, H. G., Jr., and R. H. Whittaker. 1972b. Comparison of ordination techniques. Ecology 53:868–875.

Gauch, H. G., Jr., R. H. Whittaker, and T. R. Wentworth. 1977. A comparative study of reciprocal averaging and other techniques. Journal of Ecology 65:157–174.

Gordon, A. D. 1982. Numerical methods in Quaternary ecology. V. Simultaneous graphical representation of the levels and taxa in a pollen diagram. Review of Paleobotany and Palynology 37:155–183.

Gower, J. C. 1967. Multivariate analysis and multivariate geometry. Statistician 17:13–28.

Greenacre, M. J. 1984. Theory and application of correspondence analysis. Academic Press, London, England.

Greenacre, M. J., and T. Hastie. 1987. The geometrical interpretation of correspondence analysis. Journal of the American Statistical Association 65:984–997.

Greenacre, M. J., and E. S. Vrba. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. Ecology 67:984–997.

Hasnaoui, B. 1979. Etude structurale des trouées de régénération naturelle en forêts humides de la plaine d'Alsace. Thesis. University of Strasbourg, Strasbourg, France.

Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. Journal of Ecology 61:237–249.

———. 1974. Correspondence analysis: a neglected multivariate method. Journal of the Royal Statistical Society C23:340–354.

———. 1977. Use of simple discriminant functions to classify quantitative phytosociological data. Pages 181–199 in E. Diday, editor. Proceedings of the First International Symposium on Data Analysis and Informatics. Institut Na-

tional de la Recherche en Informatique et Automatique (INRIA), Rocquencourt, France.

Hill, M. O., and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

LaFrance, C. R. 1972. Sampling and ordination characteristics of computer-simulated individualistic communities. Ecology 53:387–397.

Laurec, A., P. Chardy, P. De La Salle, and M. Rickaert. 1979. Use of dual structures in inertia analysis: ecological implications. Pages 127–174 in L. Orloci, C. R. Rao, and W. M. Stiteler, editors. Multivariate methods in ecological works. International Co-operative Publishing House, Fairland, Maryland, USA.

Lebart, L., A. Morineau, and N. Tabard. 1977. Techniques de la description statistique. Méthodes et logiciels pour l'analyse des grands tableaux. Bordas, Paris, France.

Lebart, L., A. Morineau, and K. M. Warwick. 1984. Multivariate descriptive analysis: correspondence and related techniques for large matrices. Wiley, New York, New York, USA.

McDonnell, M. J., and S. T. A. Pickett. 1990. Ecosystem structure and function along urban–rural gradients: an unexploited opportunity for ecology. Ecology 71:1232–1237.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science 167:131–139.

Nishisato, S. 1980. Analysis of categorical data: dual scaling and its applications. University of Toronto Press, Toronto, Canada.

Noy-Meir, I., D. Walker, and W. T. Williams. 1975. Data transformation in ecological ordination. II On the meaning of data standardization. Journal of Ecology 63:779–800.

Noy-Meir, I., and R. H. Whittaker. 1977. Continuous multivariate methods in community analysis: some problems and developments. Vegetatio 33:79–98.

Oksanen, J. 1987. Problems of joint display of species and site scores in correspondence analysis. Vegetatio 72:51–57.

Persson, S. 1981. Ecological indicator values as an aid in the interpretation of ordination diagrams. Journal of Ecology 69:71–84.

Sabo, S. R., and R. H. Whittaker. 1979. Bird niches in a subalpine forest: an indirect ordination. Proceeding of the National Academy of Sciences (USA) 76:1338–1341.

Tatibouet, F., and J. Broyer. 1980. Etude des peuplements d'oiseaux nicheurs de la zone urbaine de Lyon. Pages 106–156 in Rapport final du Contrat 237-01-78-00314, Ministère de l'Environnement (Ecologie Urbaine), France.

ter Braak, C. J. F. 1983. Principal component biplots and alpha and beta diversity. Ecology 64:454–462.

———. 1985. Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. Biometrics 41:859–873.

———. 1986. Canonical correspondence analysis: a new eigenvector method for multivariate direct gradient analysis. Ecology 67:1167–1179.

———. 1987. Unimodal models to relate species to environment. Agricultural Mathematics Group, Wageningen, The Netherlands.

———. 1988. Partial canonical correspondence analysis. Pages 551–558 in H. M. Bock, editor. Classification and related methods of data analysis. North Holland, Amsterdam, The Netherlands.

Thioulouse, J. 1989. Statistical analysis and graphical display of multivariate data on the Macintosh. Computer Applications in the Biosciences 5:287–292.

———. 1990. MacMul and GraphMu: two Macintosh programs for the display and analysis of multivariate data. Computers and Geosciences 16:1235–1240.

Usseglio-Polaterra, P., and M. Bournaud. 1989. Trichoptera and Ephemeroptera as indicators of environmental changes

of the Rhone river at Lyon over the past twenty five years. Regulated Rivers: Research and Management 4:249–262.

Van Der Aart, P. J. M., and N. Smeek-Enserik. 1975. Correlation between distribution of hunting spiders (Lycosidae, Ctenidae) and environmental characteristics in a dune area. Netherlands Journal of Zoology 25:1–45.

Van Der Maarel, E. 1980. On the interpretability of ordination diagrams. Vegetatio 42:43–45.

Wartenberg, D., S. Ferson, and F. J. Rohlf. 1987. Putting things in order: a critique of detrended correspondence analysis. American Naturalist 129:434–448.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Reviews 42:207–264.

Whittaker, R. H., W. A. Niering, and M. D. Crisp. 1979. Structure, pattern and diversity of a mallee community in New South Wales. Vegetatio 39:65–76.