The Mantel Test Versus Pearson's Correlation Analysis: Assessment of the Differences for Biological and Environmental Studies

Pierre DUTILLEUL, Jason D. STOCKWELL, Dominic FRIGON, and Pierre LEGENDRE

The space-time clustering procedure of Mantel was originally designed to relate a matrix of spatial distance measures and a matrix of temporal distance measures in a generalized regression approach. The procedure, known as the Mantel test in the biological and environmental sciences, includes any analysis relating two distance matrices or, more generally, two proximity matrices. In this paper, we discuss the extent to which a Mantel type of analysis between two proximity matrices agrees with Pearson's correlation analysis when both methods are applicable (i.e., the raw data used to calculate proximities are available). First, we demonstrate that the Mantel test and Pearson's correlation analysis should lead to a similar decision regarding their respective null hypothesis when squared Euclidean distances are used in the Mantel test and the raw bivariate data are normally distributed. Then we use fish and zooplankton biomass data from Lake Erie (North American Great Lakes) to show that Pearson's correlation statistic may be nonsignificant while the Mantel statistic calculated on nonsquared Euclidean distances is significant. After small-size artificial examples, seven bivariate distributional models are tried to simulate data reproducing the difference between analyses, among which three do reproduce it. These results and some extensions are discussed. In conclusion, particular attention must be paid whenever relations established between proximities are backtransposed to raw data, especially when these may display patterns described in the body of this paper.

Key Words: Bivariate distributions; Correlation analysis with raw data; Mantel test with proximity matrices; Parametric and permutational methods.

1. INTRODUCTION

Two statistical tools commonly used for investigating relationships among variables in biological or environmental data sets are (1) the parametric linear correlation analysis

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based on Pearson's r-statistic and performed on raw data between two variables of observation (e.g., Sokal and Rohlf 1995) and (2) a permutational testing procedure initiated by Mantel (1967) and further developed in Mantel and Valand (1970), which judges whether closeness in one set of variables is related to closeness in another set of variables. Mantel (1967) called his procedure generalized regression because it was performed between two matrices of distance measures. Since then, the procedure has become known as the Mantel test in the biological and environmental sciences. It is also referred to as Mantel and Valand's nonparametric MANOVA technique in the statistical sciences, being a special case of multiresponse permutation procedures (Mielke 1988).

Both the Mantel test and Pearson's correlation analysis can be used when the raw data are available so that the Euclidean distance or any proximity measure between two observational units can be derived from them. Naturally, a question then arises: Do the two methods of analysis always agree by leading to similar decisions regarding their respective null hypotheses? In other words, is a (non)significant Pearson's r-statistic calculated between two n-vectors of observations for variables X and Y always accompanied by a (non)significant Mantel's statistic between the two derived $n \times n$ distance matrices D_X and D_Y? The question is critical because, if the answer is no, conclusions drawn in the space of proximities cannot always be validly backtransposed into the space of raw data. The question is all the more critical because the Mantel test has been increasingly used since 1967, especially after the development of derived forms (e.g., Dow and Cheverud 1985; Manly 1986; Oden and Sokal 1986; Smouse, Long, and Sokal 1986; Sokal 1986; Clarke 1993; Legendre, Lapointe, and Casgrain 1994) and the promotion of the method in the biological and environmental sciences (Legendre and Fortin 1989; Fortin and Gurevitch 1993; Manly 1997; Legendre and Legendre 1998).

Despite the increasing number of its applications, the Mantel test may not have disclosed all of its secrets to users. In particular, it has never been demonstrated that the null hypothesis of no linear relationship between two vectors of observations should be rejected (accepted) whenever the null hypothesis of no linear relationship between the derived distance matrices is rejected (accepted). Such a demonstration or, alternatively, the finding of counterexamples to the previous statement motivated the present study.

The objective of this paper is threefold: first, observing that Pearson's r-statistic calculated between the X and Y sample data (from which D_X and D_Y are derived) can be close to zero (and hence nonsignificant) when the Mantel test indicates a significant (positive or negative) relationship between the distance matrices D_X and D_Y; second, understanding when such differences between analyses arise; and finally, assessing our understanding of these differences by being able to reproduce them.

Accordingly, we proceed in three steps. Step 1: We analyze seven data sets of planktivorous fish biomass and zooplankton biomass that were collected along transects in Lake Erie (Stockwell 1996). Step 2: Using results for the Lake Erie data, we study small-size artificial examples for which Pearson's r is 0.0 in relation with the corresponding Mantel statistic for different point densities in the biplot of raw data. Step 3: Following the small-size artificial examples of step 2, we try seven bivariate distributional models to simulate data reproducing the differences observed between the Mantel test and Pearson's correlation analysis on Lake Erie data.

In Section 2, we review the principles of the two methods of analysis, describe the Lake Erie example, and give the design of our simulation study. Theoretical results as well as empirical results obtained on real data and in the simulation study are presented and discussed in Section 3. The theoretical results specify situations in which both methods lead to similar decisions regarding their respective null hypothesis, whereas empirical results show situations in which differences between analyses arise. Closing remarks are given in Section 4, where the bivariate distributional models found to produce differences between analyses and some extensions of our results are discussed further.

2. MATERIALS AND METHODS

2.1 PEARSON'S CORRELATION ANALYSIS

To test whether ρ, the linear correlation between variables X and Y, is zero against a given alternative hypothesis, the following product-moment statistic was defined by Karl Pearson:

$$r = \frac{\sum_{i=1}^{n}(X_i - \bar{X})(Y_i - \bar{Y})}{\sqrt{\left[\sum_{i=1}^{n}(X_i - \bar{X})^2\right]\left[\sum_{i=1}^{n}(Y_i - \bar{Y})^2\right]}}, \tag{2.1}$$

where $X_1, \ldots, X_n, Y_1, \ldots, Y_n$, and $\bar{X}$ and $\bar{Y}$ denote random samples of size n for variables X and Y and the corresponding sample means, respectively. In the parametric approach, the calculation of the probability of significance for r is based on a t-test with $n-2$ d.f. (Sokal and Rohlf 1995, p. 575), i.e.,

$$t(n-2) = \frac{r}{\sqrt{\frac{1-r^2}{n-2}}}. \tag{2.2}$$

The null hypothesis of no linear correlation between X and Y is not true when the two variables covary positively (i.e., $\rho > 0$) or negatively (i.e., $\rho < 0$). Recall that a small (large) value of X is likely to be associated with a small (large) value of Y when $\rho > 0$, whereas a small (large) value of X is likely to be associated with a large (small) value of Y when $\rho < 0$. In hypothesis testing, we consider both the case of a one-tailed alternative and that of the two-tailed alternative. For the Lake Erie data, parametric linear correlation analysis was carried out with SAS procedure CORR (SAS Institute 1990a). In the simulation study, it was incorporated in a computer program performing the permutational Mantel analysis on the derived Euclidean distances.

2.2 THE MANTEL TEST

If $d_{X,ii'}$ and $d_{Y,ii'}$ represent the distances between observational units i and i', as derived from the observations for variables X and Y, let $D_X = (d_{X,ii'})$ and $D_Y = (d_{Y,ii'})$ denote the corresponding $n \times n$ distance matrices. In the Lake Erie example, X is planktivorous fish biomass, whereas Y is zooplankton biomass; the observational units are sampling sites along a transect; distances are Euclidean for both variables, so $d_{X,ii'} = |X_i - X_{i'}|$ and $d_{Y,ii'} = |Y_i - Y_{i'}|$.

The normalized Mantel statistic, defined as the product-moment coefficient of linear correlation between distance matrices D_X and D_Y, is

$$\frac{\sum\sum(d_{X,ii'} - \bar{d}_X)(d_{Y,ii'} - \bar{d}_Y)}{\sqrt{\left[\sum\sum(d_{X,ii'} - \bar{d}_X)^2\right]\left[\sum\sum(d_{Y,ii'} - \bar{d}_Y)^2\right]}}, \tag{2.3}$$

where $\Sigma\,\Sigma$ denotes the double summation over i and i' with i ranging from one to n and $i < i'$ by symmetry of D_X and D_Y, and $\bar{d}_X$ and $\bar{d}_Y$ are the means of distances derived from the X and Y raw data, respectively. The null hypothesis of no linear relationship between D_X and D_Y is likely to be rejected when small (large) distances d_X are associated with small (large) distances d_Y (positive relationship) or when points far apart along the Y-axis tend to be close to each other along the X-axis and reversely (negative relationship). Following Mantel and Valand's (1970) terminology, statistic (2.3) judges whether closeness in one variable or set of variables is related to closeness in another variable or set of variables.

Significance of the normalized Mantel statistic was assessed by permutations in our study by randomly reassigning labels $i = 1, \ldots, n$ to X-observations while keeping labels of Y-observations fixed and by calculating the value of the normalized Mantel statistic for each permutation. The one-tailed significance probability was provided by the proportion of permutations for which the value of statistic (2.3) was greater (smaller) than or equal to the initial value when this was positive (negative); the two-tailed significance probability was provided by the proportion of permutations for which the value of statistic (2.3) was greater than or equal to the initial value in absolute value. Each significance probability was calculated from 1,000 permutations, as recommended by Manly (1997), and the initial labeling was included among the permutations, following Hope (1968). For the Lake Erie data and in the simulation study, the permutational Mantel analysis was carried out with our own computer program written in the SAS/IML language (SAS Institute 1989).

Originally, the Mantel method is related to the analysis of n events, each event involving a time of occurrence and a location of occurrence. For a pair of events, the temporal separation between the two events and the spatial separation between them are of interest. The Mantel (1967) approach was to consider the exact separation, suggesting the use of measures of closeness. This problem was initially addressed by Knox (1964), who had considered whether, for each pair of events, both the temporal separation and the spatial separation were of some limited magnitude (Nathan Mantel, personal communication). Mantel and Valand (1970) relaxed the restriction to spatial and temporal distance measures by considering any two matrices of distances. Accordingly, the Mantel statistic in this paper is a coefficient of linear correlation between D_X and D_Y. However, the Mantel test here does not include tests of *a priori* classifications or multiresponse permutation procedures (Mielke, Berry, and Johnson 1976), although our results may have implications for other forms of the Mantel test such as the Mantel correlogram (see Section 4.2).

2.3 The Lake Erie Data

Seven data sets of planktivorous fish and zooplankton biomass were collected simultaneously at night along transects in Lake Erie (North American Great Lakes) during May and September 1994 (Stockwell and Sprules 1995; Stockwell 1996). An optical plankton counter (Model OPC-1 T, Focal Technologies, Inc., Dartmouth, Canada) mounted on a hydrodynamic V-fin (Endeco/YSI, Inc., Marion, USA) was used to sample zooplankton biomass along each transect. The V-fin was deployed in an undulating fashion to profile the water column as the ship traversed each transect. Zooplankton biomass estimates were recorded at 1-second intervals along the towpath. These estimates were collapsed into one dimension by vertically integrating the data. Integration was accomplished by taking the mean of all biomass estimates for each pair of nonoverlapping ascents and descents of the V-fin towpath (Stockwell 1996). Fish biomass was measured along each transect with a Biosonics model 102 dual beam echosounder operating at 120 kHz. Calibration of the acoustic system was done following Foote and MacLennan (1983). Only fish with lengths of 12–200 mm were used to estimate biomass because fish in this size range in Lake Erie are predominantly planktivores. Mass of individual targets was calculated using length–mass relationships from trawl data. Biomass was estimated by summing individual masses and dividing by sampling volume over 1-m depth intervals. These data were spatially aligned with the V-fin towpath, and water column means were calculated over the corresponding horizontal and vertical distances to match the integrated zooplankton biomass data collected from the optical plankton counter.

The resulting data sets are coded Erie 1–7. They consist of mean water column estimates of paired planktivorous fish biomass (X) (fresh g/m^3) and zooplankton biomass (Y) (fresh μg/L) spatially distributed along a transect. The sample size n ranges from 35 to 94, depending on the data set. For each data set, the n sample data for X were transformed to an $n \times n$ matrix of Euclidean distances D_X, and so were the n sample data for Y, with D_Y as the outcome. The presence of outliers in two of the initial seven data sets led to further analyses after removal of the outlier(s), providing a total of nine data sets analyzed; the two additional data sets are coded Erie 2^* and Erie 7^*. Results are reported for six data sets. The Lake Erie data analyzed in this paper are available from the second author on request.

For each data set, the raw data were submitted to parametric linear correlation analysis based on Pearson's r-statistic (Section 2.1), whereas the matrices of Euclidean distances were submitted to the Mantel test (Section 2.2). For use in the discussion, Geary's c spatial correlograms and Spearman's rank correlation coefficient were calculated on the raw data using the R package (Legendre and Vaudor 1991) and SAS procedure CORR (SAS Institute

1990a), respectively. For the same reason, the Mantel correlogram (Oden and Sokal 1986; Sokal 1986) was computed on the Euclidean distances d_Y versus d_X and the Mantel test was performed on $n \times n$ matrices of ranks corresponding to the distance classes in which Euclidean distances d_X and d_Y fall, given a number of defined classes; the R package was used in both cases. Equal-frequency distance classes were defined following Dutilleul and Legendre (1993).

2.4 Design of the Simulation Study

Following the Lake Erie example in which a nonsignificant Pearson's r is observed while the Mantel statistic is significant for some transects (see Section 3.2), we focused on the $\rho = 0$ case in our simulations. In practice, this situation may have more serious implications than the reverse (i.e., significant Pearson's r for a nonsignificant Mantel statistic). In fact, when the raw data are not available, erroneously concluding there is a linear correlation between X and Y when the Mantel statistic is significant may have more severe consequences than erroneously concluding there is no linear correlation between X and Y because the Mantel test indicates no relationship between D_X and D_Y. Moreover, a perfect linear relationship between raw data (i.e., $Y_i = a + bX_i$ with $b = \rho(\sigma_Y/\sigma_X)$ and $\rho \neq 0$) automatically implies a perfect linear relationship without intercept for the derived Euclidean distances (i.e., $d_{Y,ii'} = |Y_i - Y_{i'}| = |b||X_i - X_{i'}| = |b|d_{X,ii'}$) or squared Euclidean distances (i.e., $d^2_{Y,ii'} = b^2 d^2_{X,ii'}$).

After experimenting with small-size artificial examples, we consider seven distributional models for the random couple (X, Y) (Table 1). The first three models (i.e., arrow 1, arrow 2, arrow 3) are unimodal in Y. They differ in the point density along the X-axis, which is higher on the left for arrow 1, in the middle for arrow 2, and on the right for arrow 3. Arrow 1 is directly inspired from the pattern of some data sets in the Lake Erie example. The fourth model (i.e., U transposed) is bimodal in Y. This model originates from the quadratic relationship $Y = X^2$, for which $r = 0.0$ over a symmetric range of negative and positive values for X. Here the U, which extends to $0.0 \leq Y \leq X^2$, has been

Table 1. Bivariate Distributional Models Used in the Simulation Study

Name	*Description*
Arrow 1	$X = \exp + 1.0,\ Y \mid x = \text{norm}/x^2$
Arrow 2	$X = \text{norm} + 3.0,\ Y \mid x = \text{norm}/x^2$
Arrow 3	$X = 4.0 - \exp,\ Y \mid x = \text{norm}/x^2$
U transposed	$X = \exp + 1.0,\ Y \mid x = \text{uni1}/x^2$ if $\text{uni2} \geq 0.5$ and $2.0 - \text{uni1}/x^2$ otherwise
Circle 1 (uniform)	$X = 2.0(\text{uni1} - 0.5),\ Y \mid x = 2.0(\text{uni2} - 0.5)(1 - x^2)^{1/2}$
Circle 2 (concentric)	$X = \text{uni1}\cos(2\pi\text{uni2}),\ Y \mid x = \text{uni1}\sin(2\pi\text{uni2})$
Square	$X = \text{uni1},\ Y \mid x = \text{uni2}$

Exp, exponential distribution with parameter $\lambda = 1.0$; norm, normal distribution with zero mean and unit variance; uni1 and uni2, two independent uniform distributions over the $[0, 1]$ interval; $Y \mid x$, conditional distribution of Y given x.

transposed and moved in order to ensure positive values for both X and Y. The last three models (i.e., circle 1, circle 2, square) are more classical. The two circular models differ in the point density within the circle, which is uniform for circle 1 and concentric for circle 2.

The RANEXP, RANNOR, and RANUNI functions of SAS (SAS Institute 1990b) were used to simulate data. One thousand samples of size 100 were generated for each model; we tried different sample sizes (e.g., 50, 100, 150) but present results only for $n = 100$. We used our own computer program written in the SAS/IML language (SAS Institute 1989) to simulate data and perform the parametric correlation analysis on the raw data and the permutational Mantel analysis on the Euclidean distances. Empirical significance levels represent mean rates of rejection of the null hypothesis over 1,000 samples of size 100 for a 0.05 theoretical level.

3. RESULTS AND DISCUSSION

3.1 SITUATIONS OF AGREEMENT

Our primary effort here is to delineate the situations in which the Mantel test and Pearson's correlation analysis lead to similar decisions regarding their respective null hypothesis (i.e., situations of agreement). We also want to go beyond the perfect linear relationship $Y = a+bX$ mentioned in Section 2.4. Therefore, consider sample data (X_i, Y_i) $(i = 1, \ldots, n)$ from a bivariate distribution so that $\mathrm{E}[Y_i \mid X_i] = a + bX_i$. Let $\mathrm{E}[X_i] = \mu_X$ and $\mathrm{E}[Y_i] = \mu_Y$ for $i = 1, \ldots, n$ and $\boldsymbol{\Sigma_x}$, $\boldsymbol{\Sigma_y}$ denote the autocovariance matrices associated with the $n \times 1$ random vectors $\boldsymbol{x} = (X_1, \ldots, X_n)'$ and $\boldsymbol{y} = (Y_1, \ldots, Y_n)'$, where $'$ is the transpose operator. The multivariate normal model for $(\boldsymbol{x}', \boldsymbol{y}')'$ may then be written as

$$\mathrm{N}_{2n}\left[\begin{pmatrix}\mu_X \mathbf{1}_n \\ \mu_Y \mathbf{1}_n\end{pmatrix}, \begin{pmatrix}\boldsymbol{\Sigma_x} & \boldsymbol{\Sigma_{xy}} \\ \boldsymbol{\Sigma_{xy}} & \boldsymbol{\Sigma_y}\end{pmatrix}\right], \tag{3.1}$$

where $\mathbf{1}_n$ denotes the $n \times 1$ vector of ones and $\boldsymbol{\Sigma_{xy}}$ is the matrix of cross-covariances $\mathrm{cov}(\boldsymbol{x}, \boldsymbol{y})$.

To benefit from the properties of quadratic forms in the normal vector (e.g., Searle 1971) and because $d_{Y,ii'} = |b| d_{X,ii'}$ is equivalent to $d^2_{Y,ii'} = b^2 d^2_{X,ii'}$, we work below with squared Euclidean distances and calculate $\mathrm{cov}(d^2_{X,ii'}, d^2_{Y,ii'})$ for any pair (i, i') under model (3.1). Any squared Euclidean distance $d^2_{X,ii'}$ can be written as a quadratic form in $\boldsymbol{x}$, defined by a given $n \times n$ matrix $\boldsymbol{A}_{i,i'}$. This matrix is full of zeros except entries (i, i) and (i', i'), which are equal to 1.0, and entries (i, i') and (i', i), which are equal to -1.0. The same applies to $d^2_{Y,ii'}$ with random vector $\boldsymbol{y}$ and the same matrix $\boldsymbol{A}_{i,i'}$. The calculation of $\mathrm{cov}(d^2_{X,ii'}, d^2_{Y,ii'})$ then becomes the calculation of $\mathrm{cov}(\boldsymbol{x}'\boldsymbol{A}_{i,i'}\boldsymbol{x}, \boldsymbol{y}'\boldsymbol{A}_{i,i'}\boldsymbol{y})$, which can be rewritten as the covariance between two quadratic forms in the $2n \times 1$ random vector $(\boldsymbol{x}', \boldsymbol{y}')'$. Matrix $\boldsymbol{A}_{i,i'}$ simply needs to be completed by three $n \times n$ matrices of zeros (the completion of $\boldsymbol{A}_{i,i'}$ differs depending on whether it is for $d^2_{X,ii'}$ or $d^2_{Y,ii'}$), which finally provides two $2n \times 2n$ matrices $\boldsymbol{B_x}$ and $\boldsymbol{B_y}$ that define the quadratic forms in $(\boldsymbol{x}', \boldsymbol{y}')'$ that are equivalent to $\boldsymbol{x}'\boldsymbol{A}_{i,i'}\boldsymbol{x}$ and $\boldsymbol{y}'\boldsymbol{A}_{i,i'}\boldsymbol{y}$. The second-order properties of quadratic forms in the normal vector (Searle 1971, p. 66), combined with the assumed constancy of $\mathrm{E}[X_i]$ and $\mathrm{E}[Y_i]$ for $i = 1, \ldots, n$, then provide that $\mathrm{cov}(d^2_{X,ii'}, d^2_{Y,ii'})$ is equal to 0.0 or not, depending on whether $\mathrm{cov}(\boldsymbol{x}, \boldsymbol{y}) = \mathbf{0}$ or not, whatever the autocovariance structure of random vectors $\boldsymbol{x}$ and $\boldsymbol{y}$.

More precisely, under a spherical variance–covariance structure for $\boldsymbol{x}$ and $\boldsymbol{y}$ (i.e., $\boldsymbol{\Sigma}_{\boldsymbol{x}} = \sigma^2_X \boldsymbol{I}_n$ and $\boldsymbol{\Sigma}_{\boldsymbol{y}} = \sigma^2_Y \boldsymbol{I}_n$), it can be proven that

$$\mathrm{corr}(d^2_{X,ii'}, d^2_{Y,ii'}) = \rho^2 \tag{3.2}$$

if $\boldsymbol{\Sigma}_{\boldsymbol{xy}} = \rho \boldsymbol{I}_n$. On the other hand, if $\boldsymbol{x}$ and $\boldsymbol{y}$ follow two processes with autocovariances inversely proportional to the distance between points [i.e., $\mathrm{cov}(X_i, X_{i'}) = \sigma^2_X \rho_X^{d_{X_{i,i'}}}$ and $\mathrm{cov}(Y_i, Y_{i'}) = \sigma^2_Y \rho_Y^{d_{Y_{i,i'}}}$ with ρ_X and ρ_Y the autocorrelation parameters], then

$$\mathrm{corr}(d^2_{X,ii'}, d^2_{Y,ii'}) = \frac{\rho^2}{(1-\rho_X)(1-\rho_Y)}. \tag{3.3}$$

We verified equality (3.2) empirically. At the same time, we also investigated the relationship between $\mathrm{corr}(d_{X,ii'}, d_{Y,ii'})$ and ρ empirically since the second-order properties of quadratic forms in the normal vector are not applicable in that case. The numerical results reported in Table 2 confirm the correctness of equality (3.2). In comparison, $\mathrm{corr}(d_{X,ii'}, d_{Y,ii'})$ tends to be lower than $\mathrm{corr}(d^2_{X,ii'}, d^2_{Y,ii'})$ by about 10%. For smaller sample sizes, equality (3.2) may be approximate due to some underestimation of ρ by r (results not reported).

Thus, under the multivariate normal distribution model, the direct measurement of association on raw data is equivalent to the indirect measurement of association on squared Euclidean distances in that $\mathrm{corr}(d^2_{X,ii'}, d^2_{Y,ii'}) = 0.0$ for any (i, i') if and only if $\boldsymbol{\Sigma}_{\boldsymbol{xy}} = \mathbf{0}$, whatever $\boldsymbol{\Sigma}_{\boldsymbol{x}}$ and $\boldsymbol{\Sigma}_{\boldsymbol{y}}$. When $\rho > 0.0$, the correlation for the raw data and the correlation for the derived squared Euclidean distances agree in sign, with autocorrelation decreasing

Table 2. Theoretical Values of Correlation for the Raw Data and the Derived Squared Euclidean Distances Versus Empirical Mean Values of Correlation for the Raw Data and the Derived Euclidean Distances and Squared Euclidean Distances From 1,000 Samples of Bivariate Raw Data of Size 100

Theoretical ρ	*Theoretical correlation between squared Euclidean distances*	*Empirical mean of* ρ	*Empirical mean of Mantel statistic*[a] *between Euclidean distances*	*Empirical mean of Mantel statistic*[a] *between squared Euclidean distances*
0.0	0.00	−0.0033	0.0011	0.0017
0.1	0.01	0.0961	0.0093	0.0107
0.2	0.04	0.1956	0.0346	0.0391
0.3	0.09	0.2952	0.0777	0.0872
0.4	0.16	0.3951	0.1390	0.1551
0.5	0.25	0.4951	0.2194	0.2432
0.6	0.36	0.5954	0.3202	0.3519
0.7	0.49	0.6961	0.4437	0.4815
0.8	0.64	0.7971	0.5930	0.6323
0.9	0.81	0.8984	0.7732	0.8050

[a] The normalized version of the statistic is reported. See Section 3.1 for details.

Table 3. Parametric Linear Correlation Analysis on Raw Data and Permutational Mantel Analysis on Derived Euclidean Distances for Six Sets of Lake Erie Biomass Data

	Pearson's correlation analysis			*Mantel test*		
Data set[a]	*Statistic*	*One-tailed p*[b]	*Two-tailed p*[b]	*Statistic*[c]	*One-tailed p*[b]	*Two-tailed p*
Erie 1 ($n = 54$)	0.072	0.302	0.605	−0.061	0.125	0.264
Erie 2 ($n = 87$)	0.084	0.219	0.437	0.030	0.238	0.674
Erie 2* ($n = 86$)	0.057	0.302	0.604	0.065	0.155	0.292
Erie 5 ($n = 38$)	−0.058	0.364	0.727	−0.144	0.026	0.116
Erie 7 ($n = 63$)	−0.023	0.429	0.857	−0.091	0.005	0.137
Erie 7* ($n = 61$)	−0.064	0.313	0.626	−0.110	0.018	0.069

[a] Data sets Erie 2^* and Erie 7^* were obtained from Erie 2 and Erie 7 by removing the outlier(s) on the right-hand side of the Y versus X scattergram in Figure 1(b) and (d).

[b] The one-tailed significance probability was calculated as the probability of having a statistic value greater than the one observed when this was positive and as 1.0 minus that probability when the observed value of the statistic was negative. A t-distribution with $n - 2$ d.f. was used in Pearson's correlation analysis, whereas 1,000 permutations were used in the Mantel test. This explains why the one-tailed p is equal to 0.5 times the two-tailed p for Pearson's correlation analysis but not for the Mantel test. The one-tailed p is reported for both methods of analysis to facilitate the comparison between results.

[c] The normalized version of the statistic is reported.

or increasing $\text{corr}(d^2_{X,ii'}, d^2_{Y,ii'})$ with respect to ρ^2. When $\rho < 0.0$, $\text{corr}(d^2_{X,ii'}, d^2_{Y,ii'})$ differs from 0.0 but is positive. In other words, under the multivariate normal distribution model, when the mean of Y varies in relation with the mean of X (strictly speaking, the conditional expectation of Y given x depends on x), so do the corresponding variances or between-individual dispersion (proximity) measures provided by squared Euclidean distances, with a disagreement in sign between correlations when $\rho < 0.0$. The theoretical approach followed here is not readily available for mixtures of normal and exponential distributions as in the arrow 1–3 and U-transposed models of Section 3.4, which justifies the empirical approach followed there. Moreover, we shall see that, outside the multivariate normal distribution model, Mantel statistic values can be significantly different from 0.0, while Pearson's r-values equal 0.0.

3.2 THE LAKE ERIE EXAMPLE

Numerical results are reported in Table 3. On the basis of the two-tailed significance probability $p > |r|$, none of the nine data sets analyzed showed a linear correlation between planktivorous fish biomass (X) and zooplankton biomass (Y) that was significant at the 0.05 level. However, for three data sets (i.e., Erie 5, Erie 7, Erie 7*), the normalized Mantel statistic calculated between Euclidean distances (d_X and d_Y) was negative and significant at the 0.05 level, based on the left-hand one-tailed p. This disagreement is illustrated in

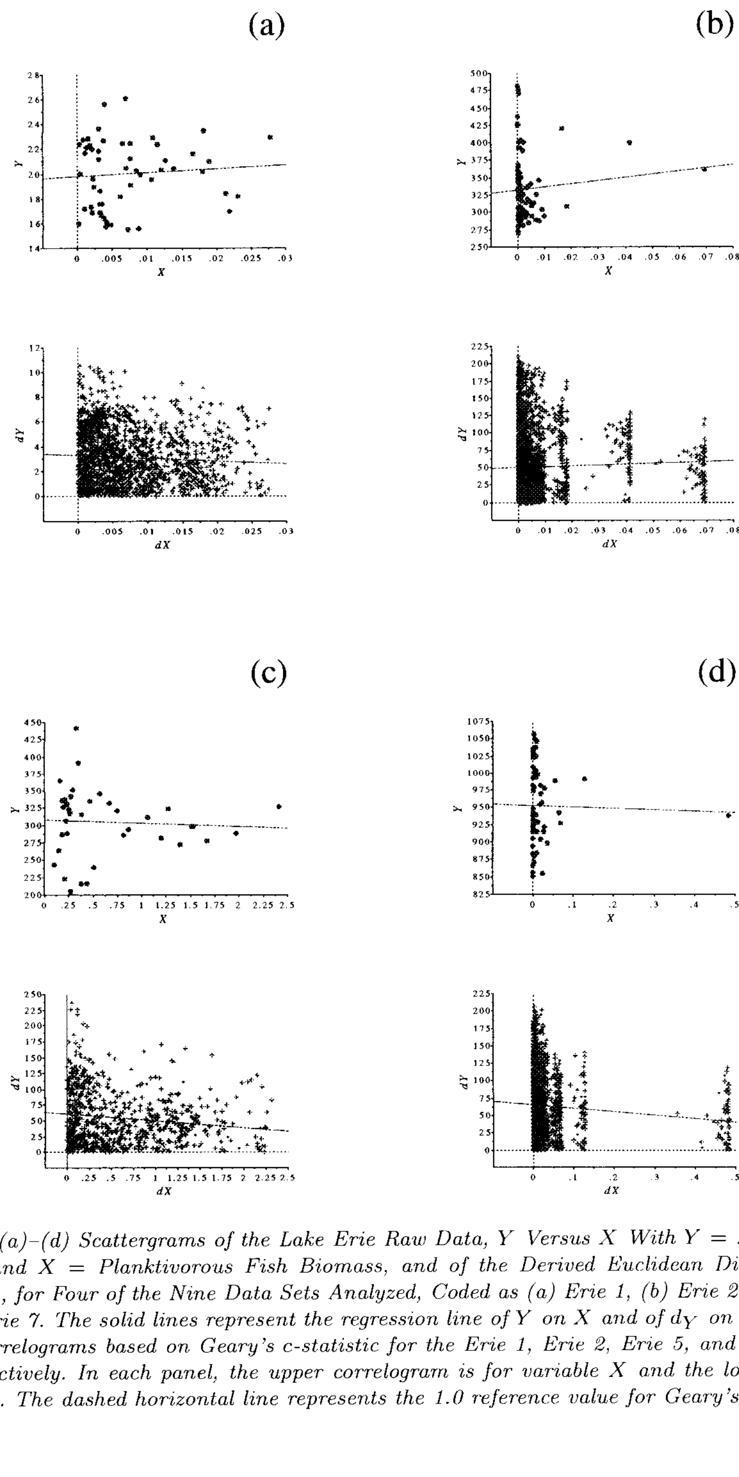

Figure 1. (a)–(d) Scattergrams of the Lake Erie Raw Data, Y Versus X With Y = Zooplankton Biomass and X = Planktivorous Fish Biomass, and of the Derived Euclidean Distances, d_Y Versus d_X, for Four of the Nine Data Sets Analyzed, Coded as (a) Erie 1, (b) Erie 2, (c) Erie 5, and (d) Erie 7. The solid lines represent the regression line of Y on X and of d_Y on d_X. (e)–(h) Spatial correlograms based on Geary's c-statistic for the Erie 1, Erie 2, Erie 5, and Erie 7 data sets, respectively. In each panel, the upper correlogram is for variable X and the lower one for variable Y. The dashed horizontal line represents the 1.0 reference value for Geary's c-statistic.

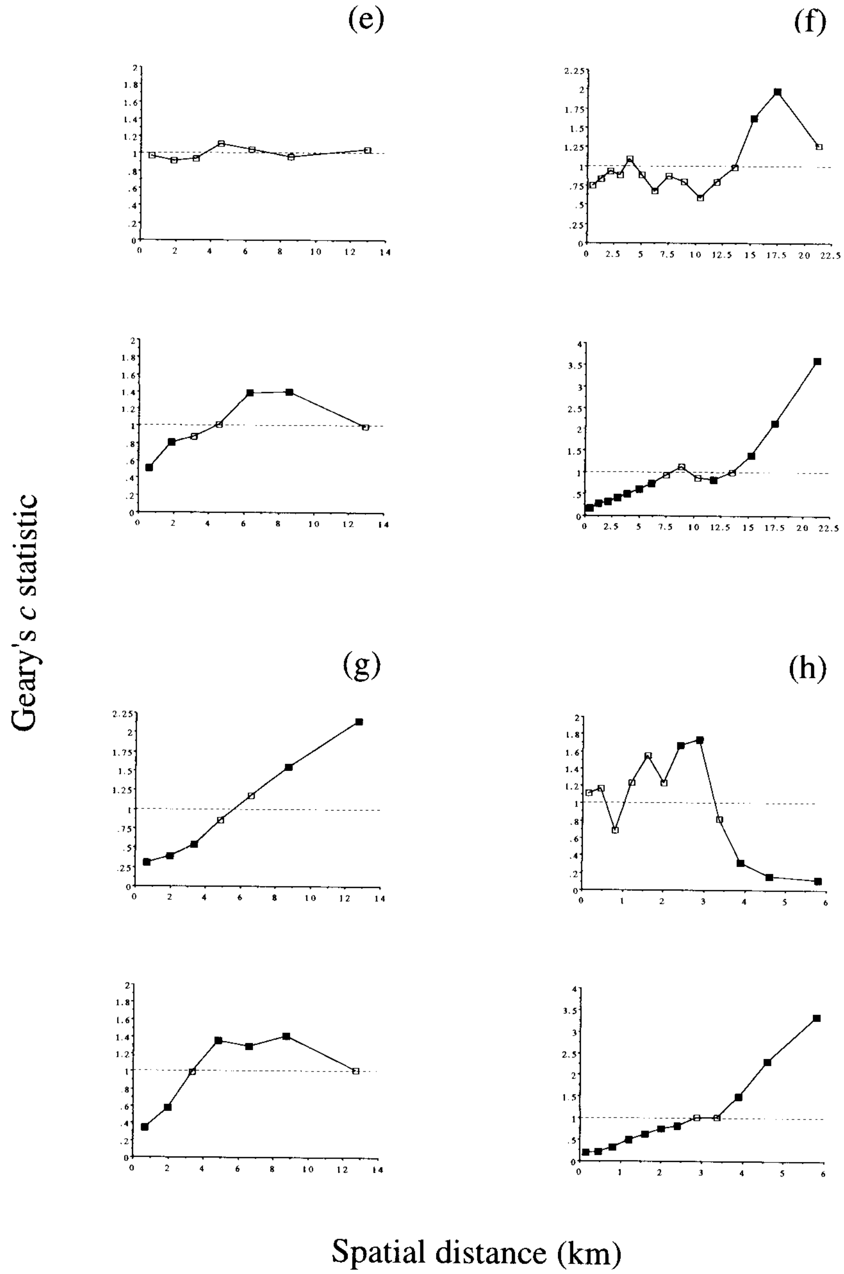

Figure 1. Continued.

Figure 1(c) and (d) for Erie 5 and Erie 7. Two data sets, which do not present the disagreement (i.e., Erie 1 and Erie 2), are also presented [Fig. 1(a), (b)].

Data sets Erie 2 and Erie 7 are characterized by outliers on the right-hand side of the Y versus X scattergram, resulting from a high concentration of fish at a few sampling sites.

The analyses redone after removing the outlier of Erie 2 and the two outliers of Erie 7 provided similar results (see Erie 2* and Erie 7* in Table 3). Thus, the origin of the agreement and disagreement between the Mantel test and Pearson's correlation analysis for Erie 2 and Erie 7 is not in the outliers. It is also not in the autocorrelation of the raw data and its nuisance effects on the correlation analysis of spatial processes. In fact, X presents no spatial autocorrelation at small distance classes and Y is characterized by a spatial structure of trend type for both data sets. The only difference is in the sign of spatial autocorrelation at larger distance classes for an extent that is wider in Erie 2 than in Erie 7 [see Geary's c spatial correlograms of Fig. 1(f), (h)]. Furthermore, for the disagreement between analyses to become an agreement in the case of Erie 7, Pearson's r-statistic must be declared significant, assuming the null hypothesis is correctly rejected in the Mantel test. However, the modified t-test recommended in the correlation analysis of spatial processes cannot change to a significant correlation coefficient smaller than 0.1 in absolute value for the sample sizes considered, even though the modification may result in an increase of the number of degrees of freedom of the t-test (Dutilleul 1993). A similar argument applies to the lack of normality of the raw data; this point is addressed in Section 4.

In this context, the usefulness of Geary's c-statistic is greater than that of Moran's I, for example. In fact, although Geary's c is based on squared differences between observations (i.e., squared Euclidean distances) while the Mantel test is applied to matrices of nonsquared Euclidean distances here, the outcome of some Mantel tests might be anticipated from the spatial correlograms displayed in Figure 1(e)–(h). For instance, the nonsignificance of the normalized Mantel statistic for Erie 1 can be predicted from the flatness of Geary's c-correlogram for X compared with the patchy type of correlogram for Y. Similarly, a negative normalized Mantel statistic can be expected for Erie 7 from the diverging Geary's c-correlograms for X and Y. The constancy of Geary's c-statistic over the major portion of the correlogram for X may also explain the lack of significance of the normalized Mantel statistic for Erie 2. This reasoning does not apply to Erie 5 because it should lead to a positive normalized Mantel statistic while it actually is significant but negative (Table 3). The plots of the transect data of X and Y for Erie 5 (not reported here) resolve this question. In some parts of the transect, X-values were relatively constant while there were jumps in Y at given sampling sites so that small distances d_X were associated with large distances d_Y. In some other parts of the transect, the reverse phenomenon was observed, i.e., jumps were in X while Y-values were constant. Jumps were of intermediate magnitude, so the data points were not outliers. Their number was not large enough to affect spatial autocorrelation at small distance classes but was sufficient to provide a negative and significant normalized Mantel statistic.

The comparison of the Y versus X scattergrams for Erie 1 and 2 to those for Erie 5 and 7 [Fig. 1(a)–(d)] leads to the following observations: (1) Erie 1 displays a diffuse cloud of points, whereas the other three data sets present arrow-shaped scattergrams characterized by a higher concentration of points on the left-hand side of the X-axis; (2) the main difference between Erie 2 and Erie 5 and 7 is in the distribution of Y, which is symmetrical for Erie 5 and 7 and skewed toward the higher values for Erie 2. Actually, this is why we retained the arrow pattern of symmetrical type (arrow 1) as the basis for one of the distributional models for (X, Y) in the simulation study. Moreover, we decided to base the simulations of the arrow pattern on the exponential distribution for X instead of the log-normal distribution, e.g., because of the rationale of the former in relation to Poisson events (e.g., the presence of a bank of fish in the example); Poisson refers to the stochastic process.

3.3 SMALL-SIZE ARTIFICIAL EXAMPLES

The first four configurations that we consider are directly inspired by the Lake Erie example, with two triangular patterns as rough approximations of the arrow pattern of symmetrical type (head to the right) and two configurations with extra points in the middle

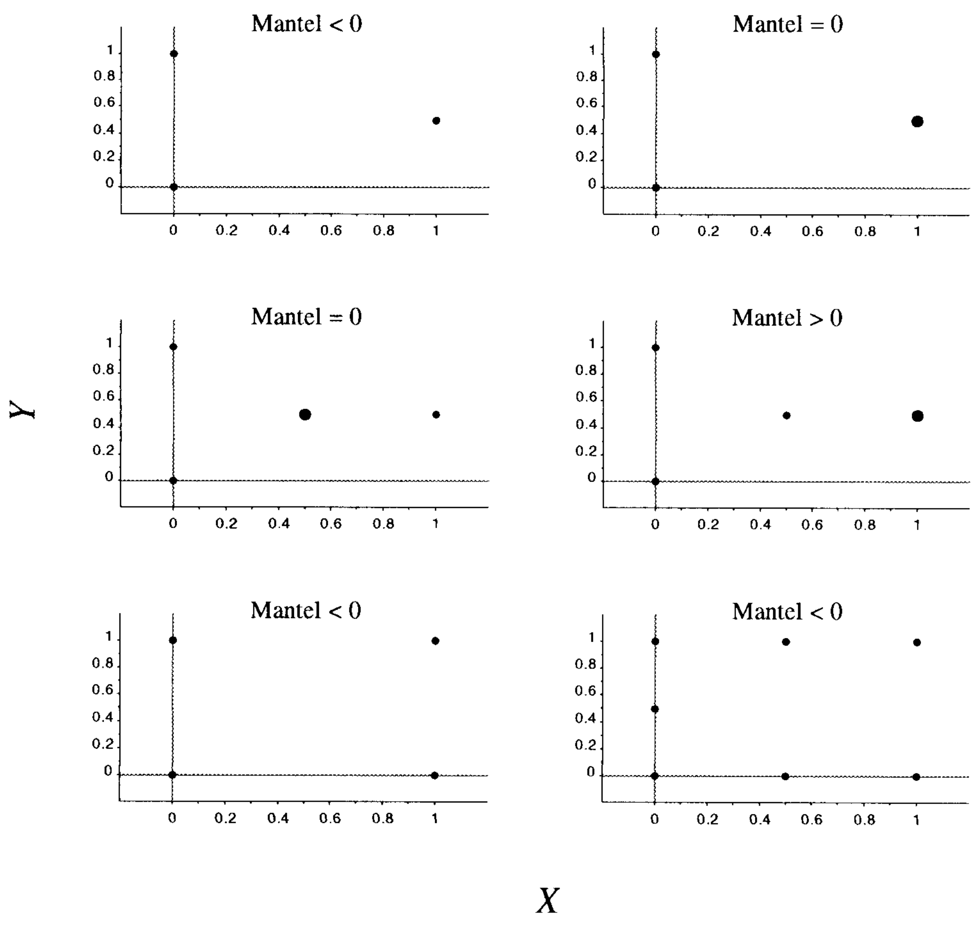

Figure 2. Artificial Small-Size Examples Used in the Development of the Arrow and U-Transposed Bivariate Distributional Models for (X, Y). For all of them, Pearson's r-statistic is equal to zero, whereas the Mantel statistic may be negative, zero, or positive, depending on the pattern and the density of points. A bigger point represents two superimposed observations. The scattergrams of Euclidean distances are not plotted; only the sign of the Mantel statistic is reported.

of the biplot, in which the arrow tends to appear more clearly (Fig. 2). The last two configurations are a square and a U transposed, the latter following from the square by the consideration of some intermediate points (Fig. 2). The presence of superimposed points (see the bigger points) allows a preassessment of point density effects on the sign of the Mantel statistic.

While Pearson's r is 0.0 for all six configurations, it can easily be shown that the Mantel statistic calculated on the Euclidean distances is negative for three of the configurations, zero for two, and positive for one (Fig. 2). Disagreement between analyses arises in the triangular pattern (approximate arrow) with no superimposed points, the arrow pattern with superimposed points on the right, the (empty) square, and the U transposed. Thus, not only the configuration but also the density of points may have an effect on the outcome of the Mantel test and its agreement or disagreement with Pearson's correlation analysis. The density of points is not related to the sampling effort that would concentrate more on some parts of the (X, Y) biplot but follows instead from the theoretical bivariate distribution of (X, Y).

In practice, scattergrams of raw data displaying a symmetrical pattern of the arrow or U-transposed type would be indicative of potential differences between the two methods of analysis, depending on the density of points. The small-size artificial examples presented here are completed in the next section by filling the arrow, U-transformed, and square configurations with simulations and by considering two circular configurations (Table 1).

3.4 The Simulation Study

Simulation results are summarized in Table 4. For each of the seven models, the mean value of Pearson's r was very close to 0.0. Also, the empirical 95% confidence interval for ρ contained 0.0 for all seven models. On the other hand, the one-tailed and two-tailed empirical significance levels were largely above the 0.05 theoretical level for two of the models, namely arrow 2 and arrow 3. This result does not contradict the previous ones but simply reflects the uniform instead of bell-shaped distribution of Pearson's r for these two models (histograms not shown). At the same time, the mean value of the Mantel statistic was close to 0.0 and the empirical 95% confidence interval for $\mathrm{corr}(d_X, d_Y)$ contained the 0.0 value only for the circle 2 and square models. The two-tailed empirical significance level was above 0.90 for models arrow 2, arrow 3, U transposed, and circle 1. The left-hand one-tailed empirical significance level equaled 0.0 for arrow 2, arrow 3, and U transposed, while the right-hand one (not reported in Table 4) was 0.984, 0.992, and 0.920, respectively. These values compare with the 0.992 left-hand one-tailed empirical significance level of circle 1. Arrow 1 was the only model for which the left-hand one-tailed empirical significance level was largely above the 0.05 theoretical level, while the two-tailed empirical significance level was not.

Thus, there are three models in seven for which there is some or much evidence for a correlation between Euclidean distances while there is none for the raw data. These three models are arrow 1, U transposed, and circle 1. For the arrow 2 and arrow 3 models with

Table 4. Parametric Linear Correlation Analysis on Raw Data and Permutational Mantel Analysis on Derived Euclidean Distances for 1,000 Samples of Size 100 Simulated Under Each of Seven Bivariate Distributional Models for (X, Y)

	Pearson's correlation analysis[a]			*Mantel test*[a]		
Model[b]	*Mean value of statistic*	*One-tailed empirical significance level*	*Two-tailed empirical significance level*	*Mean value of statistic*	*One-tailed empirical significance level*	*Two-tailed empirical significance level*
Arrow 1	−0.002	0.029	0.026	−0.077	0.339	0.015
	[−0.170, 0.163]			[−0.122, −0.013]		
Arrow 2	0.003	0.294	0.521	0.300	0.000	0.982
	[−0.351, 0.361]			[0.128, 0.444]		
Arrow 3	−0.006	0.402	0.737	0.404	0.000	0.992
	[−0.485, 0.450]			[0.213, 0.644]		
U transposed	0.003	0.067	0.080	0.059	0.000	0.918
	[−0.204, 0.230]			[0.028, 0.103]		
Circle 1	0.000	0.018	0.010	−0.095	0.992	0.975
	[−0.157, 0.144]			[−0.130, −0.052]		
Circle 2	0.000	0.036	0.039	−0.006	0.028	0.016
	[−0.182, 0.187]			[−0.072, 0.076]		
Square	0.003	0.037	0.041	−0.001	0.050	0.041
	[−0.183, 0.193]			[−0.045, 0.050]		

[a]For each method of analysis, a mean value of the statistic was calculated over the 1,000 samples for each model; the normalized version of the Mantel statistic was used. Each mean value of a statistic is followed, below in brackets, by the corresponding empirical 95% confidence interval. The empirical significance levels represent mean rates of rejection of the null hypothesis over 1,000 samples of size 100 for a 0.05 theoretical level. One-tailed empirical significance levels are left-hand thoroughly. See text for further details.

[b]See Table 1 for the description of models.

higher density of points in the middle and on the head of the arrow, Pearson's r is equal to 0.0 on average and the Mantel statistic is likely to be strictly positive, although the Pearson and Mantel analyses provide a high proportion of significant results in hypothesis testing. For models circle 2 and square, both analyses agree on nonsignificant results.

As the density of points increased from left to right in the arrow pattern (head to the right), the Mantel statistic changed its sign from negative to positive [Fig. 3(a)–(c)]. This phenomenon is mainly due to an increase in the proportion of small d_X and d_Y distances from arrow 1 to arrow 3, combined with the formation of a cloud of larger distances. A similar observation can be made for circle 1 (negative and highly significant Mantel statistic) and circle 2 (negative but nonsignificant Mantel statistic).

The arrow 1 model [Fig. 3(a)] mimics very well the pattern displayed by the Erie 5 data set of the example [Fig. 1(c)]. In arrow 1, variable X follows an exponential distribution $+1.0$, while the conditional distribution of Y given x is normal with a variance equal to $1/x^4$ (Table 1).

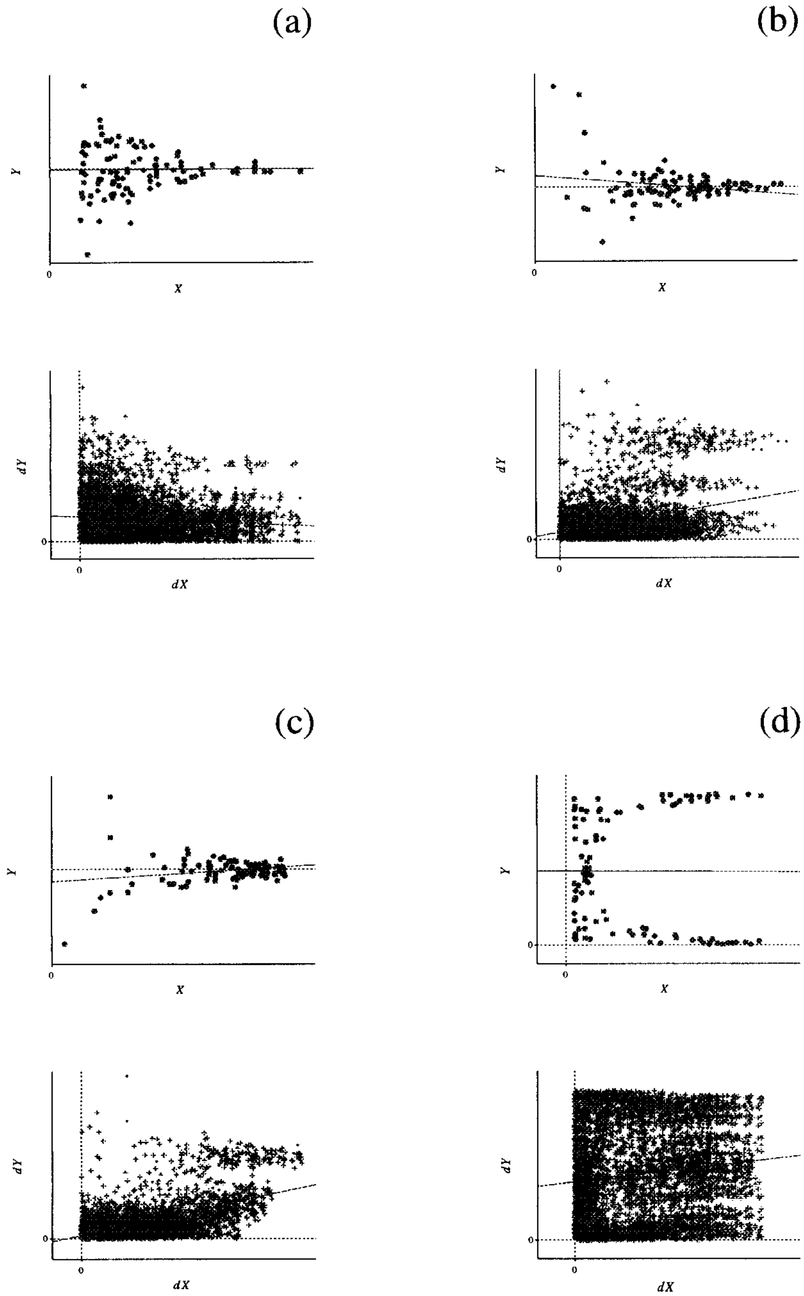

Figure 3. An Illustrative Example of the Scattergrams of Raw Data and Derived Euclidean Distances for One Simulation Replicate From Each of the Seven Models Listed in Table 1 With $n = 100$*: (a)–(c) Arrows 1–3, (d) U transposed, (e)–(f) circles 1–2, and (g) square. Only the zero value is represented on the axes, when justified. The dotted lines represent symmetry axes, when existing, whereas the solid lines represent the regression line of* Y *on* X *and of* d_Y *on* d_X*.*

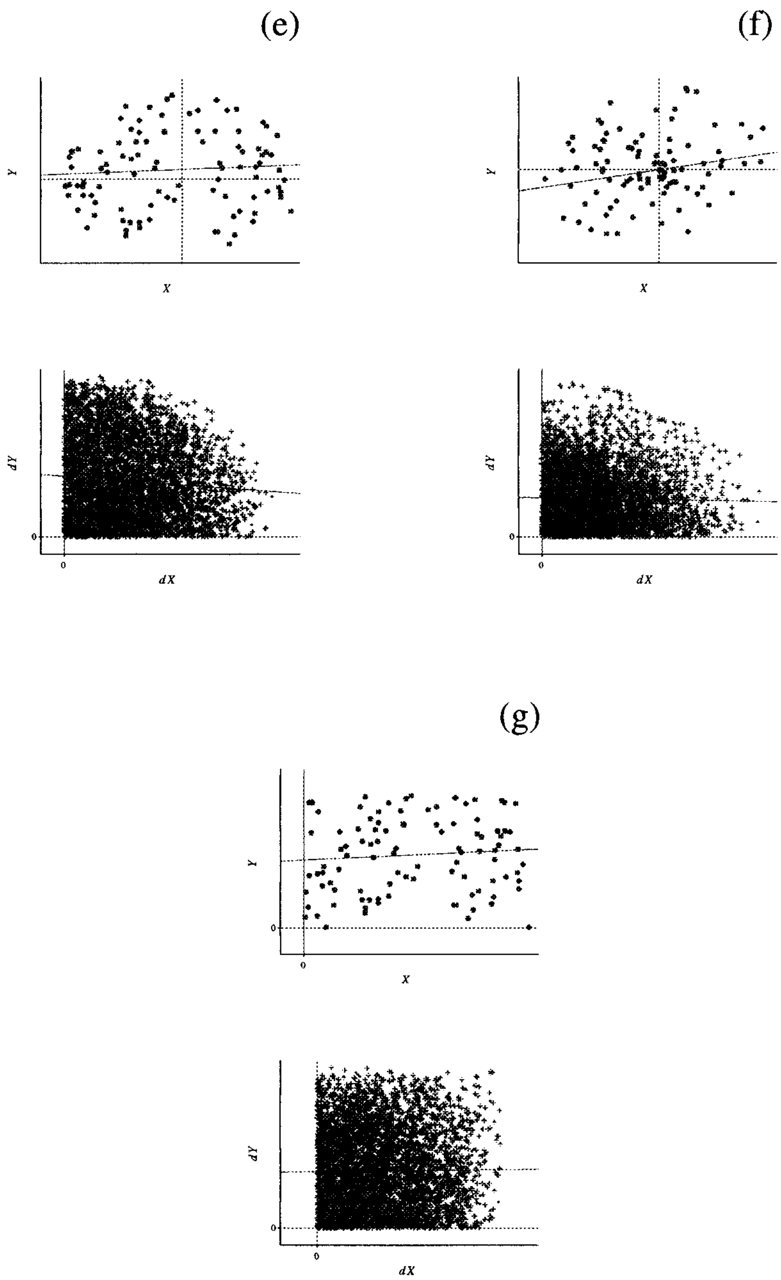

Figure 3. Continued.

4. CLOSING REMARKS

The Mantel test and Pearson's correlation analysis are likely to disagree when the values of variable X vary independently of those of variable Y, while the variation in X as measured by the distances d_X is related, positively or negatively, to the variation in Y as measured by the distances d_Y. Our analyses of the Lake Erie data showed this can indeed occur with real data, as three of the nine data sets analyzed presented such a disagreement. We also reported three bivariate distributional models for (X, Y) that reproduced this disagreement, of which one (i.e., arrow 1) mimicked the Erie 5 and Erie 7 data sets. The density of points in the raw data space seems to be of crucial importance to the outcome of the Mantel test, as shown by the change in sign of the Mantel statistic from the arrow 1 (high density on the left of the head) to the arrow 3 (high density on the right) model. For only one of the nine Lake Erie data sets analyzed (i.e., Erie 6) was the right-hand one-tailed significance probability of Pearson's r below the 0.05 level (i.e., $r = 0.197$, $p = 0.028$), while the 0.045 value of the normalized Mantel statistic was not significant at the 0.05 level, whatever the alternative hypothesis. This disagreement was not investigated in our study because of its low frequency of observation in the Lake Erie example.

Our findings concerning disagreement were obtained by using Euclidean distances in the Mantel test. In the one-dimensional case, they extend to any distance derived from a norm of the Minkowski family (e.g., Manhattan, supremum) because all the Minkowski norms are equivalent in that case. Our results also seem to extend to the nonparametric versions of both methods of analysis. For example, the Erie 7 data set provided a Spearman's rank correlation coefficient of 0.080 ($p = 0.263$), while the normalized rank-based Mantel statistic was -0.101 ($p = 0.006$) by using 20 equal-frequency distance classes. To assess whether the lack of normality of the raw data had an effect on our findings, we recalculated the significance probability of Pearson's r by permutations with similar results; e.g., the one-tailed permutational p of Pearson's r was 0.366 for Erie 5 and 0.454 for Erie 7.

Actually, on the basis of the marginal distribution for X and the conditional distribution of Y given x, it is possible to calculate the theoretical covariance between X and Y from the joint probability density function of (X, Y). Accordingly, for each of the three bivariate distributional models that produced differences between the analyses in Section 3.4, it can be shown that the double integral defining $\text{cov}(X, Y)$ is 0.0. In other words, whatever the statistic calculated on the raw data and for a given Type I error risk, the correlation between X and Y should be nonsignificant for these three models. It can also be shown that an ellipse 1 model corresponding to circle 1 would provide similar results. To assess the effect of inequality of variances between X and Y on our findings, consider a bivariate distribution for (X, Y) defined by the marginal distribution of circle 1 for X and the conditional distribution of circle 1 for Y given x multiplied by a positive constant a. This defines an ellipse 1 model, for which $\text{corr}(X, Y) = \text{corr}(X_{\text{circle 1}}, aY_{\text{circle 1}})$ and $\text{corr}(d_X, d_Y) = \text{corr}(d_{X,\text{circle 1}}, ad_{Y,\text{circle 1}})$. The similarity of results for ellipse 1 and circle 1 follows from the invariance of correlations after linear transformation of data.

Any Mantel type of analysis, including partial Mantel tests, Mantel correlograms, and multiple regression on distance matrices, may replace the Mantel test in the observation of a disagreement with Pearson's correlation analysis. For example, the Mantel correlogram (Oden and Sokal 1986; Sokal 1986) that we computed for d_Y versus d_X from the Erie 5 data set had seven significant ($p < 0.05$) ordinates out of 20: four positive at intermediate d_X classes and three negative at further classes.

Users of the Mantel test, including in an analysis-of-variance approach (e.g., Mielke et al. 1976; Hubert, Golledge, and Costanzo 1982; Clarke 1993; Fortin and Gurevitch 1993), should be fully aware that the hypotheses tested are stated in terms of distances or closeness, following Mantel and Valand (1970), instead of raw data. Whether in its original form (Mantel 1967) or in its regression extensions (Manly 1986; Smouse et al. 1986; Legendre et al. 1994), the objective of the Mantel test is the detection of relationships between a dependent proximity matrix and one or several explanatory proximity matrices. On the other hand, in the Mantel correlogram of d_Y versus d_X, the null hypothesis is that, at a given distance class d_X, the mean d_Y distance within that class is equal to the mean d_Y distance from the other distance classes $d_{X'}$.

In summary, full care should be taken when drawing conclusions based on the Mantel test. Special attention should be paid when one of the two variables or sets of variables is related to the Poisson distribution in the discrete case or the associated exponential distribution in the continuous case, i.e., when the values taken by one or more of the variables may change drastically due to the scarcity of individuals of large size or the occurrence of rare events with great impact in the sampling area. In contrast, under the multivariate normal model for the raw data, the use of squared Euclidean distances in the Mantel test provides a situation in which the Mantel test and Pearson's correlation analysis agree. We hope this paper will motivate further investigation about the specific aspects of these two methods of analysis.

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Addendum

Strictly speaking, equation (3.3) is correct when $i' = i+1$ if $1 \leq i < n$ and when $i' = i-1$ if $1 < i \leq n$. Otherwise, equation (3.3) must read

$$\mathrm{corr}(d_{X,ii'}^2, d_{Y,ii'}^2) = \frac{\rho^2}{(1 - \rho_X^{|i-i'|})(1 - \rho_Y^{|i-i'|})},$$

within the limits of positive definiteness of the variance-covariance matrix of the normal vector $(\underline{\mathbf{x}}', \underline{\mathbf{y}}')'$ and the boundaries of the correlation coefficient.