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Multiple regression on distance matrices: a multivariate spatial analysis tool

Jeremy W. Lichstein
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, 08544-1003, USA; (e-mail: jwl@princeton.edu)

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Abstract

I explore the use of multiple regression on distance matrices (MRM), an extension of partial Mantel analysis, in spatial analysis of ecological data. MRM involves a multiple regression of a response matrix on any number of explanatory matrices, where each matrix contains distances or similarities (in terms of ecological, spatial, or other attributes) between all pair-wise combinations of *n* objects (sample units); tests of statistical significance are performed by permutation. The method is flexible in terms of the types of data that may be analyzed (counts, presence–absence, continuous, categorical) and the shapes of response curves. MRM offers several advantages over traditional partial Mantel analysis: (1) separating environmental distances into distinct distance matrices allows inferences to be made at the level of individual variables; (2) nonparametric or nonlinear multiple regression methods may be employed; and (3) spatial autocorrelation may be quantified and tested at different spatial scales using a series of lag matrices, each representing a geographic distance class. The MRM lag matrices model may be parameterized to yield very similar inferences regarding spatial autocorrelation as the Mantel correlogram. Unlike the correlogram, however, the lag matrices model may also include environmental distance matrices, so that spatial patterns in species abundance distances (community similarity) may be quantified while controlling for the environmental similarity between sites. Examples of spatial analyses with MRM are presented.

Introduction

Spatial patterns in species abundances reflect spatial patterns in the environment and/or spatial processes such as dispersal and disturbance (Legendre 1993). Often, spatial processes are not independent of the environment. For example, seed dispersal may be directed towards particular environments by animals (Wenny and Levey 1998), or biased by topographic effects on wind currents . Similarly, the frequency and behavior of disturbances such as wind-throw and fire are strongly influenced by the physical environment (Bergeron 1991; Johnson 1992; Everham and Brokaw 1996). Nevertheless, species data typically have some spatial structure that can not be explained by environmental variables (Borcard et al. 1992; Borcard and Legendre 1994; Lichstein et al. 2002). This nonenvironmental, or 'pure,' spatial structure has two causes. First, it is difficult to identify and measure all important aspects of the environment, so that some spatially structured environmental variation appears incorrectly in the analysis as pure spatial structure (Legendre and Legendre 1998:777). Secondly, most spatial processes are at least partially independent of the

environment. For example, seed dispersal by animals has both pure spatial (distance-limitation) and environmental (habitat-preference) components.

Correlograms, which quantify how inter-site similarity varies with inter-site distance, are frequently used in ecology to describe spatial pattern in either univariate (single-species) or multivariate (community) responses (Sokal and Oden 1978; Oden and Sokal 1986; Rossi et al. 1992; Legendre and Legendre 1998). However, correlograms alone provide no insight into the cause of the spatial pattern; i.e., it is impossible to tell from a correlogram how much of the spatial pattern is due to the environment vs. spatial processes.

In this paper, I show that multiple regression on distance matrices (MRM; Manly 1986; Smouse et al. 1986; Legendre et al. 1994; Legendre and Legendre 1998:559, 783) can be used to generate a correlogram analogue that controls for environmental variation. MRM, an extension of partial Mantel analysis, is conceptually and mathematically simple and can accommodate all common data types (i.e., presence–absence, counts, continuous, ordinal, categorical). The method can be used to investigate linear, nonlinear, or nonparametric relationships between a multivariate response distance matrix and any number of explanatory distance matrices. Although MRM has been applied in a few ecological studies (Urban et al. 2002; Tuomisto et al. 2003), spatial analysis with MRM has not been discussed in detail.

I first briefly summarize simple and partial Mantel tests and the Mantel correlogram (see Legendre and Legendre 1998 for details on these methods). I then describe MRM, focusing on its application to spatial analysis. I show how MRM can be used to incorporate the Mantel correlogram into the multiple regression framework (Legendre and Legendre 1998:783). Examples are presented using data on tree, shrub, and liana abundance in northwest Argentina.

Analysis of distance matrices

Simple Mantel test (2 matrices)

Mantel (1967) proposed a test for association between two $n \times n$ matrices whose entries are distances or similarities between all pair-wise combinations of n objects (Figure 1A). The objects may be plots, species, or any other type of sampling unit, and the pair-wise measures may reflect distance or similarity in terms of species abundance(s), environmental conditions, or geographic location (when the objects are plots); physiology, behavior, morphology, or phylogeny (when the objects are species); or any other uni- or multivariate space.

A common use of the Mantel test is to quantify the spatial structure in a species abundance distance matrix. Two $n \times n$ matrices are constructed: $\mathbf{D_Y}$, containing species abundance (e.g., Bray–Curtis) distances between the site pairs; and $\mathbf{D_{SPACE}}$, containing raw or transformed geographic (Euclidean) distances. Most distance coefficients are symmetric ($d_{ij} = d_{ji}$), so the upper right and lower left portions of the matrices

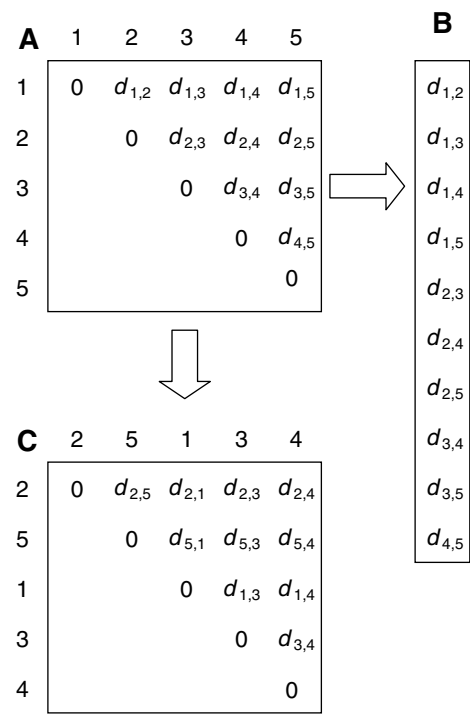


Figure 1. (A) Structure of a distance matrix with $n = 5$ objects (e.g., sample plots). Each value, d_{ij}, is the distance between objects i and j in uni- or multivariate space. Self-distances (d_{ii}) are, by definition, zero. For symmetrical distance coefficients ($d_{ij} = d_{ji}$) the lower left portion of the matrix (not shown) contains redundant values with the upper right portion. (B) The $n(n-1)/2$ nontrivial distances are unfolded into a vector for subsequent analysis. (C) The rows and associated columns of a distance matrix are simultaneously permuted to perform statistical tests of association between the matrix and one or more other distance matrices.

contain redundant values (Figure 1A). After removing the redundant values and the main diagonal (which contain self-distances), there are $n(n-1)/2$ values per matrix. Each matrix is unfolded into a vector of distances (Figure 1B), and r_M (or a nonparametric coefficient) is calculated as the correlation between the two vectors (Legendre and Legendre 1998). A large positive value of r_M would indicate that plot pairs with similar species abundances (small values in $\mathbf{D_Y}$) are close in geographic space (small values in $\mathbf{D_{SPACE}}$), and that plot pairs with very different species abundance (large values in $\mathbf{D_Y}$) are far apart (large values in $\mathbf{D_{SPACE}}$).

Valid tests for r_M may be performed by permutation or by comparing a transformed version of r_M to a standard normal deviate (Mantel 1967; Legendre and Legendre 1998:554). The permutation approach is the only method available for the extensions to the Mantel test discussed below. Due to the interdependence of the distances, it is the n objects, not the distances, which must be permuted. For each permutation, the n objects and their associated values for one set of attributes (e.g., species abundances) in the original (raw) data are randomly permuted and the distance matrix recalculated, while the other set of attributes (e.g., the spatial coordinates) is held constant. An equivalent, more efficient procedure is to simultaneously permute the rows and corresponding columns in one of the distance matrices (Figure 1C; Legendre and Legendre 1998:554; Legendre 2000). Mantel tests are usually one-tailed, because one expects objects that are similar in one set of attributes (e.g., species abundances) to also be similar in another set of attributes (e.g., space).

Partial Mantel test (3 matrices)

Partial Mantel analysis is partial correlation analysis performed on distance matrices, each unfolded into a vector (Figure 1B). The partial correlation between two distance matrices is computed while controlling for the effect of a third matrix (Smouse et al. 1986). Partial Mantel analysis is one of several methods commonly used to obtain the variance partitioning of Borcard et al. (1992), in which variation in species data is partitioned into environmental and spatial components. However, distance and raw data matrices have very different properties, and distance matrix analysis should not be used for making inferences about raw data (Legendre et al. 2005). For example, it is possible to construct a multi-species raw data matrix in which no two sites share the same set of species abundances, but whose corresponding distance matrix has zero variance (i.e., all inter-site species abundance distances are the same; Legendre et al. 2005).

Legendre (2000) used simulations to compare permutation methods for partial Mantel tests. The method described in Legendre and Legendre (1998:558), in which $\mathbf{D_Y}$ is permuted (see simple Mantel test, above; Figure 1C) and the two explanatory distance matrices are held constant, was valid except in the presence of extreme outliers (Legendre 2000).

Mantel correlogram

Oden and Sokal (1986) and Sokal (1986) used the Mantel test to compute a multivariate correlogram, which, like univariate correlograms or semivariograms, plots autocorrelation as a function of geographic distance. A Mantel correlogram, which describes the spatial structure of a distance matrix, $\mathbf{D_Y}$, may be constructed as follows: (1) the geographic distances between the n plots are divided into classes, or 'lags'; (2) for each lag, an $n \times n$ matrix is constructed containing zeroes for site pairs whose geographic distances fall within the lag class and ones otherwise; (3) simple Mantel tests are calculated between $\mathbf{D_Y}$ and each lag distance matrix, and r_M is plotted as a function of the lag mid-points. Each r_M statistic is tested for significance using the permutation procedure described above for the simple Mantel test. Some correction (e.g., Bonferroni) is needed to account for multiple testing in correlograms. Two-tailed tests are often used, because negative autocorrelation is not uncommon, particularly at the farther lags.

MRM (≥ 2 matrices)

MRM entails a multiple regression of a response distance matrix, $\mathbf{D_Y}$, on two or more environmental, spatial, or other explanatory distance

matrices, each unfolded into a distance vector (Figure 1B). The significance of an MRM model and its regression coefficients are tested by permuting $\mathbf{D_Y}$ while holding the explanatory matrices constant. When $\mathbf{D_Y}$ is an ordinary distance or similarity matrix, its rows and columns are permuted as described above for the simple Mantel test (Figure 1C; Legendre et al. 1994), and the model R^2 and regression coefficients are calculated for each permutation to generate null distributions. Legendre et al. (1994) discuss permutation procedures when $\mathbf{D_Y}$ contains distances representing a dendrogram or a phylogenetic tree. MRM, like other distance matrix analyses, provides inferences about relationships between distances, not between raw data.

MRM offers two advantages over traditional partial Mantel analysis:

(1) Polynomial, nonlinear, or nonparametric regression methods, such as generalized additive models (Yee and Mitchell 1991), can be used with MRM: Once the distance matrices have been unfolded into vectors, the calculations for fitting an MRM model are no different than those for multiple regression with raw data. The only computational difference lies in significance testing, which is performed by permuting the objects of the response distance matrix.
(2) Expanding the number of explanatory matrices allows each environmental variable to be represented by its own distance matrix. This provides an improved species–environment correlation (because the effects of important variables are not diluted by unimportant ones), and a convenient way to determine the statistical significance and relative importance of each environmental factor.

Expanding the number of explanatory distance matrices also increases the flexibility of spatial analysis. Noting that ecological (e.g., species abundance) distances may be nonlinearly related to geographic distance, Legendre and Legendre (1998:783) proposed to use a series of geographic distance matrices, each corresponding to a lag distance class, as explanatory matrices in an MRM model (hereafter, the 'lag matrices model'). The distance matrices in the lag matrices model could be the same as those used in a Mantel correlogram. The lag matrices model can fit complex nonlinear patterns and provides a significance test for spatial structure at each scale (lag distance).

If the lag matrices model is fully specified (i.e., all lags plus an intercept are included), then the model has a linear dependency and must be reparameterized. The model may be reparameterized in such a way that the regression coefficients and their *P*-values provide tests for autocorrelation at each lag distance (see Appendix A). In general, it may be undesirable to include all lags in the model, because the farthest lags will only include site pairs located on the periphery of the study area. In some cases, however, it is of interest to compare the most geographically distant sites (e.g., Condit et al. 2002), which requires that all distance classes be included in the analysis. When interpreting spatial pattern at the farthest lags, it is important to bear in mind that these patterns are more susceptible than the shorter lags to being influenced by local anomalies near the edges of the study area.

Application of MRM

I apply MRM to spatial analysis of species abundance and environmental data from northwest Argentina, Tucumán province. The study aims to understand the relative roles of seed dispersal and environmental factors on the recruitment of native and exotic plants (Lichstein et al. 2004).

Data

Sixty-four 20×20 m plots were located in secondary forest patches in a 2.2×0.65 km section of a landscape (27°30′ S, 65°40′ W; 580–710 m elevation) that was deforested for agriculture during the first half of the 20th century. Presently, the landscape consists of a mosaic of agriculture, native secondary forests, forests dominated by *Ligustrum lucidum* W. T. Aiton (Oleaceae; an invasive tree from Asia), and exotic tree plantations (*Eucalyptus* and *Pinus*). Plots were arranged in clusters of two to four adjacent plots, depending on the size of the forest patch. Small inter-plot geographic distances within clusters allowed for fine-scale resolution in spatial analyses, while larger distances between

clusters allowed for broad extent. In each plot, I recorded the diameters and identities of all woody plants (trees, shrubs, and lianas) with dbh $\geq$3 cm. In the central 10×10 m of each plot, I counted and identified all woody stems taller than 25 cm and assigned stems with dbh <3 cm to one of three size classes: 25–50 cm tall, 50–150 cm tall, and >150 cm tall. I measured environmental variables in each plot, including canopy cover and soil moisture, chemistry, and texture. See Lichstein et al. (2004) for details.

Analysis

Permutation tests for MRM models were performed with the program Permute! (http://www.fas.umontreal.ca/biol/casgrain/en/labo/permute/index.html). All other analyses were performed with SPLUS (Insightful Corporation 2002). Mantel tests and Mantel correlograms may also be computed with the R Package (http://www.fas.umontreal.ca/biol/casgrain/en/labo/R/v4/index.html). Here, I discuss general features of the methods. I describe each analysis in more detail in the examples below.

Separate $\mathbf{D_Y}$ matrices were constructed from abundances (stem counts) within each stem size class for three species groups: all species combined, native trees, and shrubs. Each $\mathbf{D_Y}$ contained Bray–Curtis distances between the 2016 plot pairs. Abundances were $\log(y+1)$ transformed to emphasize rare species.

I fit Mantel correlograms to describe spatial patterns in $\mathbf{D_Y}$. Sturge's rule (Legendre and Legendre 1998:717) determined that 12 lag classes were appropriate for 2016 distances. The first lag included all plot pairs with geographic distances <50 m ($n=94$), and the second lag included pairs with distances of 50–100 m ($n=132$). Lags 3–12 each contained 179 plot pairs and were of unequal width. Plot pairs whose inter-plot distances fell within a given lag class were assigned a value of zero in the corresponding lag matrix, and a value of one otherwise; thus, positive r_M values in Mantel correlograms imply positive autocorrelation. The significance of each r_M value in the correlograms was assessed by permutation using the progressive Bonferroni correction (Legendre and Legendre 1998:671, 721): $\alpha_i = \alpha/2i$ for the ith lag, where $\alpha = 0.05$, and the two in the denominator yields a two-tailed test.

I fit MRM lag matrices models of $\mathbf{D_Y}$ using the same lag distance classes as in the correlograms. These models contained all 12 lags and were reparameterized as in Appendix A. I fit MRM environment models using 11 environmental distance matrices containing the absolute values of inter-plot differences for the following variables: stand age; percent of plot basal area comprised by *L. lucidum*; percent canopy cover; an index of canopy gappiness; soil moisture; three principal components (PCs) describing soil texture (soil PC1), fertility (soil PC2), and pH (soil PC3); and three PCs describing soil surface rockiness (surface PC1), fine woody debris (surface PC2), and litter depth (surface PC3). In all cases, partial residual plots (Rawlings et al. 1998) indicated a linear relationship (if any) between $\mathbf{D_Y}$ and the environmental distances.

P-Values for MRM models were obtained with the program Permute! by comparing each observed regression coefficient to a distribution of 2000 values (observed + 1999 permuted values; Legendre and Legendre 1998:20–22). Nonlinear relationships between species and environment distances may be modeled with Permute! by, for example, using polynomials of the explanatory distances, although this was not necessary in the present study.

Fitting spatial patterns with MRM

A Mantel correlogram of the all species data (stems 25–50 cm tall) shows positive autocorrelation at lags 1, 2, 3, and 5, and negative autocorrelation at lags 6, 11, and 12 (Figure 2A). I use the term 'autocorrelation' to refer to the presence of a statistically significant spatial pattern, regardless of whether the pattern is thought to be caused by the environment or by an endogenous spatial process.

Figure 3 shows the fit of three linear models (Figuers 3A, C, and E) and the lag matrices model (Figure 3G) to the 2016 Bray–Curtis×geographic distances, and Mantel correlograms of the residuals from each model (Figure 3B, D, F, and H). A simple linear model (simple Mantel test between $\mathbf{D_Y}$ and a geographic distance matrix) explains 17% of the variation in $\mathbf{D_Y}$ (Figure 3A). This model fails to capture the nonlinearity in the data, and a correlogram of the residuals shows

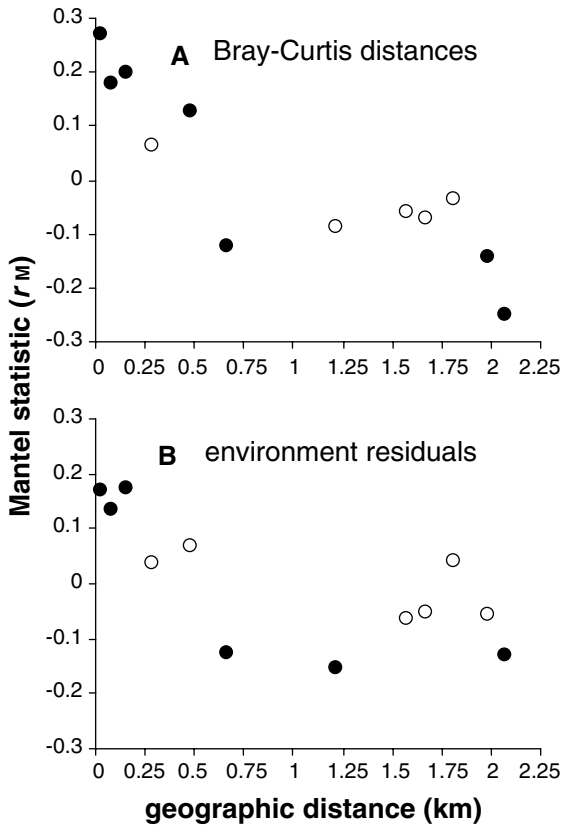


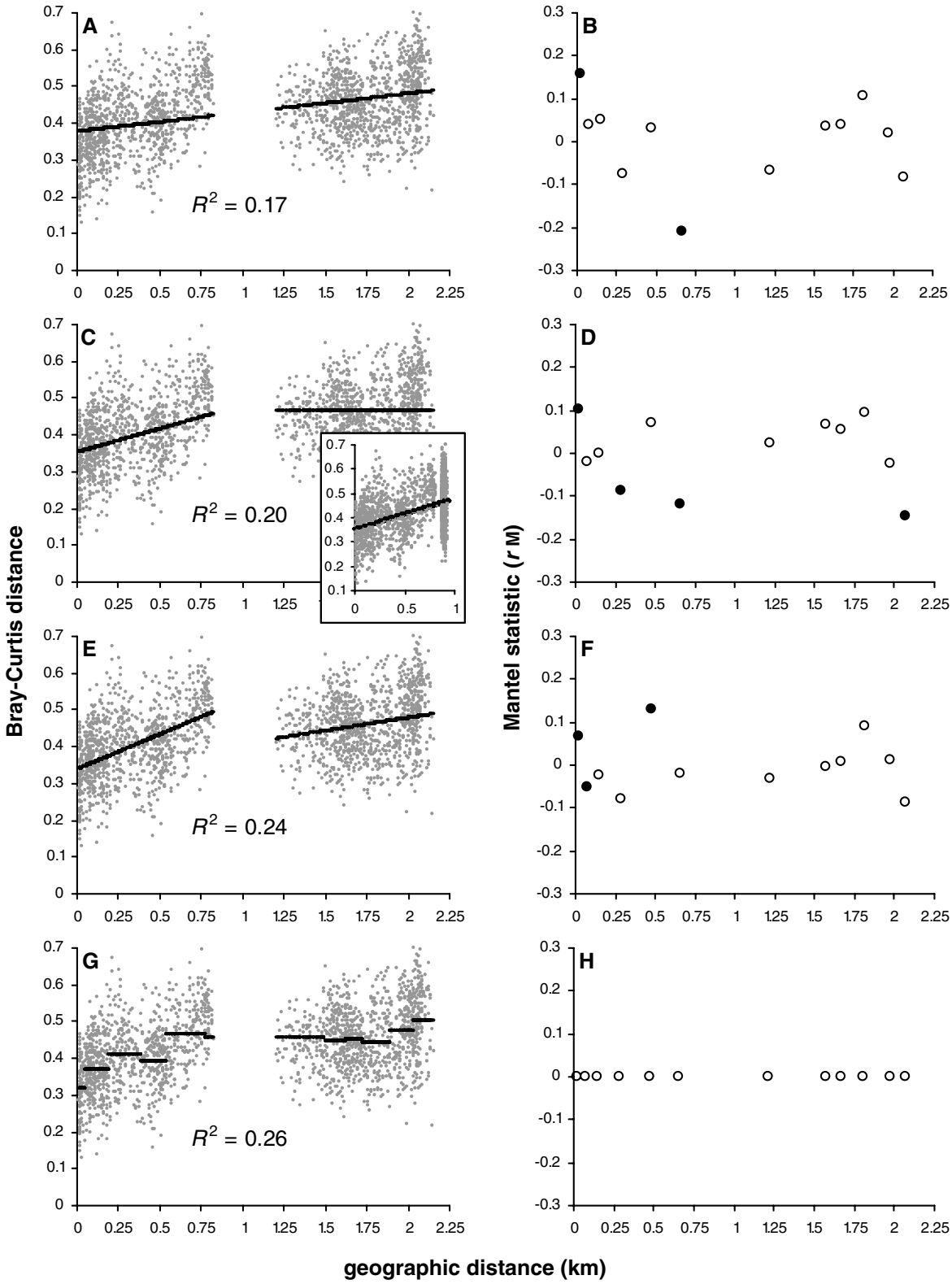
Figure 2. Mantel correlograms (r_M vs. lag mid-point) for the all species data (stems 25–50 cm tall). (A) Bray–Curtis distances: multivariate (47 species) differences in abundance between plots. (B) Residuals from MRM environment model containing the environmental variables age, soil PC1, and soil PC2. Closed symbols: r_M significantly different than zero; open symbols: $r_M$not significantly different than zero.

significant autocorrelation at the first and sixth lags (Figure 3B). An alternative to the simple linear model is to assume a linear increase in Bray–Curtis distance with geographic distance up to a break point, and no spatial pattern beyond the break. This can be achieved by re-assigning all distances beyond the break point (set arbitrarily as 900 m) to 900 m and fitting a simple linear model to the modified distances (Figure 3C inset). This model (Figure 3C) explains 20% of the variation in $\mathbf{D_Y}$, but the residuals again show autocorrelation at several lags (Figure 3D). The fit is further improved by a multiple regression of $\mathbf{D_Y}$ on two distance matrices (Figure 3E), the first containing the geographic distances between all plots located <1 km apart (with all other values in the matrix set to zero), and the second containing the geographic distances between all plots located >1 km apart (and zeros elsewhere). This model explains 24% of the variation in $\mathbf{D_Y}$ and appears to capture the primary structure of the data, although the residuals are still autocorrelated (Figure 3F).

The lag matrices model (Figure 3G) accounts for 26% of the variation in $\mathbf{D_Y}$. The correlogram of the residuals shows that the model explains all of the spatial pattern in $\mathbf{D_Y}$ (Figure 3H), which follows from the fact that the model and the correlogram both employ the same lag matrices. The statement that "the model explains all of the spatial pattern in $\mathbf{D_Y}$" must be qualified: 74% of the variation in $\mathbf{D_Y}$ is unexplained, but this variation has no spatial structure at the resolution of the lags in the correlogram. Finer subdivision into more lag classes increases the strength of autocorrelation detected in Mantel correlograms (Fortin and Payette 2002) and, by analogy, increases the amount of variation explained by the lag matrices model. To avoid arbitrarily inflating the explained spatial variation, an objective method, such as Sturge's rule (Legendre and Legendre 1998:717), should be used to determine the number of lags.

Finally, it is worthwhile to compare the lag matrices model to some nonparametric alternatives. Figure 4 shows generalized additive models with spline functions of 4 and 8 degrees of freedom, which explain 25 and 28%, respectively, of the variation in $\mathbf{D_Y}$. In terms of fitting the Bray–

Figure 3. Four parametric spatial models (A, C, E, and G) fit to the all species data (gray dots are Bray–Curtis distances vs. geographic distances; black lines are fitted values) and Mantel correlograms (r_M vs. lag mid-points) of the residuals from each model (B, D, F, and H). Due to the arrangement of the plots, no inter-plot geographic distances occur between ~0.8 and 1.2 km. (A) Simple linear regression of Bray–Curtis distances on geographic distances. (C) Simple linear regression with all distances beyond a 900 m break-point re-assigned to 900 m. (Modified data are shown in the inset; the large number of points at 900 m have been randomly off-set slightly to show overlapping points.) (E) Multiple regression on two geographic distance matrices: one matrix for inter-plot distances <1 km, and one for distances >1 km. (G) 'Lag matrices model': multiple regression on the 12 lag matrices used to construct the correlograms. The fitted values for the seventh lag in (G) span the gap in the geographic distances. Correlograms of residuals (B, D, F, and H) show decreasing amounts of spatial pattern for increasingly complex models. Symbols and significance tests in correlograms as in Figure 2.


A
B
C
D
E
F
G
H
R^2 = 0.17
R^2 = 0.20
R^2 = 0.24
R^2 = 0.26
Bray-Curtis distance
Mantel statistic (r M)
geographic distance (km)

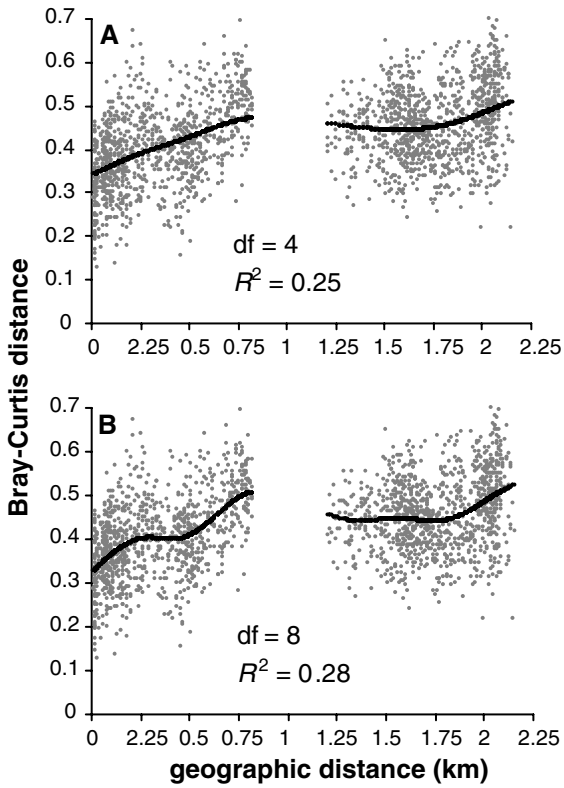


Figure 4. Nonparametric generalized additive models fit to the all species data (gray dots are Bray–Curtis distances vs. geographic distances; black lines are fitted values). Models were fit with a spline function with (A) 4 and (B) 8 degrees of freedom. R^2 was calculated as the percent deviance explained.

Curtis distances, these nonparametric models perform favorably compared to the fully specified lag matrices model, which has 12 degrees of freedom (one for each parameter, or lag). The main advantage of the lag matrices model is not its superior performance in fitting nonlinearities, but, the ability to test for autocorrelation at different spatial scales (see below). In contrast, nonparametric models, by definition, provide no such tests. (Here, 'nonparametric' refers to the form of the fitted curve, not the response distribution.)

The above analyses are all-directional: the interplot distances, but not directions, are used to construct the spatial matrices. There is no reason why directionality cannot be incorporated into the spatial matrices if there is thought to be a directional component to the spatial processes under consideration. For example, for wind-dispersed plants in a region with prevailing westerly winds, a site pair might be included in a lag class only if, in addition to their geographic distance falling within the distance class, the sites are within 60°–120° or 240°–300° azimuth bands of each other. For analyses that use the geographic distances, rather than lag classes, directionality could be accounted for by using a matrix of spatial similarities (e.g., 1/distance), weighted by the appropriate sine or cosine of the inter-site azimuths.

Lag matrices model vs. Mantel correlogram

I reparameterized the lag matrices model (Figure 3G) as in Appendix A and tested the multiple regression coefficients using Permute!. With one exception (lag 7), the coefficients in the fully specified lag matrices model (Table 1) were significant at the same lags that were significant in the Mantel correlogram (Figure 2A). The signs are reversed in the MRM model relative to the Mantel correlogram because the former was parameterized to estimate the difference between the mean Bray–Curtis distance in the *i*th lag and the overall mean Bray–Curtis distance (i.e., negative regression coefficients imply positive autocorrelation), whereas the later was coded so that positive autocorrelation would result in positive values of r_M. After accounting for the difference in sign, the two analyses lead to very similar inferences. To test the generality of this result, I fit Mantel correlograms and fully specified lag matrices models to 12 additional species abundance data sets, consisting of different species groups and stem size classes. The two approaches yielded nearly identical inferences regarding autocorrelation (Table 2). The 13 data sets are not independent (e.g., the all species data contains the smaller data sets); nevertheless, the close correspondence between the two approaches suggests that the lag matrices model incorporates the main features of the Mantel correlogram. The key functional difference between the two methods is that the correlogram simply describes spatial pattern, whereas MRM allows the lag matrices to be combined with environmental distances in a multiple regression model.

MRM space/environment models

I searched over all possible combinations of the 11 environmental distance matrices to identify the set

Table 1. Fully specified lag matrices model for all species data (Figure 3G).

Lag class	Mean/max lag distance (m)	Coefficient[a]	Mean[b]
1	26/50	−0.109*	0.316
2	78/100	−0.058*	0.367
3	146/195	−0.055*	0.370
4	286/392	−0.014	0.411
5	475/539	−0.032*	0.392
6	659/775	0.042*	0.467
7	1216/1499	0.032*	0.456
8	1571/1623	0.023	0.447
9	1669/1727	0.027	0.451
10	1810/1895	0.016	0.440
11	1976/2030	0.048*	0.472
12	2069/2157	0.080*	0.504

[a]Multiple regression coefficients are differences between the mean Bray–Curtis distance in the *i*th lag and the overall mean Bray–Curtis distance (see Appendix A). For a given lag, a negative coefficient indicates positive autocorrelation; i.e., species composition within that lag is more similar (smaller Bray–Curtis distance) than the mean similarity among all plot pairs.[b]Mean Bray–Curtis distance for $\text{lag}_i = \text{intercept} + \text{coefficient}_i$, where intercept from reparameterization of Appendix A is 0.424. Means are fitted values shown in Figure 3G.*Significant at progressive Bonferroni adjusted $\alpha_i = 0.05/2i$ for *i*th lag (two-tailed test; Legendre and Legendre 1998:671, 721).

that explained the most variation in $\mathbf{D_Y}$ (Bray–Curtis distances for the all species data, stems 25–50 cm tall). I used a Bonferroni-corrected α of $0.05/11 = 0.0045$ (one-tailed test for positive correlation). The best environment model included distance matrices for stand age, soil PC1, and soil PC2, and explained 19% of the variation in $\mathbf{D_Y}$ (Table 3). A space/environment model, including the three significant environmental matrices and the 12 lag matrices, explained 33% of the species data, compared to 26% for the pure space model (Table 1; Figure 3G). Stand age and soil PC2 remained significant, but soil PC1 was no longer significant after controlling for the spatial structure in the data (Table 3). This is reflected in the regression coefficients, which are very similar in the two models for stand age and soil PC2, but much smaller in the space/environment model compared to the environment model for soil PC1 (Table 3).

Partitioning the variation in $\mathbf{D_Y}$ into pure environment (7%), shared space/environment (14%), and pure space components (12%; Figure 5) suggests that dispersal limitation or other spatial processes are more important than environmental factors in determining community similarity. A Mantel correlogram of the residuals from the pure environment model described above shows significant autocorrelation at lags 1, 2, 3, 6, 7, and 12 (Figure 2B), reflecting the substantial pure spatial structure in $\mathbf{D_Y}$.

A useful way to visualize the extent of overlap between the spatial and environmental structure in $\mathbf{D_Y}$ is to plot the lag coefficients from fully

Table 2. Lags with significant positive (+) and negative (−) autocorrelation in Mantel correlograms (left) and fully specified MRM lag matrices models (right).[a]

	Size class[b]	Lag											
		1	2	3	4	5	6	7	8	9	10	11	12
All species	1	+/+	+/+	+/+		+/+	−/−	/−				−/−	−/−
	2	+/+	+/+	+/+			−/−					−/−	−/−
	3	+/+	+/+	+/+			−/−				/−		/−
	4	+/+	+/+	+/+		−/							−/−
Native trees	1	+/+	+/+	+/+			/−						−/−
	2	+/+	+/+	+/+		−/−							−/−
	3	+/+	+/+	+/+				+/					−/−
	4	+/+	+/+	+/+		−/−							/−
Lianas	1–2	+/+	+/+	+/+			−/−	−/−					
	3–4	+/+	+/+									−/−	−/−
Shrubs	1	+/+	+/+	+/		+/+			+/+		−/−	−/−	−/−
	2	+/+	+/+										
	3–4	+/+				/−	+/						

[a]MRM models included all 12 lags and no environmental variables, and were parameterized as in Appendix A. For both MRM models and Mantel correlograms, autocorrelation at each lag was tested at the progressive Bonferroni adjusted $\alpha_i = 0.05/2i$ for *i*th lag (two-tailed test; Legendre and Legendre 1998:671, 721).[b]Size classes: (1) 25–50 cm tall; (2) 50–150 cm tall; (3) >150 cm tall and <3 cm dbh; (4) 3–10 cm dbh.

Table 3. MRM environment and space/environment models for all species data.

Variable	Coefficient[a]	P[b]
Environment model: $R^2 = 0.19$		
Stand age	0.024	0.0005*
Soil PC1	0.019	0.0005*
Soil PC2	0.019	0.0005*
Space/environment model: $R^2 = 0.33$		
Stand age	0.018	0.0005*
Soil PC1	0.002	0.63
Soil PC2	0.018	0.0005*
Lag1	−0.081	0.0005*
Lag2	−0.052	0.0005*
Lag3	−0.054	0.0005*
Lag4	−0.016	0.061
Lag5	−0.027	0.0035*
Lag6	0.036	0.0005*
Lag7	0.043	0.0005*
Lag8	0.024	0.0035
Lag9	0.029	0.0025*
Lag10	0.008	0.45
Lag11	0.038	0.0005*
Lag12	0.053	0.0005*

[a]Environmental distances were standardized to zero mean and unit variance, so their coefficients refer to a common scale. Lag matrices were not standardized (see Appendix A). Interpretation of lag matrix coefficients as in Table 1.[b]P-values were calculated from a distribution of 2000 values (observed + 1999 permuted values); thus, the minimum possible P is 0.0005.*Significant at Bonferroni adjusted $\alpha = 0.05/11$ (environmental variables; one-tailed test) or progressive Bonferroni adjusted $\alpha_i = 0.05/2i$ for ith lag (two-tailed test; Legendre and Legendre 1998:671, 721).

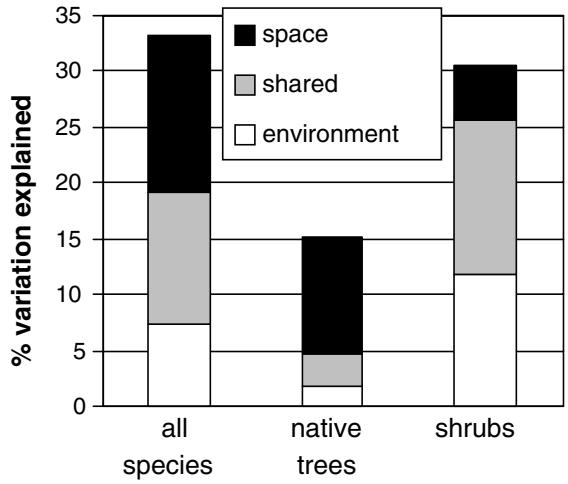


Figure 5. Explained variation in Bray–Curtis distances partitioned by MRM into pure environment, spatially structured environment ('shared'), and pure space components (Borcard et al. 1992). The total variation explained by environment models is equal to the pure environment plus shared components. The total variation explained by spatial (lag matrices) models is equal to the pure space plus shared components.

specified lag matrices models with and without environmental variables. To illustrate, I fit fully specified pure space and space/environment lag matrices models to Bray–Curtis distances calculated from the native tree data (25–50 cm tall stems) and the shrub data (25–50 cm tall stems). Environment models were selected using the procedure described above for the all species data.

Only one environmental distance, stand age, was significantly correlated with native tree Bray–Curtis distances, explaining 5% of the variation in $\mathbf{D_Y}$ (Figure 5). The coefficients and significance tests for the lags in the pure space and space/environment models were nearly identical to each other (Figure 6A). Likewise, Mantel correlograms of the native tree distances and of the residuals from the native tree environment model were also very similar (Figure 6C); i.e., the environmental distances explained so little of the variation in $\mathbf{D_Y}$ that the spatial pattern in the environment model residuals is almost the same as the spatial pattern in the original Bray–Curtis distances.

In contrast, the environment model for shrubs included three distance matrices (stand age, soil PC1, and soil PC2), explaining 26% of the variation in $\mathbf{D_Y}$. Because much of this variation was spatially structured (Figure 5), the coefficients and significance tests for the lags in fully specified space and space/environment models differed considerably (Figure 6B); i.e., there was much less spatial pattern for the lag matrices to explain in the presence of the environmental distances than in their absence. Accordingly, the correlogram of environment model residuals showed much less spatial pattern than the correlogram of the Bray–Curtis distances (Figure 6D).

Discussion

MRM extends partial Mantel analysis of three distance matrices to any number of explanatory matrices that may be related to the response (e.g., species) matrix by any multiple regression procedure (e.g., linear, nonlinear, or nonparametric). Although MRM is conceptually similar to partial Mantel analysis, moving from the partial correla-

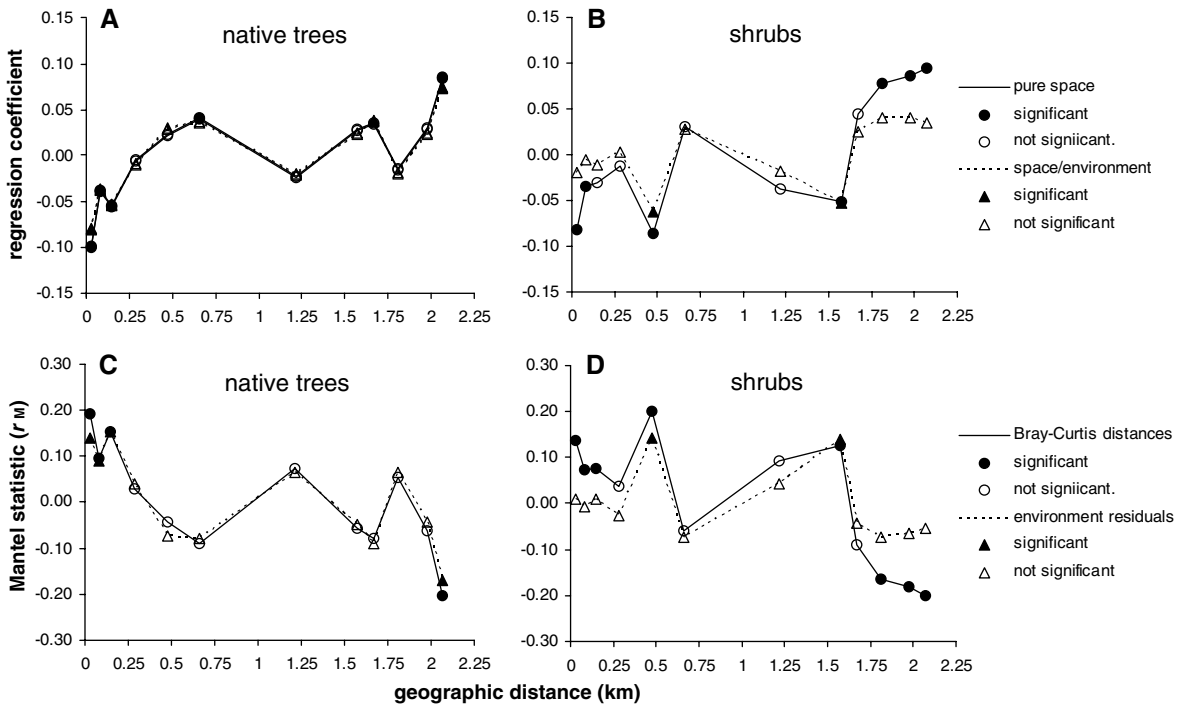


Figure 6. (A and B) Fully specified lag matrices models (parameterized as in Appendix A) for 25–50 cm tall native trees (A) and shrubs (B). For native trees (A), lag matrices had very similar coefficients in pure space (solid line, circles) and space/environment (broken line, triangles) models, because the environmental distances explained little of the variation (5%) in the Bray–Curtis distances (Figure 5). In contrast, for shrubs (B), the lag matrix coefficients diverged in pure space vs. space environment models, because the environmental distances explained a substantial amount (26%) of the variation in the Bray–Curtis distances. (C and D) Mantel correlograms of Bray–Curtis distances (solid line, circles) and residuals from environment models (broken line, triangles) for 25–50 cm tall native trees and shrubs. All four panels show positive autocorrelation at shortest lags and negative autocorrelation at the farthest lags; i.e., the difference in sign between the lag matrices models and the correlograms simply reflects the way the in which the spatial matrices are coded in the two methods.

tion to the multiple regression framework has significant advantages. First, in a space/environment partial Mantel analysis, different environmental variables must be combined into a single multivariate distance, which precludes inferences on the importance of individual environmental factors. In contrast, MRM allows the relationship between species abundance distances and each environmental factor to be assessed separately. Second, unlike partial Mantel analysis, which has traditionally investigated linear correlations, MRM provides a convenient means for modeling nonlinear species responses (e.g., Tuomisto et al. 2003). Finally, MRM allows for a special type of spatial model with lag distance matrices (Legendre and Legendre 1998:783). Although nonparametric (Figure 4) or other nonlinear MRM models with fewer parameters may fit the spatial pattern in the species data as well as, or better than, a lag matrices model (Figure 3G), only the latter provides autocorrelation indices and significance tests for particular spatial scales.

The MRM lag matrices model yields similar inferences regarding spatial autocorrelation as the Mantel correlogram (Table 2). Unlike the correlogram, however, the lag matrices model may also include environmental distance matrices, allowing autocorrelation to be quantified at different scales while controlling for the environmental similarity among sites. Condit et al. (2002) suggested that tree community similarity declines more rapidly with geographic distance in Panama than in western Amazonia due to steeper environmental gradients in Panama. MRM could be used to test this hypothesis directly. More generally, MRM could be used to test hypotheses regarding distance-decay in community similarity (Nekola and White 1999) while controlling for environmental similarity.

The lag matrices MRM model, like other forms of distance matrix analysis, can also be used to partition the explained variation in community similarity (species abundance distances) into spatial and environmental components (Borcard et al. 1992). This variation in community similarity is distinct from the variation in species abundances (Legendre et al. 2005): community similarity may differ little among site-pairs (in which case there could be little spatial or environmental structure in community similarity), despite low similarity (high species turnover) between sites. Inferences about correlations between distances may be invalid for raw data. For example, the Mantel test has low power to detect correlations between raw data vectors (see Table 2 of Legendre 2000), and, in some cases, distance matrices calculated from univariate data may be correlated even when the raw data vectors are not (Dutilleul et al. 2000). Although partial Mantel analysis is often used by ecologists to partition variation in species abundances into spatial and environmental components, this practice should be abandoned in favor of canonical ordination (Legendre et al. 2005), particularly in light of recent improvements to ordination methods (Legendre and Gallagher 2001; Borcard et al. 2004).

In addition to providing weak, or misleading, inferences about raw data, another limitation of Mantel analysis is inflated type I error in the presence of spatial autocorrelation, even when a geographic distance matrix is included in the analysis (Oden and Sokal 1992; Raufaste and Rousset 2001). Determining if this is also problematic in more flexible MRM models is an important topic for future work. Regardless, there are known valid methods to account for autocorrelation in raw data regression of univariate responses (Augustin et al. 1996; Selmi and Boulinier 2001; Lichstein et al. 2002), and, in general, there is no reason to use distance matrices when more direct univariate regression and correlogram methods are available. The lag matrices approach could be incorporated into univariate regression by defining a series of spatial neighborhood matrices, one for each lag, in autoregressive models (Augustin et al. 1996; Lichstein et al. 2002).

Finally, while MRM should capture much of the spatial pattern generated by distance-limited processes (e.g., seed dispersal), MRM and other distance methods will be ineffective at perceiving many spatial patterns generated by the environment, such as gradients on a two-dimensional sampling design (as opposed to a linear transect; Legendre et al. 2005) or patches of variable size and shape. Problems with all-directional correlograms (Legendre and Legendre 1998:724) also apply to distance matrix analysis unless directionality is accounted for in the spatial matrices.

Despite its limitations, MRM is a useful tool for studying the spatial structure of multivariate distances. In particular MRM is well-suited for quantifying the strength and scales of autocorrelation in community similarity while controlling for the environmental similarity among sites. In providing inferences about the importance of individual environmental factors and in fitting complex environmental and spatial responses, MRM offers significant advantages over traditional partial Mantel analysis.

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Appendix A

Reparameterizing the fully specified lag matrices model

If the lag matrices model is fully specified (contains all lags), interpreting and reparameterizing the model are most straight-forward when the values in the lag matrices are coded as one for plot pairs that fall within a given lag class and zero otherwise. Consider a MRM model with (1) dependent ecological distance matrix **Y** unfolded into a vector of length $n(n-1)/2$; (2) an intercept

(mean) vector of ones of length $n(n-1)/2$; and (3) a series of lag distance matrices unfolded into their corresponding distance vectors, each of length $n(n-1)/2$. (For simplicity, I have excluded environmental variables, but the reparameterization derived below is unchanged if other explanatory distance matrices are also included.) Consider $n=5$ sites (as in Figure 1) and five lag classes, each containing two of the $n(n-1)/2=10$ inter-site pairs (in reality, each lag class should contain at least 30 pairs). In matrix notation, the model is $\mathbf{Y}=\mathbf{X}\boldsymbol{\beta}+\boldsymbol{\varepsilon}$:

$$\begin{pmatrix} d_{1,2} \\ d_{1,3} \\ d_{1,4} \\ d_{1,5} \\ d_{2,3} \\ d_{2,4} \\ d_{2,5} \\ d_{3,4} \\ d_{3,5} \\ d_{4,5} \end{pmatrix} = \begin{pmatrix} y_{11} \\ y_{12} \\ y_{21} \\ y_{22} \\ y_{31} \\ y_{32} \\ y_{41} \\ y_{42} \\ y_{51} \\ y_{52} \end{pmatrix} = \begin{bmatrix} 1&1&0&0&0&0 \\ 1&1&0&0&0&0 \\ 1&0&1&0&0&0 \\ 1&0&1&0&0&0 \\ 1&0&0&1&0&0 \\ 1&0&0&1&0&0 \\ 1&0&0&0&1&0 \\ 1&0&0&0&1&0 \\ 1&0&0&0&0&1 \\ 1&0&0&0&0&1 \end{bmatrix} \begin{pmatrix} \mu \\ \tau_1 \\ \tau_2 \\ \tau_3 \\ \tau_4 \\ \tau_5 \end{pmatrix} + \begin{pmatrix} \varepsilon_{11} \\ \varepsilon_{12} \\ \varepsilon_{21} \\ \varepsilon_{22} \\ \varepsilon_{31} \\ \varepsilon_{32} \\ \varepsilon_{41} \\ \varepsilon_{42} \\ \varepsilon_{51} \\ \varepsilon_{52} \end{pmatrix}, \tag{A.1}$$

where μ is the overall mean response, τ_i is the mean departure of y in the ith lag from μ, and $\boldsymbol{\varepsilon}$ is the vector of errors. $\mathbf{Y}$ is expressed in two different notations above because in regards to the parameterization of the multiple regression model, the $n(n-1)/2$ inter-site distances ($d_{1,2}$, $d_{1,3}$,..., $d_{4,5}$) should be thought of as y_{ij}: the jth replicate within the ith treatment group (lag class). (In this example, two of the 10 distances, d_{ab}, were arbitrarily assigned to each of the five lags; in a real analysis the geographic distances would determine these assignments.) The fully specified lag matrices model, then, is equivalent to a one-way ANOVA design, and differs from ANOVA only in that significance tests must be performed by permutation (Legendre et al. 1994). Like ANOVA models, the fully specified lag matrices model is not full rank; i.e., there is a linear dependency between the lag vectors (which sum to a vector of ones) and the intercept. Thus, the model has no unique solution and must be reparameterized to a full rank model (Rawlings et al. 1998, Chapter 9).

There are several common reparameterizations, each leading to the identical R^2 but allowing different hypotheses to be tested. In particular, we wish to test the hypotheses that the τ_i are different from their mean (i.e., $\tau_i-\bar{\tau}\neq 0$), where $\tau_i-\bar{\tau}$ is an autocorrelation index for the ith lag. Eliminating the intercept from the model leads to a reparameterization in which, rather than estimating μ and each τ_i, we estimate each $\mu_i=\mu+\tau_i$ (Rawlings et al. 1998:274). This reparameterization does not yield useful hypothesis tests: the μ_i (e.g., the predicted values in Figure 4G) may all be significantly different from zero, but not different from each other (in which case there would be no spatial pattern in the data).

To test the hypotheses of interest ($\tau_i-\bar{\tau}\neq 0$), we impose the constraint that $\Sigma\tau_i=0$. Thus, for the model above with five lags, we have

$$\tau_5=-(\tau_1+\tau_2+\tau_3+\tau_4). \tag{A.2}$$

The model for the distances (y) in the fifth lag class ($y_{51}=d_{3,5}$ and $y_{52}=d_{4,5}$ in our example),

$$y_{5j}=\mu+\tau_5+\varepsilon_{5j}, \tag{A.3}$$

can now be re-written as

$$y_{5j}=\mu+(-\tau_1-\tau_2-\tau_3-\tau_4)+\varepsilon_{5j}. \tag{A.4}$$

The parameter τ_5 may now be eliminated and the model re-defined as $\mathbf{Y}=\mathbf{X}^*\boldsymbol{\beta}^*+\boldsymbol{\varepsilon}$ (Rawlings et al. 1998:278):

$$\begin{pmatrix} y_{11} \\ y_{12} \\ y_{21} \\ y_{22} \\ y_{31} \\ y_{32} \\ y_{41} \\ y_{42} \\ y_{51} \\ y_{52} \end{pmatrix} = \begin{bmatrix} 1&1&0&0&0 \\ 1&1&0&0&0 \\ 1&0&1&0&0 \\ 1&0&1&0&0 \\ 1&0&0&1&0 \\ 1&0&0&1&0 \\ 1&0&0&0&1 \\ 1&0&0&0&1 \\ 1&-1&-1&-1&-1 \\ 1&-1&-1&-1&-1 \end{bmatrix} \begin{pmatrix} \mu^* \\ \tau_1^* \\ \tau_2^* \\ \tau_3^* \\ \tau_4^* \end{pmatrix} + \begin{pmatrix} \varepsilon_{11} \\ \varepsilon_{12} \\ \varepsilon_{21} \\ \varepsilon_{22} \\ \varepsilon_{31} \\ \varepsilon_{32} \\ \varepsilon_{41} \\ \varepsilon_{42} \\ \varepsilon_{51} \\ \varepsilon_{52} \end{pmatrix}. \tag{A.5}$$

Note that the linear dependency has been removed, so the reparameterized model has a unique solution. In terms of the original model parameters, the expectation of the ordinary least squares estimate of $\boldsymbol{\beta}^*$ is (Rawlings et al. 1998:278):

$$\mathrm{E}(\hat{\boldsymbol{\beta}}*) = \begin{pmatrix} \mu + \bar{\tau} \\ \tau_1 - \bar{\tau} \\ \tau_2 - \bar{\tau} \\ \tau_3 - \bar{\tau} \\ \tau_4 - \bar{\tau} \end{pmatrix} = \begin{pmatrix} \bar{\mu} \\ \bar{\mu}_1 - \bar{\mu} \\ \bar{\mu}_2 - \bar{\mu} \\ \bar{\mu}_3 - \bar{\mu} \\ \bar{\mu}_4 - \bar{\mu} \end{pmatrix}. \qquad \text{(A.6)}$$

Thus, the coefficients $\hat{\tau}_1^*, \hat{\tau}_2^*, \hat{\tau}_3^*$, and $\hat{\tau}_4^*$ in $\hat{\boldsymbol{\beta}}^*$ provide autocorrelation indices $(\tau_i - \bar{\tau})$ for lags 1–4; significance tests for the coefficients are performed using the MRM permutation method described in this paper and in Legendre et al. (1994).

All that remains now is to estimate $\tau_5 - \bar{\tau}$ and determine if the estimator is significantly different than zero. An unbiased estimator for $\tau_5 - \bar{\tau}$ is (Rawlings et al. 1998:279):

$$\hat{\tau}_5^* = -(\hat{\tau}_1^* + \hat{\tau}_2^* + \hat{\tau}_3^* + \hat{\tau}_4^*). \qquad \text{(A.7)}$$

In order to implement a permutation test for the hypothesis $\tau_5^* \neq 0$ (i.e., $\tau_5 - \bar{\tau} \neq 0$), it is necessary to reparameterize the model in the identical manner as before, but retaining τ_5 and eliminating instead any one of the other τ_i. For example, we could eliminate τ_1, in which case Eq. (A.5) would become:

$$\begin{pmatrix} y_{11} \\ y_{12} \\ y_{21} \\ y_{22} \\ y_{31} \\ y_{32} \\ y_{41} \\ y_{42} \\ y_{51} \\ y_{52} \end{pmatrix} = \begin{bmatrix} 1 & -1 & -1 & -1 & -1 \\ 1 & -1 & -1 & -1 & -1 \\ 1 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{pmatrix} \mu^* \\ \tau_2^* \\ \tau_3^* \\ \tau_4^* \\ \tau_5^* \end{pmatrix} + \begin{pmatrix} \varepsilon_{11} \\ \varepsilon_{12} \\ \varepsilon_{21} \\ \varepsilon_{22} \\ \varepsilon_{31} \\ \varepsilon_{32} \\ \varepsilon_{41} \\ \varepsilon_{42} \\ \varepsilon_{51} \\ \varepsilon_{52} \end{pmatrix}. \qquad \text{(A.8)}$$

The estimated coefficients $\hat{\tau}_i^*$ for the model in Eq. (A.8) should be identical to those for the model in Eq. (A.5), and the permutation tests for the two models should yield the same results.

In summary, the fully specified lag matrices model is reparameterized and tested as follows:

(a) Eliminate any one of the lags (τ_i) from the model by removing its column from **X** and, for the rows in **X** corresponding to the removed lag, replace each zero in the **X** columns of the retained lags with negative one. For example, Eq. (A.5) is the reparameterization of Eq. (A.1) after removing the fifth lag.
(b) For the lags retained in the reparameterized model, the ordinary least squares multiple regression coefficients provide autocorrelation indices $(\tau_i - \bar{\tau})$, and the MRM permutation method provides tests of the null hypotheses $\tau_i - \bar{\tau} = 0$.
(c) To obtain the autocorrelation index and significance test for the lag eliminated in step (a), repeat steps (a) and (b), but this time eliminating one of the other τ_i instead. For example, Eq. (A.8) is the reparameterization of Eq. (A.1) after removing the first lag.

Finally, two notes of caution are in order:

(1) Standardizing the unfolded distance vectors to mean zero and unit variance, which references the regression coefficients for different explanatory variables to a common scale, is often desirable. However, the coefficients of the fully specified lag matrices model are not interpretable in terms of the original response (e.g., Bray–Curtis distances) if the columns of **X** are standardized. Therefore, the **X** matrix for the fully specified lag matrices model should be coded with ones and zeros as in Eq. (A.1), and the re-defined $\mathbf{X}^*$ matrices with ones, zeros, and negative ones as in Eqs. (A.5) and (A.8). Note that the program Permute! (Casgrain 2002) reports standardized regression coefficients. This standardization affects the values of the coefficients, but not their *P*-values. Nonstandardized coefficients (which reflect the original coding of the variables) may be obtained from any standard regression software.

Another reason not to standardize the **X** matrix in the fully specified lag matrices model is the following: If there are unequal numbers of plot pairs in the different lag classes, then standardization will cause the columns in **X** to have different codings, and Eqs. (A.2)–(A.8) will no longer hold.

(2) Reparameterizing the lag matrices model is neither necessary nor desirable if only some of the lags are included in the model. For example, if the Mantel correlogram is used to determine at which lags there is significant autocorrelation, and only these lags are included in an MRM model, then there is no reason to reparameterize the lag

matrices: The linear dependency between the intercept and the lag matrices only arises only if all lag matrices are included in the model, and the interpretation of the reparameterization discussed above only holds for the fully specified model.

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