

# Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study

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**Abstract.** The Mantel correlogram is an elegant way to compute a correlogram for multivariate data. However, recent papers raised concerns about the power of the Mantel test itself. Hence the question: Is the Mantel correlogram powerful enough to be useful? To explore this issue, we compared the performances of the Mantel correlogram to those of other methods, using numerical simulations based on random, normally distributed data. For a single response variable, we compared it to the Moran and Geary correlograms. Type I error rates of the three methods were correct. Power of the Mantel correlogram was nearly as high as that of the univariate methods. For the multivariate case, the test of the multivariate variogram developed in the context of multiscale ordination is in fact a Mantel test, so that the power of the two methods is the same by definition. We devised an alternative permutation test based on the variance, which yielded similar results. Overall, the power of the Mantel test was high, the method successfully detecting spatial correlation at rates similar to the permutation test of the variance statistic in multivariate variograms. We conclude that the Mantel correlogram deserves its place in the ecologist's toolbox.

**Key words:** autocorrelation; correlogram; Geary; Mantel; Moran; multiscale ordination; multivariate variogram; simulation study; spatial correlation.

## INTRODUCTION

A traditional way of measuring spatial correlation in a univariate quantitative variable is to resort either to Moran's  $I$  (Moran 1950) or Geary's  $c$  (Geary 1954) spatial correlation statistics (Cliff and Ord 1981). These structure functions, each in its manner, measure the resemblance of pairs of values located within predefined distance classes. Practically, one computes a matrix of geographical distances among sampling sites and converts these distances into a vector of classes  $\mathbf{d}$ . The statistic is then computed in turn within each distance class  $d$ .

Moran's  $I$  formula bears a close resemblance to the Pearson correlation coefficient:

$$I(d) = \frac{\frac{1}{W} \sum_{h=1}^n \sum_{i=1}^n w_{hi} (y_h - \bar{y})(y_i - \bar{y})}{\frac{1}{n} \sum_{i=1}^n (y_i - \bar{y})^2} \quad \text{for } h \neq i \quad (1)$$

whereas Geary's  $c$  is akin to a squared distance measure

$$c(d) = \frac{\frac{1}{2W} \sum_{h=1}^n \sum_{i=1}^n w_{hi} (y_h - y_i)^2}{\frac{1}{n-1} \sum_{i=1}^n (y_i - \bar{y})^2} \quad \text{for } h \neq i \quad (2)$$

$y_h$  and  $y_i$  are the values of variable  $y$  at pairs of sites  $h$  and  $i$ ,  $\bar{y}$  is the mean of variable  $y$  over all sites and  $n$  is the number of observations (sites). Both formulas show the computation of the index value for a class of inter-site distance  $d$ .  $W$  is the number of pairs of points in the distance class considered. The weights  $w_{hi}$  have value 1 for pairs of sites belonging to distance class  $d$ , and 0 otherwise.

The expected value of Moran's  $I$  for no spatial correlation is  $E(I) = -1/(n-1)$ . For Geary's  $c$ , the expected value is 1.

For multivariate data, Sokal (1986) and Oden and Sokal (1986) proposed to construct a spatial correlation function on the basis of the Mantel (1967) test of matrix correlation. The principle goes as follows: one computes an appropriate resemblance matrix  $\mathbf{X}$  among sites on the basis of the ecological (or other) data, and for each geographical distance class, this matrix is compared using the standardized Mantel statistic  $r_M$  to a model matrix  $\mathbf{Y}$  where pairs of sites belonging to the same distance class receive value 1 and the other pairs receive value 0. The resemblance matrix subjected to testing can be computed in any way appropriate to the application field, e.g., using an ecological or genetic distance function. It does not have to be computed using the Euclidean distance formula. The standardized Mantel statistic has the same formula as the Pearson correlation coefficient, but computed between the values in distance or similarity matrices  $\mathbf{X}$  and  $\mathbf{Y}$  (the lower [or upper] triangular values only are used in the common case of a symmetric matrix  $\mathbf{X}$ ; the diagonal values are trivial and

Manuscript received 22 September 2011; revised 1 February 2012; accepted 2 February 2012. Corresponding Editor: B. D. Inouye.

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not used in the calculation):

$$r_M = \frac{1}{d-1} \sum_{i=2}^n \sum_{j=1}^{i-1} \left( \frac{x_{ij} - \bar{x}}{s_x} \right) \left( \frac{y_{ij} - \bar{y}}{s_y} \right) \quad (3)$$

where  $\bar{x}$  and  $\bar{y}$  are the means of the values in each of the lower-triangular distance matrices  $\mathbf{X}$  and  $\mathbf{Y}$  and  $s_x$  and  $s_y$  are their standard deviations;  $d = [n(n-1)/2]$  is the number of distances in the lower triangular part of each distance matrix. The expected value for no correlation is 0.

Note that despite the mathematical relationship between Pearson's  $r$  and Mantel's  $r_M$ , one should not try to interpret the actual  $r_M$  values as if they were equivalent to correlation coefficients among variables. Dutilleul et al. (2000) showed that for pairs of simulated variables with normal distributions, the  $r_M$  statistic computed between Euclidean distance matrices derived from these variables was always much smaller than the theoretical correlation between the simulated variables. They explained this phenomenon by showing, theoretically and empirically, that  $r_M$  calculated between matrices of squared Euclidean distances computed from these variables is equal to the squared Pearson's  $r$  between the original variables; the demonstration holds for the bivariate normal case only. When interpreting a Mantel correlogram, one should not look for high values of the statistic, but for the shape drawn by the significant  $r_M$  values. The sign of the coefficient is important, however. A positive (and significant)  $r_M$  indicates that for the given distance class, the multivariate similarity among sites is higher than expected by chance (i.e., the mean within-class similarity is higher than the mean among-class similarity). The reverse is true for negative  $r_M$  values: communities that are at the corresponding distance are more different than expected by chance. This interpretation is valid for  $r_M$  statistics computed between an ecological *similarity* matrix and distance class model matrices with value 1 for pairs of sites belonging to distance class  $d$ , and 0 otherwise. If the calculation is based on an ecological *distance* matrix, the sign of  $r_M$  has to be changed for the correlogram to display positive values in cases of positive spatial correlation. This change of sign is done automatically in function `mantel.correlog()` in R (R Development Core Team 2010).

Parametric tests exist for Moran's  $I$  and Geary's  $c$  coefficients. The Mantel statistic is generally tested by permutations, although a normal approximation exists for large data sets. Furthermore, the Appendix shows that a permutational test of Mantel's  $r_M$  on a matrix of squared Euclidean distances computed from univariate data and a distance model matrix is equivalent to a permutational test of Geary's  $c$  computed on the same data. It is also equivalent to a permutation test of the univariate semi-variance statistic used in variograms.

A correlogram is a graph representing the spatial correlation values against the distance classes. Correlo-

grams can be drawn on the basis of any of the three functions described above. Depending on the way that the distance classes have been constructed, a correlogram can be all-directional (when the variable of interest is isotropic) or directional (when the geographic distances have been calculated in a geographic direction determined by the user). Interpretation of correlograms, which can be tricky, is explained by Legendre and Fortin (1989) and Legendre and Legendre (1998, 2012: Chapter 13).

Apart from the Mantel correlogram, techniques to assess multivariate spatial structures by means of structure functions are scarce. One interesting approach is multiscale ordination (MSO; Wagner 2003, 2004). MSO allows a spatial partitioning of community variation among distance classes and a representation and testing of the community spatial structure in the form of a multivariate variogram, which is simply the sum of the univariate variograms (Wagner 2003, Legendre and Legendre 2012: Chapter 13).

The Mantel correlogram is an elegant idea, but recent papers have raised concerns about the power of the Mantel test of matrix correlation itself (Legendre et al. 2005, 2008, Legendre and Fortin 2010). Therefore, it is appropriate to investigate whether the Mantel correlogram has sufficient power to be useful to ecologists. This is why we set out to compare it to the performance of Moran's  $I$  and Geary's  $c$  in the univariate context (the use of a Mantel correlogram in the univariate context was needed only for comparison purposes), and to the multivariate variogram in the multivariate context, by using simulated data. We chose to base our simulations on random normal data compared using the Euclidean distance to provide a comparison of the Mantel correlogram with Moran and Geary correlograms in situations where the latter two are expected to perform at their best. The question addressed in this paper is thus: how does the Mantel correlogram compare to the other methods in terms of type I error rate and power in the case of random normal data and Euclidean distance matrices?

## MATERIALS AND METHODS

### *Data simulations*

The shape of our simulated data surface was a square (100 × 100 pixel) grid populated by values drawn at random from the normal distribution, which were autocorrelated.

A necessary preliminary step to a power study is to verify that the method under investigation has a correct rate of type I error. To that effect, we populated our grid with values drawn at random from a normal distribution with mean  $\mu = 0$  and standard deviation  $\sigma = 1$ . These values were generated using function `rnorm()` of the R language base package.

The random autocorrelated data were generated using an R function derived from the Fortran program

SimSSD (Legendre et al. 2002, 2004, 2005). SimSSD is available as a Supplement to Legendre et al. (2005).

Data generation was done as follows: random normal data were modified using conditional sequential Gaussian simulations based on a variogram, which produced data with isotropic spatial correlation. The spherical variogram model was controlled by values of the range parameter; values for this parameter were provided for each simulation run. In all simulations, the nugget variance was set to 0. The range parameter of the variogram was set using the following values: 5, 10, 20, 50, and 100, i.e., spatial correlation was made to vary among simulated data set from below the smallest range theoretically perceptible by the sampling design up to the point of encompassing the whole data set (100 units). The data were actually generated on a simulation grid larger than  $100 \times 100$  pixel to avoid border effects.

The sampling design was a regular  $10 \times 10$  grid overlaid on the  $100 \times 100$  grid; every 10th point was sampled in both directions. This resolution allowed us to sample data that were autocorrelated at scales starting well below the sampling interval (i.e., spatial correlation that should not be detected by analysis of the sample of observations), and ranging up to the broadest possible scale. Every simulation run consisted of 1000 independent replicate data with the same characteristics.

The multivariate data for the Mantel correlograms and multivariate variograms were made of two blocks of five independent variables. The first five variables were autocorrelated over the ranges defined above (except for the type I error rate simulations) whereas the last five variables were random normal variates with mean  $\mu = 0$  and standard deviation  $\sigma = 2$ . We added this amount of noise to the data to prevent the spatial correlation from being too strong and thus detectable with 100% power by all methods under investigation. All data sets, including the random normal variates, were generated prior to their use in the test runs, so that the exact same data could be submitted to the different statistical methods.

#### *Computation and tests of spatial statistics*

All correlograms were computed for the same distance classes to make them comparable. The class interval, measured in units on the simulated surface, was equal to 8.6 pixels.

The line of reasoning developed in the Appendix led us to run two sets of Mantel tests for univariate data: one set where a matrix of Euclidean distances computed on the simulated data was used and another set where the distances were squared.

A set of computations consisted of the following steps: (1) sample the next vector available among the 1000 data sets. (2) compute the statistics (Moran's  $I$ , Geary's  $c$ , multivariate variogram and Mantel's  $r_M$ ) for the seven first distance classes. (3) Test the coefficients. Variances in the variograms and correlations  $r_M$  in Mantel correlograms and in multivariate variograms

were tested by 999 permutations; the other two tests are parametric. (4) Write the values of the statistics and the associated probabilities to an output file. (5). Repeat steps 1 to 4 for the 1000 data sets. (6) Compute summary statistics: mean value of the statistics, rejection rates of  $H_0$  at  $\alpha = 0.05$  and their confidence intervals.

The Mantel correlogram was computed using the function `mantel.correlog()` of the `vegan` R package (*available online*).<sup>2</sup> Moran's  $I$  and Geary's  $c$  correlograms were obtained using a modified version of function `correlog()` of the package `pgirmess` (*available online*).<sup>3</sup> The multivariate variogram was obtained through a modified version of function `mso()` (`vegan` package): `correlog()` computes one-tailed tests in the direction of positive spatial correlation; `mso()` computes two-tailed tests. Therefore, we modified `correlog()` and `mso()` to allow the tests to be one-tailed in the direction of the sign of  $r_M$ , i.e., the same test as the default in `mantel.correlog()`. This may seem an overly liberal decision, but we justify it by the fact that when computing a correlogram one often has one-tailed hypotheses of positive spatial correlation for the first few distance classes. For these classes, a two-tailed test would be too conservative. Conversely, many spatial structures induce *negative* spatial correlation at larger distances, which are detected by one-tailed tests in the direction of the sign (which detect negative as well as positive correlations). A side effect of this decision is that in the simulations for type I error, one expects the overall rejection rate to be twice the  $\alpha$  significance level. For instance, for  $\alpha = 0.05$ , a test is expected to reject  $H_0$  in 5% of the runs in each tail, i.e., in 10% of the runs.

In its current version, the variogram test provided by function `mso()` is in fact the exact same Mantel test as performed by the function `mantel.correlog()` when the latter is computed on squared Euclidean distances. Consequently, we had no independent test to which we could compare the performance of the Mantel correlogram. This led us to devise another test based on a different statistic. The Mantel test is based on the correlation between a matrix of (ecological) distances among sites and a binary matrix representing the membership of sites to the distance class being tested. In our new test, the variogram statistic (variance) corresponding to each distance class is tested by random permutations of the data rows followed by recomputation of the statistic. The test is one-tailed in the direction of the sign of the difference between the statistic and the total variance of the data, which is the mathematical expectation of the variogram statistic. The test is run as follows for a given distance class  $k$ : (1) compute the variance of class  $k$ ,  $s_k^2$ , and the total variance,  $s_{tot}^2$ , of the data; (2) note the sign of the statistic obtained by subtracting  $s_{tot}^2$  from  $s_k^2$ ; (2) permute the rows of the data table; (3) recompute the variance of the permuted data

<sup>2</sup> <http://cran.r-project.org/package=vegan>

<sup>3</sup> <http://CRAN.R-project.org/package=pgirmess>

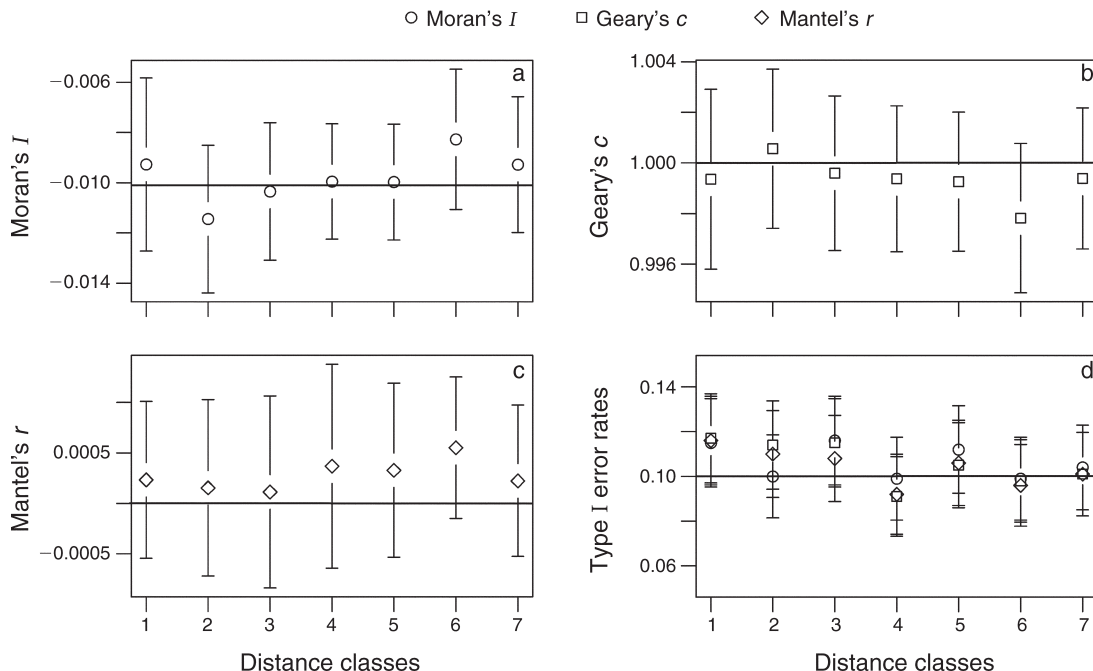


FIG. 1. (a, b, c) Values of the statistics and (d) type I error rates for seven distance classes of Moran (circles), Geary (squares) and Mantel (diamonds) correlograms run on random normal data (1000 independent runs). The Mantel correlograms were computed on squared distances. Type I error rates are for a significance level  $\alpha = 0.05$ , one-tailed on the side of the sign. The expected rejection rate under  $H_0$  was thus 0.10. Horizontal lines in the graphs indicate (a, b, c) the expectation of the statistic or (d) the type I error rate. Error bars show 95% confidence intervals.

in class  $k$ ,  $s_{k,perm}^2$ : (4) compare  $s_{k,perm}^2$  to the distribution of  $s_k^2$  obtained by permutation, in the tail given by the sign noted at step 2.

Another issue is the correction for multiple testing often applied to correlograms. Repeated testing on a given data set increases the overall risk of type I error. An overview of the most often-used correction procedures can be found in Legendre and Legendre (2012:23). In the simulations, we opted for no correction in order to obtain and compare the raw probabilities in each distance class.

RESULTS

Type I error rate

Fig. 1 shows the results of the type I error simulations for completely random, uncorrelated data in the univariate case. Fig. 4a and b provide the same type of results in the multivariate case; the Mantel correlogram and variance-based test of the multivariate variogram had very similar results. As can be seen, all methods investigated are valid for all distance classes. A statistical test is valid when the rejection rate of  $H_0$  is not larger than the significance level  $\alpha$ , for any value of  $\alpha$ , when  $H_0$  is true (Edgington 1995). Validity has been verified for other  $\alpha$  levels as well (not illustrated). Type I error rates were always correct (i.e., close to the expected value of 10% in our simulations). All statistics showed values close to their expectation at all distance classes. The results are the same for data that were autocorrelated

with a range of five units, i.e., half the sampling interval (not illustrated). This is normal, since the spatial correlation range was below the detection limit of the sampling design. In spite of the development presented in the Appendix, there are slight differences between the Mantel and Geary results, due to the fact that the tests of Geary correlograms were parametric.

Power

The results reported below always refer to the Mantel correlogram computed on squared Euclidean distances because this version of the  $r_M$  statistic is mathematically closer to Geary's  $c$ , as demonstrated in Appendix A. Small but nonsignificant differences between results based on Euclidean distances and squared Euclidean distances are due to the randomness of the permutations.

Univariate data.—Overall and as expected, the power of the three methods increased with the range of the spatial correlation in the data. The power of the three methods was approximately the same, with a slight advantage to Moran and Geary (for which our simulations used parametric tests, compared to permutational tests for the Mantel correlogram).

Fig. 2a–d shows the results of the simulations for data autocorrelated with a range of 10 units, i.e., corresponding to the sampling interval. Interestingly, over the 1000 independent runs, the three coefficients detected spatial correlation at the first distance class enough times to

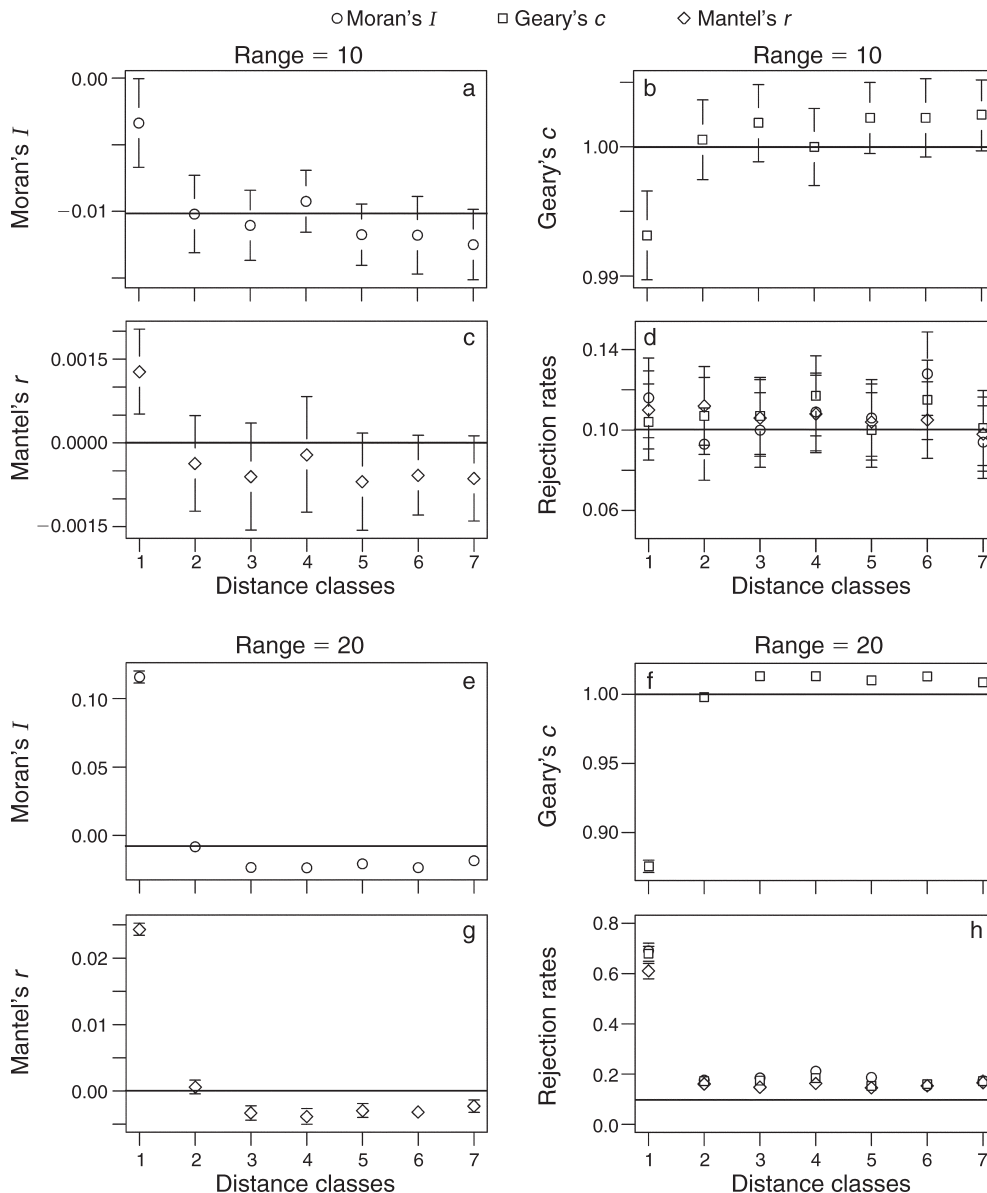


FIG. 2. Values of the statistics of (a, e) Moran's  $I$  (circles), (b, f) Geary's  $c$  (squares), and (c, g) Mantel's  $r$  (diamonds) correlograms, and (d, h) rejection rates of  $H_0$  for normal data autocorrelated with a range of (a-d) 10 units and (d-g) 20 units on the simulated surface and sampled every 10th unit in both directions. Rejection rates are for a significance level  $\alpha = 0.05$ , one-tailed on the side of the sign. The expected rejection rate under  $H_0$  was thus 0.10. Horizontal lines in the graphs indicate (a, b, c, e, f, g) the expectation of the statistic or (d, h) the expected rejection rate under  $H_0$ . Error bars show 95% confidence intervals; confidence intervals are omitted when they are smaller than the symbols.

change the mean values of the statistics by a very slight amount (Fig. 2a-c, where the scale of the ordinate was chosen to show tiny differences), but the power of these methods did not reach over the level of type I error (Fig. 2d). This means that even in the cases where these three methods reacted to short-range spatial correlation with a higher coefficient value, these values were not more often significant than with uncorrelated data. This is due to the fact that, in order to be consistently detected by the test, spatial correlation has to be larger than the class interval.

Increasing the range of spatial correlation increased the rates of detection at short range (first distance classes) and at progressively larger ranges. With a spatial correlation range of 20 units (Fig. 2e-h), the powers of the Moran and Geary coefficients for the first distance class were near 0.7. Mantel's  $r$  was slightly less powerful, at 0.6 (Fig. 2h). The power of the three coefficients dropped to around or below 0.20 for the second distance class, and remained slightly above the type I error level for the other five classes.



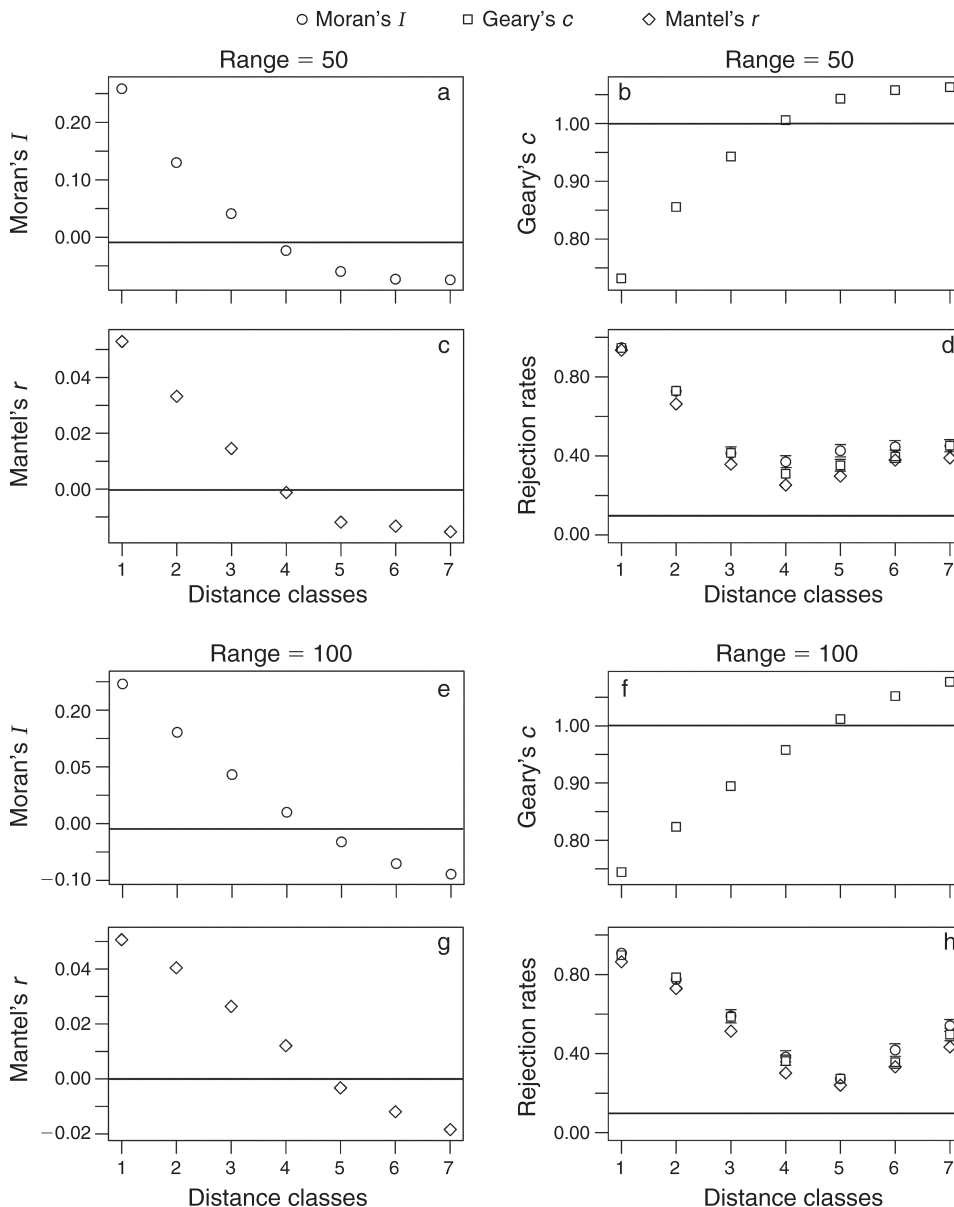


FIG. 3. Values of the statistics of (a, e) Moran's *I* (circles), (b, f) Geary's *c* (squares), and (c, g) Mantel's *r* (diamonds) correlograms, and (d, h) rejection rates of  $H_0$  for normal data autocorrelated with a range of (a–d) 50 units and (d–g) 100 units on the simulated surface and sampled every tenth unit in both directions. For details, see caption of Fig. 2.

With a spatial correlation range of 50 units (Fig. 3a–d), the power of the three statistics was high for the first two distance classes (close to 0.90; Fig. 3d). Spatial correlation was detected in approximately 40% of the cases in the third distance class. The rate dropped to around 0.3 in class 4, but increased slightly in the next classes, which displayed negative spatial correlation. When the spatial correlation range reached the extent of the simulated surface (range = 100), the results (Fig. 3e–h) resembled those obtained for a range of 50 units, but with the smallest rates of rejection in distance class 5

(Fig. 3h), and negative spatial correlation detected in around 40–55% of the cases in classes 6 and 7.

The conclusion from this part of the study is that the three methods performed in a very comparable manner, the Mantel correlogram being only slightly less powerful for univariate normal data than its classical univariate parametric counterparts.

*Multivariate data.*—For reasons explained in *Materials and methods*, the type I error and rejection rates of the Mantel correlogram and of the multivariate variogram in the form implemented in the version of mso()

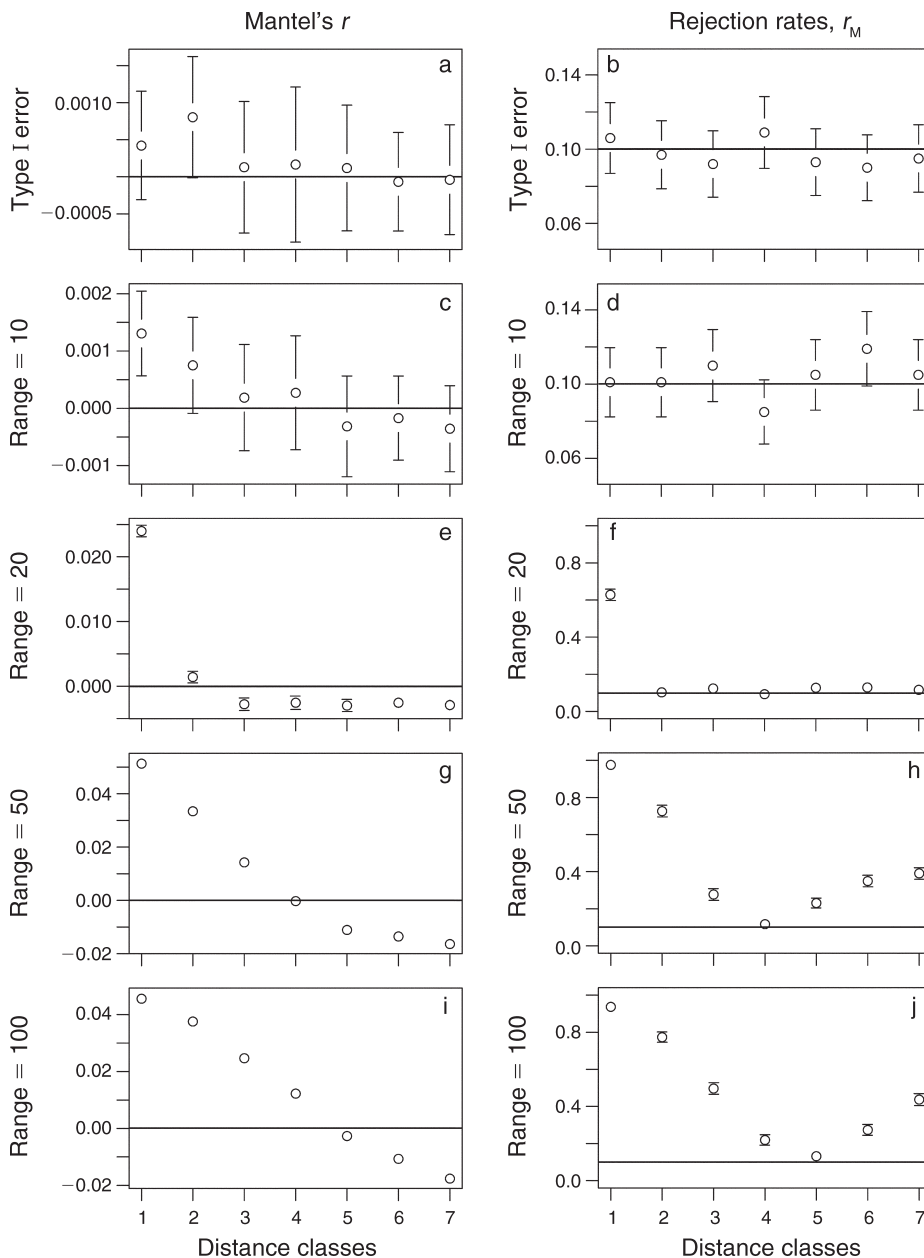


FIG. 4. Values of the (a, c, e, g, i) statistics, (b) type I error rates, and (d, f, h, j) power (which is the rejection rate of  $H_0$  when spatial correlation is present) for seven distance classes of multivariate Mantel correlograms run on (a, b) random normal data and (c–j) spatially correlated data in each of 1000 independent runs. For type I error and rejection rates, see caption of Fig. 2. Error bars show 95% confidence intervals.

currently distributed with `vegan` on CRAN were identical to within a few random permutations. This equivalence holds because the test used in `mso()` is a Mantel test based on Euclidean distances. A Mantel test based on a matrix of non-Euclidean (e.g., Bray-Curtis) ecological distances would of course not be equivalent to a multivariate variogram computed on raw data. Normality of distributions, however, plays no role in this equivalence because the tests are permutational. Furthermore, the power of our new test of the

multivariate variogram, based on variances, was undistinguishable from that of the Mantel correlogram for all spatial correlation ranges and distance classes. Therefore, only the results for the Mantel correlogram are presented.

Fig. 4c–j shows the distributions of  $r_M$  statistics and rejection rates of the Mantel correlogram for four ranges of spatial correlation. Overall, the properties observed here are the same as the ones displayed by the univariate Mantel correlogram. As soon as the range of spatial

correlation exceeds the sampling distance, the power of the Mantel correlogram increases, first in the first distance class, and then in the following ones when the range increases. Note the power to detect negative spatial correlation, lying at about 40% in class 7 of ranges 50 (Fig. 4h) and 100 (Fig. 4j).

The conclusion of this part of the study is that the Mantel test in multivariate correlogram analysis had the same type I error rate and power as the permutation test of the new variogram statistic. Furthermore, it displayed a power comparable to those of the univariate methods for normally distributed data with similar ranges of spatial correlation.

### Conclusion

All results reported above are dependent on the relationship between the range of the spatial patterns or correlation and the grain, i.e., the width of the distance classes chosen in the analyses. In this study based on a square grid with intersite distances equal to 10, we chose a class interval (8.6) that allowed the first class to encompass sites that were related horizontally, vertically and diagonally, since the interval [8.6, 17.4) contains the diagonal distance  $\sqrt{200} = 14.14$  (remember, the points are 10 units apart horizontally and vertically). The second class contained the second neighbors, and so on. It was important to choose a class interval that was both compatible with the grain of the study and the aim of the analysis. Since this condition was fulfilled, our study showed that, despite the recent concerns about the power of the Mantel test, which is at the core of the Mantel correlogram, this method provided a reliable assessment of the presence of spatial correlation in univariate as well as multivariate data. The concerns expressed in recent literature about the Mantel test are related to situations where alternative methods are available to address the scientific hypotheses more appropriately and to test them with more power. When looking for a multivariate assessment of spatial correlation, however, few alternatives exist to compute correlograms, which test hypotheses formulated in terms of distances. Therefore, our simulation results can be seen from two viewpoints: (1) comparisons between the Mantel correlogram and other approaches using data compatible with all methods showed that the Mantel correlogram behaves well; (2) in its own field, in the absence of equivalent methods, the Mantel correlogram has an acceptable power. For univariate data, the test of significance in the Mantel correlogram based on a Euclidean distance matrix is equivalent to the test of Geary's  $c$ , which is also the method to test autocorrelation values in univariate variograms. For multivariate data, the test used in Mantel correlograms has the exact same power as the only alternative method, which is the test of the multivariate variogram.

To be able to compare the methods with data compatible with all of them, we ran our simulations on random normal variables projected on sites that were

compared using the Euclidean distance, this class including distances that can be obtained by transforming the data followed by calculation of the Euclidean distance formula; see Legendre and Gallagher (2001) and Legendre and Legendre (2012: Section 7.7). However, the real value of the Mantel correlogram is for studies where the response data are modeled by a distance function that is not Euclidean. Among these are most of the coefficients developed for the analysis of species presence-absence data, for example, the coefficients of Jaccard and Sørensen, as well as quantitative distances for species abundance data, such as the asymmetric Gower coefficient, the geodesic metric, the Whittaker, Canberra, Clark, percentage difference, and mean character difference modified for species data. Distance coefficients intended for data other than species are, for example, the symmetric Gower, Estabrook-Rogers, and the generalized Mahalanobis distance for groups of observations. See Legendre and Legendre (2012) for descriptions of these coefficients, which can all be used in Mantel correlogram studies and in none of the other methods. Further simulations are needed to assess the behavior of the Mantel correlogram with nonnormal data and non-Euclidean distances.

### ACKNOWLEDGMENTS

This paper is dedicated to the memory of Robert R. Sokal who passed away on 9 April 2012. Professor Sokal was at the origin of the Mantel correlogram discussed in this paper.

We are grateful to Alena Motorina for help at the beginning of the simulation process, and to two anonymous reviewers for very insightful comments on the manuscript. This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) grant no. 7738 to P. Legendre.

### LITERATURE CITED

- Cliff, A. D., and J. K. Ord. 1981. Spatial processes. Pion, London, UK.
- Dutilleul, P., J. D. Stockwell, D. Frigon, and P. Legendre. 2000. The Mantel test versus Pearson's correlation analysis: assessment of the differences for biological and environmental studies. *Journal of Agricultural, Biological and Environmental Statistics* 5:131–150.
- Edgington, E. S. 1995. Randomization tests. Third edition. Marcel Dekker, New York, New York, USA.
- Geary, R. C. 1954. The contiguity ratio and statistical mapping. *Incorporated Statistician* 5:115–145.
- Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435–450.
- Legendre, P., D. Borcard, and P. R. Peres-Neto. 2008. Analyzing or explaining beta diversity: comment. *Ecology* 89:3238–3244.
- Legendre, P., M. R. T. Dale, M.-J. Fortin, P. Casgrain, and J. Gurevitch. 2004. Effects of spatial structures on the results of field experiments. *Ecology* 85:3202–3214.
- Legendre, P., M. R. T. Dale, M.-J. Fortin, J. Gurevitch, M. Hohn, and D. Myers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25:601–615.
- Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107–138.
- Legendre, P., and M.-J. Fortin. 2010. Comparison of the Mantel test and alternative approaches for detecting complex



- multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources* 10:831–844.
- Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second English edition. Elsevier Science BV, Amsterdam, The Netherlands.
- Legendre, P., and L. Legendre. 2012. *Numerical ecology*. Third English edition. Elsevier Science BV, Amsterdam, The Netherlands.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.
- Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37:17–23.
- Oden, N. L., and R. R. Sokal. 1986. Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Systematic Zoology* 35:608–617.
- R Development Core Team. 2010. R version 2.11.1. R Project for Statistical Computing, Vienna, Austria. [www.r-project.org](http://www.r-project.org)
- Sokal, R. R. 1986. Spatial data analysis and historical processes. Pages 29–43 in E. Diday, Y. Escoufier, L. Lebart, J. Pagès, Y. Schektman, and R. Tomassone, editors. *Data analysis and informatics, IV*. North-Holland, Amsterdam, The Netherlands.
- Wagner, H. H. 2003. Spatial covariance in plant communities: integrating ordination, variogram modeling, and variance testing. *Ecology* 84:1045–1057.
- Wagner, H. H. 2004. Direct multi-scale ordination with canonical correspondence analysis. *Ecology* 85:342–351.

#### SUPPLEMENTAL MATERIAL

##### Appendix

A demonstration of the equivalence between the permutational tests of the semi-variance, Geary's  $c$ , and Mantel's  $z_M$  statistics (*Ecological Archives* E093-129-A1).

**Borcard, D. and P. Legendre. 2012. Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. *Ecology* 93(6): 1473-1481.**

### Appendix A

A demonstration of the equivalence between the permutational tests of the semi-variance, Geary's  $c$ , and Mantel's  $z_M$  statistics

We demonstrate here that in the form used in the Mantel correlogram, the original Mantel statistic  $z_M$  is closely related to Geary's  $c$  and should produce the exact same permutational results when the Mantel correlogram is computed on squared distances. The demonstration concerns  $z_M$  instead of the widely used standardized coefficient  $r_M$ , but in practical terms this is not important since both forms also produce the exact same permutational test results. The comparison is made for the analysis of a single variable and the distance used to compute the Mantel correlogram statistic is the Euclidean distance.

1. Consider a matrix  $\mathbf{D}$  of Euclidean distances computed on the variable of interest. In the Mantel correlogram, for a given class of geographical distance  $d$ ,  $z_M$  is the scalar product of matrix  $\mathbf{D}$  and a binary model matrix built as explained in the Introduction, after transforming (stringing out) both matrices into vectors. Only the upper (or lower) triangular portion of each matrix need be used in the calculation since a Euclidean distance matrix is symmetric. Therefore,  $z_M$  is simply the sum of the distances of  $\mathbf{D}$  that belong to distance class  $d$ .

2. The semi-variance (Legendre and Legendre 1998 eq. 13.10) is the numerator of Geary's  $c$ :

$$\gamma(d) = \frac{1}{2W} \sum_{h=1}^{n-1} \sum_{i=h+1}^n w_{hi} (y_h - y_i)^2 \quad (\text{A1})$$

- Therefore, a permutational test of Geary's  $c$  is equivalent to a permutational test of  $\gamma$  since the two statistics differ only by the denominator of  $c$ , which is a constant.

- $w_{ih}$  is used to select the pairs belonging to class  $d$ ; it plays a role equivalent to the binary model matrix in the Mantel correlogram test.

- $W$  is the numbers of pairs in distance class  $d$ ; since this number is constant across the permutations, one can eliminate it without changing the result of the test.

- The computation of Mantel's  $z_M$  differs from  $\gamma$  by a single point: to obtain  $z_M$ , one sums the Euclidean distances between pairs of objects, whereas to obtain  $\gamma$  one sums *squared* Euclidean distances.

**Conclusion:** one can obtain a test equivalent to a *permutational* test of the semi-variance statistic or Geary's  $c$  by squaring the distances in  $\mathbf{D}$  before submitting them to the Mantel test.