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Matching species traits to environmental variables: a new three-table ordination method

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This paper addresses the question of studying the joint structure of three data tables **R**, **L** and **Q**. In our motivating ecological example, the central table **L** is a sites-by-species table that contains the number of organisms of a set of species that occurs at a set of sites. At the margins of **L** are the sites-by-environment data table **R** and the species-by-trait data table **Q**. For relating the biological traits of organisms to the characteristics of the environment in which they live, we propose a statistical technique called RLQ analysis (R-mode linked to Q-mode), which consists in the general singular value decomposition of the triplet $(\mathbf{R}^t\mathbf{D}_I\mathbf{L}\mathbf{D}_J\mathbf{Q},\mathbf{D}_q,\mathbf{D}_p)$ where $\mathbf{D}_I$, $\mathbf{D}_J$, $\mathbf{D}_q$, $\mathbf{D}_p$ are diagonal weight matrices, which are chosen in relation to the type of data that is being analyzed (quantitative, qualitative, etc.). In the special case where the central table is analysed by correspondence analysis, RLQ maximizes the covariance between linear combinations of columns of **R** and **Q**. An example in bird ecology illustrates the potential of this method for community ecologists.

Keywords: Correspondence analysis, three-table ordination, randomization tests, RLQ analysis, species-trait-environment relationships, statistical graphics

1. Introduction

A current theoretical concept in ecology extensively studied in a special issue of *Freshwater Biology* (Statzner *et al.*, 1994a) focuses on the notion of the habitat template. This concept views the habitat as a template for ecological responses and thereby deals with the linkage between life history and other traits of species and habitat conditions. The underlying hypothesis originating from the work of Southwood (1977, 1988) is that habitat provides the template upon which evolution forges characteristic species traits. Also, through the concepts of assembly and response rules, Keddy (1992) suggested the creation of a general model that could be used to predict the organization of plant (and animal) communities. Keddy (1992) emphasizes that this objective requires at least two data sets for ecological communities: a total species pool, and a table giving the traits of species in this pool. This should enable the specification of 'whether or not certain traits (or a set of them) will permit a species to persist under a defined set of environmental conditions' (Keddy, 1992, p. 159).

As a first step towards such a general model, Rice *et al.* (1983) suggested that bird ecologists were able to accurately predict the species composition of common habitats. They related this ability to

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one important objective of evolutionary ecology, i.e. developing a theoretical framework, which incorporates the prediction of 'habitat associations and other similar natural-history attributes of species' (Rice *et al.*, 1983, p. 263). Likewise, Bayley and Li (1992) depicted expected attributes of fish species and assemblages, in terms of body size and migration, across different combinations of hydrological attributes. Finally, in the context of stream ecology, Townsend and Hildrew (1994) elaborated a set of predictions about species traits expected in particular habitats defined by their environmental variations.

It is evident that these developments in theoretical concepts of ecology are a source for stimulating interactions between ecology and statistics. For example, to investigate the relationships between community organization and environmental changes, community ecologists usually collect a number of species in a number of sampling units and record environmental variables in the same sampling units. Thereby, the study of the relationships between a fauna (or a flora) and its environment leads to two data tables (Lebreton *et al.*, 1991): (1) a species–composition table that contains the abundance or occurrence of a number of species (as columns) in a set of sampling units (as rows), and (2) an environmental table that includes quantitative or categorical measurements (as columns) from the same sampling units (as rows). One of the community ecologist's task is to arrange the sampling units and/or the species along environmental gradients (see for example Whittaker, 1967; Austin, 1968) and to derive patterns that enable this arrangement. As emphasized by Palmer (1993), ordination techniques such as correspondence analysis and its detrending version are increasingly used for gradient analysis. Moreover, a number of statistical methods have been devoted to the simultaneous study of the two above matrices to investigate the species–environment relationships (reviewed in Dolédec and Chessel, 1994; Ter Braak and Verdonschot, 1995). Non-symmetric multivariate techniques such as canonical correspondence analysis (multivariate direct gradient analysis of Ter Braak, 1986) look for an inference of the faunistic variation from the environmental variation. In contrast, weighted averaging partial least squares regression (Ter Braak and Juggins, 1993) aims to reconstruct environmental variables from species assemblages. Symmetric analyses such as canonical correlation analysis (reviewed by Gittins, 1985) and co-inertia analysis (Mercier *et al.*, 1992; Dolédec and Chessel, 1994), examine the covariation between a sample–unit ordination computed from the faunistic table and a sample–unit ordination computed from the environmental table.

The use of the habitat template concept requires more depth than the common study of the species–environment relationships because life history traits of species (rather than the species themselves) are to be related to the environmental conditions (Statzner *et al.*, 1994b). A first attempt in this direction has been made by Grime (1974) who studied three determinants of plant strategies to elaborate a habitat template. Therefore, as Keddy (1992) and Chevenet *et al* (1994) have indicated, knowledge concerning the traits of species must be coded into a third table. Some authors have already undertaken the elaboration of this third table. For example, Haefner (1978) looked for the habitat requirements of foliage-gleaning passerine birds. Wiens (1991) used a set of life-history attributes to compare the Australian and the North American shrub-desert avifauna. Bournaud *et al.* (1992) described the affinity of up to 100 aquatic Coleoptera species using a set of ecological requirements. A dozen papers in Statzner *et al.* (1994a) related the traits of about 600 plant and animal species to the spatio-temporal variability of the habitats in a river and its floodplain, using weighted averaging.

Responding to these demands of ecologists to link the contents of more than two tables, our objective is to describe a new statistical technique, called RLQ analysis (R-mode; Q-mode; and L-link between R and Q), which permits the simultaneous ordination of the three tables of interest (Fig. 1). In the above ecological context, this technique enables the species traits to be incorporated into the analysis of the species–environment relationship and thus the study of the relationships

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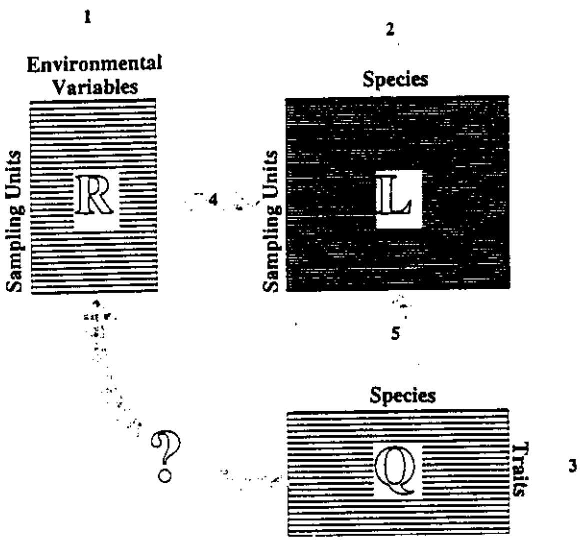

Fig. 1. The various possibilities for analysing three data tables: towards a three-table ordination. Table **R** is the environmental table; table **L** is the species composition table and describes the habitat utilization of species; and table **Q** is the species–trait table. Single arrows (numbered 1–3) indicate the use of a single ordination technique (principal components analysis, correspondence analysis or alternatives). Double arrows (numbered 4 and 5) indicate the simultaneous ordination of two arrays (e.g. canonical correspondence analysis, co-inertia analysis). These five potential multivariate analyses can be summarized by the RLQ analysis. In this case, the aim of RLQ analysis (noted by the question mark) is to relate the species–trait table to the environmental table.

between species traits and the environmental conditions. We include an example of RLQ analysis concerning a bird assemblage to illustrate the potential of this method for community ecologists.

2. Theory

If marginal tables are available, separate ordinations of L, R, and Q constitute a first step. A further step consists in exploring the joint structure of the three tables via RLQ analysis.

2.1 *Separate analyses*

2.1.1 *Analysis of the central table* L

Let L be a table having I rows and J columns derived from a raw data table by any kind of transformation (Noy-Meir, 1973). Let $(\mathbf{L}, \mathbf{D}_J, \mathbf{D}_I)$ be the resulting statistical triplet or duality diagram (Escoufier, 1987). $\mathbf{D}_J$ contains the weight associated with the columns of L and forms the diagonal of a square matrix with J rows and J columns. $\mathbf{D}_I$ contains the weight associated with the rows of L and forms the diagonal of a square matrix with I rows and I columns.

The general singular value decomposition (GSVD; see for example Greenacre, 1984, pp. 344–6) of the statistical triplet $(\mathbf{L}, \mathbf{D}_J, \mathbf{D}_I)$ consists in finding a $\mathbf{D}_J$-normed axis $\mathbf{u}_1$ (first principal axis) and a

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$\mathbf{D}_I$-normed component $\mathbf{v}_1$ (first principal component) so that the inner products

$$(\mathbf{LD}_J\mathbf{u}_1|\mathbf{v}_1)_{\mathbf{D}_I} = \mathbf{u}_1^t\mathbf{D}_J\mathbf{L}^t\mathbf{D}_I\mathbf{v}_1 = \mathbf{v}_1^t\mathbf{D}_I\mathbf{LD}_J\mathbf{u}_1 = (\mathbf{L}^t\mathbf{D}_I\mathbf{v}_1|\mathbf{u}_1)_{\mathbf{D}_J}$$

and the quadratic forms $Q(\mathbf{u}_1)$ and $S(\mathbf{v}_1)$

$$Q(\mathbf{u}_1) = \|\mathbf{LD}_J\mathbf{u}_1\|^2_{\mathbf{D}_I} = \mathbf{u}_1^t\mathbf{D}_J\mathbf{L}^t\mathbf{D}_I\mathbf{LD}_J\mathbf{u}_1$$

$$S(\mathbf{v}_1) = \|\mathbf{L}^t\mathbf{D}_I\mathbf{v}_1\|^2_{\mathbf{D}_J} = \mathbf{v}_1^t\mathbf{D}_I\mathbf{LD}_J\mathbf{L}^t\mathbf{D}_I\mathbf{v}_1$$

are maximized under the constraints that $\|\mathbf{u}_1\|^2_{\mathbf{D}_J} = \mathbf{u}_1^t\mathbf{D}_J\mathbf{u}_1 = \|\mathbf{v}_1\|^2_{\mathbf{D}_I} = \mathbf{v}_1^t\mathbf{D}_I\mathbf{v}_1 = 1$.

The achieved maximum of the above inner product is equal to the first singular value. The solution vectors $\mathbf{u}_1$ and $\mathbf{v}_1$ can also be obtained as the right-hand eigenvectors of $\mathbf{L}^t\mathbf{D}_I\mathbf{LD}_J$ and $\mathbf{LD}_J\mathbf{L}^t\mathbf{D}_I$, respectively, and the achieved maximum of $Q(\mathbf{u}_1)$ and $S(\mathbf{v}_1)$ are equal and given by the first eigenvalue of these matrices (which is the square of the above-mentioned first singular value). The rows of $\mathbf{L}$ can be $\mathbf{D}_J$-projected on $\mathbf{u}_1$ and the columns of $\mathbf{L}$ can be $\mathbf{D}_I$-projected on $\mathbf{v}_1$ resulting in the first scores $\mathbf{x}_1$ and $\mathbf{y}_1$ as follows:

$$\mathbf{x}_1 = \mathbf{LD}_J\mathbf{u}_1 \quad \text{and} \quad \mathbf{y}_1 = \mathbf{L}^t\mathbf{D}_I\mathbf{v}_1$$

If r is the rank of table $\mathbf{L}$, then the second and further principal axes $(\mathbf{u}_2, \mathbf{u}_3, \ldots, \mathbf{u}_r)$ and the second and further principal components $(\mathbf{v}_2, \mathbf{v}_3, \ldots, \mathbf{v}_r)$ maximize the same inner products and norms, but subject to extra constraints of orthogonality, i.e. for all $s \neq t$, $(\mathbf{u}_s|\mathbf{u}_t)_{\mathbf{D}_J} = (\mathbf{v}_s|\mathbf{v}_t)_{\mathbf{D}_I} = 0$.

This general procedure embraces various types of analyses such as correspondence analysis (CA; Greenacre, 1984), multiple correspondence analysis (MCA; Tenenhaus and Young, 1985), fuzzy correspondence analysis (FCA; Chevenet *et al.*, 1994) and the various kinds of principal components analyses (PCA; Escoufier, 1987) (non-centred, row centred, column centred, etc.).

2.1.2 *Analysis of the marginal tables* R *and* Q

Let $\mathbf{R}$, the first marginal table, have I rows and p columns. Let $(\mathbf{R}, \mathbf{D}_p, \mathbf{D}_I)$ be the resulting statistical triplet. $\mathbf{D}_p$ contains the weight associated with the columns of $\mathbf{R}$. $\mathbf{D}_I$ contains the weight associated with the rows of $\mathbf{R}$. Table $\mathbf{R}$ can be associated with $\mathbf{L}$ since the row weights of the two tables are identical ($\mathbf{D}_I$). As indicated above the nature of the triplet $(\mathbf{R}, \mathbf{D}_p, \mathbf{D}_I)$ is determined by the nature of data (quantitative, qualitative, fuzzy coded, etc.) and by the transformation option. Consequently, the GSVD of $(\mathbf{R}, \mathbf{D}_p, \mathbf{D}_I)$ results in various types of multivariate analysis (PCA, CA, MCA, FCA).

Furthermore, let $\mathbf{Q}$, the second marginal table, have J rows and q columns. Let $(\mathbf{Q}, \mathbf{D}_q, \mathbf{D}_J)$ be the resulting statistical triplet. $\mathbf{D}_q$ contains the weight associated with the columns of $\mathbf{Q}$. $\mathbf{D}_J$ contains the weight associated with the rows of $\mathbf{Q}$. Table $\mathbf{Q}$ can be associated with $\mathbf{L}$ since the row weights of $\mathbf{Q}$ agree with the column weights of $\mathbf{L}(\mathbf{D}_J)$. Similarly to the above triplet, the GSVD of $(\mathbf{Q}, \mathbf{D}_q, \mathbf{D}_J)$ results in various types of multivariate analyses (PCA, CA, MCA, FCA).

2.2 *RLQ analysis*

Instead of carrying out three separate ordinations of the triplets $(\mathbf{L}, \mathbf{D}_J, \mathbf{D}_I)$, $(\mathbf{R}, \mathbf{D}_p, \mathbf{D}_I)$ and $(\mathbf{Q}, \mathbf{D}_q, \mathbf{D}_J)$ respectively, RLQ analysis aims to investigate the joint structure of $\mathbf{R}$, $\mathbf{L}$ and $\mathbf{Q}$.

We define RLQ analysis as the GSVD of the statistical triplet $(\mathbf{R}^t\mathbf{D}_I\mathbf{LD}_J\mathbf{Q}, \mathbf{D}_q, \mathbf{D}_p)$, which is equivalent to the GSVD of $(\mathbf{Q}^t\mathbf{D}_J, \mathbf{L}^t\mathbf{D}_I\mathbf{R}, \mathbf{D}_p, \mathbf{D}_q)$.

According to the properties of GSVD (Section 2.1.1), the objective of RLQ analysis is to find

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a $\mathbf{D}_p$-normed axis $\mathbf{b}_1$ in $\mathbb{R}^p$ and a $\mathbf{D}_q$-normed axis $\mathbf{c}_1$ in $\mathbb{R}^q$ so that the inner product

$$(\mathbf{R}^t\mathbf{D}_I\mathbf{L}\mathbf{D}_J\mathbf{Q}\mathbf{D}_q\mathbf{c}_1|\mathbf{b}_1)_{\mathbf{D}_p} = (\mathbf{Q}^t\mathbf{D}_J\mathbf{L}^t\mathbf{D}_I\mathbf{R}\mathbf{D}_p\mathbf{b}_1|\mathbf{c}_1)_{\mathbf{D}_q}$$

is maximized.

To get more insight into the properties of RLQ analysis, let $\mathbf{x}_1 = \mathbf{R}\mathbf{D}_p\mathbf{b}_1$ and let $\bar{\mathbf{x}}_1$ be the corresponding normed vector

$$\bar{\mathbf{x}}_1 = \frac{\mathbf{R}\mathbf{D}_p\mathbf{b}_1}{\|\mathbf{R}\mathbf{D}_p\mathbf{b}_1\|_{\mathbf{D}_I}}$$

Furthermore, let $\mathbf{y}_1 = \mathbf{Q}\mathbf{D}_q\mathbf{c}_1$ and let $\tilde{\mathbf{y}}_1$ be the corresponding normed vector

$$\tilde{\mathbf{y}}_1 = \frac{\mathbf{Q}\mathbf{D}_q\mathbf{c}_1}{\|\mathbf{Q}\mathbf{D}_q\mathbf{c}_1\|_{\mathbf{D}_J}}$$

Then, the inner product maximized by RLQ analysis can be rewritten as

$$(\mathbf{L}\mathbf{D}_J\mathbf{Q}\mathbf{D}_q\mathbf{c}_1|\mathbf{R}\mathbf{D}_p\mathbf{b}_1)_{\mathbf{D}_I} = \mathbf{x}^t\mathbf{D}_I\mathbf{L}\mathbf{D}_J\mathbf{y} = (\mathbf{L}\mathbf{D}_J\tilde{\mathbf{y}}_1|\bar{\mathbf{x}}_1)_{\mathbf{D}_I}\|\mathbf{R}\mathbf{D}_p\mathbf{b}_1\|_{\mathbf{D}_I}\|\mathbf{Q}\mathbf{D}_q\mathbf{c}_1\|_{\mathbf{D}_J} \tag{1}$$

The right-hand side of (1) can be seen to be the product of three criteria: the first one is optimized by the analysis of **L**, the second one (to the square) is optimized by the analysis of **R**, and the third one (to the square) is optimized by the analysis of **Q**.

Consequently, RLQ analysis results in a compromise among the three separate ordinations. According to the separate ordinations used for each of the three data tables (PCA, CA, MCA, etc.), this general model involves a large range of possibilities. In the following section we describe some practical specifications of RLQ analysis.

2.3. *RLQ analysis based on CA of the central table*

In this case, **L** is derived from the raw table $\mathbf{N} = [n_{ij}]$ having I rows (sampling units) and J columns (species). Let n_{ij}, for $1 \leq i \leq I$ and $1 \leq j \leq J$, be the abundance of the jth species in the ith sampling unit. Moreover, let $n_{i.} = \sum_{j=1}^{J} n_{ij}$, $n_{.j} = \sum_{i=1}^{I} n_{ij}$, and $n_{..} = \sum_{i=1}^{I} n_{i.} = \sum_{j=1}^{J} n_{.j}$ be the row totals, the column totals and the grand total, respectively.

Table $\mathbf{P} = [p_{ij}]$ of relative frequencies has I rows and J columns with p_{ij} being the proportion of the cell (i, j) as follows:

$$p_{ij} = n_{ij}/n_{..} \qquad \text{for } 1 \leq i \leq I \quad \text{and} \quad 1 \leq j \leq J$$

The row and column weights are respectively denoted by $p_{i.} = n_{i.}/n_{..}$ and $p_{.j} - n_{.j}/n_{..}$. Let $\mathbf{D}_I = \text{Diag}(p_{1.}, \ldots, p_{i.}, \ldots, p_{I.})$ and $\mathbf{D}_J = \text{Diag}(p_{.1}, \ldots, p_{.j}, \ldots p_{.J})$ be respectively the diagonal matrices of row weights and column weights.

The correspondence analysis of the central table **N** is the GSVD of $(\mathbf{L}, \mathbf{D}_J, \mathbf{D}_I)$ with $\mathbf{L} = \mathbf{D}_I^{-1}\mathbf{P}\mathbf{D}_J^{-1} - \mathbf{1}_{IJ}$. This decomposition involving a first eigenvalue equal to 0 is analogue to the GSVD of $(\mathbf{D}_I^{-1}\mathbf{P}\mathbf{D}_J^{-1}, \mathbf{D}_J, \mathbf{D}_I)$ yielding a first eigenvalue equal to 1 (Escoufier, 1982). This operation (Greenacre, 1984, p. 348–9; Escoufier, 1987) results in a $\mathbf{D}_J$-normed vector $\mathbf{u}_1$ and a $\mathbf{D}_I$-normed vector $\mathbf{v}_1$ maximizing

$$\mathbf{v}_1^t\mathbf{D}_I\mathbf{L}\mathbf{D}_J\mathbf{u}_1 = \mathbf{v}_1^t(\mathbf{P} - \mathbf{D}_I\mathbf{1}_{IJ}\mathbf{D}_J)\mathbf{u}_1 = \text{Cov}_{\mathbf{P}}(\mathbf{u}_1, \mathbf{v}_1) \tag{2}$$

As stated by Williams (1952) and emphasized by Hill (1973), CA results in row and column scores having a maximal correlation. Because these scores are standardized (by orthogonality to $\mathbf{1}_I$ and $\mathbf{1}_J$)

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this correlation is similar to a covariance (Equation 2). As a result, CA allows the interpretation of maximizing a covariance.

This property extends to RLQ analysis for which the maximization criterion (Equation 1) turns into the following covariance maximization problem

$$(\mathbf{LD}_J\tilde{\mathbf{y}}_1|\tilde{\mathbf{x}}_1)_{\mathbf{D}_I}\|\mathbf{RD}_p\mathbf{b}_1\|_{\mathbf{D}_I}\|\mathbf{QD}_q\mathbf{c}_1\|_{\mathbf{D}_J} = \mathrm{Cor}_{\mathbf{P}}(\mathbf{x}_1,\mathbf{y}_1)\sqrt{\mathrm{Var}(\mathbf{x}_1)}\sqrt{\mathrm{Var}(\mathbf{y}_1)}$$

since the two vectors $\mathbf{x}_1$ and $\mathbf{y}_1$ are centred either because the columns of **R** are $\mathbf{D}_I$-centred and the columns of **Q** are $\mathbf{D}_J$-centred or because $\mathbf{x}_1$ and $\mathbf{y}_1$ are $\mathbf{D}_I$-orthogonal to $\mathbf{1}_I$ and $\mathbf{D}_J$-orthogonal to $\mathbf{1}_J$ via the GSVD.

In other words, in the case of a central table processed by CA, RLQ analysis aims to find a vector $\mathbf{b}_1$ (environmental axis in Fig. 2) and a vector $\mathbf{c}_1$ (species–trait axis in Fig. 2), such that the covariance between the site scores $\mathbf{x}_1 = \mathbf{RD}_p\mathbf{b}_1$ and species scores $\mathbf{y}_1 = \mathbf{QD}_q\mathbf{c}_1$ is maximum. Notice the coordinates in $\mathbf{x}_1$ and $\mathbf{y}_1$ are the projection points of the I rows of **R** and the J rows of **Q** on $\mathbf{b}_1$ and $\mathbf{c}_1$, respectively. Because

$$\mathrm{Cov}_{\mathbf{P}}(\mathbf{x}_1,\mathbf{y}_1) = \mathrm{Cor}_{\mathbf{P}}(\mathbf{x}_1,\mathbf{y}_1)\sqrt{\mathrm{Var}(\mathbf{x}_1)}\sqrt{\mathrm{Var}(\mathbf{y}_1)}$$

this results in the best joint combination of the ordination of sampling units by environmental variables (optimization of $\mathrm{Var}(\mathbf{x}_1)$), the ordination of species by species traits (optimization of $\mathrm{Var}(\mathbf{y}_1)$) and simultaneous ordination of species and sampling units (optimization of $\mathrm{Cor}_{\mathbf{P}}(\mathbf{x}_1,\mathbf{y}_1)$).

2.3.1 **R** *and* **Q** *both quantitative*

We focus here on the case where the central table **L** is processed by CA and where the marginal tables **R** and **Q** both incorporate quantitative variables.

Let z_{ik} be a quantitative measurement of the kth environmental variable for the ith sampling unit. The average and the variance of the kth variable are $\bar{z}_k = \sum_{i=1}^{I} p_{i.}z_{ik}$ and $\mathrm{Var}_k = \sum_{i=1}^{I} p_{i.}(z_{ik} - \bar{z}_k)^2$ respectively. Note that $p_{i.}$ weights associated with the rows of **L** are used in these definitions. Let $\mathbf{R} = [r_{ik}] = [(z_{ik} - \bar{z}_k)/\sqrt{\mathrm{Var}_k}]$ be the resulting normalized table. The principal components analysis (PCA) of **R** corresponds to the GSVD of $(\mathbf{R}, \mathbf{Id}_p, \mathbf{D}_I)$ where $\mathbf{Id}_p$ corresponds to the identity matrix with p rows and p columns.

Let y_{jl} be a quantitative measurement of the lth biological variable for the jth species. The average and the variance of the lth variable are $\bar{y}_k = \sum_{j=1}^{J} p_{.j}y_{jl}$ and $\mathrm{Var}_l = \sum_{j=1}^{J} p_{.j}(y_{jl} - \bar{y}_l)^2$ respectively. Note that $p_{.j}$ weights associated with the columns of **L** are used in these definitions. Let $\mathbf{Q} = [q_{jl}] = [(y_{jl} - \bar{y_l})/\sqrt{\mathrm{Var}_l}]$ be the resulting normalized table. PCA of **Q** corresponds to the GSVD of $(\mathbf{Q}, \mathbf{ID}_q, \mathbf{D}_J)$ where $\mathbf{Id}_q$ corresponds to the identity matrix with q rows and q columns.

In that case, RLQ analysis is the GSVD of $(\mathbf{R}^t\mathbf{D}_I\mathbf{LD}_J\mathbf{Q}, \mathbf{Id}_q, \mathbf{Id}_p)$. Note that $\mathbf{R}^t\mathbf{D}_I\mathbf{LD}_J\mathbf{Q} = \mathbf{R}^t\mathbf{PQ}$, which is the covariance matrix between the two sets of variables (environmental and biological). One searches here for a linear combination of variables of **R** and a linear combination of variables of

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Fig. 2. Principle of RLQ analysis in the case of a central table computed by a CA. From table Q, RLQ analysis displays a $\mathbf{D}_q$-normed ordination axis (species–trait axis) in the multidimensional space $\mathbb{R}^q$ resulting in scores for species (letters from a to h, in squares). Simultaneously, a $\mathbf{D}_p$-normed ordination axis (environmental axis) is computed from table R in the multidimensional space $\mathbb{R}^p$ resulting in scores for sampling units (numbered from 1–6, in squares). The resulting sets of scores are used to rearrange the species composition table L so that the covariance between sampling-units (S.U.) scores constrained by the environmental attributes and species scores constrained by their traits is maximal (the size of the circles is proportional to the abundance of species in S.U.)

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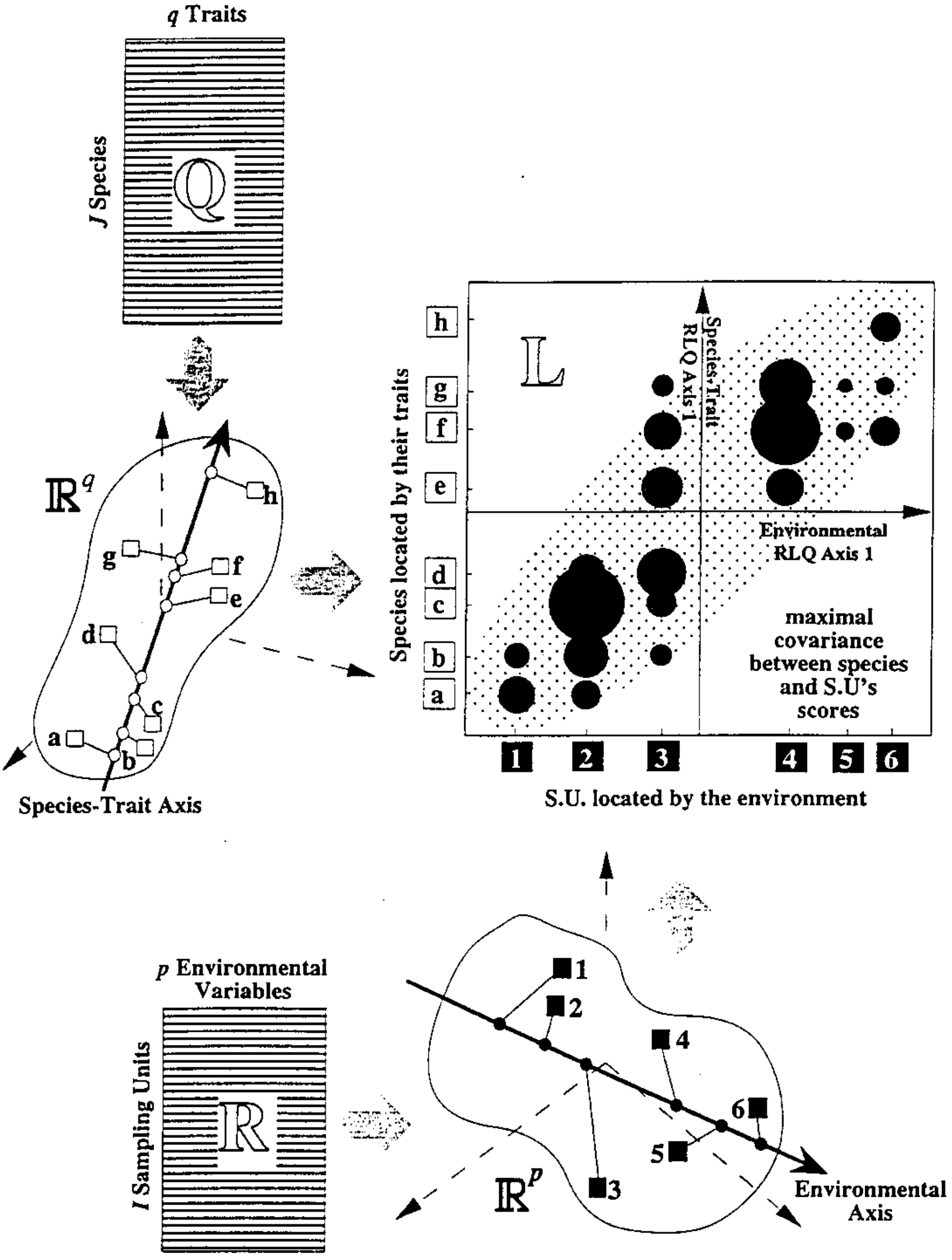

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Q maximizing their covariance. This particular case of RLQ represents an extension of the two separate PCAs, which results in axes that maximize the variances, and co-inertia analysis which results in axes that maximize the usual covariance.

2.3.2 **R** *and* **Q** *both qualitative*

In the subsequent ecological application (Section 3) we propose a special case of RLQ analysis where the central table **L** is again processed by CA and where the marginal tables **R** and **Q** are both composed of nominal variables.

Let $\mathbf{X} = [x_{ik}]$ be a complete disjunctive array (multivariate indicator matrix in Greenacre, 1984, p. 138). For $1 \leq i \leq I$ sites and $1 \leq k \leq p$ categories, $x_{ik} = 1$ if the kth category is present in the ith site and $x_{ik} = 0$ if it is absent. Let ω_k be the column totals of the kth category:

$$\omega_k = \sum_{i=1}^{I} x_{ik} p_{i.} \quad \text{and} \quad \sum_{k=1}^{m} \omega_k = \nu$$

(where $\nu =$ number of qualitative variables of **X**, $m = p$) so that $\mathbf{D}_m = \mathrm{Diag}(\omega_1, \ldots, \omega_k, \ldots, \omega_m) = \mathbf{X}^t\mathbf{D}_I\mathbf{1}_{mI}$.

Let $\mathbf{D}_p = 1/\nu\mathbf{D}_m$ be the diagonal matrix of column weights and let $\mathbf{R} = \mathbf{X}\mathbf{D}_m^{-1} - \mathbf{1}_{Im}$ be the **X**-transformed table in the metric defined by $\mathbf{D}_I$ ($p_{i.}$ weights associated with the rows of **L**). Multiple correspondence analysis of **X** is the GSVD of $(\mathbf{R}, 1/\nu\mathbf{D}_m, \mathbf{D}_I)$ and comes here as an extension of the MCA proposed by Tenenhaus and Young (1985).

Let $\mathbf{Y} = [y_{jk}]$ be a complete disjunctive array. For $1 \leq j \leq J$ species and $1 \leq k \leq t$ categories, $y_{jk} = 1$ if the jth species presents the kth category and $y_{jk} = 0$ if not. Let π_k be the column totals of the kth category:

$$\pi_k = \sum_{j=1}^{J} y_{jk} p_{.j} \quad \text{and} \quad \sum_{k=1}^{t} \pi_k = w$$

(where w is the number of qualitative variables of **Y**, $q = t$), so that $\mathbf{D}_t = \mathrm{Diag}(\pi_1, \ldots, \pi_k, \ldots, \pi_t) = \mathbf{Y}^t\mathbf{D}_J\mathbf{1}_{tJ}$.

Let $\mathbf{D}_q = 1/w\mathbf{D}_t$ be the diagonal matrix of column weights and let $\mathbf{Q} = \mathbf{Y}\mathbf{D}_t^{-1} - \mathbf{1}_{Jt}$ be the **Y**-transformed table in the metric defined by $\mathbf{D}_J$ ($p_{.j}$ weight associated with the columns of **L**). Multiple correspondence analysis of **Y** corresponds to the GSVD of $(\mathbf{Q}, 1/w\mathbf{D}_t, \mathbf{D}_J)$. From the above specification for **R** and **Q** and the general definition of RLQ (Section 2.2) it follows that RLQ analysis amounts here to the GSVD of

$$\left((\mathbf{R}\mathbf{D}_m^{-1} - \mathbf{1}_{Im})^t\mathbf{D}_I\mathbf{L}\mathbf{D}_J(\mathbf{Q}\mathbf{D}_t^{-1} - \mathbf{1}_{Jt}),\ 1/w\mathbf{D}_t,\ 1/\nu\mathbf{D}_m\right)$$

If we consider that

$$\mathbf{D}_I\mathbf{L}\mathbf{D}_J = \mathbf{D}_I(\mathbf{D}_I^{-1}\mathbf{P}\mathbf{D}_J^{-1})\mathbf{D}_J = \mathbf{P} - \mathbf{D}_I\mathbf{1}_{IJ}\mathbf{D}_J = \mathbf{P}_0$$

then

$$(\mathbf{R}\mathbf{D}_m^{-1} - \mathbf{1}_{Im})^t\mathbf{P}_0(\mathbf{Q}\mathbf{D}_t^{-1} - \mathbf{1}_{Jt}) = \mathbf{D}_m^{-1}\mathbf{R}^t\mathbf{P}\mathbf{Q}\mathbf{D}_t^{-1} - \mathbf{1}_{mt}$$

As a result, RLQ analysis amounts here to the correspondence analysis of $\mathbf{R}^t\mathbf{P}\mathbf{Q}$.

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Table 1. Bird species (and their family membership) referred to in this study including scientific and common names

Family name	*No.*	*English name*	*Scientific name*
Accipitidae	1	Montagu's Harrier	*Circus pygargus*
Falconidae	2	Kestrel	*Falco tinnunculus*
Laridae	3	Black Headed Gull	*Larus ridibundus*
Columbidae	4	Rock Dove	*Columbia livia*
	5	Turtle Dove	*Streptopelia turtur*
	6	Collared Dove	*Streptopelia decaocto*
Cuculidae	7	Cuckoo	*Cuculus canorus*
Apodidae	8	Swift	*Apus apus*
Alaudidae	9	Sky Lark	*Alauda arvensis*
Hirundinidae	10	Swallow	*Hirundo rustica*
	11	House Martin	*Delichon urbica*
Motacillidae	12	Wagtail	*Motacilla flava*
Troglodytidae	13	Wren	*Troglodytes troglodytes*
Turdidae	14	Whinchat	*Saxicola rubetra*
	15	Stonechat	*Saxicola torquata*
	16	Black Redstart	*Phoenicurus ochruros*
	17	Redstart	*Phoenicurus phoenicurus*
	18	Nightingale	*Luscinia megarhynchos*
	19	Blackbird	*Turdus merula*
Sylviidae	20	Melodious Warbler	*Hippolais polyglotta*
	21	Garden Warbler	*Sylvia borin*
	22	Blackcap	*Sylvia atricapilla*
	23	Willow Warbler	*Phylloscopus trochilus*
	24	Chiffchaff	*Phylloscopus collybita*
Paridae	25	Blue Tit	*Parus caeruleus*
	26	Great Tit	*Parus major*
Emberizidae	27	Corn Bunting	*Emberiza calandra*
	28	Cirl Bunting	*Emberiza cirlus*
Passeridae	29	House Sparrow	*Passer domesticus*
	30	Tree Sparrow	*Passer montanus*
Fringillidae	31	Chaffinch	*Fringilla coelebs*
	32	Greenfinch	*Carduelis chloris*
	33	Goldfinch	*Carduelis carduelis*
	34	Linnet	*Carduelis cannabina*
	35	Serin	*Serinus serinus*
Sturnidae	36	Starling	*Sturnus vulgaris*
Oriolidae	37	Golden Oriole	*Oriolus oriolus*
Corvidae	38	Magpie	*Pica pica*
	39	Jackdaw	*Corvus monedula*
	40	Carrion crow	*Corvus corone*

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3. Ecological application

As indicated by Lebreton and Yoccoz (1987), basic bird count data incorporate a species-by-sample table with qualitative or quantitative variables associated to the species and the sampling units. Consequently, to illustrate the technique of the RLQ procedure, we selected an example from the work of Tatibouet (1981) on bird assemblages. Data are presented in the Appendix. The aim of the author was to describe the simultaneous changes in avifauna and environmental attributes along an urban–rural gradient.

3.1. *Data sets*

A total of 51 sites were surveyed along a transect depicting an urban–rural gradient. At these sites, 40 bird species were recorded (Table 1) using a method derived from the IPA (point indices of abundance) method (Blondel *et al.*, 1981). It consisted in listening to bird songs at each locality for a period of 15 minutes. In each site, 11 habitat attributes (Table 2) describing the degree of

Table 2. Environmental variables and categories (and the letters used as labels in the figures) used in the analyses

No.	*Environmental variable*	*Code*	*Modality*
1	Farms or villages	p	Presence
		a	Absence
2	Small buldings	p	Presence
		a	Absence
3	High buildings	p	Presence
		a	Absence
4	Industry	p	Presence
		a	Absence
5	Fields	p	Presence
		a	Absence
6	Grassland	p	Presence
		a	Absence
7	Scrubby areas	p	Presence
		a	Absence
8	Deciduous woods	p	Presence
		a	Absence
9	Coniferous woods	p	Presence
		a	Absence
10	Noisy area	p	Presence
		a	Absence
11	Vegetation cover	a	100%
		b	[97–100%]
		c	[90–97%]
		d	[75–90%]
		e	[50–75%]
		f	[25–50%]
		g	[10–25%]
		h	[0–10%]

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Table 3. Species traits and categories (and the letters used as labels in the figures) of the 40 bird species used in the analyses

No.	*Species trait*	*Code*	*Modality*
1	Feeding habit	a	Insectivore
		b	Granivore
		c	Omnivore
2	Feeding stratum	a	Ground
		b	Aerial
		c	Scrub and foliage
3	Breeding stratum	a	Ground
		b	Building
		c	Scrub
		d	Foliage
4	Migratory strategy	a	Resident
		b	Migrant

urbanization (presence of villages, buildings, human activities such as roadworks, factories) and the architecture of the landscape (vegetation cover) were recorded. These habitat attributes were coded using categories (or categories), i.e. one category for each habitat characteristic was assigned to each site. Moreover, four species traits associated with the feeding and breeding attributes of the 40 species were also coded using categories, i.e. one category for each trait was assigned to each species (Table 3).

3.2. *Separate analyses*

The study of the species composition table (**L**) was made by Thioulouse and Chessel (1992) using a correspondence analysis and we will present here the separate analyses of habitat attributes and species traits.

3.2.1 *Structure of the habitat: analysis of* **R**

To describe the habitat structure only, we performed a statistical ordination of the sites. The initial 51 sites × 28 categories ($\nu = 11$ qualitative variables) habitat table was therefore investigated by multiple correspondence analysis based on the GSVD of ($\mathbf{R}, 1/\nu\mathbf{D}_m, \mathbf{D}_I$) as specified in Section 2.3.2.

The first two eigenvalues were $\lambda_1 = 0.272$ and $\lambda_1 = 0.213$ with 17.6% and 13.8% of the variance respectively (Fig. 3A). The first axis (denoted by F1 in Fig. 3B) opposes urban and rural areas. According to the highest correlation ratios, sites in the urban area characterized by the absence of farms or villages, the presence of buildings, a high level of noise and a low vegetation cover (<50%) are positioned on the negative side of the first axis. In contrast, sites in the rural area are positioned on the positive side of the first axis. The second axis (denoted by F2 in Fig. 3B) demonstrates the redundancy among the variables describing human influences (e.g. roadworks, factories and gravel pits) and the vegetation cover, especially the category that represents a vegetation cover <10% (denoted by h in Fig. 3B).

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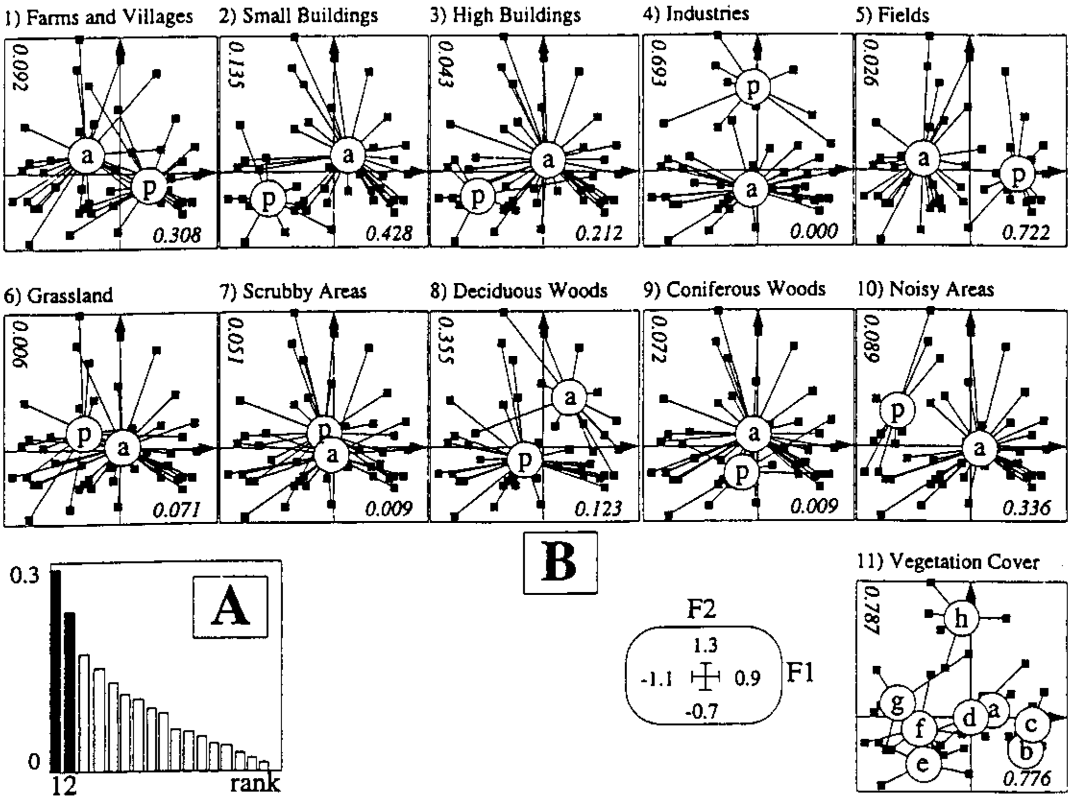

Fig. 3. Ordination of environmental variables by multiple correspondence analysis: A, histogram of eigenvalues; B, distribution of categories (the letters in circles; p: presence; a: absence) on the first factorial plane (see Table 2 for full labels of variables and categories). The scale box indicates the limits for the first and second axes (denoted by F1 and F2 respectively). Correlation ratios for each environmental variable are indicated in italics for the two selected axes. Small squares represent sites. Each category is positioned at the weighted average factorial scores of sites representing that category.

3.2.2 *Relationships among species traits: analysis of* Q

The initial 40 species × 12 categories ($w = 4$ qualitative variables) of species traits was also investigated by multiple correspondence analysis based on the GSVD of $(\mathbf{Q}, 1/w\mathbf{D}_t, \mathbf{D}_J)$ as specified in Section 2.3.2.

Only the first two eigenvalues were selected ($\lambda_1 = 0.651$ and $\lambda_1 = 0.399$ with 32.5% and 20% of the variance respectively; see Fig. 4A). A two-axes representation enables the visualization of how categories are discriminated within traits (Fig. 4B). On the basis of this elementary set of traits, one can see a strong association between insectivore and migratory species (the categories a and b occupy an almost identical position). On the negative side of the first axis, omnivore and granivore species are associated with resident species. On the second axis, scrub and foliage (category c of 'feeding stratum') and scrub (category c of 'breeding stratum') are associated and separated from the other categories.

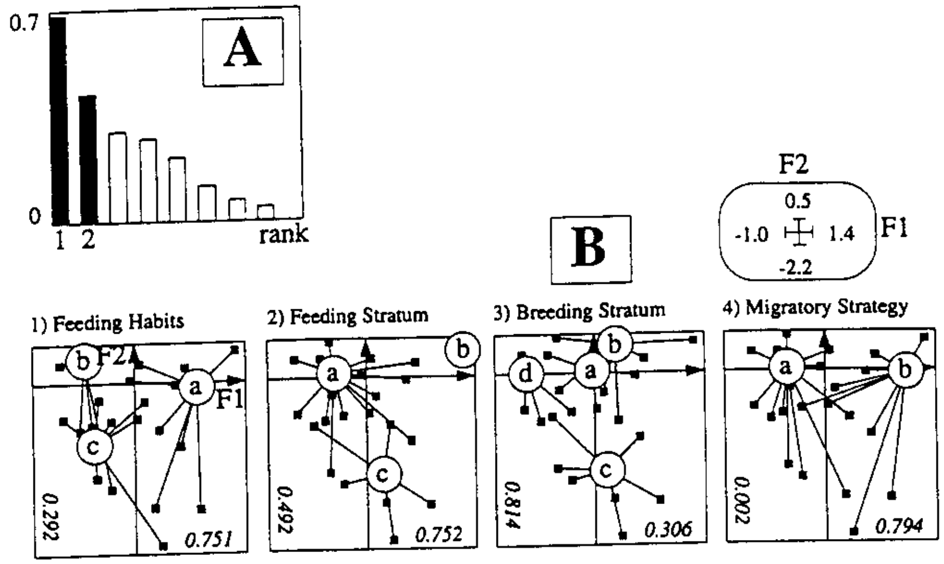

Fig. 4. Ordination of species traits by multiple correspondence analysis: A, histogram of eigenvalues; B, distribution of categories (the letters in circles) on the first factorial plane (see Table 3 for full labels of species traits and trait categories). The scale box indicates the limits for the first and second axes (denoted by F1 and F2 respectively). Correlation ratios for each species trait are indicated in italics for the two selected axes. Small squares represent species. Each category is positioned at the weighted average factorial scores of species representing that category.

3.3. *Relationships between species traits and habitat structure*

3.3.1 *Test of significance*

The statistical significance of the relationship between **R** and **Q** may be evaluated by a random permutation test. The works of Kazi-Aoual *et al.* (1995) and Fraile *et al.* (1993) suggest that total inertia is a coherent index for multivariate inference that tests the independence between two data tables. As a result, we use a permutation test that focuses on $z = \mathrm{Tr}(\mathbf{Z}^t\mathbf{D}_p\mathbf{Z}\mathbf{D}_q)$ with $\mathbf{Z} = \mathbf{R}^t\mathbf{D}_I\mathbf{L}\mathbf{D}_J\mathbf{Q}$, which represents the total inertia computed via RLQ analysis. This total inertia increases with the intensity of the link between **R** and **Q** through **L**. Under the null hypothesis, the rows of **R** and **Q** can be randomly permuted. The null distribution of z can be generated from the complete set of permutations. In practice we used a Monte Carlo version of the test.

The test demonstrated a significant relationship between the habitat attributes (**R**) and the species traits (**Q**) ($p = 0.018$). This means that 18 permutations out of 1000 yield greater values than the observed total inertia. Consequently, the link between environmental variables and species traits can be further investigated.

3.3.2 *Decomposition of inertia*

The proportion of variance attributed to each of the three tables by RLQ analysis can be compared to the separate analyses and to the two-table ordinations (Table 4). RLQ analysis represents partial inertia analyses of the environmental table (denoted by **R** in Table 4), the species trait table (denoted by **Q** in Table 4) and the species composition table (denoted by **L** in Table 4). In the following, we

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Table 4. Comparison of inertia resulting from (a) the separate analyses (**R**, **L** and **Q** alone), and (b) the co-inertia analyses (**R-L** and **Q-L**: two-table ordinations) and the RLQ analysis (**RLQ**: three-table ordination). The two first axes of the analyses (denoted by F1 and F2) are considered. Inertia, maximal projected variability; Var, variance of the set of factorial scores computed for one axis; Cov, covariance of the two sets of factorial scores projected either onto the first and second co-inertia axes (co-inertia analysis) or onto the first and second RLQ axes (RLQ analysis). These values correspond to the latent roots of the analyses; Cor, correlation between the two sets of factorial scores resulting from the co-inertia analysis or the RLQ analysis

(a)	*Inertia*	*VarF1*	*VarF2*
Separate analyses			
R	1.545	0.272	0.213
L	2.659	0.414	0.272
Q	2.000	0.651	0.399

(b)	*Inertia*	*VarF1*	*VarF2*	*CovF1*	*CovF2*	*CorF1*	*CorF2*
Co-inertia analyses							
R/R-L	0.1578	0.253	0.144	0.281	0.149	0.844	0.801
Q/Q-L	0.3972	0.336	0.405	0.366	0.334	0.878	0.710
RLQ analyses							
R/RLQ	0.0165	0.221	0.155	0.104	0.057	0.383	0.236
Q/RLQ	0.0165	0.335	0.372	0.104	0.057	0.383	0.236

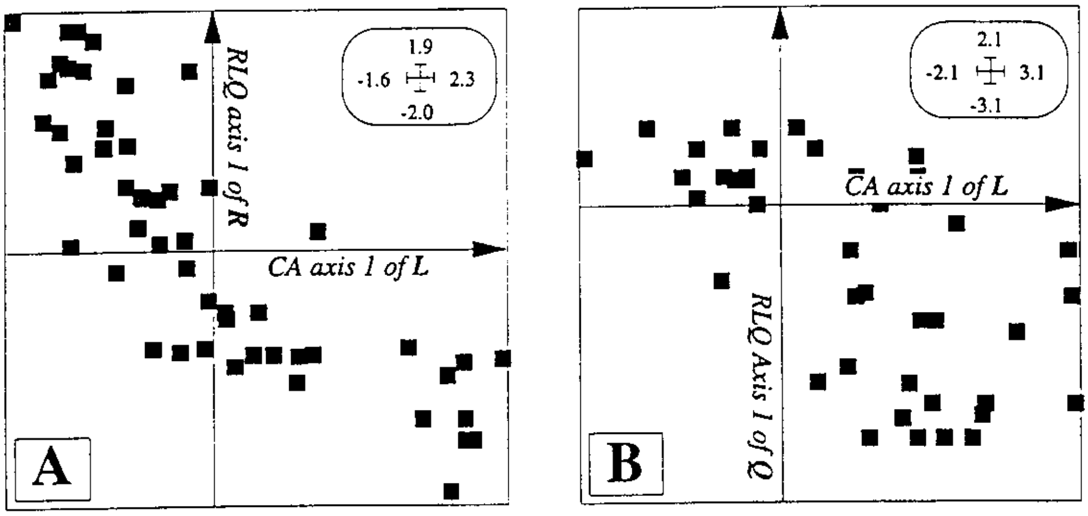

Fig. 5. A, correlation between the standardized scores of sites resulting from the correspondence analysis of **L** and the standardized scores of sites resulting from the RLQ analysis ($R = -0.817$; $n = 51$); B, correlation between the standardized species scores resulting from the correspondence analysis of **L** and the standardized species scores resulting from the RLQ analysis ($R = -0.723$; $n = 40$).

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have only considered the first axis of the RLQ analysis because the proportion of variability extracted by this axis (0.104; see Table 4b) is twice that of the second axis (0.057; see Table 4b). Consequently, we assume that this first axis represents the main part of the co-structure between **R** and **Q**.

If we consider the environmental table **R**, the first axis of the RLQ analysis takes into account 81% (equal to 0.221/0.272; see Table 4a and b) of the potential projected inertia (given by the separate analysis; see Table 4a). By contrast, this axis only accounts for 51% (equal to 0.335/0.651; see Table 4a and b) of the projected inertia of the separate analysis of the species trait table **Q**. As seen before, the optimal correlation between sampling units and species within the species composition table **L** is given by the square root of the first eigenvalue of the correspondence analysis. This value is equal to 0.643 ($\sqrt{0.414}$; see Table 4a) and must be compared to the correlation

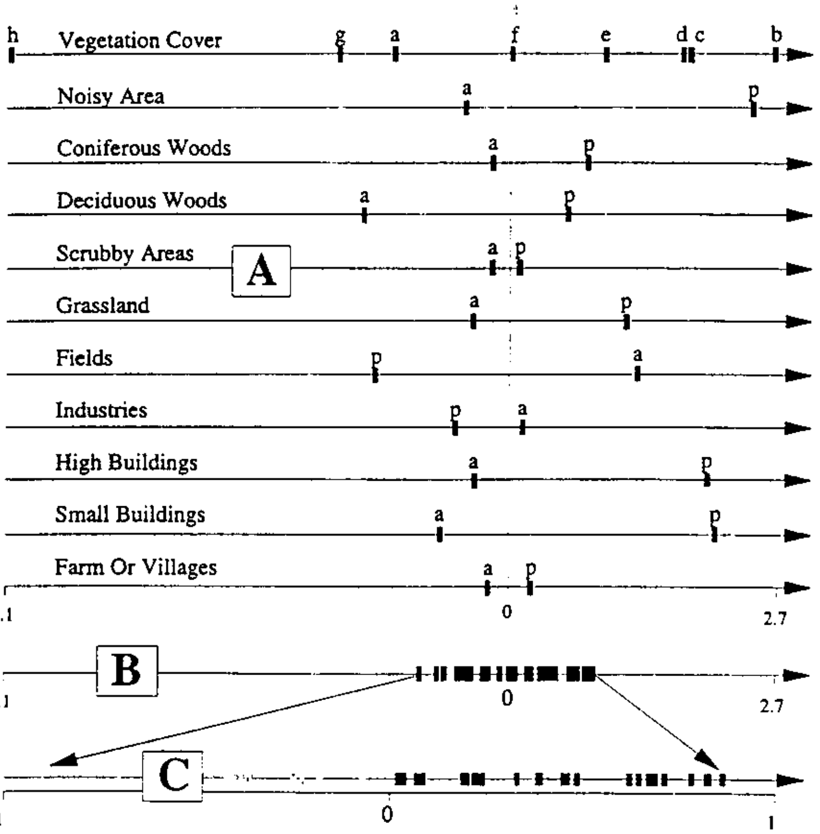

Fig. 6. A, ordination of categories of environmental variables separated by variable along the first RLQ axis. The marks along each arrow represent the positions of categories, which are identified by small letters (see Table 1 for full labels; p: presence; a: absence). B, ordination of sites (represented by marks) along the first RLQ axis. Sites are positioned at the weighted average of categories of environmental variables that they represent. C, Standardization of the first RLQ axis scores of sites on the interval [−1, 1]. This procedure is used for the readability of further graphs. Grey marks indicate the sites most associated to the rural area whereas black marks indicate the sites most associated to the urban area.

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value resulting from the RLQ analysis. The canonical correlation resulting from RLQ analysis shows a decrease (0.383 in comparison to 0.643; see Table 4b). As a result, by maximizing the covariance between the site scores and the species scores, the RLQ analysis partly maximizes the correlation of these scores and partly their variances (standard deviations). The observed decrease results from the species trait records which are too elementary in this example to reconstruct the complete original data, i.e. the species ordination of the separate analysis of L.

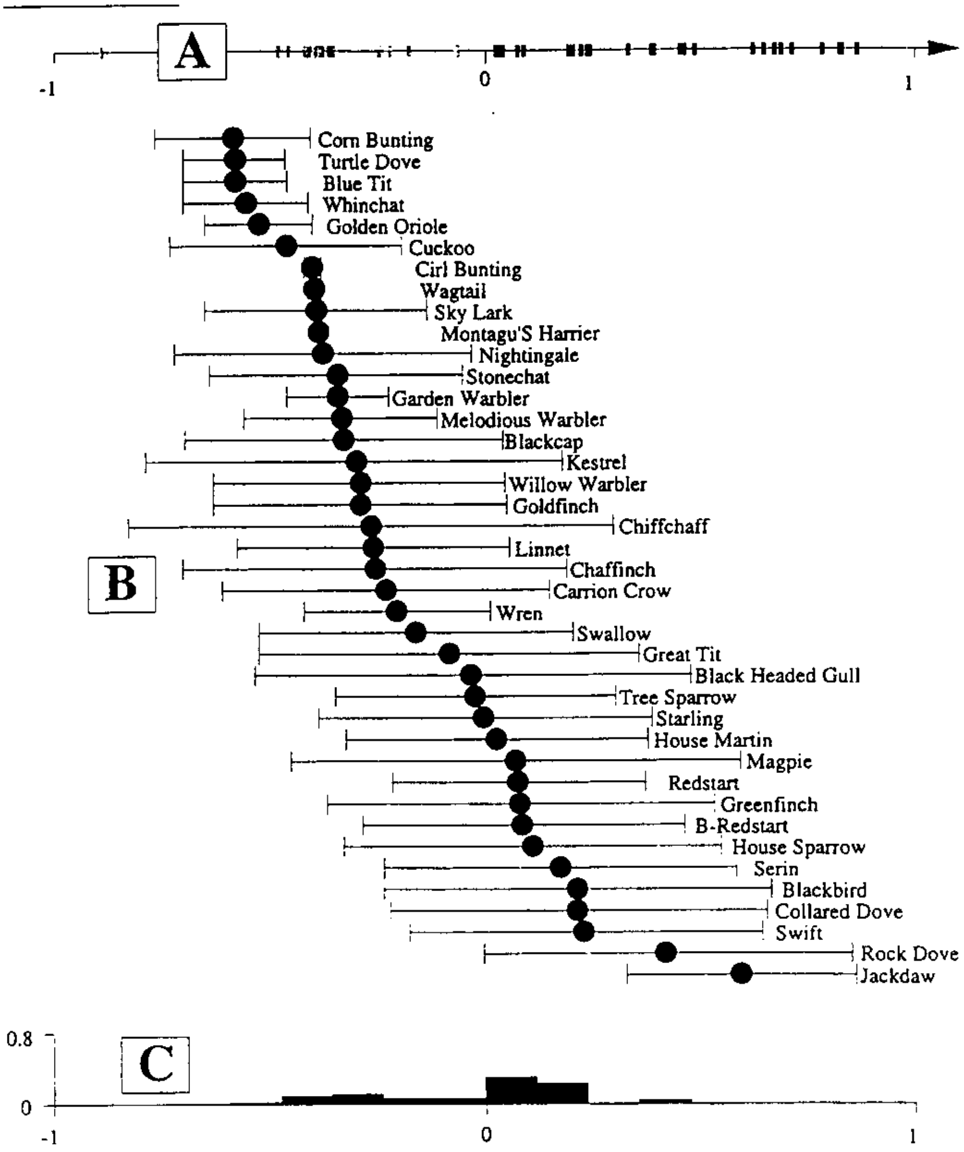

Fig. 7. A, ordination of the sites along the first RLQ axis defining the environmental gradient (equal to Fig. 7C). B, ordination of species along the first RLQ axis. Species are positioned at the weighted average (circles) of sites where they occur. The whisker represents the distribution amplitude of the species (standard deviation). Species are arranged according to their weighted average. C, distribution in 10 classes of the species abundance along the first RLQ axis.

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However, the weighted standardized scores for sites and species respectively, computed by the RLQ analysis for the tables **R** and **Q**, are well correlated with the row and column scores of the correspondence analysis of table **L** (Fig. 5).

3.3.3 *Display of the three-table ordination*

To summarize the RLQ analysis results, we have used a graphical display of the three-table ordination along with the first axis of the RLQ analysis. Three steps can be incorporated.

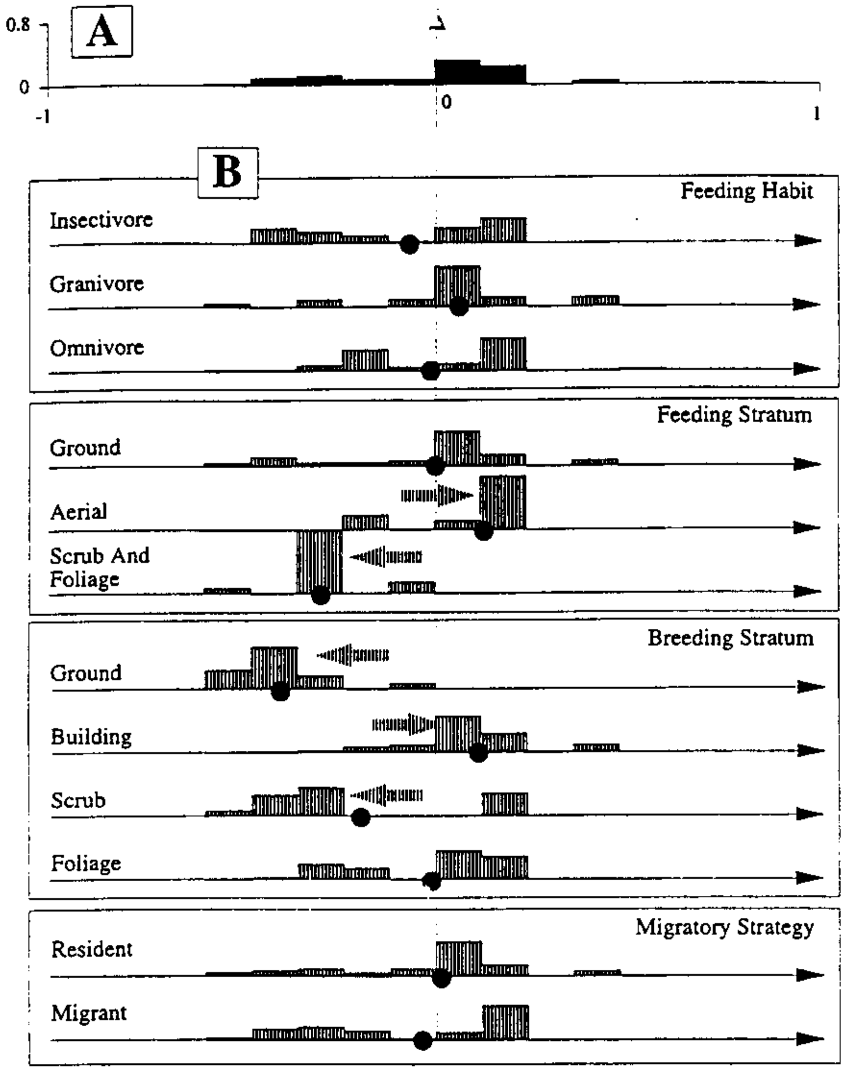

Fig. 8. A, distribution in 10 classes of the species abundance along with the environmental gradient (equal to Fig. 8C). B, presentation of species traits along the first RLQ axis. Each category of species trait has a frequency distribution of its use by a species. The circle below each distribution represents the weighted average of that distribution and defines the position of each category of traits. The RLQ analysis maximizes the between-trait average variance of these positions. The arrows underscore the separation of the corresponding category within a trait.

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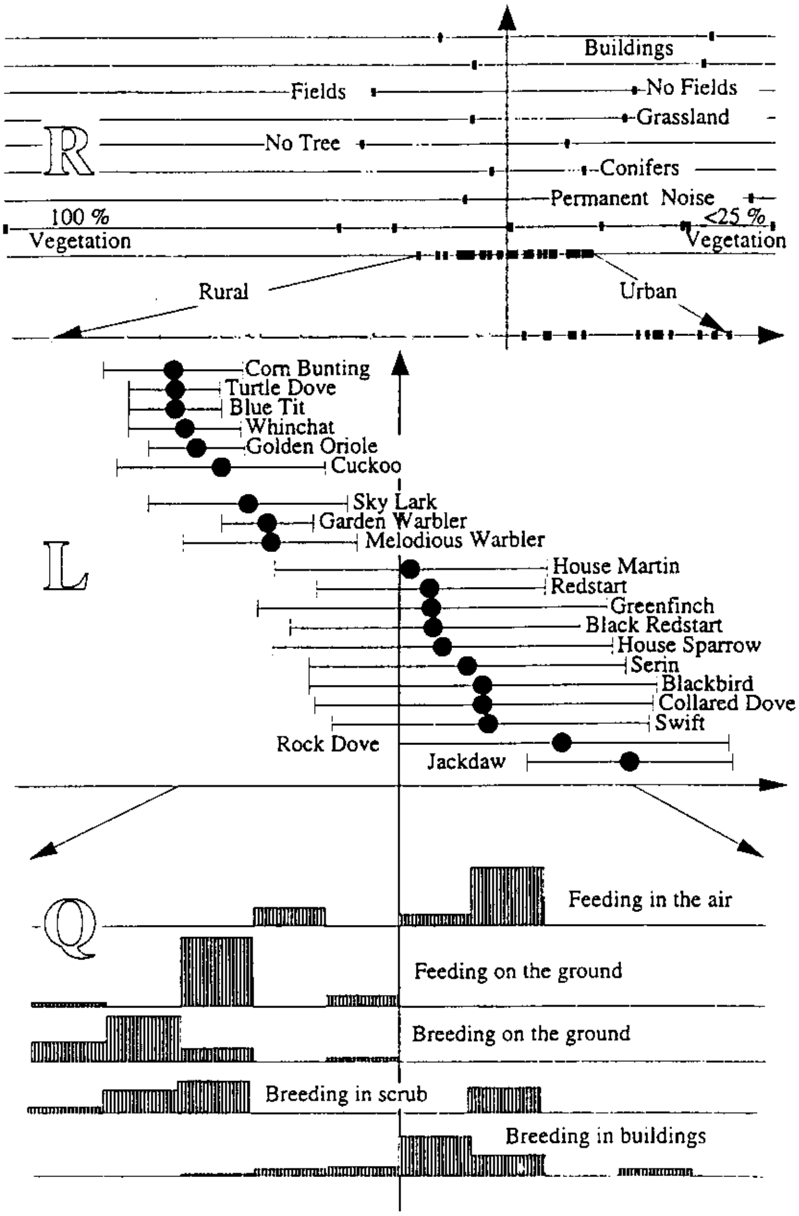

Fig. 9. Succession of averaging operated with the scores resulting from the RLQ analysis (see Figs 6–8 for details). The environmental characteristics of sites depict a gradient of urbanization (ordination of **R**). Main species are distributed along this gradient (ordination of **L**). Main category of traits are distributed along the environmental gradient according to species that present these categories (ordination of **Q**).

1. Location of the categories of environmental variables (**R**) by numerical scores centred for each variable and with an average variance (among variables) equal to 1 (Fig. 6A). Basically, a multiple correspondence analysis of **R** can provide such scores. As seen earlier, RLQ analysis takes into account the major part of these scores (81%). Furthermore, each site

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can be located at the weighted average of categories that are presented by this site (Fig. 6B). The standardization of these scores for readability prevents further computed scores (for species and categories of species traits) tending towards zero (Fig. 6C). Consequently, sites are arranged according to their environmental attributes.

2. Each species has a frequency distribution among sites. In other words, species can be located by their conditional means among the sites where they occur (Fig. 7B). By using the site scores defined in Fig. 6C (and repeated in Fig. 7A), the resulting species scores locate species along the gradient of urbanization. The frequency distribution of the conditional means of all species along the gradient is then derived (Fig. 7C).
3. Using this frequency distribution of conditional means for species (Fig. 8A), we locate each category of the species (Q) along the gradient.at the weighted average of species that present that category (Fig. 8B). For example, the categories of 'feeding habit' and 'migratory strategy' are not well separated, i.e. the weighted average positions (circles in Fig. 8B) are close together within each of these traits. In contrast, the categories of 'feeding stratum' and 'breeding stratum' are better distinguished on the first RLQ axis (arrows in Fig. 8B).

One can then define the variance of the average positions of categories within each trait and the between-category variance for all the traits. A high value of the between-category variance for all the traits underlines the relevance of the first numerical scores selected for environmental variables and indicates a coherent relationship between the four elements of the analysis, i.e. the categories of environmental variables, the sites, the species and the species traits. The optimal values are obtained by the RLQ analysis.

This procedure is symmetrical because an arrangement of species may be derived from the species traits, resulting in an ordination of sites and consequently a location of categories of environmental variables.

A summary of all these manipulations provides the visualization of the simultaneous ordination of the three tables (Fig. 9). As seen above, the RLQ analysis retains the urban–rural gradient from the set of environmental variables (**R**). Species are arranged (**L**) according to this gradient and to a selected set of traits (**Q**). As a result, the RLQ analysis mainly distinguishes among categories associated with feeding layers. Ground feeding is expectedly much more frequent in rural areas whereas birds taking their prey in flight occur in urban areas. Furthermore, birds breed on the ground and on the lower strata in rural areas whereas buildings are frequently used for breeding in urban areas.

4. Discussion

The selected ecological example was intended to enable a demonstration of the coherence of the RLQ methodology using already known biological material. It is of special interest to show whether the procedure automatically finds associations between the three tables. In our experiment, RLQ analysis exhibits an ordination of sites based on a combination of environmental variables that corresponds to an ordination of species resulting from their traits.

It can be noted that the traits which are the most correlated among species (i.e. feeding habit and migratory strategy) are not those traits correlated to the selected environmental attributes (i.e. feeding layer and breeding layer). As a result, RLQ analysis operates as a filter among variables to analyze ecological information organized in three tables. This methodology is implied in the work of Hansen and Urban (1992) by undertaking the relationships between bird life-history traits and the utilization of particular landscape attributes by these birds.

In the example, we have used an 'averaging' practice to interpret the scores resulting from the RLQ analysis (see Figs 6, 7 and 8). This approach, tackled by Whittaker (1967) and detailed by Ter Braak and Barendregt (1986) with the so-called direct gradient analysis justifies the utilization of an analysis belonging to the correspondence analysis family (Palmer, 1993). Classical correspondence analysis (Hill, 1973) and its extension to instrumental variables (Ter Braak, 1986; Chessel *et al.*, 1987; Lebreton *et al.*, 1991) represent multivariate analyses clearly associated with this gradient approach.

Our example was a particular case of RLQ analysis. In Section 2.3.2 this RLQ analysis was shown to be equivalent to a classical correspondence analysis. As seen above, if **R** and **Q** incorporates quantitative variables, then RLQ analysis amounts to the GSVD of $(\mathbf{R}^t\mathbf{L}\mathbf{Q}, \mathbf{Id}_q, \mathbf{Id}_p)$ and effectively analyses the **L**-weighted covariance matrix of the variables of **R** and **Q**. By analogy with the specifications in Section 2.3.1 and 2.3.2, it is straightforward to specify the appropriate analysis when **R** contains quantitative variables and **Q** qualitative variables or vice versa.

These empirical practices fit in the general framework of RLQ analysis, which consists in the GSVD of $(\mathbf{R}^t\mathbf{P}\mathbf{Q}, \mathbf{D}_q, \mathbf{D}_p)$ and can take into account any type of data table as marginal arrays. Takane and Shibayama (1991) investigated the question of three-table ordination in psychometry and proposed an alternative in terms of modelling. In their example, the central table (**L**) represented a multivariate judgment of *p* referees on *n* products. Information associated with the referees (e.g. sex, age, educational level) formed a table **R**, and information on the products were available as a **Q** array. These authors proposed the reconstruction of the central table by

$$\mathbf{L} = \mathbf{R}\mathbf{M}\mathbf{Q}^t + \mathbf{B}\mathbf{Q}^t + \mathbf{R}\mathbf{C} + \mathbf{E}$$

with **M**, **B**, and **C** representing three matrices, for which the coefficients should be estimated, and **E** being the table of residuals. Our approach is in line with the double constrained correspondence analysis (Böckenholt and Böckenholt, 1990) which consists of the GSVD of $(\mathbf{X}^t\mathbf{P}\mathbf{Y}, (\mathbf{Y}^t\mathbf{D}_J\mathbf{Y})^-, (\mathbf{X}^t\mathbf{D}_I\mathbf{X})^-)$. Observational data are often very unbalanced, so that the norms $\mathbf{Y}^t\mathbf{D}_J\mathbf{Y}$ and/or $\mathbf{X}^t\mathbf{D}_I\mathbf{X}$ are near singular, leading to solution vectors that are numerically unstable or that have poor predictive power. Our method therefore differs from those of Takane and Shibayama (1991) and Bockenhölt and Bockenhölt (1990) in that we omit the terms that involve the norm inversion. Our solution is therefore stable, also for multicollinear observational data.

A more general perception of the different kind of multivariate analyses available for community ecologists can now be elaborated. This perception leads to the fact that (1) discriminant analysis and (2) between-groups analysis; (1) PCA with respect to instrumental variables and (2) co-inertia analysis; (1) double constrained correspondence analysis and (2) RLQ analysis are alternatives for one, two and three tables having the same relationships. The preference for the latter analyses (labelled 2 above) is related to their greater numerical stability, especially if a large number of variables is taken into account.

5. Conclusion

Because RLQ analysis allows the investigation of the joint structure among three tables it could be helpful for a wide class of ecological problems. For example, the study of the relation between species traits and habitat attributes through species composition is useful to investigate theoretical concepts in ecology such as those concerned with habitat templates and associated predictions (see for example Townsend and Hildrew, 1994).

The hypothesis of these authors involves the study of the link between species traits and environmental variability or, at least, the link betwen species traits and species utilization of environmental units with a particular spatial and temporal variability. In our example on birds, we have defined the

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habitat conditions using the state of environmental variables, i.e. mean values. However, according to the general definition of RLQ analysis, the environmental table may be composed of the variability of variables defining the spatial and temporal variability of habitats (see for example, Poff and Ward, 1990; Cellot *et al.*, 1994).

Furthermore, various kind of transformation (Noy-Meir, 1973) can be used in **R** (environmental table in our example), L (species-composition table in our example), and Q (species–trait table in our example). As a result, RLQ analysis offers a powerful framework to improve the procedure used in Statzner *et al.* (1994a) to elaborate a model based on the relationships between species traits and spatial and temporal variability of habitats.

6. Software

Software to perform RLQ analysis is incorporated in ADE version 4.0 and later versions (Thioulouse *et al.*, 1995). The ADE-4 package and basic documentation (ADE QuickStart and ADE HyperCard interface) is freely available on the Internet by anonymous FTP to biom3.univ-lyon1.fr. You can also use the following WWW page to download ADE-4:

http://biomserv.univ-lyon1.fr/ADE-4.html

Details for acquiring the full documentation of ADE are available on request to the senior author of this paper.

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Appendix: Data analysed in Section 3

R is the environmental table (51 sites × 11 variables), **L** is the species composition table (51 sites × 40 species), and Q is the species–trait table (4 traits × 40 species). The positions of a table is as processed in the RLQ analysis (for full labels of rows and columns see Tables 1, 2 and 3).

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S. Dolédec teaches biology, ecology and data analysis at the University of Lyon 1. He belongs to an ecological research unit in the Laboratoire d'Ecologie des Eaux Douces et des Grands Fleuves of the same university. His research deals with the elaboration of a framework that incorporates data analysis and current ecological theories to serve ecologically oriented management.

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R

	1	2	3	4	5	6	7	8	9	10	11
1	1	2	2	2	1	2	2	1	2	2	2
2	1	2	2	2	2	1	1	2	2	2	4
3	2	2	2	2	1	2	1	1	2	2	1
4	2	2	2	2	1	2	1	2	2	2	1
5	2	2	2	1	2	2	1	2	2	2	8
6	2	2	2	1	2	1	1	2	2	1	8
7	2	2	2	1	2	2	1	2	2	2	8
8	2	2	2	2	2	2	1	1	2	2	1
9	1	2	2	2	1	2	2	1	2	2	3
10	2	2	2	2	1	2	1	1	2	2	1
11	2	2	2	2	1	2	2	1	2	2	2
12	1	2	2	2	1	2	2	1	2	2	2
13	1	2	2	2	1	2	2	2	2	2	3
14	2	1	2	2	2	2	2	1	1	2	4
15	1	2	2	2	1	2	1	1	2	2	2
16	1	2	1	2	1	2	1	2	2	2	3
17	1	1	2	2	2	1	1	1	1	2	5
18	1	1	2	2	1	2	1	1	2	2	5
19	1	2	2	1	1	2	1	2	2	2	4
20	2	1	2	2	2	2	1	1	2	2	4
21	2	2	2	2	2	2	2	1	1	2	6
22	2	2	2	2	2	1	1	1	1	1	6
23	2	1	1	2	2	2	2	1	2	1	6
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25	2	1	2	1	2	2	1	1	2	1	7
26	2	1	1	2	2	2	1	1	2	2	6
27	2	1	1	2	2	2	2	1	2	2	7
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35	2	2	2	1	2	2	1	1	2	1	8
36	2	1	1	2	2	1	2	1	1	2	5
37	2	1	2	2	2	2	2	2	2	1	6
38	2	2	2	2	2	1	1	1	2	2	8
39	2	2	2	2	1	2	1	1	1	2	4
40	2	1	2	2	2	1	2	1	2	1	5
41	1	2	2	2	2	2	1	1	2	2	5
42	1	2	2	2	1	1	1	2	2	2	3
43	1	2	2	1	2	1	2	1	2	1	8
44	2	2	2	2	1	2	1	1	2	2	2
45	1	2	2	2	1	2	2	2	1	2	2
46	1	2	2	2	1	2	2	1	2	2	2
47	1	2	2	2	1	1	1	1	2	2	3
48	1	2	2	1	1	2	2	2	1	2	3
49	2	2	2	1	1	2	2	2	2	2	8
50	2	2	2	1	1	2	2	2	2	2	8
51	1	2	2	2	1	2	2	1	2	2	3

L

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1							1									1		1	1			1				1			4			1	1		1					1
2							1						1					2	1			1		1		1			4	4	1	1	1							
3		2					1		1					1				2				1				1	1		1		1		1							1
4							1		1						1			2				1		1			2		1		1	1	1					1		
5									2						1	1		1				1				1	1		1	1	1									
6																1													4	1		1	1	2	1	2				
7				4					1	1						1		1	1										4	1		1	1			1				
8					1								1					2	1		1	1	1	1	1	1			1		1				1	1	1			1
9				1		1		1		4	4		1			1		1				1	1						3	2	1	1				2				
10					2				1									1	1			2	1	1	1		1		1	1	2	1	1	1			1			1
11		1				1	1	3		1								1	2			1				1		1	3	1		1	1	1	1	2	1			
12	1						1	2	1		1	1			1			1	1			1					1	1	4			1	1		1					1
13									1	1		1		1	2	1																	1							1
14								3			3					1			1										3			2	1		1					
15				2		1	1	2	1	1							1	1	1	1		1							3	1								1		1
16								3		1								1	1	1		1							3		1	2			1	1		2		1
17				3				3		2								1	1			1		1		1			3	2		1			1			1		1
18						1		3			3						1		2							1			3	2		2			1	1				1
19		1				1		3	1	1						1			1	1		1							3			1			1					
20								3								1			1										2	1		1			1				1	
21			1					3											1				1						1	1	1	3			3					
22				3				3																					3			1						1		
23				3				3											1										2			1							1	
24				1		1		3									1		2										3			1								
25				3		1		3																					3			1			1					1
26				1				3								1			2							1			3		1	1			1					
27			1	3				2								1			2										3			2			1	2				
28				3		1		3											1										3			1			1					
29				3		1		3		1									1										3			1			1					
30		1		2				3											1										2							1				
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32								3			2					1													3			1								
33						1		3											1										3	1		1			1	2				2
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35				1				3	1																				3				1							
36				1		1		4								1			2										4			1			1					
37				1		1		3			2											1							2						1					
38								3		1					1		1		1										3				1							
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44	1				1				1	1								1		1		1					1													2
45		1						2	2											1		1					1		3			1	1		1					2
46	1							3	2	3										1		1							2	1										
47								3	1	3	2					1										1			4	4		1			1					
48			1					3	3	3					1												1		2			1				1				3
49									3									1									1					1								
50			1		2		1		3	2	2				1					2							2			2		1								
51										1	1							1			1								3			1	1			2				1

Q

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
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