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Matrix Correlation Analysis in Anthropology and Genetics

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ABSTRACT The comparative analysis of the population variation patterns exhibited by different types of information has long been a genuine anthropological/genetic preoccupation. One of the generic problems attracting repeated attention is the connection between genetic and cultural consequences of population isolation; we expect both patterns and amounts of variation to reflect the same history of group fission and fusion, but what do we see in practice? Numerous techniques have been employed in such work, all based on comparison of different matrices of pairwise distances/affinities. A basic difficulty with all of these methods is that the $N(N - 1)$ pairwise elements of an $(N \times N)$ matrix cannot be mutually independent. Recently, a versatile test of matrix correlation that allows for this fact, originally developed by Mantel but since extensively modified and extended, has gained popularity in anthropology, as well as geography, ecology, sociology, psychometrics, population biology, and systematics. We present here a general framework for many of these efforts, based on the Mantel test, and then illustrate its use with four examples from our own work and that of our colleagues: a) genetic affinity and migrational separation in the Bainwa, b) clinal versus cluster variation in the Yanomama, c) genetic, linguistic, and geographic affinities among the Chibcha-speaking tribes, and d) migration and genetic affinity in the Gainj and Kalam. The technique is nonparametric and so general that it is useful for many different types of pattern comparison, even when the connections between different types of information are poorly understood. Greater analytic potential is generally realized when there are definite theoretical connections between the patterns being compared. With theoretical care and a bit of imagination, one can combine the advantages of parametric assumptions with the robustness of nonparametric analysis. Novel analyses and anthropological opportunities are emerging continuously. © 1992 Wiley-Liss, Inc.

Many anthropological questions are profitably approached by comparing the patterns of population differences/similarities obtained with different sorts of information. For example, isolation between populations will produce both genetic and cultural divergence, with both patterns and amounts of variation reflecting the same history of group fissions and fusions. Several different techniques have been employed in such comparative work, all relying on matrices of pairwise distances or affinities. The difficulty encountered with all of these methods is that

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$N(N-1)$ pairwise elements of an $(N \times N)$ matrix cannot be mutually independent; in fact, there can be no more than $(N-1)$ independent comparisons among a set of N elements. Notwithstanding the difficulties, the need to make such comparisons and the development of new methods to facilitate them have been genuine anthropological preoccupations for some time. Techniques of dealing with this problem that are familiar in the anthropological literature are: 1) matrix correlation techniques (Sokal and Rohlf, 1962; Sneath and Sokal, 1973), 2) matrix dilation and rotation techniques (Schönemann and Carrol, 1970; Gower, 1971), and 3) smallest space techniques (Lingoes, 1965; Guttman, 1968). There are also techniques that rely less directly on matrices of distances, such as 4) comparisons of phyletic networks (Sokal and Rohlf, 1962; Spielman, 1973; Spielman et al., 1974), 5) spatial autocorrelation (Sokal and Oden, 1978a,b; Sokal, 1979, 1983a,b, 1986, 1988; Jones et al., 1980; Sokal et al., 1980, 1985, 1986, 1987a,b,c, 1989; Cliff and Ord, 1981; Sokal and Riska, 1981; Sokal and Wartenberg, 1981, 1983; Caugant et al., 1982; Sokal and Friedlaender, 1982; Sokal and Menozzi, 1982; Winkler and Sokal, 1987; Barbujani, 1987; Sokal and Thompson, 1987; Sokal and Uytterschaut, 1987; Sokal and Winkler, 1987), and 6) map-quadrat techniques (Derish and Sokal, 1988).

Recently, a versatile test of matrix correspondence, originally developed by Mantel (1967), has gained wide popularity in geography (Hubert and Golledge, 1982), ecology (Manly, 1986; Burgman, 1987), psychometrics (Hubert and Baker, 1978; Hubert, 1979a,b, 1985, 1987; Hubert and Subkoviak, 1979; Hubert and Golledge, 1981), population biology (Sokal, 1979; Sokal et al., 1980; Douglas and Endler, 1982; Schnell et al., 1985, 1986), and systematics (Dietz, 1983), as well as in anthropology (Dow and Cheverud, 1985; Salzano et al., 1986; Sokal et al., 1986; Smouse et al., 1986; Dow et al., 1987; Long et al., 1987; O'Brien, 1987; Smouse and Wood, 1987; Barrantes et al., 1990). The Mantel test has been generalized in different fashions (Hubert, 1985, 1987; Dow and Cheverud, 1985; Manly, 1986; Smouse et al., 1986; Krackhardt, 1987, 1988; Dow and de Waal, 1989), and provides a useful analytical framework for matrix correlation analysis.

The purpose of this review is to show how a large number of efforts in matrix correlation analysis can be subsumed under a single analytical framework based on the Mantel test, and to illustrate its use with a number of examples from our own work and that of our colleagues. We shall restrict attention in this way, because much of the critical anthropological information that makes a problem interesting in the first place is unpublished, and we need to capitalize on everything we know about the situation in each case. In the process of pursuing these examples, we shall nevertheless present some new analyses, rather than simply recapitulating the published record. The picture that will emerge is that while maximum analytic potential is best realized when there is a clear theoretical motivation for the connection between two or more patterns, the technique is so general that it can be useful for a great many different types of pattern comparison, even where the theoretical connections are poorly understood.

THE MANTEL TEST OF MATRIX CORRELATION

Our basic tool here will be the Mantel test of matrix correspondence. We begin with a set of N populations, for which a full set of $N(N-1)$ pairwise distances (or affinities) are computed from two different types of data, one set denoted X and the other Y. In practice, most distance measures of interest are symmetric, $\Delta_{ij} = \Delta_{ji}$, but we can deal equally well with antisymmetric measures, $\Delta_{ij} = -\Delta_{ji}$, or with asymmetric measures, $\Delta_{ij} \neq \Delta_{ji}$. An example of a symmetric relationship would be the straight line distance between two points,

$$\Delta_{ij} = |X_i - X_j| = \Delta_{ji}, \tag{1a}$$

where direction is of no particular theoretical interest. An example of an antisymmetric relationship would be the difference in dominance rank between two individuals,

TABLE 1. Example distance matrices for a quartet of populations

a. Symmetric distance matrix

Population	1	2	3	4
1	—	0.75	0.34	0.65
2	0.75	—	0.51	0.14
3	0.34	0.51	—	0.10
4	0.65	0.14	0.10	—

b. Antisymmetric distance matrix

Population	1	2	3	4
1	—	+.27	−.09	+.45
2	−.27	—	+.68	−.36
3	+.09	−.68	—	+.53
4	−.45	+.36	−.53	—

c. Asymmetric distance matrix

Population	1	2	3	4
1	—	0.22	0.68	0.40
2	0.31	—	0.50	0.74
3	0.70	0.50	—	0.85
4	0.10	0.91	0.62	—

Entries are stylized.

$$\Delta_{ij} = (X_i - X_j) = -\Delta_{ji}, \tag{1b}$$

where direction does have a potentially important impact, the implications of such a difference being anything but symmetrical. An example of an asymmetric relationship might be the degree of relationship between two individuals, measured by the fraction of genes shared in common for a sex-linked trait. A male shares all of his sex-linked genes with his full sister, but she shares only half of hers with her brother. This sort of measure is also asymmetric for maternal and paternal half sibs. In this case, we have:

$$\Delta_{ij} \neq \pm\Delta_{ji}. \tag{1c}$$

It is convenient to package these distance measures into a square matrix of dimension N (Table 1). Most distance matrices have zero diagonal elements, the distance from an item to itself being zero, but even that is not essential. Alternatively, we can define square matrices of pairwise affinities (e.g., kinship coefficients among a set of individuals), where the affinity of an item with itself is unity, and maximum departure from affinity is represented by zero.

Given two matrices of distances between the same set of items, each matrix based on a different type of information, we wish to determine the level of correspondence. There are various ways to define correspondence, and depending on the definition, various types of test-related measures have been defined. Probably the most widely used measure is that of Mantel (1967), who devised a test of matrix correspondence based on a general regression approach. Let the two matrices be denoted $\mathbf{D}_{XX} = \{\Delta_{Xij}\}$ and $\mathbf{D}_{YY} = \{\Delta_{Yij}\}$, respectively, both of dimension N. Compute the measure Z_{XY}, a summation of element-by-element product of the two matrices (Hadamard product),

$$Z_{XY} = \mathbf{D}_{XX}{}^{*}\mathbf{D}_{YY} = \sum_{i \neq j}^{N} \Delta_{Xij}\Delta_{Yij}. \tag{2}$$

As mentioned earlier, the elements of the $\mathbf{D}_{XX}$ are not mutually independent; there are no more than $(N - 1)$ independent contrasts. If there are $L < (N - 1)$ variables involved in the definition of Δ_{Xij}, then the rank of the matrix is only L. Similar strictures apply to $\mathbf{D}_{YY}$. We need to allow for this fact in our test procedure. Mantel (1967) provided a normal distribution test of Z_{XY} for large matrices. Mielke et al. (1981) have advocated the use of a Pearson Type III distribution for Z_{XY}, a two-parameter exponential family distribution that is flexible enough in shape to fit most empiric data sets. The safest method is permutational evaluation of the null distribution (Mantel, 1967; Cliff and Ord, 1981), which requires no assumptions about the distribution of Z_{XY} at all—an important consideration, since we sometimes know very little about how Δ_{Xij} and Δ_{Yij} are distributed.

Although we can test Z_{XY} easily enough, it is difficult to interpret. We can, however, transform Z_{XY} into a standardized regression coefficient or even a correlation coefficient whose magnitude is not scale dependent, the choice depending on whether we view Δ_{Xij} as fixed and measured without error or as a random variable, measured with error. For many of the examples that follow, the random definition makes sense, but since the computed values of Z_{XY}, r_{XY}, and b_{YX} map one to one in any case, we will concentrate on the correlational measures. The first step is to subtract the average element of $\mathbf{D}_{XX}$ from each of the individual elements, and similarly for $\mathbf{D}_{YY}$ (Smouse et al., 1986). We then compute sums of squares and cross-products, using these deviations, δ_{Xij} and δ_{Yij}, variables that have been centered around the mean

$$SS(\mathbf{X}) = \sum_{i \neq j}^{N} (\Delta_{Xij} - \bar{\Delta}_{X..})^2 = \sum_{i \neq j}^{N} \delta_{Xij}^2, \tag{3a}$$

$$SS(\mathbf{Y}) = \sum_{i \neq j}^{N} (\Delta_{Yij} - \bar{\Delta}_{Y..})^2 = \sum_{i \neq j}^{N} \delta_{Yij}^2, \tag{3b}$$

$$SP(\mathbf{X},\mathbf{Y}) = \sum_{i \neq j}^{N} \delta_{Xij}\delta_{Yij}. \tag{3c}$$

With these sums of squares and products, we can compute both a regression coefficient (b_{YX}) and a correlation coefficient r_{XY} as follows

$$b_{YX} = \frac{SP(\mathbf{X},\mathbf{Y})}{SS(\mathbf{X})} \quad \text{and} \quad r_{XY} = \frac{SP(\mathbf{X},\mathbf{Y})}{[SS(\mathbf{X}) \cdot SS(\mathbf{Y})]^{1/2}}. \tag{4}$$

In the case where $\mathbf{X}$ is itself treated as a random variable (rather than as a fixed predictor of $\mathbf{Y}$), r_{XY} is the standard Pearson correlation coefficient. If the two matrices have nothing to do with each other, then we should expect b_{YX} and r_{XY} to be zero.

To test whether the observed value of r_{XY} is significantly different from zero, we need the null hypothesis distribution, obtained in permutational fashion (Mantel,

1967; Cliff and Ord, 1981). Hold one of the matrices constant, say $\mathbf{D}_{XX}$, and permute rows (and corresponding columns) of the other. What that amounts to is a permutation of the ID numbers on the items themselves. If the two sets of measures are truly independent, it should not matter at all which of the Ys goes with which of the Xs. Given the permutation of $\mathbf{D}_{YY}$, compute the value or r_{XY} and tally the result. Still holding $\mathbf{D}_{XX}$ constant, permute $\mathbf{D}_{YY}$ again, compute a new r_{XY}, tally it, and continue. With matrices of dimension N, there are $N!$ possible permutations. For example, the distance matrix in Table 1a has four populations and six pairwise distances. There are $4! = 24$ different arrangements of these values for the upper triangular portion of the matrix; the distances are symmetric, so the arrangement of the lower triangle always reflects the upper triangle exactly. That requires renumbering the rows columns in the same order. For small matrices (say $N \leq 7$), we can exhaustively enumerate the permutations, but for larger matrices, we require a random subsample of the full $N!$ permutations.

Note that the denominator of Equation (4) is constant with respect to permutation, since we are merely renaming the elements of Equations (3a) and (3b). Because the means of the two matrices are constant with respect to row (and corresponding column) permutation, we see that Z_{XY} and r_{XY} represent a one-to-one transformation. The null distribution for r_{XY} is identical to that for Z_{XY}, barring a scale transformation and centering. We have also allowed explicitly for the internal correlations of $\mathbf{D}_{XX}$ and $\mathbf{D}_{YY}$, since permutation preserves those correlations; the test is thus conditioned on the internal structure of the two matrices. We have taken two rigid $(N - 1)$-dimensional figures, and rotated one of them in space (by randomizing the labels of the vertices), and then asked how well the two match (without regard to orientation). For example, with $N = 4$, each of the distance matrices represents an irregular tetrahedron in three-dimensional space. We assess the degree to which they are the same shape, subject only to rotation and scale translation. The null distribution is obtained simply by reassigning names to the four vertices of one of the tetrahedrons in all possible $(4! = 24)$ ways. Given a permutationally derived null distribution for r_{XY}, we determine how many of our randomly permuted distance matrices, $\mathbf{D}_{YY}$, yield an r_{XY} value at least as large as the value we actually observed. In principle, we could have either a positive or negative r_{XY}, so a two-tailed test of the null hypothesis would be appropriate. In most anthropological/genetic applications, theory postulates a directional alternative model, and a one-tailed test is in order.

This procedure is so general that it can be used on just about any pair of distance/affinity matrices imaginable, but it has a special relationship to standard correlation and regression analyses that deserves a mention. Consider two variables, X and Y, for each of which we define antisymmetric distance measures as per Equation (1b). It turns out that b_{YX} and r_{XY} are precisely the values we would get if we were to do a correlation analysis of the original X and Y values (Li, 1976). The permutational null distribution amounts to holding the Xs constant and permuting the Ys, as might be appropriate if we were unwilling to assume that the Ys were normally distributed.

For a single character in each matrix, there is seldom anything to be gained by translating the Xs and Ys to distance matrix form, but the fact that we can do so is revealing. In the case where both X and Y are Bernoulli variables (taking values 0 and 1 only), then the Mantel distribution leads exactly to Fisher's exact contingency test. On the other hand, in the case of data that are inherently dyadic (say the number of agonistic interactions between two individuals), standard univariate regression and correlation measures are not available; pairwise distance analysis is unavoidable. In the case where $\mathbf{X}$ and $\mathbf{Y}$ are multivariate vectors, we can do a variety of multivariate analyses of the correlations between the two vectors, but they might be more work than a simple Mantel test.

There are a number of extensions of this basic treatment that permit even wider deployment of pattern correlation analysis. Consider two collections of variables, $\mathbf{W}$ and $\mathbf{X}$, used to describe the patterns in a third set, $\mathbf{Y}$. Instead of two matrices,

we have a trio. We treat the analysis as a multiple regression or correlation problem (Smouse et al., 1986), defining a model

$$\delta_{Yij} = b_{YW}\,\delta_{Wij} + b_{YX}\,\delta_{Xij} + \epsilon_{ij}. \tag{5}$$

To analyze, we begin with the sums of squares and cross-products

$$SS(\mathbf{W}) = \sum_{i \neq j}^{N} \delta_{Wij}^2 \quad \text{and} \quad SS(\mathbf{X}) = \sum_{i \neq j}^{N} \delta_{Xij}^2, \tag{6a}$$

$$SS(\mathbf{Y}) = \sum_{i \neq j}^{N} \delta_{Yij}^2, \tag{6b}$$

$$SP(\mathbf{X},\mathbf{Y}) = \sum_{i \neq j}^{N} \delta_{Wij}\delta_{Yij} \quad \text{and} \quad SP(\mathbf{X},\mathbf{Y}) = \sum_{i \neq j}^{N} \delta_{Xij}\delta_{Yij}, \tag{6c}$$

$$SP(\mathbf{W},\mathbf{X}) = \sum_{i \neq j}^{N} \delta_{Wij}\delta_{Xij}. \tag{6d}$$

All the standard multiple-regression machinery can be derived from Equations (6a–d). Using such definitions, we can define a vector of regression coefficients, B, which is estimated in the usual matrix fashion. Define

$$\mathbf{B} = \begin{bmatrix} \beta_{YW} \\ \beta_{YX} \end{bmatrix}, \mathbf{X}'\mathbf{Y} = \begin{bmatrix} SP(\mathbf{W},\mathbf{Y}) \\ Sp(\mathbf{X},\mathbf{Y}) \end{bmatrix}, \mathbf{X}'\mathbf{X} = \begin{bmatrix} SS(\mathbf{W}) & SP(\mathbf{W},\mathbf{X}) \\ SP(\mathbf{W},\mathbf{X}) & SS(\mathbf{X}) \end{bmatrix}. \tag{7}$$

The vector of estimated regression coefficients is

$$\hat{\mathbf{B}} = (\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'\mathbf{Y}, \tag{8}$$

and the coefficient of multiple determination is

$$R^2 = \frac{\mathbf{Y}'\mathbf{X}(\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'\mathbf{Y}}{\mathbf{Y}'\mathbf{Y}}. \tag{9a}$$

In the case where $\mathbf{D}_{WW}$, $\mathbf{D}_{XX}$, and $\mathbf{D}_{YY}$ are all random and measured with error, we can rewrite Equation (9a) as

$$R^2 = 1 - (1 - r_{XY}^2)(1 - r_{WY \cdot X}^2), \tag{9b}$$

where r_{WY} and r_{XY} are the usual correlation coefficients and $r_{XY \cdot W}$ and $r_{WY \cdot X}$ are the respective partial correlation coefficients

$$r_{WY \cdot X} = \frac{r_{WY} - r_{XY}r_{WX}}{[(1 - r_{XY}^2)(1 - r_{WX}^2)]^{1/2}}, \tag{10a}$$

$$r_{XY \cdot W} = \frac{r_{XY} - r_{WY}r_{WX}}{[(1 - r_{WY}^2)(1 - r_{WX}^2)]^{1/2}}. \tag{10b}$$

Using the latter, we can assess how much of the variation in $\mathbf{D}_{YY}$ is accounted for by variation in $\mathbf{D}_{WW}$, while holding $\mathbf{D}_{XX}$ constant, and the reverse. A proper permutational test for this situation depends on whether $\mathbf{D}_{XX}$ and $\mathbf{D}_{WW}$ are viewed as fixed and measured without error, in the usual regression sense, or whether they are viewed as variable and/or measured with error. In the first case, we hold $\mathbf{D}_{XX}$ and $\mathbf{D}_{WW}$ constant, permuting $\mathbf{D}_{YY}$, a procedure that protects the interrelations of the two predictor sets, thought to be associated. In the latter case, we compute the regression of $\mathbf{D}_{YY}$ on $\mathbf{D}_{XX}$ and obtain the residuals, denoted $\mathbf{D}_{YY \cdot XX}$. We also compute the regression of $\mathbf{D}_{WW}$ on $\mathbf{D}_{XX}$ and obtain the residuals, denoted $\mathbf{D}_{WW \cdot XX}$. Finally, we compute the correlation between the two sets of residual matrices to

get the partial correlation between $\mathbf{D}_{YY}$ and $\mathbf{D}_{WW}$, with $\mathbf{D}_{XX}$ fixed. Holding either of the two residual matrices constant, permute the other to evaluate the null distribution. Extension of these procedures to multiple predictor (**X** and **W**) and multiple predicted (**Y** and **Z**) matrices is a straightforward extension of multivariate least squares analysis (Smouse et al., 1986; Krackhardt, 1987, 1988), but the permutational null distribution frees us from the (generally inappropriate) multivariate normality assumptions.

The final point we need to make at this juncture is less concerned with the computational aspects of the problem than it is with the choice of inputs. The procedures are so simple that we can handle almost any matrices that we can define. That permits analysis of variables that do not have well-behaved or even well-understood distributional properties, an advantageous property of no mean proportions. On the other hand, the results will never be better than the input data. Optimal payoff will come with careful attention to the details of how the distance matrices are defined. In practical terms, theory-motivated analysis is best, where the variables make sense in the context of the problem. The best way to illustrate this comment is by example. We turn to a series of real examples from our own work and that of our collaborators, for each of which an attempt has been made to capitalize on the background and theoretical information that made the problem interesting in the first place.

GENETIC AFFINITY AND MIGRATIONAL SEPARATION IN THE BANIWA

Salzano et al. (1986) have recently completed a demographic and genetic study of the Baniwa, an Arawak-speaking tribe of northern Brazil. The broad objectives were to compare this tribe with other groups from northern Brazil and neighboring Venezuela, most of whom are not Arawak-speakers. Several communities were studied, all of them found along the Rio Içana or Rio Negro (Fig. 1). In the course of this cross-tribal study, it became important to examine the pattern of genetic affinities among the various Baniwa communities. Travel in this part of the world is almost entirely riverine, and we suspected that the genetic affinities among these Baniwa communities would decrease with travel distance along the river system. The obvious way to compare geographic separation and genetic distance is by means of a Mantel test. For this purpose, we used a Euclidean genetic distance metric [see Equation (14) below], and postulated that genetic distance (Δ_{Gij}) was related to river distance (Δ_{Rij}) in linear fashion

$$\Delta_{Gij} \propto \alpha \Delta_{Rij}. \tag{11}$$

Relative distances along the river were measured with a planimeter from the map, and the genetic distances were computed from ten polymorphic genetic loci (Salzano et al., 1986). Both genetic (Δ_{Gij}) and riverine travel (Δ_{Rij}) distances are presented in Table 2; analysis yields $r_{GR} = .501$. The dimension of both matrices is only 5, so there are only $5! = 120$ permutations to evaluate; there were 8/120 stronger random correlations, so $P \leq .075$. Although Jandu Cachoeira (the most isolated community) is genetically the most disparate, as might be expected from its map position, the other populations do not show genetic affinities that are entirely consistent with map order. Study of the recent demographic histories of the communities reveals a clear reason for these seemingly anomalous results. In Amazonâs, there is a general tendency for acculturation (and its attendant admixture) to move progressively upriver, from major towns into the hinterlands, and the Baniwa illustrate this point nicely. All of these populations have come into contact with neo-Brazilian society over the last hundred years or so. The time depth and degree of contact decreases (but only in a rough way) as one moves upriver from Boa Vista. The interesting feature is that the admixture history of what are rapidly becoming communities of the "regional melting pot" can still be deciphered from careful pedigree reconstruction (Salzano et al., 1986).

The non-Baniwa in-migrants have themselves been a mixed lot. The Arekena

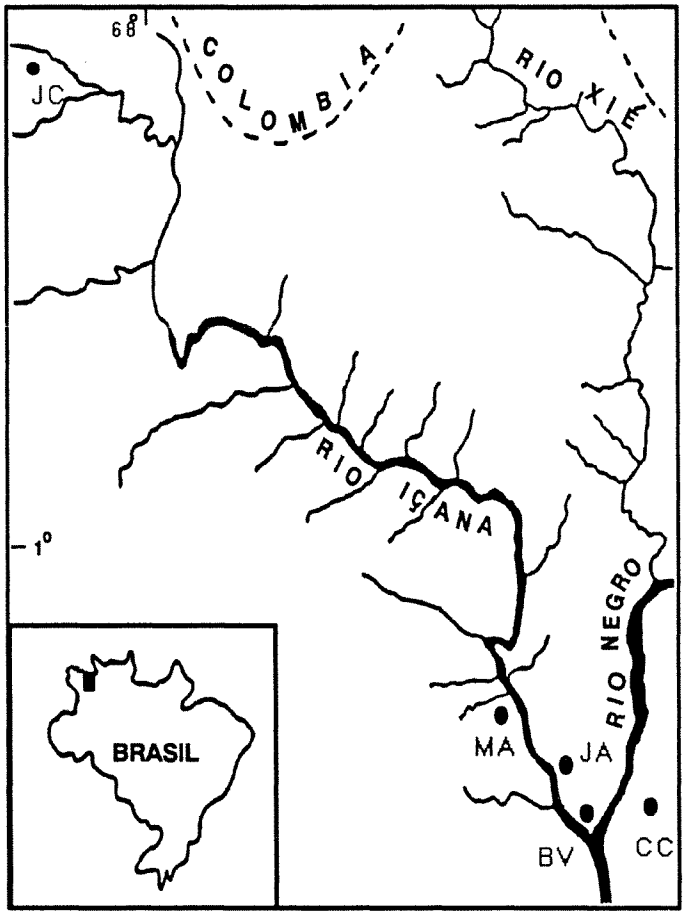

Fig. 1. Baniwa communities along the Rio Içana and Rio Negro of northern Brazil: CC, Cué Cué; MA, Maracajá; BV, Boa Vista; JA, Jauacanã; JC, Jandu Cachoeira (modified from Salzano et al., 1986).

TABLE 2. Distances among five Baniwa communities

	CC	MA	BV	JA	JC	*m* value
CC	—	.17	.05	.09	1.00	.82
MA	.41	—	.11	.08	.83	.68
BV	.51	.32	—	.04	.95	.61
JA	.48	.35	.48	—	.91	.52
JC	.61	.40	.52	.49	—	.04

CC, Cué Cué; MA, Maracajá; BV, Boa Vista; JA, Jauacaná; JC, Jandu Cachoeira. The river distances, standardized so the largest is 1.00, are presented above the diagonal; genetic distances are presented below the diagonal; migrational inputs from non-Arawakan groups are presented to the right (data drawn from Salzano et al., 1986). $r_{GR} = .501, P \leq .075$; $r_{GM} = .613, P \leq .025$; $r_{GR \cdot M} = -0.191, P \leq .668$; $r_{GM \cdot R} = .445, P \leq .110$; multiple $R_{G(RM)} = .631, P \leq .010$.

are a neighboring Arawak tribe with whom the Baniwa have intermarried to some extent, but they were probably genetically fairly similar, and we will lump them with the Baniwa for purposes of analysis; the "Baniwa" thus represent the regional "Arawakan" gene pool. There are several additional Amerindian contributors to the regional gene pool, among them the Tucano, Cubeo, and Tariana. In addition, there are many individuals in these communities who are representatives of the

regional (agglomerated and no longer differentiable) Amerindian gene pool, called "Nyengatu" (really a linguistic designation for the regional lingua franca, based on a Tucano dialect disseminated by the missionaries). In addition, several of these communities are admixed with neo-Brazilian settlers of European and African ancestry. Non-Arawakan percentages among the nominal "Baniwa" communities are: Cué Cué, 82%; Maracajá, 68%; Boa Vista, 61%; Jauacaná, 52%; and Jandu Cachoeira, 4% (no overt evidence but routine allowance for some undetected admixture). River position is *not* an infallible predictor of admixture history, although there is a rough correspondence. We were led to ask whether admixture history might be a better predictor of affinity among the Baniwa communities than strict travel distance along the river system.

On the premise that all of these communities have received genes from the same regional (non-Arawakan) population, there is a regular relationship that should obtain between differential admixture and genetic distance in this situation. Consider first a single, two-allele locus. Denote the ancestral/recipient "Arawakan" frequency of A_1 as p_A and that of the non-Arawakan donor gene pool as p_N. Then the frequencies for the ith Baniwa community should be

$$p_i = (1 - m_i)p_A + m_i p_N, \tag{12}$$

where the m_i values represent the accumulated influx of non-Arawakan genes into the ith community. Algebraic manipulation shows that the squared genetic distance between the ith and jth communities takes the simple form

$$\Delta^2_{Gij} = [p_i - p_j]^2 = [m_i - m_j]^2[p_A - p_N]^2 = [m_i - m_j]^2\Delta^2_{AN} \tag{13}$$

We next need to replace the single-locus, two-allele distance measure with its multiple-allele, multiple-locus analogue, a Mahalanobis distance measure on the pattern of Kurczynski (1970), Smouse and Williams (1982), and Chakraborty (1992)

$$\Delta^2_{Gij} = \sum_{\ell=1}^{L}\sum_{k=1}^{K_\ell}\frac{[p_{ik\ell} - p_{jk\ell}]^2}{\bar{p}_{\cdot k\ell}}/(K - L), \tag{14}$$

where we sum over all $K = \Sigma_\ell K_\ell$ alleles and $\ell = 1, \ldots, L$ loci, and where $\bar{p}_{\cdot k\ell}$ is the average allele frequency for the five communities. We substitute Equation (14) for the left hand (observed) side of Equation (13).

We do not know the ancestral frequencies of either the Arawakan or the non-Arawakan gene pools with any precision, of course, but whatever they were, we take the value of Δ^2_{AN} as a constant for each of the pairwise contrasts of Baniwa communities. Taking square roots of both sides of Equation (13), we *expect*

$$\mathrm{E}(\Delta_{Gij}) \propto |m_i - m_j| \cdot \Delta_{AN}, \tag{15}$$

and we define $D_{Mij} = |m_i - m_j|$ as the "migrational distance" between the ith and jth communities. The genealogy derived migrational estimates (Salzano et al., 1986) are presented on the far right in Table 2. The observed correlation between genotypic and migrational distance is $r_{GM} = .613$. With migrational distance instead of river distance, only 2/120 random permutations provide higher correlations, so $P \leq .025$. Is it possible to do better by using both river and migrational distance? The two are highly correlated ($r_{MR} = .916$), so there will be considerable redundancy of information. Using Equations (10a) and (10b), we see that $r_{GR \cdot M} = -.191$ and $r_{GM \cdot R} = .445$. The coefficient of multiple determination is $R^2 = .398$, computed via Equation (9b). Taking the square root of this value, we have $R_{G(RM)} = .631 > r_{GM} = .613$; the improvement is small. In summary, physical isolation is correlated with genetic divergence, but is less important than the history of gene flow from the outside. We need to translate travel distance into its admixture consequences if we are to elicit the full value of our anthropological knowledge.

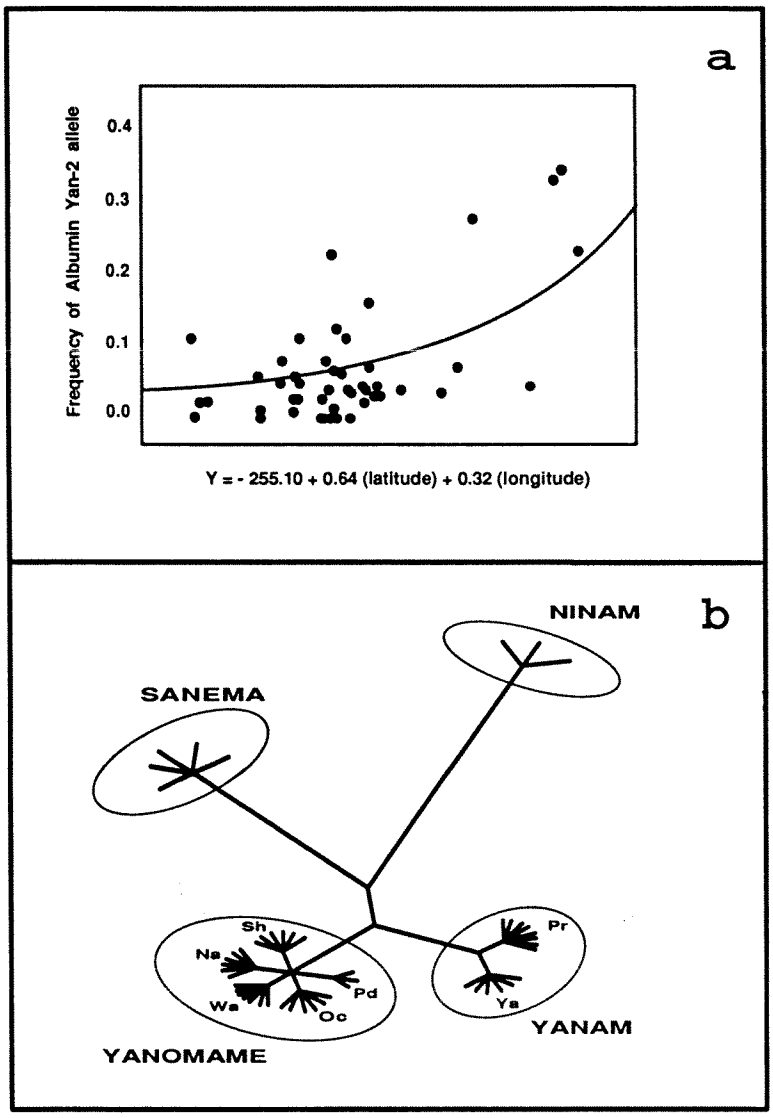

Fig. 2. Internal genetic structure of the Yanomama. a: The logarithm [p/q] of ALB*YAN-2 along a NW–SE transect through the tribe (modified from Tanis et al., 1974). b: Historical separation network, with dialect groups, miniclusters, and villages (modified from Sokal et al., 1986).

CLINAL VERSUS CLUSTER VARIATION IN THE YANOMAMA

Our studies of the Yanomama from Venezuela and northern Brazil have shown that the internal genetic structure of the tribe can be traced to important social and demographic forces that impinge on the group (e.g., Neel, 1978a,b; Smouse, 1982). We have described a very striking cline in the frequency of ALB*YAN-2 within the tribe (Tanis et al., 1974), an allele that is highly polymorphic within the tribe but which does not occur in the surrounding groups. The result is shown in Figure 2a. Later analyses (Ward and Neel, 1976) showed that six of 11 polymorphic loci showed clinal variation within the tribe but that the clines ran in several

different directions. Our best interpretation was that these clines were the result of centrifugal expansion of the tribe at an earlier historical stage.

Parallel efforts to elucidate the internal genetic structure of the tribe (Ward, 1972; Spielman, 1973; Spielman et al., 1974; Spielman and Smouse, 1976; Smouse and Neel, 1977; Smouse and Ward, 1978; Smouse et al., 1982, 1983) have made it clear that genetic variation within the tribe is hierarchically organized, largely as a residual feature of this same expansion history, with villages grouped into miniclusters (of a few decades duration), miniclusters grouped within dialect clusters (of a few centuries duration), and dialect clusters grouped within the tribe (Fig. 2b). The dialect clusters would be called different tribes in other anthropological situations, but the distinctiveness of the Yanomama sensu lato from their neighbors (of distantly related Carib and Arawak ethnicity) has made the "dialect-cluster" terminology attractive. The hierarchical structure of the tribe is defined on the basis of verbal history (Ward, 1972) and linguistic affinity (Spielman et al., 1974).

Since the hierarchical groupings are spatially organized within the 150,000-square-mile territory of the Yanomama, we had always wondered whether the clinal variation was merely a consequence of the cluster structure. Using a set of 15 allele frequencies for each of 50 Yanomama villages, we subsequently completed several analyses addressed to that question (Sokal et al., 1986). The essence of the problem is to compute matrices of genetic, geographic, and historical distances, and to determine whether history or geography better describes genetic population structure within the tribe.

For that study, we used Nei's (1972) standardized genetic distance measure to gauge the genetic divergence between pairs of villages. This is a different type of measure from Equation (14), and in fact it is not Euclidean, but it is particularly useful here, and we shall use it again later. Briefly, we define a measure of genetic affinity, I_{ij}, for the ith and jth villages, where the $p_{ik\ell}$ and $p_{jk\ell}$ are defined as for Equation (14)

$$I_{ij} = \frac{\sum_{\ell=1}^{L} \sum_{k=1}^{K_\ell} p_{ik\ell} p_{jk\ell}}{\left[\sum_{\ell=1}^{L} \sum_{k=1}^{K_\ell} p_{ik\ell}^2 \times \sum_{\ell=1}^{L} \sum_{k=1}^{K_\ell} p_{jk\ell}^2 \right]^{1/2}}. \tag{16}$$

Nei and Feldman (1972) have shown that under the neutral mutation model of evolution, genetic affinity decays exponentially with time, so that we expect

$$I_{ij} \sim \exp\{-2\alpha t\}, \tag{17a}$$

where α is the rate constant for decay, assumed to be the same for all neutral genetic loci, and t is measured in generations. They define a genetic distance measure, Δ_{Gij}, whose neutral expectation is linear in time

$$\Delta_{Gij} = -\log\{I_{ij}\} \sim 2\alpha t. \tag{17b}$$

We can obtain rough measures of relative times since divergence that are independent of the genetic data from information on historical and linguistic divergence, and can place the 50 villages into a crude network, with length along the internodes and legs measured in decades since separation (Fig. 2b). The precise value of the constant α is not known with any certainty, but for our purposes, the only important point is that all pairwise comparisons employ the same value. Measuring genetic distance along the network should give us a roughly time-proportional and time-linear pattern of divergence.

Geographic distance is measured in the usual straight-line fashion, using the map coordinates of the villages. Travel is most surely not accomplished in straight line fashion in the lowland rainforest, but for this study, we had no realistic

alternative. If we view genetic affinity as a consequence of gene flow (genetic diffusion), then I_{ij} can be related to geographic distance in the classical "isolation by distance" form (Morton et al., 1968, 1971; Malécot, 1969; Morton, 1969)

$$I_{ij} \sim \exp\{-\alpha D_{ij}\} \text{ or } \Delta_{Gij} = -\log\{I_{ij}\} \sim \alpha\Delta_{Dij}. \tag{18}$$

Both fission and diffusion processes have probably been important in the pattern of genetic affinities and differences among Yanomama villages, and we were attempting to determine which was the more important factor. The basic outcome is that the correlation between genetic (G) and geographic (D) distance is $r_{GD} = .415$ ($P \leq .0001$), while that between genetic (G) and historical (H) distance is $r_{GH} = .374$ ($P \leq .0002$). To determine how much of the cluster structure is inherent in sheer geographic separation and vice versa, we use the partial correlation analysis presented in Equations (9a) and (9b), derived in Smouse et al. (1986). The correlation between geographic (D) and historical (H) distance is $r_{DH} = .777$ ($P \leq .0001$), confirming that geography and cluster structure are highly confounded. The partial correlation of genetic (G) and geographic (D) distance, with historical (H) distance held constant, is $r_{GD \cdot H} = .213$. That of genetic (G) and historical (H) distance, with geographic (D) distance held constant, is $r_{GH \cdot D} = .090$. The coefficient of multiple determination is $R^2 = .1789$; the square root of that number is $R_{G(DH)} = .423$, as compared with $r_{GD} = .415$; there is nothing much to be gained by adding historical connections, once geography has been factored into the argument, since most cluster structure is inherent in the geography. This is a reversal of the Baniwa pattern presented earlier. Although hierarchical genetic organization may have been created by centrifugal expansion of the tribe, as postulated by Ward and Neal (1976), there has obviously been enough subsequent gene flow among these groups to "blur the boundaries" between them.

GENETIC, LINGUISTIC, AND GEOGRAPHIC AFFINITIES IN LOWER CENTRAL AMERICA

The lower Central American corridor is a critical archaeological region for any understanding of the peopling of South America (reviewed in Barrantes et al., 1990). One of the interesting questions that arises from our ongoing studies of the genetic structure within and affinities among a series of Chibcha-speaking Indian tribes from lower Central America (Fig. 3) is whether the current tribes are descended from the original migrants who first crossed the Isthmus, or whether they represent a much later wave of colonization from either the north or the south. We also need to know how they are related to each other. A lot has been learned about the genetic (Tanis et al., 1977; Spielman et al., 1979; Barrantes et al., 1982, 1990; Mohrenweiser and Novotny, 1982a,b) and linguistic (Constenla, 1984, 1985; Vargas, 1986) affinities of these people in the last decade, as well as their archaeological history (Linares and Ranere, 1980; Cooke, 1984, 1986; Lange and Stone, 1984; Snarskis, 1984; Irving, 1985), and we have recently attempted a composite evolutionary reconstruction (Barrantes et al., 1990).

Our measure of genetic distance is defined as in Equation (17b), because of its expected linearity with time since divergence and with geographic distance. We are able to define a similar measure of linguistic divergence, using cognate percentages from Constenla (1985) and Vargas (1986). Recall that glottochronological work begins with a standard word list (Swadesh, 1955, 1967) consisting of numerous lexical items. For each item, the ith and jth languages are judged to be cognate if the name for the item is the same, within the limits of systematic phonemic changes. Given W lexical items, the fraction that is cognate between the ith and jth languages is denoted K_{ij}, by analogy with I_{ij} in Equation (17a). Statistical analysis of written languages has shown (Hymes, 1960; Greenberg, 1987) that K_{ij} decays in roughly time-linear form, described by

$$K_{ij} \sim \exp(-2\beta t), \tag{19a}$$

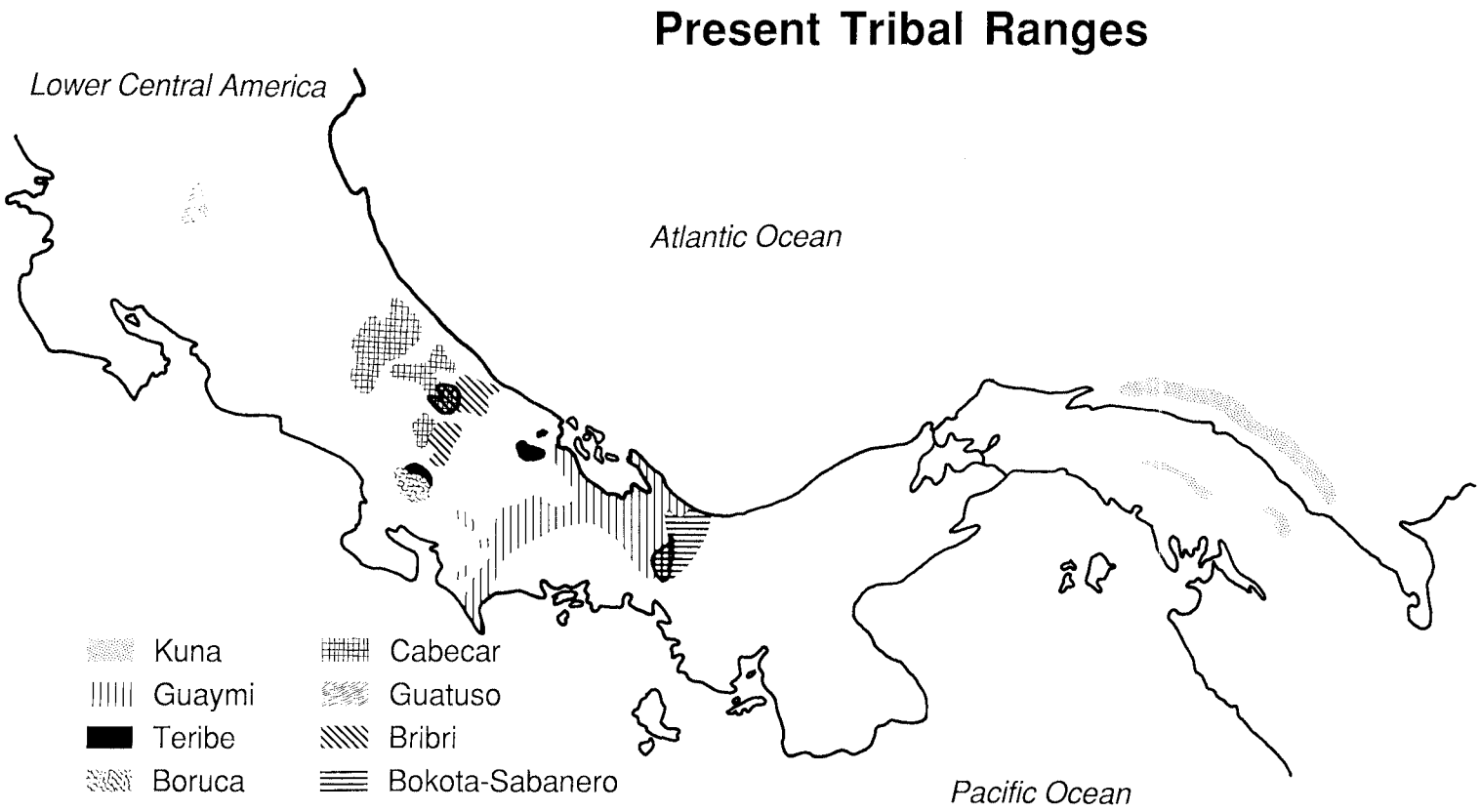

Fig. 3. Postcolumbian distributions of the Chibcha-speaking tribes of lower Central America (Reprinted from Barrantes et al., 1990).

where β is the rate constant for decay, assumed to be the same for all lexical items, and t is measured in years. By analogy with the genetic analysis in Equations (17a) and (17b), we can define a linguistic distance metric, C_{ij}, which should be linear with time since divergence

$$C_{ij} = -\log(K_{ij}) \sim 2\beta t. \tag{19b}$$

If both D_{ij} and C_{ij} were time-linear, they should be colinear with each other. If D_{ij} were linear with geographic distance, as postulated in Equation (18), then we should also expect colinearity of C_{ij} and G_{ij}. Using ten Chibcha population samples for which we have geographic position, genetic, and linguistic data, we plot C_{ij} against D_{ij} in Figure 4a. Mantel analysis shows that the correlation is highly significant ($r_{CD} = .69, P \leq .001$), but there are severe departures from linearity, suggesting that the decay of linguistic affinity, C_{ij}, is *not* colinear with D_{ij}. Comparison of C_{ij} with G_{ij} (not shown) shows the same trend. Although our Mantel test does not actually require any assumptions about linearity, we conclude that C_{ij} is neither linear with genetic divergence nor with geographic separation. It is probably not linear with time, either.

One of the critical theoretical assumptions that leads to time-linearity of both D_{ij} and C_{ij} is homogeneity of the decay rate constants α and β across genetic loci and lexical items, respectively; any departure from decay rate homogeneity leads to departures from strict time-linearity. Nei et al. (1976) had earlier shown that α varies among genetic loci, finding it mathematically convenient to describe the variation of α values among loci with a gamma distribution. The relationship between I_{ij} and the average value of α (say $\bar{\alpha}$) then takes the form (Nei et al., 1976)

$$\tilde{I}_{ij} \simeq \left[\frac{a}{a + 2\bar{\alpha}t}\right]^a, \tag{20a}$$

where a is the coefficient of variation of decay rates, α, across genetic loci. We can translated into a new measure ($\tilde{D}_{ij}$) which has time-linear expectation

$$\tilde{D}_{ij} = [1 - \tilde{I}_{ij}^{-a}]/a \cdot [\tilde{I}_{ij}^{-a}] \sim 2\bar{\alpha}t, \tag{21a}$$

The coefficient of variation in α values is thought to be about 0.8 in human studies (Nei et al., 1976), but we really cannot distinguish among a values over a range from ($0.0 \leq a \leq 2.0$) with our data. For small values of $\bar{\alpha}t$, this will always be the case. We use $a = 1.0$ for convenience.

Rate heterogeneity is also known to affect the decay rate of linguistic affinity across lexical items (Hymes, 1960; Greenberg, 1987). Using the same sort of gamma-distribution arguments concerning the average rate constant $\bar{\beta}$, we see that the relationship between K_{ij} and time is

$$\tilde{K}_{ij} \simeq \left[\frac{b}{b + 2\bar{\beta}t}\right]^b, \tag{20b}$$

where b is the coefficient of variation of decay rates, β, across the lexical items. This formula can be translated into an equation for $\tilde{C}_{ij}$

$$\tilde{C}_{ij} = [1 - \tilde{K}_{ij}^{-b}]/b \cdot [\tilde{K}_{ij}^{-b}] \sim 2\bar{\beta}t. \tag{21b}$$

In contrast to the experience with genetic distances, C_{ij} and $\tilde{C}_{ij}$ are not colinear over a reasonable range of b, because $2\bar{\beta}t >> 2\bar{\alpha}t$. Some correction for heterogeneity in β is clearly in order, but there is no extraneous information available to tell us what values of b we should use. Having arbitrarily set $a = 1.0$, we chose a value of b such that $\tilde{C}_{ij}$ and $\tilde{D}_{ij}$ are roughly colinear. A little trial and error fitting makes it clear that a value of $b = 0.5$ linearizes the relationship adequately, yielding a value of $r_{CD} = .735$. We claim no special virtue for this value except that it reduces the plot of $\tilde{C}_{ij}$ and $\tilde{D}_{ij}$ to roughly colinear form (Fig. 4b). It also reduces

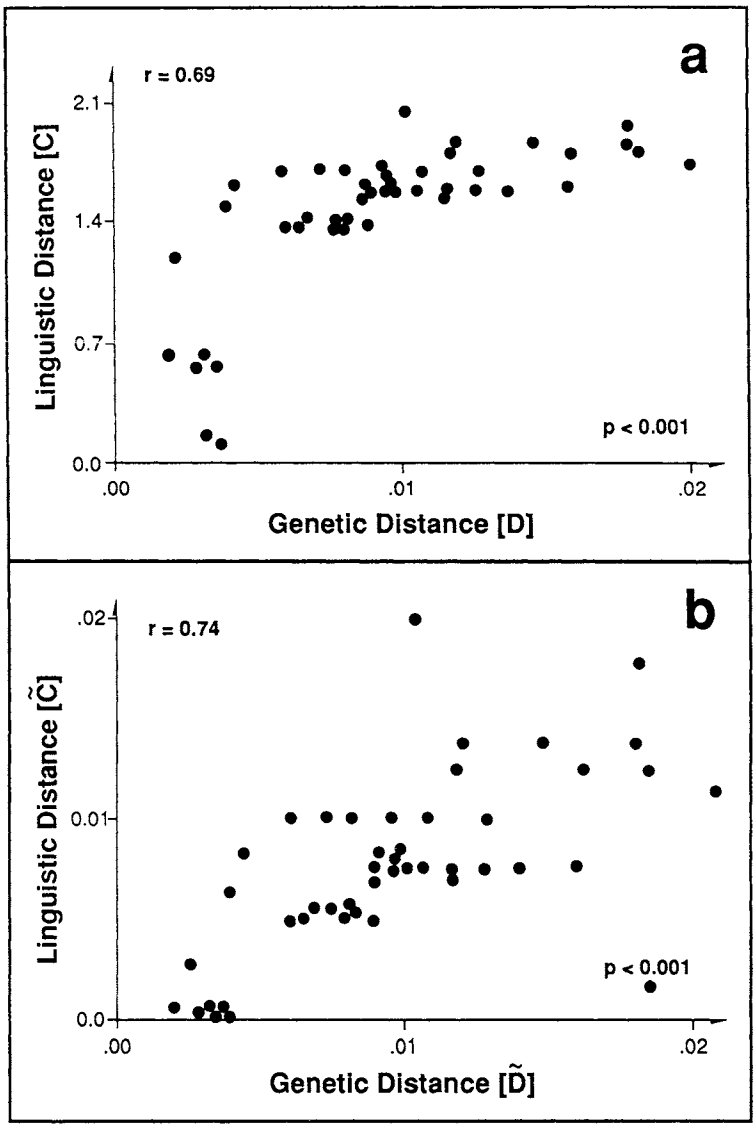

Fig. 4. Relationships between linguistic (C) and genetic distances (D) among eight Chibcha-speaking groups of lower Central America. a: Plot of C_{ij} against D_{ij}; b: plot of $\tilde{C}_{ij}$ against $\tilde{D}_{ij}$. The distances are defined in the text (from Barrantes et al., 1990).

that of $\tilde{C}_{ij}$ and G_{ij} to roughly colinear form (not shown). Neither of the geographic plots is very compelling, especially in view of the essentially corridor-like geography, but we might want to adjust the linguistic-genetic correlation for the common geographic component in any case; we obtain $r_{CD \cdot G} = .652$ (with P still $\leq .001$). Linearity is not essential for the test, of course, but its initial failure told us something useful about the validity of our theoretical predictions. The strong correlation between analogous genetic and linguistic measures of affinity confirms our initial supposition that the processes of genetic and linguistic diversification are strongly parallel.

A COMPARISON OF MIGRATION AND GENETIC AFFINITY PATTERNS IN NEW GUINEA

Many of applications of the Mantel test and our extensions have been developed in connection with our long-term studies on gene flow and genetic differentiation in the Gainj- and Kalam-speaking populations of Papua New Guinea (Wood et al., 1982, 1985; Long, 1986; Wood, 1986, 1987; Wood and Smouse, 1982; Long et al., 1986, 1987; Smouse and Wood, 1987; Smouse and Long, 1988), studies that elucidate the relationships between human population structure and their underlying demographic determinants. We have sought to explain the pattern of migration and genetic differentiation among Gainj and Kalam communities in terms of four primary demographic features; population size, endemicity (the tendency for offspring to be born in the same parish as their parents), geographic location, and the mix of the Gainj and Kalam languages spoken. Two distinct analytical strategies have been carried in parallel. Our first strategy has been the multiple-regression approach described above (Long et al., 1987). Our second strategy relied on prediction of a steady-state genetic distance matrix from primary demographic/cultural variables and comparison of this predicted matrix with observations on genetic markers, using the Mantel test. A pilot version of this approach was presented by Smouse and Wood (1987); a more complete analysis is presented here.

A brief description of the salient features of Gainj and Kalam population structure is in order before we present our analyses and conclusions. Both groups reside on the northern fringe of Papua New Guinea's central highlands, and both are subdivided into local groups called parishes (Fig. 5). Each parish contains between 20 and 200 individuals, and parish exogamy and patrilocal postmarital residence are usual (Johnson, 1982). We expect that the level of genetic differentiation among parishes will reflect a balance between the disruptive effects of genetic drift and the homogenizing effects of gene flow. Genetic drift among Gainj/Kalam parishes is due to small parish population sizes, and is exacerbated by cultural practices such as polygyny (Johnson, 1982). Interparish migration rates are structured according to underlying factors such as geography, language, exogamy, and population size. How genetic drift is counterbalanced by migration and the extent to which cultural and demographic variables influence this process remain to be demonstrated.

We examined the demography of a set of 18 parishes, including seven composed primarily of Kalam speakers, six composed primarily of Gainj speakers, and five with varying mixtures of the two (Fig. 5). As might be expected, the linguistic mix of a parish is not independent of its geographical location. For these 18 subpopulations, we have data on parish size (Wood et al., 1982; Long et al., 1986), Gainj/Kalam linguistic mix (Wood et al., 1985; Long et al., 1987), and the distance along primarily trail routes between parishes (Wood et al., 1985). All of these primary variables influence the patterns of migration and genetic affinities in one way or another. We have an estimated migration matrix (Wood et al., 1985) on the full set of 18 parishes and genetic data for 17 of the 18 (Wood et al., 1982; Long et al., 1986).

Multiple-regression approach

Long et al. (1987) used the Mantel multiple-regression method for empiric evaluation of the impact of the four aspects of Gainj/Kalam population structure on genetic distance: parish (population) size, endemicity, geographic distance, and linguistic distance. The population sizes of the different parishes were found to exert the greatest effect on the pattern of genetic distances ($R^2 = .31$). As expected, the smallest parishes were the most divergent and the largest parishes were the least divergent. More surprisingly, endemicity (i.e., the tendency for individuals to be born in the same parish as their parents) showed no effect on genetic distances, once parish sizes were accounted for. Geographic and linguistic distances both showed statistically significant but very weak ($R^2 < .07$) effects on the pattern of genetic distances. We were unable, however, to demonstrate an effect of linguistic distance, independent of geographic distance.

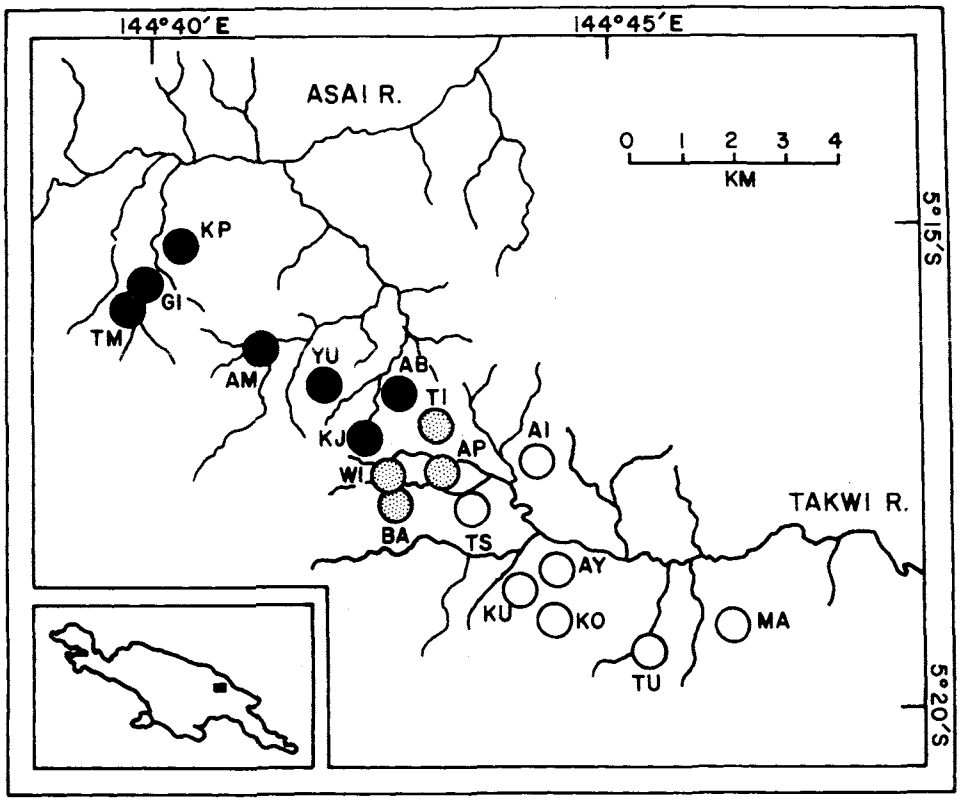

Fig. 5. A map of Gainj and Kalam parishes from the Takwi and Asai valleys of northern Papua New Guinea, with linguistic mix indicated by cross-hatching; blackened parishes have greater than 90% Kalam-speakers; open parishes have greater than 90% Gainj-speakers; hatched parishes have an intermediate mix (from Wood et al., 1985).

Population structure models

We have also modeled the patterns of interparish migration, in terms of primary demographic, geographic, and linguistic variables (Wood et al., 1985), using a modified "gravity model." This model predicts pairwise interparish migration rates from the equation

$$\log[m_{ij}/m_{ii}] = \mu + \alpha(S_i - S_j) + \gamma G_{ij} + \delta L_{ij} + e_{ij}, \tag{22}$$

where m_{ij} is the fraction of the parents for children who were born in the ith parish who were themselves born in the jth parish, and m_{ii} is corresponding fraction born in the same parish. The term μ is the endemicity parameter, reflecting the cultural strength of the tendency for parents and offspring to be born in the same parish. The term $\alpha(S_i - S_j)$ measures the tendency for parents to be recruited from larger to smaller parishes (or the reverse). The terms γG_{ij} and δL_{ij} measure the effects of geographic separation and linguistic isolation on migration rates, respectively. The e_{ij} is an error term. Geographic distance was measured with a pedometer along major travel routes, and L_{ij} has been defined (Wood et al., 1985) as

$$L_{ij} = \left| \log\frac{\%Kalam(i)}{\%\,Gainj(i)} - \log\frac{\%Kalam(j)}{\%Gainj(j)} \right|, \tag{23}$$

TABLE 3. Mantel correlations between observed genetic distances among Gainj and Kalam parishes and those predicted by the migration model theory

Migrational model	Model parameters included	Residual χ^2		Degrees of freedom	Mantel outcomes	
		Male	Female		r	P
0	none	6073.94	2465.82	306	.000	.500
1	μ	856.59	1680.82	305	.443	.005
2	μ, α	828.16	1549.82	304	.419	.012
3	μ, γ	778.45	1199.30	304	.288	.058
4	μ, δ	655.12	1175.41	304	.428	.000
5	μ, α, γ	750.51	1044.40	303	.178	.144
6	μ, α, δ	627.39	1030.58	303	.294	.012
7	μ, γ, δ	652.21	1054.66	303	.400	.010
8	μ, α, γ, δ	624.48	896.46	302	.260	.027
Observed	complete fit	0.00	0.00	0	.412	.001

Both the observed migration matrix and the migration models of Wood et al. (1985) were used, along with residual χ^2 values for those models; μ, endemicity effect; α, population density effect; γ, geographic distance effect; δ, linguistic divergence effect.

where the percentages represent the proportions of individuals within the ith and jth parishes who identify their primary language as either Kalam or Gainj, respectively. The log-linear form for linguistic distance was chosen to match the log-linear form of the migrational model.

Wood et al. (1985) have described the various parameter estimation and hypothesis testing techniques for the log-linear model, Equation (23); basically, we obtain parameter estimates and a set of χ^2 goodness-of-fit test criteria; the reader is referred to that paper for the details. Exhaustive analysis provides the results in Table 3, where we have separated male and female components of migration for the 18 parishes. We have migrational data on one parish for which we have no genetic data, but will include it in the migrational analysis to establish the predicted genetic outcomes. Endemicity accounts for most (85%) of the χ^2 variation in migration rates for males and a substantial fraction (32%) of that for females. The parameter estimates ($\mu_f = -2.11$, $\mu_m = -4.47$) indicate that males are more philopatric than are females. After accounting for the level of endemicity, linguistic distance is the most important variable, as seen by comparing the residual χ^2 for H4 with those for H2 or H3. The estimated linguistic divergence coefficient is slightly greater in magnitude for females ($\delta_f = -0.42$, $\delta_m = -0.34$); females are slightly more constrained by linguistic differences than are males. Geographic distance is also a barrier to migration, with females again being more constrained than males ($\gamma_f = -0.13$, $\gamma_m = -0.08$). Population densities of donor and recipient parishes also have a small effect, with recruitment being preferentially from larger to smaller parishes in both sexes ($\alpha_f = -0.008$, $\alpha_m = -0.006$). The full model accounts for 90% of the migrational variation in males but only 64% of that in females. There is some confounding in the full model; geographic and linguistic distances are highly correlated, and a clean separation of their effects is problematic. Considering that we begin with 306 degrees of freedom and use only four to fit the model, we have achieved a compelling and parsimonious description of the migration matrix.

The next step in our analysis was to convert these predicted migration matrices into predicted genetic distance matrices. We accomplished that by applying the "migration matrix theory" developed by others (Bodmer and Cavalli-Sforza, 1968; Smith, 1969; Imaizumi et al., 1970; Harpending and Jenkins, 1974; Wood, 1986; Rogers, 1987). The Mantel test is then applied to assess the level of correspondence between each of these predicted genetic distance matrices and the actual (observed) matrix. The essential strategy of the migration matrix theory is to predict a matrix, $\mathbf{V}(t) = \{v_{ij}(t)\}$, where

$$v_{ij}(t) = \frac{[q_i(t) - \bar{q}][q_j(t) - \bar{q}]}{\bar{q}(1 - \bar{q})}. \tag{24}$$

The elements of this expression are $q_i(t)$ and $q_j(t)$, the allele frequencies at a given locus for the ith and jth parishes in generation t, respectively, and $\bar{q}$, the expected allele frequency at the same locus, assumed to be identical across all parishes. The diagonal elements of $\mathbf{V}(t)$ are the variances of allele frequencies within populations, and the off-diagonal elements are the covariances of allele frequencies among populations. Division by $\bar{q}(1 - \bar{q})$ in the expression for $v_{ij}(t)$ removes the effect of scale, so that the same $v_{ij}(t)$ values pertain to all alleles at all loci. The values of $v_{ij}(t)$ will change from generation (t) to generation $(t + 1)$ until an equilibrium is reached. The predictions of this matrix are not made from allele frequencies! Rather, they are made from the migration matrix, $\mathbf{M} = \{m_{ij}\}$, where m_{ij} is the proportion of alleles in the ith subpopulation that originated in the jth subpopulation in the previous generation, and from a diagonal matrix $\mathbf{U}(t) = [1 - v_{ii}(t - 1)]/2N_{ei}$, with N_{ei} defined as the effective population size of the ith subpopulation. The theory predicts that

$$\mathbf{V}(t) = \sum_{r=0}^{t} [\mathbf{M}']^r \mathbf{U}(r)[\mathbf{M}]^r. \tag{25}$$

Harpending and Ward (1982) have used a spectral decomposition of $\mathbf{M}$ to power the equation, showing that the results are more robust to computer rounding error. We will only need to power for three to four generations for our example (see below), so we will not need that additional wrinkle here.

Another sort of prediction that can be obtained from the migration matrix theory, and the type we need here, is the set of expectations for the $N(N - 1)/2$ pairwise genetic distances among subpopulations for the tth generation

$$\mathbf{D}_{GG}(t) = \{d_{ij}(t)\} = v_{ii}(t) + v_{jj}(t) - 2v_{ij}(t). \tag{26}$$

Wood (1986) has shown that $\mathbf{D}_{GG}(t)$ converges rapidly to an equilibrium solution, $\mathbf{D}_{GG}(*)$, when the level of migration is as high as it is here. Since each sex contributes half the genes of the next generation, we have used an unweighted average of the predicted migration matrices for the two sexes to construct $\mathbf{M}$ for Equation (25), one set of predicted matrices for each demographic model tested. We estimated the effective population size (N_{ei}) of each parish to be roughly half the census number (S_i), in accord with the results of a detailed demographic analyses by Wood (1987). Given $\mathbf{M}$ and $\mathbf{U}$, we constructed a predicted genetic distance matrix for each of our migrational models. Using only the 17 parishes for which we have genetic data, we compared the predicted equilibrium matrix, $\mathbf{D}_{GG}(*)$, with our observed distance matrix, $\mathbf{D}_{GG}$, using the Mantel test.

For initial evaluation, we obtained a predicted genetic distance matrix from an observed migration matrix, reflecting the details of movement from one parish to another over a two-generation period. The predicted and observed genetic distance matrices exhibit a moderate but highly significant correlation ($r = .412, P \leq .001$). For subsequent analyses, we used the model migration matrices generated from each of the modified gravity models in Table 3 to predict genetic distance matrices. The results are presented in the final two columns of Table 3 and are a little surprising. For the model (0) using only the endemicity parameter μ, predicted genetic distances are more highly correlated ($r = .443, P \leq .005$, as in Table 3) with observed genetic distances than are the genetic distances generated from the observed migration matrix. The estimated endemicity parameter μ is the same for all parishes, so differences in pairwise predicted genetic distances are a reflection only of differences in the effective sizes, N_{ei}, of the several parishes. Basically, smaller parishes drift more than large ones, and with random migration among them at a constant level, the affinities among parishes reflect the effective size differences.

The genetic distance predictions from all of our other migration models are less correlated with observed genetic distances than is model (0). Although the genetic distances generated from migration models that include linguistic distance are no worse than those with endemicity alone, they are also no better. When geographic distance is included in the model, correlations between predicted and actual genetic distances are severely diminished. The effects of population density on migration rates do not appear to affect the pattern of genetic distances, *except* insofar as they influence $\mathbf{U}(t)$ via differences in N_{ei}, the same drift effect we described earlier.

These results illustrate some important considerations both for migration matrix theory and for applications of the Mantel test. Migration matrix theory is appealing in principle, because it provides expected genetic distances for a set of N populations, given their effective population sizes and pairwise migration rates. Nevertheless, it carries the assumptions that the effective population sizes and pairwise migration rates have remained constant for many generations and that they are known without error. Neither assumption is ever strictly true in the analysis of natural populations. Furthermore, since the actual genetic distance between two parishes is a random variable, and the migration matrix theory provides only an expectation for this random variable, we cannot expect our observed genetic distances to equal our predicted values precisely, even if the model assumptions were met in precise detail. Moreover, the data always depart from precise theory to some degree. For example, Rogers and Harpending (1986) and Rogers (1987) show that both the age structure of the population and the familial component of nonrandom gene flow can have an influence on the outcome. Neither effect is allowed for in the elaborate (but still relatively oversimplified) models above.

It is unfortunate that prediction of the standard errors of the genetic distances is beyond the current scope of migration matrix theory; we cannot conduct a rigorous analysis of correspondence between the observed and expected values, based on stringent distributional assumptions. The best we can hope for is to demonstrate empirically a significant correspondence between the predictions of our idealized theory and our observations. Herein lies the strength of the Mantel test. Whether or not we accept the correlation between our observed genetic distances and those predicted from the observed migration matrix ($r = .412$) as being important, it is surely of interest that some of our predicted migration matrices do equally well or better than the observed matrix, despite the fact that only a few salient features of Gainj/Kalam population structure have been used to predict those migration matrices.

Our results also provide some insight on Gainj/Kalam population structure. The structure of genetic differentiation among Gainj and Kalam parishes is not the same as the structure of migration. Geographic distance and language have modest impact on migration but virtually no impact on genetic differentiation. While this seems counterintuitive at first glance, it is consistent with the theoretical balance between drift, due to small effective population size, and migration. From first principles, we know that N_e is inversely related to the magnitude of genetic drift. Parish effective population sizes in this region of New Guinea are small, so there is considerable random dispersion each generation. There is also, however, considerable migration; about 50% of the genes born in a parish derive from other parishes in the previous generation. This high level of migration can be expected to "erase" any accumulated genetic pattern rapidly. As a consequence, the genetic structure we observe at any given moment is correlated with the most recent burst of genetic drift, embodied in the N_{ei} values, with the overall exchange rate, embodied in the endemicity parameter μ, and little else. If we can extract the essential pattern of drift and the magnitude of gene flow, we are doing about as well as we can expect. In this case, the pursuit of more exquisite anthropological/demographic detail was not productive, though that was not obvious at the outset. The multiple-Mantel treatment developed by Smouse et al. (1986) and deployed by

Long et al. (1987) would seem to provide about as much precision as the data will support.

DISCUSSION

We have made much of the relationship between matrix correlation analysis and standard regression and correlation techniques. We should mention briefly an additional extension holding promise in anthropological genetics context. Livshits et al. (1991) have turned to the deployment of $\mathbf{D}_{XX}$ matrices that are of the "design" or "contrast" form so familiar and useful in traditional analysis of variance. Using a whole series of design matrices for $\mathbf{D}_{XX}$, they have investigated the pattern of genetic variation among worldwide Jewish populations and their non-Jewish countrymen. The basic question, an old one, is whether separated Jewish populations have remained genetically isolated since the diaspora, or whether they have admixed with their respective non-Jewish neighbors. The analyses, as might be expected, show that the truth is somewhere in between; Jewish populations do show strong traces of their shared ancestry, but they also show affinities with their non-Jewish neighbors. The whole topic has been the subject of much discussion, and the results have shed some welcome light on the matter. Quite apart from clarifying an interesting anthropological situation, Livshits et al. (1991) have provided the beginnings of an important technical breakthrough that warrants additional attention in future work.

There have been three other noteworthy extensions of the Mantel procedure to multiple matrices. The first of these is described by Dow and Cheverud (1985), based on an idea first presented by Hubert and Golledge (1981). Where there are two matrices ($\mathbf{D}_{XX}$ and $\mathbf{D}_{WW}$), both thought to be predictive of another matrix ($\mathbf{D}_{YY}$), but correlated among themselves, the suggested procedure is to compare $\mathbf{D}_{YY}$ with the difference matrix

$$D_{XX-WW} = D_{XX} - D_{WW} = \{\Delta_{Xij} - \Delta_{Wij}\}. \tag{27}$$

If the b or r values are positive, X is said to be the better predictor; if the value of b or r is negative, W is said to be the better predictor. To employ this technique, it is first necessary to transform both $\mathbf{D}_{XX}$ and $\mathbf{D}_{WW}$ to a common scale, usually accomplished by subtracting the average element and dividing by the standard deviation, i.e. normalization. Using this procedure, Dow and Cheverud (1985) examined genetic, anthropometric, and geographic variation among 19 Yanomama villages, using data from Spielman (1973), finding that anthropometric and geographic distances are more correlated than are genetic and geographic distances. Sokal et al. (1986) used the same approach to examine the 50-village Yanomama data set we described earlier, but were unable to choose between geographic and historical separation as predictors of genetic distance. Oden (1992) has shown that the Dow-Cheverud technique is vulnerable to spatial autocorrelation, and the whole matter needs further investigation.

The second extension is described by Hubert (1985). This method is based on a different view of the way in which various sets of measures "interact." With this procedure, $\mathbf{D}_{YY}$ is contrasted with the element by element (Hadamard) product of $\mathbf{D}_{XX}$ and $\mathbf{D}_{WW}$

$$\mathbf{D}_{XX*WW} = \mathbf{D}_{XX}{}^{*}\mathbf{D}_{WW} = \{\Delta_{Xij}\Delta_{Wij}\}. \tag{28}$$

Here it is the nonlinear interactions of the two predictor matrices that are of interest. Using this procedure, Sokal et al. (1986), once again examining the 50-village Yanomama data set described above, have shown that genetic distance is not credibly correlated with this Hadamard product (interaction) of geographic and temporal separation. If we compare the three analyses of our 50-village Yanomama set, we are led to the conclusion that geographic and temporal separation are highly confounded and largely interchangeable as predictors of genetic distance; they do not show any nonlinear interactive effects.

Manly (1986) has derived an alternative regression model, predicting one distance matrix as a linear combination of several others. He also normalizes, and then computes partial correlation coefficients. Barring the normalization, which is mere scale transformation, Manly's formulation is identical to that of Smouse et al. (1986), used extensively here. Where Manly's procedure departs from ours is in his attempt to place confidence intervals on his estimated r coefficients. Permutational analysis under the null hypothesis provides both a test and a confidence interval around ($r = 0$), but that is not what Manly has done. His effort is directed toward placing a confidence interval around the observed correlation ($r \neq 0$); he uses a more elaborate sampling scheme. Oden and Sokal (1992) have raised some questions about Manly's confidence intervals, but technical questions aside, the central idea has merit; matrix correlation analysis is commonly conducted with the a priori expectation that the null hypothesis is *not* true, constituting a convenient statistical straw man. That being the case, a confidence interval on the nonzero correlation would be useful. Evaluating the same 19 Yanomama Indian villages as Dow and Cheverud (1985), Manly obtains the same qualitative conclusions. His coefficient of multiple determination is $R^2 = .733$ ($P \leq .001$), when predicting genetic data from geographic and anthropometric data, so that would be our value as well.

Oden and Sokal (1992) have recently compared all four of these methods for the case where $\mathbf{D}_{XX}$ and $\mathbf{D}_{YY}$ both contain internal spatial autocorrelation, due to geographic patterns embedded within $\mathbf{D}_{WW}$. Both the Dow-Cheverud (1985) and Hubert (1985) procedures are highly vulnerable to spatial autocorrelation, particularly if the pattern is nonlinear (fairly typical, if our experience is any indication). Oden and Sokal (1992) show that the P values are seriously underestimated by permutational analysis. The Manly confidence intervals appear to be seriously underestimated as well. The size of the problem in each case increases with the level of spatial autocorrelation. The Smouse et al. (1986) method favored here seems to be more resistant to spatial autocorrelation. We can partial $\mathbf{D}_{WW}$ out of the linear correlation between $\mathbf{D}_{XX}$ and $\mathbf{D}_{YY}$, but when the spatial autocorrelation is very large and highly nonlinear, even the present method is vulnerable. Krackhardt (1987, 1988) has shown that generalizations of the current approach to multiple matrices are remarkably unbiased in the face of *linear* autocorrelation, but it makes sense that nonlinear relationships are difficult to deal with, using a technique designed for linear relationships.

Two additional comments are in order. 1) We have shown with the Chibcha example that the appropriate way to deal with nonlinear relationships is to linearize them before conducting the analysis. On the other hand, if we have no theory to guide us or if we have no data on geographic connections, we cannot protect ourselves; but that has ever been the price of ignorance. Moreover, and as we have shown with our examples, even if we have information on geography, there are cases where it can actually obfuscate the issue. 2) Manly's (1986) estimated confidence intervals are too narrow, but since his matrix correlation analysis is isomorphic to ours, permutational evaluation of the *null* hypothesis should yield the same result as our method, which is somewhat more robust. Oden and Sokal's (1992) results indicate that a reexamination of Manly's confidence interval procedure is in order. Confidence intervals on $r \neq 0$ would be useful, if they were reliable, a problem that will have to be left for the future. The strengths and limitations of permutational testing procedures are matters that need further work, because it is hard to imagine a credible alternative. If the relatively forgiving nonparametric procedures are vulnerable, then the assumption-laden distributional alternatives almost have to be more so.

Statistical quibbles aside, the Dow-Cheverud and Hubert approaches capture the essence of two different types of dependency of $\mathbf{D}_{YY}$ on a pair of predictor matrices, $\mathbf{D}_{XX}$ and $\mathbf{D}_{WW}$. The Dow-Cheverud approach detects additive relationships, while the Hubert approach tests for nonadditive interactions. The general-

ized regression approach advocated here can easily incorporate both types of dependency, since we can always write

$$\Delta_{Yij} = a_1\Delta_{Xij} + a_2\Delta_{Wij} + a_3\Delta_{Xij}\Delta_{Wij} + e_{ij}. \tag{29}$$

Dow-Cheverud have (implicitly) set $a_1 = -a_2$ and $a_3 = 0$; Hubert has implicitly set $a_1 = 0 = a_2$. Both approaches are thus special cases of the quadratic model (29), a more general version of which we have used for analysis of the Gainj and Kalam (Long et al., 1987)

$$\Delta_{Yij} = b_1\Delta_{Xij} + b_2\Delta_{Wij} + c_{11}\Delta^2_{Xij} + c_{12}\Delta_{Xij}\Delta_{Wij} + c_{22}\Delta^2_{Wij} + e_{ij}. \tag{30}$$

We found no significant quadratic effects, but (in fairness) we also found only one linear effect (see above). There may well be situations where higher order effects will provide useful information. Dow and de Waal (1989), citing Hubert (1987), develop a cubic version of the Mantel model that is designed to search for these higher order effects, and use them to elucidate subgroup interactions among sets of different elements. The method is reminiscent of that provided by Livshits et al. (1991), based on the idea of contrasts.

Comparative work with different distance and affinity measures has a long history in anthropology, and there is every reason to anticipate still further developments. We show here that there are simple techniques available that can be used in concert with as much social, demographic, and historical information as we can bring to bear. In anthropological context, there are two lessons to be learned. 1) There are many anthropological problems that can be handled in this same general fashion; all that is needed is a little imagination. We have stressed anthropological *genetics* here, because that is our area of expertise, but other arenas are equally amenable to examination. The basic methodology is simple, and standard programs are readily available. Our examples were chosen to span a range of extraneous information we could expect to elicit in social, historical, demographic, and linguistic context. 2) Within broad limits, we conclude that the more we know, the more we can learn with matrix correlation analysis. We have shown that theory-guided efforts are especially fruitful, even where (as in our Chibcha and Gainj/Kalam examples) we encounter some surprises. Even in cases where traditional analyses are equivalent, there is much to be learned by comparing pairwise data. For problems where the data are inherently pairwise, these matrix correlation methods provide one of the few natural, yet powerful tools for analytical exploration.

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