Research

Ecography 32: 161–168, 2009
doi: 10.1111/j.1600-0587.2008.05567.x

Subject Editor: Pedro Peres-Neto. Accepted 26 August 2008

Finding essential scales of spatial variation in ecological data: a multivariate approach

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The identification of spatial structures is a key step in understanding the ecological processes structuring the distribution of organisms. Spatial patterns in species distributions result from a combination of several processes occuring at different scales: identifying these scales is thus a crucial issue. Recent studies have proposed a new family of spatial predictors (PCNM: principal coordinates of neighbours matrices; MEMs: Moran's eigenvectors maps) that allow for modelling of spatial variation on different scales. To assess the multi-scale spatial patterns in multivariate data, these variables are often used as predictors in constrained ordination methods. However, the selection of the appropriate spatial predictors is still troublesome, and the identification of the main scales of spatial variation remains an open question. This paper presents a new statistical tool to tackle this issue: the multi-scale pattern analysis (MSPA). This ordination method uses MEMs to decompose ecological variability into several spatial scales and then summarizes this decomposition using graphical representations. A canonical form of MSPA can also be used to assess the spatial scales of the species-environment relationships. MSPA is compared to constrained ordination using simulated data, and illustrated using the famous oribatid mites dataset. The method is implemented in the free software R.

The study of spatial patterns has been and still is a fecund paradigm in ecology (Legendre 1993). Indeed, the identification of spatial structures is a key step toward an improved understanding of the ecological processes structuring the distribution of organisms (Legendre and Fortin 1989). The distribution of species is influenced by several environmental variables, some of which are inherently spatially structured; the resulting spatial patterns observed in species communities are referred to as induced spatial dependence (Legendre 1993, Wagner and Fortin 2005). Such patterns are mainly expected to occur on broad scales (Wiens 1989, Legendre 1993). In contrast, contagious biotic processes like dispersal, mating or competition can give rise to spatial autocorrelation which likely results in intermediate to small-scale spatial structures (Wiens 1989, Legendre 1993, Wagner and Fortin 2005). In fact, any empirically observed spatial pattern can be a combination of several processes occuring on different scales, the identification of which is a crucial issue in ecological studies (Wiens 1989, Menge and Olson 1990, Dungan et al. 2002).

The study of spatial processes led to several methodological innovations, for which the modelling of spatial patterns retained particular attention (Legendre and Fortin 1989, Legendre 1993, Legendre and Legendre 1998). Several approaches have been proposed to introduce space into ecological models in order to identify spatial patterns or on the contrary to remove the effects of spatial structures. Trend surface analysis (Legendre and Fortin 1989, Borcard et al. 1992) has used polynomial expressions of spatial coordinates to create spatial predictors. However, this approach suffered from certain flaws, the strongest being the non-independence of the created variables and difficulties in interpreting high-degree terms of the polynomials. Another limitation was that trend surface analysis could not correctly model fine-scale patterns (Borcard and Legendre 2002).

Borcard and Legendre (2002) proposed the use of principal coordinates of neighbours matrices (PCNM) as spatial predictors. PCNM are uncorrelated variables dissecting the spatial variability into different but complementary scales. The fact that PCNM are uncorrelated variables makes them ideal candidates as predictors in linear models because they are not subject to multicollinearity troubles (Borcard and Legendre 2002, Griffith and Peres-Neto 2006 Dray et al. 2006). Recent theoretical works (Griffith and Peres-Neto 2006, Dray et al. 2006) demonstrated that PCNM are in fact particular cases of eigenvectors of a spatial weighting matrix (Griffith 1996, 2000), called Moran's eigenvectors maps (MEMs) by Dray et al. (2006). In geography, these eigenvectors are used for spatial filtering purposes, i.e. to remove spatial autocorrelation from residuals of a model so that standard statistical tools can be used (Getis and Griffith 2002). In ecology, PCNM and MEMs are used to dissect the spatial patterns of the

ecological variability into separate scales. These variables can be used as spatial predictors in multiple regressions (Brind'Amour et al. 2005). When dealing with multivariate data, PCNM and MEMs can also serve as spatial predictors in constrained ordinations (Borcard et al. 2004) such as redundancy analysis (RDA, Rao 1964) or canonical correspondence analysis (CCA, Ter Braak 1986). It should be noted that for "n" sites, PCNM and MEM approaches respectively produce 2n/3 and $(n-1)$ spatial predictors. Hence, variables must be selected in order to avoid overfitting in statistical models. Due to differences of objectives in geography and ecology, the selection procedures are different. In geography, Tiefelsdorf and Griffith (2007) developed a method to select spatial predictors that minimize the autocorrelation in residuals. However, ecologists favored the classical forward selection that optimizes the fit of the model. Unfortunately, this approach often overestimates the number of retained predictors (Dray et al. 2006): methods based on forward selection thus tend to identify more structuring scales than there actually are. Therefore, the question remains as how to pin down the main scales of spatial variation in ecological data.

In this paper, we propose a new exploratory approach to tackle this issue. This method, called multi-scale pattern analysis (MSPA), describes the correlation structure among a set of ecological variables and all possible scales of variation modelled by MEM, and can be applied to both quantitative and qualitative variables. The MSPA yields graphical representations allowing a visual assessment of the essential scales of spatial variation along with the variables exhibiting the strongest spatial patterns. After describing the method, we compare the results of MSPA and RDA using simulated data. An application of MSPA is also provided using the famous oribatid mites dataset (Borcard et al. 1992, Borcard and Legendre 1994) which raises the question about the scales of variation in species-environment relationships. For this purpose, we show how MSPA can be conducted after a multivariate regression to obtain a canonical MSPA. MSPA is implemented in the free software R (R Development Core Team 2008).

Statistical method

Our approach involves two steps: 1) the decomposition of a set of ecological variables in terms of spatial scales and 2) the analysis of this decomposition. The whole procedure is summarized in Fig. 1, and computation details are provided in Supplementary material, Appendix 1.

Decomposing variables in terms of spatial scales

As advocated in recent papers (Griffith and Peres-Neto 2006, Dray et al. 2006), MEMs can efficiently decompose the spatial variability of a variable into a set of different scales. The spatial distribution of "n" sites is first modelled by a connection network (Legendre and Legendre 1998, pp. 752–756). The doubly centred spatial weighting matrix of this network is then diagonalized as described in Dray et al. (2006) to obtain $(n-1)$ centred, scaled, and uncorrelated MEMs ($\mathbf{u}_j$, $j=1,\ldots, n-1$). The vectors $\mathbf{u}_j$ model spatial patterns at different scales, from the largest scale ($\mathbf{u}_1$) to the finest scale ($\mathbf{u}_{n-1}$). They can be used to decompose the variability of quantitative or qualitative variables in terms of scales.

While a quantitative variable can be used as it is, a qualitative variable needs to be transformed first. Each level of a qualitative variable $\mathbf{x}$ is recoded by a dummy variable, i.e. a vector whose components are 1 where the level is observed and 0 otherwise. For instance, a variable $\mathbf{x}=[a, a, b, b, c]$ will be recoded by three vectors: $\mathbf{x}_a=[1, 1, 0, 0, 0]$, $\mathbf{x}_b=[0, 0, 1, 1, 0]$, and $\mathbf{x}_c=[0, 0, 0, 0, 1]$. This transformation allows levels of a factor to be treated like quantitative variables. Henceforward, we shall consider a centred and scaled variable $\mathbf{y}$ which can correspond to a quantitative variable or to the level of a factor. In some cases, one may be more interested in studying the variability of $\mathbf{y}$ which can be predicted by a set of explanatory variables, rather than in $\mathbf{y}$ itself. For instance, one can seek multi-scale spatial patterns in the environmental component of a species variability. In such a case, we can proceed like in other canonical approaches (Rao 1964, Ter Braak 1986): $\mathbf{y}$ can be submitted to a linear regression onto a set of variables to obtain a predicted vector $\hat{\mathbf{y}}$. The canonical MSPA is then a usual MSPA in which vectors of predictions $\hat{\mathbf{y}}$ replace original observations $\mathbf{y}$ (Supplementary material, Appendix 1). Similarly, one could perform a partial canonical MSPA to study multi-scale spatial patterns in a variable after removing the effects of a set of covariates. For instance, we could investigate the main scales of spatial variation in species varibility that is not explained by a set of environmental variables. This can be achieved using the same approach as in canonical MSPA, but using the residuals of linear regression onto covariates ($\mathbf{y}-\hat{\mathbf{y}}$) rather than the predicted values ($\hat{\mathbf{y}}$) in further computations.

The variability of $\mathbf{y}$ is decomposed through linear regressions using the set of vectors $\mathbf{u}_j$ as explanatory variables. It is worth recalling that as all $\mathbf{u}_j$ are uncorrelated, they explain different and complementary components of variation and are not subject to multicollinearity problems. Moreover, as there are $(n-1)$ regressors, this model explains 100% of the variance of $\mathbf{y}$. Determination coefficients (R^2) are used to measure the strength of association between $\mathbf{y}$ and the different MEMs: they represent the proportion of the variance of $\mathbf{y}$ explained by each MEM (all R^2 summing to one). The $(n-1)$ coefficients of determination compose the scale profile of $\mathbf{y}$. A strong $R^2(\mathbf{y}, \mathbf{u}_j)$ would indicate that $\mathbf{y}$ exhibits spatial patterns at the jth scale, while $(n-1)$ evenly distributed coefficients would denote an absence of spatial pattern.

This operation can be extended to multivariate data. Let $\mathbf{Y}$ be a "n" by "q" matrix of transformed variables, i.e. including centred and scaled quantitative variables and dummy vectors. The "q" by $(n-1)$ matrix of coefficients of determination $\mathbf{S}$ is then obtained by:

$$\mathbf{S}=\frac{1}{n^2}(\mathbf{Y}^T\mathbf{U}*\mathbf{Y}^T\mathbf{U})$$

where "*" denotes the Hadamard product (i.e. element-wise product) and where $\mathbf{Y}^T$ is the transposed matrix of $\mathbf{Y}$. Each row of $\mathbf{S}$ corresponds to a variable (or to a level of a factor) and sums to one, while each column corresponds to a MEM.

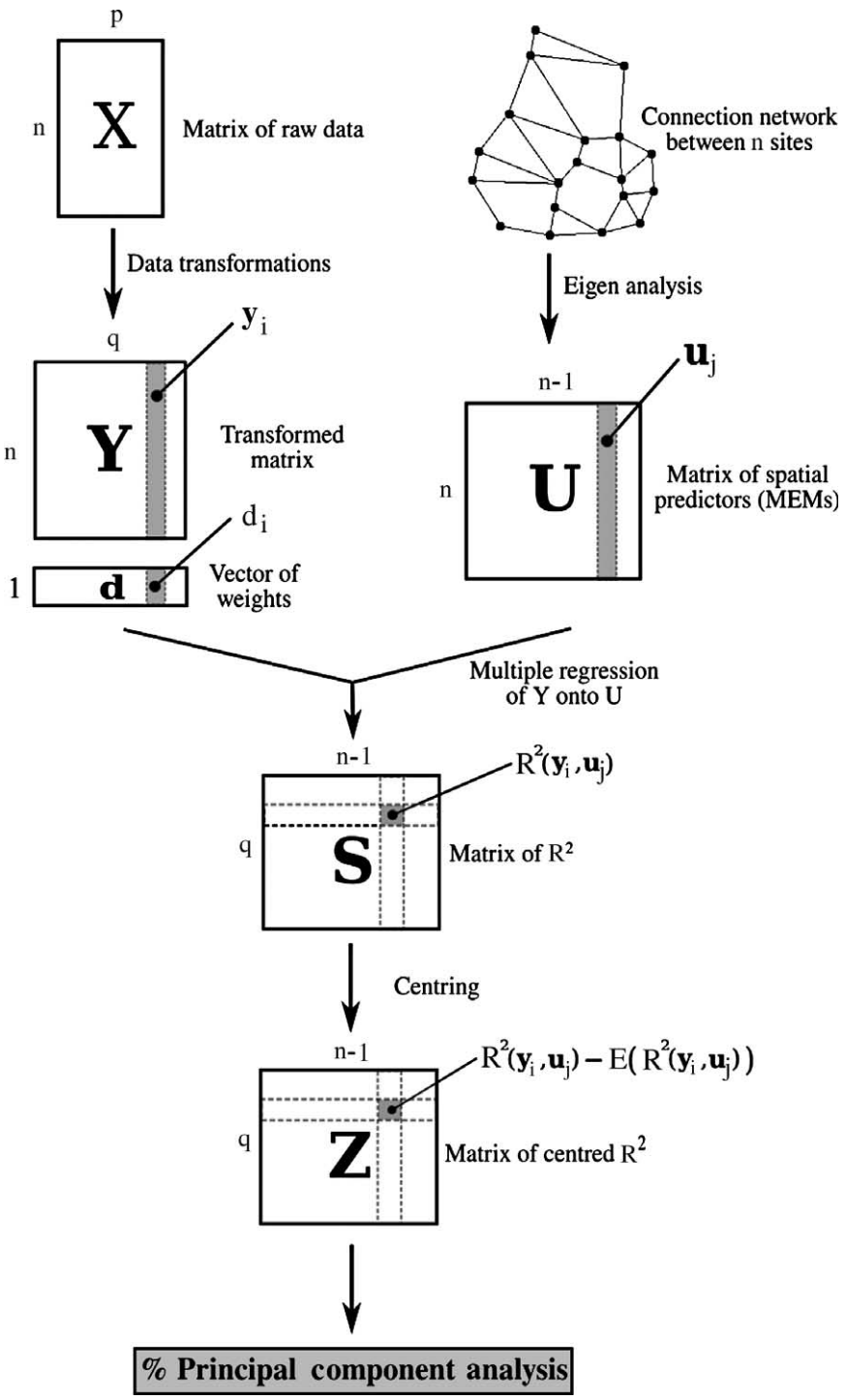

Figure 1. Diagram of the computations of MSPA. Computation details are provided in Supplementary material, Appendix 1. ''MEMs'' stands for ''Moran's eigenvector maps''.

Finding essential scales of spatial variation

The matrix **S** is analysed using an adapted version of PCA. This adaptation involves three points: 1) a particular centring, 2) an adapted row weighting, and 3) a graphical representation exploiting the row-sum constraint of **S** (i.e. all R^2 of a single variable sum to one).

First, columns of **S** must be centred to define a point of reference corresponding to a non-informative state. Usual centring by subtracting the mean of the columns to each value of **S** is irrelevant as it would reduce the information given by the most structuring scales (i.e. MEMs having high R^2 on average). Here, centring should be done by subtracting the value of R^2 that would be observed when a variable is not spatially structured at any scale. In the case of normally-distributed variables, this expected R^2 equals $1/(n-1)$ (Kendall and Stuart 1961, p. 341). In the case of non-normal variables, the expected value of R^2 is determined

using a non-parametric approach proposed by Peres-Neto et al. (2006): the rows of **Y** are randomly permuted, breaking possible spatial structures in the data, and a new matrix of R^2 is computed. This operation is performed a large number of times (1000 by default), giving a distribution of expected R^2 for each value in **S**. The means of these distributions are used as centring values. In both parametric and non-parametric cases, the expected R^2 (denoted $E(R^2(\mathbf{y}_i, \mathbf{u}_j))$ in Fig. 1) are subtracted from the terms of **S**, yielding a matrix **Z**. Each row of **Z** measures the difference between the scale profile of a variable and the expected profile of a variable exhibiting no spatial structure at any scale (i.e. the ''null profile'').

Second, it must be considered that ordinary PCA would give equal weights (1/q) to all rows of **Z**. This would be unfortunate as these rows can correspond to a quantitative variable or to a level of a qualitative variable. In other words, a qualitative variable with four levels would have four times the weight of a quantitative variable in the analysis. Moreover, centred and scaled dummy vectors coding a qualitative variable are, by construction, linearly dependent. This could induce spurious correlations between the corresponding scale profiles. Hence, if a level exhibits spatial structures at particular scales, the other levels of the same variable also convey, in part, this information. To avoid such redundancies to affect the method, we define row weights for **Z** so that all variables (quantitative and qualitative) have the same weight. If there were originally ''p'' variables, the weight given to each one should be 1/p. As in multiple correspondence analysis, dummy vectors are weighted proportionnally to the number of observations of the corresponding level: a modality observed ''k'' times would be given the weight k/(pn), so that all modalities of a single variable sum to 1/p. The diagonal matrix of row weights is denoted **D**. MSPA is a PCA of **Z** in which rows are weighted by **D**, without additional centring or scaling of the columns of **Z**. This PCA is the eigen analysis of $\mathbf{Z}^T\mathbf{DZ}$. Note that because the columns of **Z** are neither centred to mean zero nor scaled to unitary variance, the diagonalized matrix $\mathbf{Z}^T\mathbf{DZ}$ is not a covariance nor a correlation matrix. In fact, $\mathbf{Z}^T\mathbf{DZ}$ simply is the symmetric matrix of scalar products between the columns of **Z** computed with the metric **D**. MSPA yields synthetic scales summarizing the differences between the variables according to their multi-scale spatial patterns. Principal axes provide a new orthonormal basis onto which variables are represented so that their inertia (i.e. the squared Euclidean distances between the scale profiles) is maximized.

Third, it must be emphasized that the analysed matrix **S** contains compositional data, as each scale profile sums to one (Aitchison 2003). de Crespin de Billy et al. (2000) developed a PCA for compositional data (%PCA) which is employed here. The %PCA generates biplots using the principal axes previously defined, but each variable is represented at the centre of the MEM coordinates weighted by its original profile (R^2 coefficients). Technically, this is achieved by projecting the non-centred matrix **S** instead of **Z** onto the principal axes. Note that the squared distances among scale profiles are still optimized by this projection. What %PCA adds to PCA is that a scale profile can be inferred by the position of a variable with respect to the MEMs: the closer a variable is to a given scale, the closer the corresponding R^2 is to one.

Finally, MSPA provides informative biplots representing the most structured variables inside an envelope formed by the most structuring scales. As usual in reduced space ordination methods, the number of retained axes should be chosen according to the decrease of eigenvalues, which represents the amount of structure explained by each axis. MSPA will be implemented in the next release of the ade4 package (Chessel et al. 2004, Dray et al. 2007) of the free software R (R Development Core Team 2008). Functions in R language are provided in Supplementary material, Appendix 2.

Illustrations

The R code allowing the reproduction of these analyses is provided in Supplementary material, Appendix 3.

Simulated data

The construction of this dataset is detailed in Supplementary material, Appendix 4. It contains measurements of 35 variables (V1–V35) for 100 observations distributed on a 10 by 10 regular grid and linked using the rook connection (i.e. neighbours share one edge, Legendre and Legendre 1998, p. 752). The MEMs ranged from u_1 (largest scale) to u_{99} (finest scale). Seven spatially structured variables (V1–V7) were obtained by linear combinations of MEMs with the addition of random noise (Supplementary material, Appendix 4). The other variables (V8–V35) were drawn randomly from a normal distribution. Variables V1–V3 exhibited spatial patterns at the largest scales (u_1, u_2, and u_3), while V4 was structured at an intermediate scale (u_{44}, u_{45}, and u_{46}), and V5–V7 were structured at the finest scales (u_{97}, u_{98}, and u_{99}).

This dataset was analysed using both MSPA and RDA. MSPA clearly showed three axes to be retained (Fig. 2A–B). On the MSPA biplots (Fig. 2A–B), the most structuring scales correspond to the MEMs that are the closest to the circle of radius one. Note that because MEMs are orthogonal, a variable cannot be perfectly correlated to several MEMs at the same time. Hence, it is unlikely that several MEMs will be given a strong loading on the same axis of MSPA. The variables exhibiting the strongest spatial patterns are the furthest from the origin. The first axis identified variables V5–V7 as being structured at the finest scales, while the second axis retrieved large-scale structured variables V1–V3 (Fig. 2A). The third axis (Fig. 2B) found the medium-scale pattern in V4. It is worth noting that MSPA successfully identified all structures of these simulated data, without finding any artifactual patterns.

Prior to the RDA, forward selection was applied to choose the relevant MEMs using the R package ''packfor'' proposed by S. Dray <http://biomserv.univ-lyon1.fr/~dray/software.php>. The best model for a theoretical α level of 5% retained 14 MEMs, including the 9 structuring and 5 non-structuring MEMs (see Supplementary material, Appendix 5 for complete results). This reinforces the criticisms made by Dray et al. (2006) about using forward

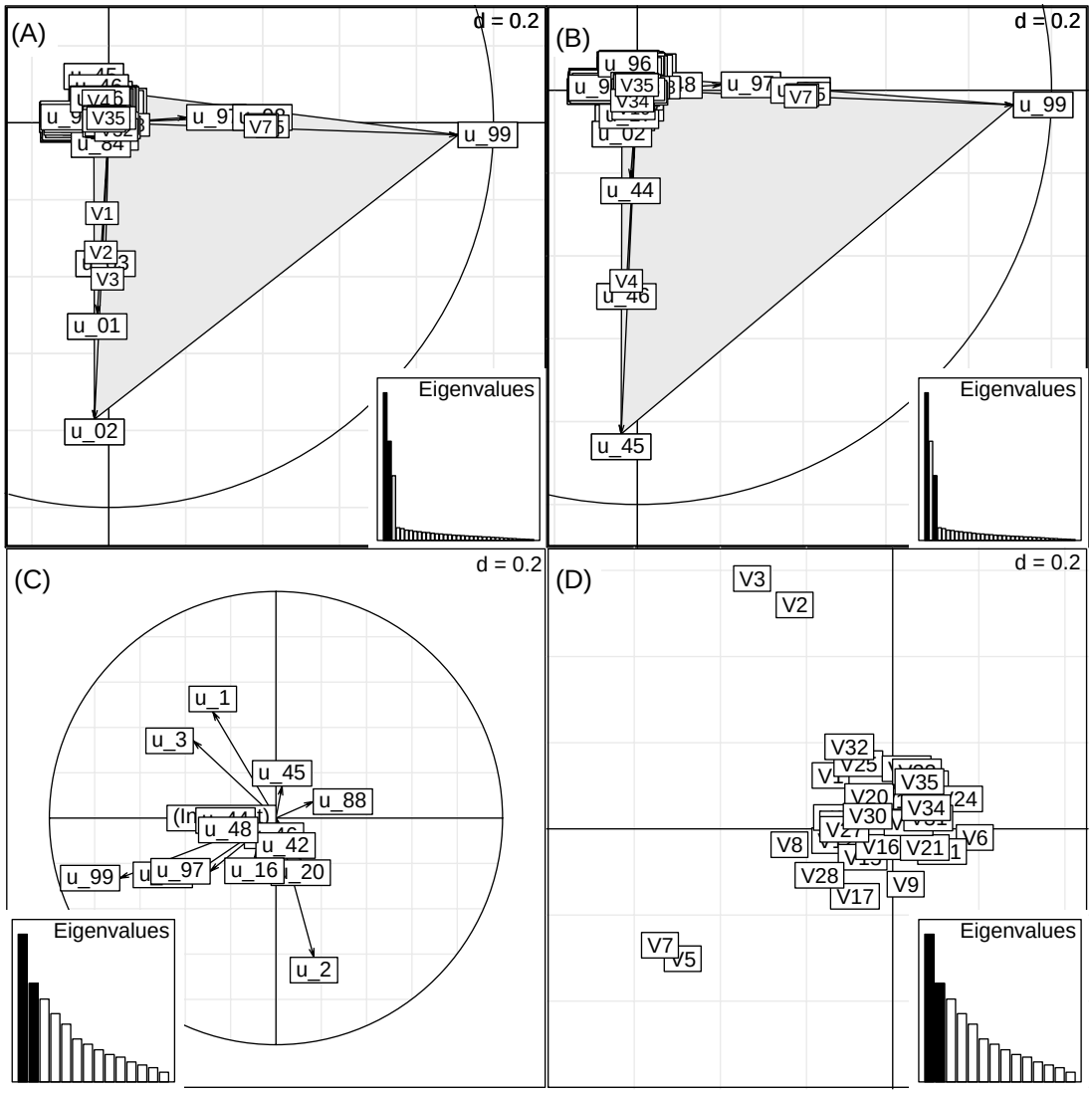

Figure 2. Analyses of simulated data: (A) MSPA biplot, axes 1–2; screeplot indicates displayed eigenvalues in black and retained ones in grey. MEMs are represented by arrows; those being well represented are close to the circle of unity radius; ''d'' indicates the mesh of the grid. (B) MSPA biplot, axes 1–3. (C) Correlation circle of the RDA of simulated data predicted by 14 MEMs selected by forward selection. (D) Variable scores of the RDA of simulated data (14 MEMs retained as predictors).

selection to select relevant MEMs. RDA was performed with simulated data as response variables and the 14 selected MEMs as predictors. Two axes were interpreted although the decrease of eigenvalues suggested only one axis (Fig. 2C–D). The analysis detected large and fine scales but ommited the intermediate one (Fig. 2C). However, the difference between structuring and non-structuring scales was far less obvious than in MSPA (Fig. 2A–C). Moreover, all structured variables were not revealed: only V2, V3, V5, and V7 seemed to contain spatial patterns (Fig. 2D).

Empirical data: oribatid mites

This illustration involves the famous oribatid mites dataset (Borcard et al. 1992, Borcard and Legendre 1994), which is available in the ade4 package as the dataset ''oribatid''. The data contained a table of 5 environmental variables (quantitative and qualitative data) measured on 70 georeferenced sites and a table giving counts of oribatid mites for 35 species at the same sites. Our purpose was 1) to investigate the scales of spatial variation in both tables separately and 2) to study how species multi-scale patterns were linked to those of the environment. We used the Delaunay triangulation (Upton and Fingleton 1985) to model the spatial connectivity among the sites. MEMs ranged for both datasets from u_1 (largest scale) to u_{69} (finest scale). Both species and environmental data were regressed onto spatial coordinates, as it was done in previous studies, to yield comparable results (Borcard et al. 2004).

The eigenvalues of the MSPA of environmental data showed that two axes should be retained (Fig. 3A). The principal axes mainly represented two large scales (u_2 and u_3), but other finer scales like u_6 or u_{13} also contributed fairly to both. The density of shrub cover (qualitative variable ''shrub'') displayed the strongest structuring: a high density of shrubs (''shrub.many'') exhibited a strong pattern at scale u_3, while the absence of shrubs (''shrub.none'') was

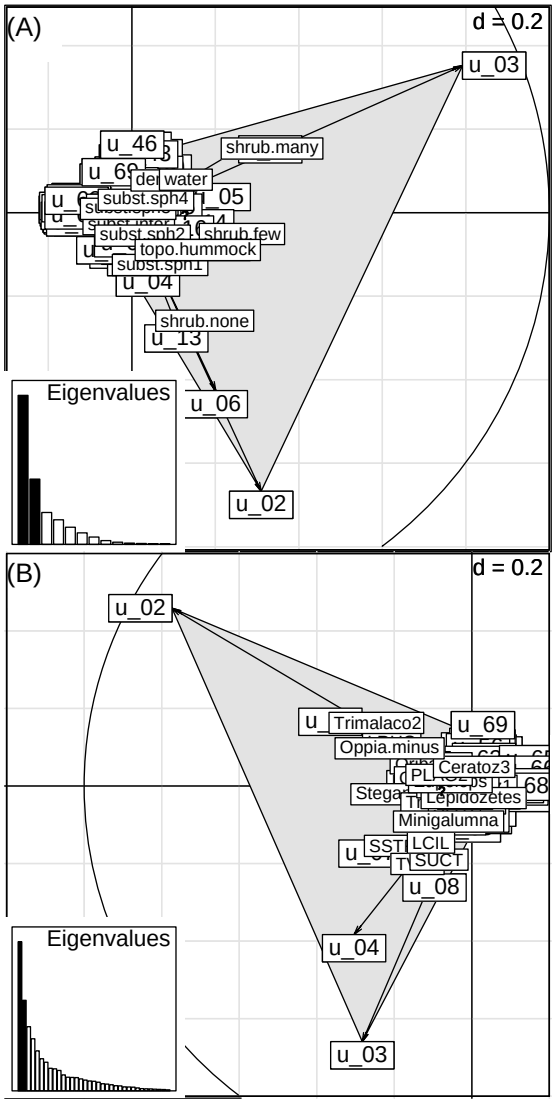

Figure 3. Biplots of the MSPA of oribatid mites dataset (same representations as in Fig. 1A–B). The qualitative variables are positioned at the average of the coordinates of their modalities. (A) MSPA of environmental variables. (B) MSPA of species.

linked to the scale u_2. These results are consistent with previous results of Borcard et al. (2004).

Species data were Hellinger-transformed prior to MSPA (Legendre and Gallagher 2001). Two principal axes were retained (Fig. 3B). The species were mainly structured at large scales (u_2, u_3, and u_4), but intermediate scales also contributed to the axes (u_4, u_5, u_7, and u_8). Some species displayed moderate spatial patterns at the largest scales (R^2 around 0.3), but none were distinguished from the others by a strong spatial pattern.

These results raised the question of how the multi-scale spatial patterns of species are determined by environmental variables. To study species-environment relationships at multiple scales, a canonical MSPA was performed: species data were predicted by multiple regression onto environmental variables, and the obtained predictions were submitted to a MSPA. This method can be employed to investigate the environmental components of the multi-scale spatial patterns of the species. The first two eigenvalues were clearly larger than the others and were therefore retained (Fig. 4A). Environmental variables were projected onto the principal axes as supplementary individuals (Fig. 4B): the first spatial structure (u_2) was mainly related to the absence of shrubs ("shrub.none"), while the second pattern (u_3) was linked to large quantities of shrubs ("shrub. many"). Strikingly, the multi-scale structuring of species was no longer composed of large and intermediate scales as seen in the previous analysis (Fig. 3B), but only consisted of two large scales (u_2 and u_3, Fig. 4A). Moreover, some species like TVEL (*Tecticepheus velatus*) or Trimalaco2 (*Trimalaconothrus* species) exhibited stronger structuring than others, with R^2 values around 0.5, showing that half of the variance predicted by environment was of spatial essence (Fig. 4A). This analysis reinforced the idea that spatial dependence (i.e. spatial patterns of species induced by environment) mainly occurs at relatively large scales, as opposed to spatial autocorrelation.

Discussion

This paper presents multi-scale pattern analysis (MSPA) as a new tool to investigate the scales of spatial variation in ecological data, using quantitative and qualitative variables. Classically, such investigation has been performed by constrained ordinations in which MEMs are used as spatial predictors after a forward selection procedure. However, as underlined by Dray et al. (2006) and shown in our simulated example, this method can provide very large type I error: it tends to find more structuring scales than there actually are. On the contrary, MSPA does not rely on testing procedures; it can be used for a preliminary exploration of data, to assess the existence of multi-scale spatial patterns (using the eigenvalues screeplot) and to identify both structuring scales and structured variables (using biplots). Moreover, MSPA can be extended to canonical and partial canonical MSPA by performing a multivariate regression of data onto a set of explanatory variables, as done in constrained ordinations (Rao 1964, Ter Braak 1986, 1988). Canonical MSPA can be used to extract the environmental component of the multi-scale spatial patterns of species, thereby focusing on spatial dependence. Partial canonical MSPA can be employed to study multi-scale spatial patterns in species after removing the environmental effect from species data; provided all relevant environmental variables have been used in this operation, one would get rid of spatial dependence and observe true spatial autocorrelation (sensu Wagner 2004).

Several points concerning the method shall be discussed. First, we used MEMs to model spatial scales, which was not their initial purpose: they were by-products of the decomposition of Moran's index of spatial autocorrelation (de Jong et al. 1984, Tiefelsdorf and Boots 1995). But, as underlined by Griffith (2000), these vectors have excellent properties to be used as multi-scale spatial predictors. They are centred (all MEMs have a mean of zero), scaled (all MEMs have a norm equaling one), orthogonal and uncorrelated (MEMs are not subject to multicollinearity problems), and each MEM models a different scale of variation. It could be argued that modelling the concept of scale (which is continuous and can involve an infinite

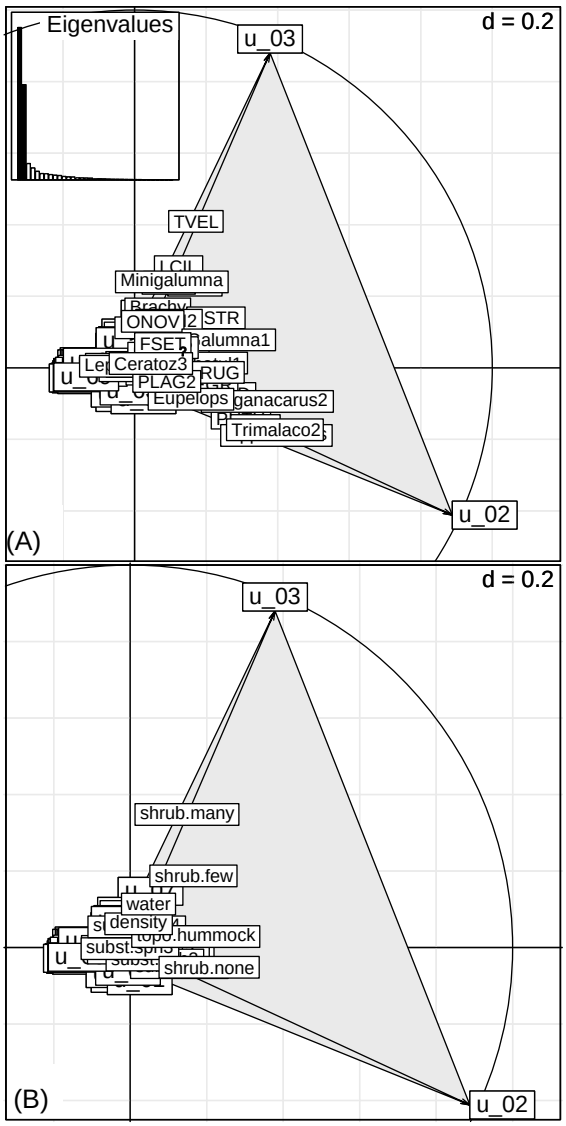

Figure 4. MSPA of oribatid mite species predicted by environmental data. (A) MSPA biplot. (B) projection of environmental variables onto MSPA axes.

number of levels) using a discrete approach (the number of MEMs is finite) is somewhat clumsy. This would not be justified, however, because MSPA seeks linear combinations of MEMs; there is an infinite number of such combinations, which likely enables the method to detect very complex spatial patterns.

Other spatial predictors besides MEM may have been considered, such as PCNM (Borcard and Legendre 2002, Borcard et al. 2004). Indeed, many of the mathematical properties of MEM (e.g. orthonormality) are also found in PCNM (Borcard and Legendre 2002, Borcard et al. 2004) because these are particular cases of MEM (Dray et al. 2006). However, the original PCNM approach yields 2n/3 spatial predictors, which is usually insufficient to decompose the whole variability of "n" observations. On the contrary, (n − 1) MEMs always explain 100% of the variability of n centred observations. Moreover, MEMs are not contingent upon the choice of a particular threshold, contrary to PCNM.

A last concern is about the dimensionality of the matrix of centred R^2 (**Z**) which is submitted to a particular PCA. This matrix has "q" variables (or species) in rows and (n − 1) MEMs in columns, where "q" would often be lower than (n − 1). In such cases, the results of PCA can be numerically instable: adding or removing a variable could induce important changes in the principal components (Costello and Osborne 2004, 2005). Numerical instability would be problematic when one wants to draw conclusions beyond the sample that is studied, to make inferences about the population from which observations were drawn (Costello and Osborne 2005). In some cases, ecological descriptors could be used to infer the multi-scale spatial structuring of a larger set of variables (or species), such as an ecosystem. Then, numerical stability would be required, since introducing a new descriptor in MSPA should not change the assessment of the main structuring scales of the ecosystem. To achieve numerical stability, it would be necessary to measure all relevant descriptors of the ecosystem at a large number of sites, which would likely result in an extensive experimental design. However, MSPA will most often be employed to describe the main scales of spatial variation in a set of variables or species, without drawing conclusions about other variables or species. In such cases, the PCA of **Z** is simply used as a descriptive tool, to summarize the information contained by the matrix of scale profiles into a few dimensions, and numerical stability is no longer required (Joliffe 2004, Costello and Osborne 2005).

As a conclusion, MSPA is an exploratory tool adapted to the multi-scale nature of spatial patterns. Its function is to peer at the ecological variability through "scale filters" – the MEMs – which can detect many different scales of spatial variation. Furthemore, MSPA could also be applied in other domains in which MEMs can be used, for instance in time series and in phylogeny (Peres-Neto 2006), which increases significantly the potential of the method.

Acknowledgements – We are grateful to Pedro Peres-Neto and two anonymous reviewers for providing constructive comments on an earlier version of the manuscript.

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