



News and Views

Alternatives to the partial Mantel test in the study of environmental factors shaping human morphological variation

S. Ivan Perez^{a,*}, José Alexandre Felizola Diniz-Filho^b, Valeria Bernal^a, Paula N. Gonzalez^a

^a CONICET, División Antropología, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900, La Plata, Argentina

^b Departamento de Ecología, ICB, Universidade Federal de Goiás, CP 131, 74001-970, Goiânia, Goiás, Brazil

ARTICLE INFO

Article history:

Received 18 October 2009

Accepted 30 July 2010

Keywords:

Spatial autocorrelation

Partial Mantel correlation

Spatial regression techniques

The importance of ecological factors in shaping morphological differences among human populations is highly debated despite numerous studies that have examined worldwide patterns of morphological variation (Roberts, 1953; Beals et al., 1984; Katzmarzyk and Leonard, 1998; Relethford, 2004a; Roseman, 2004; Harvati and Weaver, 2006; Betti et al., 2010). Some craniofacial studies have pointed out that the main forces behind cranial shape variation are random factors such as genetic drift and mutation (Relethford, 2004a; Manica et al., 2007; Betti et al., 2010). Conversely, other studies have suggested that craniofacial form and size variation, as well as dental size and postcranial morphological variables, are associated with environmental variation (Beals et al., 1984; Katzmarzyk and Leonard, 1998; Roseman, 2004; Harvati and Weaver, 2006; Perez and Monteiro, 2009; Bernal et al., 2010).

The above studies generally assess the importance of ecological factors using correlative analyses of morphological (e.g., cranial shape, body size) and environmental (e.g., minimum temperature) variables. However, one of the major problems with this approach is that spatial structure may be present in the morphological variable (Legendre and Legendre, 1998). First, morphological variation may be related to other environmental or non-environmental variables that are spatially structured, generating *spatial dependence* among populations (Legendre and Legendre, 1998). For instance, repeated migration from one particular locale into another results in spatial structure—a well-defined cline—leading to high morphological similarity between groups in close geographic proximity as well as

greater morphological differentiation of more distant groups (Sokal et al., 1989). Second, recent common ancestry, genetic exchange, and/or local environmental conditions can cause populations to become *autocorrelated*, i.e., they tend to be more similar to each other—more than what is expected only by chance and independent of the environmental variation—for a given morphological variable (Legendre, 1993; Legendre and Legendre, 1998; Felsenstein, 2002; Ives and Zhu, 2006). Gene flow, restricted by geographical distance, is particularly important in generating a high degree of biological similarity among human populations at small geographical scales (Cavalli-Sforza et al., 1994; Relethford, 2004a). The presence of spatial structure biases estimates and significance tests of standard statistical techniques used to calculate correlations between morphological and environmental variables. For example, if a population attained a wide cranium due to the influence of temperature, neighboring populations may have a similar cranial breadth as the result of gene flow with the former, even though temperature does not directly affect them. Therefore, such similar cranial breadth should not be taken as a proof of temperature response (Felsenstein, 2002).

In order to test the association between morphological and environmental variables, it is necessary to use statistical techniques that take into account the existence of spatial structure (i.e., autocorrelation or spatial dependence). Partial Mantel tests are the most widely used test for this purpose in biological anthropology (e.g., Oden and Sokal, 1992; Relethford, 2004b; Betti et al., 2010). In this paper, we assess the efficacy of the partial Mantel test. First, we describe Mantel and partial Mantel correlation (Smouse et al., 1986). Then, we briefly outline the spatial regression techniques that are designed to solve the problem of spatial structure among human populations (Dormann et al., 2007; Diniz-Filho et al., 2009; Perez et al., 2009a). Finally, we use a simple example to illustrate the performance of Mantel, partial Mantel correlations, and spatial regression techniques to test the association between morphological and environmental variables.

Mantel and partial Mantel tests

The comparison of distance matrices using Mantel-based tests is commonly used in biological anthropology to test the association between morphological and environmental variables, even when its statistical properties in this context are unknown (also see

* Corresponding author.

E-mail address: iperez@fcnym.unlp.edu.ar (S.I. Perez).

Harmon and Glor, 2010). The first step is to calculate the distances between samples (e.g., Euclidean distances for morphometric, geographical, and environmental data) using vector data (e.g., variables). Mantel (1967) introduced a method that can be used to directly estimate the correlation between two distance matrices. The Mantel Z statistic is the sum of the cross-products of the elements in two matrices, $Z_{XY} = \sum(XY)$, where X and Y are unfolded distance matrices describing the independent variables and the trait variation, respectively (i.e., the distance matrices are unfolded column by column to form a long vector, excluding the diagonal elements; Smouse et al., 1986; Legendre et al., 1994; Legendre and Legendre, 1998). The Pearson product–moment correlation coefficient, $r_{XY} = \sum(XY)/[\sum(X^2)\sum(Y^2)]^{1/2}$, is monotonically associated to Z, and it is generally preferred in anthropological studies because it has the advantage of being expressed in standardized units (Smouse et al., 1986). Given the fact that elements in a distance matrix are related to one another, Z and r statistics cannot be parametrically tested for significance. Therefore, a randomization test is used to estimate the significance of the Z and r statistics (Smouse et al., 1986; Legendre et al., 1994).

If a correlation between morphological variation and geography (i.e., spatial structure in the morphological variable) is detected, a partial Mantel test can be used to account for spatial structure (Oden and Sokal, 1992; Relethford, 2004b; Betti et al., 2010). The partial Mantel test, or Mantel method for three matrices, computes the partial correlation between the matrices X and Y, conditional upon a third matrix, V, which describes the geographical distances (Smouse et al., 1986; Legendre and Legendre, 1998). First, the elements of X are regressed on the elements of V to obtain a matrix of residuals. Second, the same procedure is used to obtain a matrix of residuals of Y on V. Finally, the correlation between the residual matrices (i.e., Z and r statistics) is calculated and its significance is tested by performing a randomization test (Smouse et al., 1986). Therefore, the partial Mantel matrix correlation, as well as the simple partial correlation, is a linear correction that removes all variation in the matrices X and Y that is correlated to the matrix V, e.g., geography (Smouse et al., 1986; Oden and Sokal, 1992; Legendre and Legendre, 1998).

Spatial regression models

Several regression techniques have been recently proposed to test whether or not a morphological variable could be associated with environmental variation. These techniques directly model the morphological and environmental variables (i.e., the vector dataset) and take into account the spatial structure in the data (for recent reviews, see Diniz-Filho et al., 2009; Perez et al., 2009a). These models have the general structure of a regression model such as: $y = Xb + \epsilon$, where y is the vector that describes the trait variation, X is the matrix of independent variables, b is the vector of regression coefficients, and ϵ is the error term, normally distributed with constant variance and independently distributed among observations (Legendre and Legendre, 1998). Thus, the covariance matrix C among residuals is $C = \sigma^2 I$, where σ^2 is the variance of the residuals—which is constant throughout the diagonal of C —and I is an identity matrix (a matrix of ones along the diagonal and zeros elsewhere), highlighting that there is no correlation structure among the data. This simple model is usually estimated using least-squares and is commonly referred to as the ordinary least-squares regression model (OLS). All this could be easily generalized to multivariate forms (Rohlf, 2001).

When applying such a model it is assumed, after considering the effects of the environment, that residual variation is randomly distributed among local populations. However, if part of that similarity among local populations is unrelated to the environment

but instead relates to higher gene flow, local environmental conditions, or both gene flow and local environmental conditions among neighboring populations, then residuals will be autocorrelated. Statistically, this implies that $C \neq \sigma^2 I$, which violates standard OLS assumptions. Taking this into account, a number of modifications in the OLS equation can be performed, both in order to improve the understanding of morphological variation, as well as to better estimate and test model parameters (for recent reviews, see Bini et al., 2009; Diniz-Filho et al., 2009; Perez et al., 2009a). In general, we refer to these techniques as *spatial regression models*. These can be grouped together in two classes, based on the idea of incorporating spatial structure either into model residuals, by correcting the matrix C above (e.g., generalized least-squares), or into model structure (e.g., autoregression and spatial eigenvector mapping) (Diniz-Filho et al., 2009; Perez et al., 2009a).

The generalized least-squares model (GLS) is the same as the ordinary least-squares model, but incorporates autocorrelation into model residuals and thus does not assume that $C = \sigma^2 I$. Hence, the error structure in C is designed to incorporate the lack of independence expected in the observations as a consequence of the spatial distribution of the populations. In this model, the covariance matrix C is based on a matrix W (the “expected relationship matrix” or weighting matrix). For example, $C = \sigma^2 W$, which contains the correlation structure among populations. The elements of W can be estimated by different and complex inverse functions of geographic distances (d_{ij}) between populations, given by inverse distance-powered functions of the form: $w_{ij} = 1/d_{ij}^\alpha$, where α is the parameter that regulates the model (see Perez et al., 2009a). In essence, the zeros in the identity matrix (I) used in OLS are replaced by numbers that reflect the inverse of the geographic relationship among populations.

Another alternative approach for spatial regression, instead of modifying the error term, is to introduce new explanatory variables in the model that “captures” the spatial variation, thereby minimizing the autocorrelation in the residuals or removing the spatial dependence. There are several ways to incorporate spatial variables into the model structure in order to eliminate or minimize residual autocorrelation, and the general model has the form $y = Xb + G + \epsilon$, where X , b , and ϵ are as defined for OLS equation and G is a vector or matrix showing the geographic space. This spatial regression takes into account autocorrelation in the residuals by capturing spatial relationships in the G term, which can be defined in different ways. The simplest way to define space is by using spatial coordinates of local populations (e.g., latitude, longitude, or its principal components), which can be added to the model as spatial independent variables. This technique is known as trend surface analysis (TSA) and is better suited to model broad-scale trends (i.e., to remove the spatial dependence), rather than local autocorrelation in the data (Legendre and Legendre, 1998). Recent comparative evaluations (e.g., Bini et al., 2009) have suggested that a good, and presently popular, way to take into account spatial patterns into the model structure is to use *spatial eigenvector mapping* (SEVM; Griffith and Peres-Neto, 2006). In this model, G is defined by principal coordinates of the W matrix, so that eigenvectors with different eigenvalues describe the geographical patterns at different spatial scales. It is important to point out that these spatial regression techniques, as well as the partial Mantel test, assume spatial stationarity (i.e., spatial autocorrelation and effects of ecological correlates are homogeneous across regions; Dormann et al., 2007).

Performance of partial Mantel correlation and spatial regression techniques: an example

We will now use a simple example to illustrate the performance of the partial Mantel test versus other regression models in order to examine the association between morphological and environmental

variables that vary geographically. This example is based on 2D cranial landmarks and semilandmarks from ten late Holocene South American samples previously used by Bernal et al. (2006) to study robusticity. Bernal et al. (2006) and Perez and Monteiro (2009) have shown, using regression techniques and quantitative genetic models (i.e., testing the magnitude of divergence), that temperature was a significant predictor of cranial divergence found among these populations. The climate hypothesis is also supported by experimental and observational studies (Bernal et al., 2006).

The samples studied belong to prehistoric populations from different geographic and ecological regions, distributed along 3,000 km (from latitude 25–55° South; Fig. 1). Twelve landmark and twenty-five semilandmark coordinates (Fig. 2) were recorded from the digital images. They were subsequently aligned using Generalized Procrustes Analysis (GPA) and the semilandmarks were slid along the contour using the minimum Procrustes distance criteria (Mitteroecker and Gunz, 2009). Finally, a Principal Components Analysis (PCA) was performed on the Procrustes coordinates plus centroid size, in order to describe major trends in form variation (Mitteroecker and Gunz, 2009). More details about the 2D cranial dataset and morphometric analysis, as well as additional sample descriptions, are presented in Bernal et al. (2006). The first PC score, accounting for 31.85% of the total variation among sample means, is used in the example to simplify the explanation. Although we used a univariate approach to study variation among populations, the techniques discussed here can be generalized to multivariate models (Smouse et al., 1986; Legendre and Legendre, 1998; Rohlf, 2001; Perez et al., 2009b).

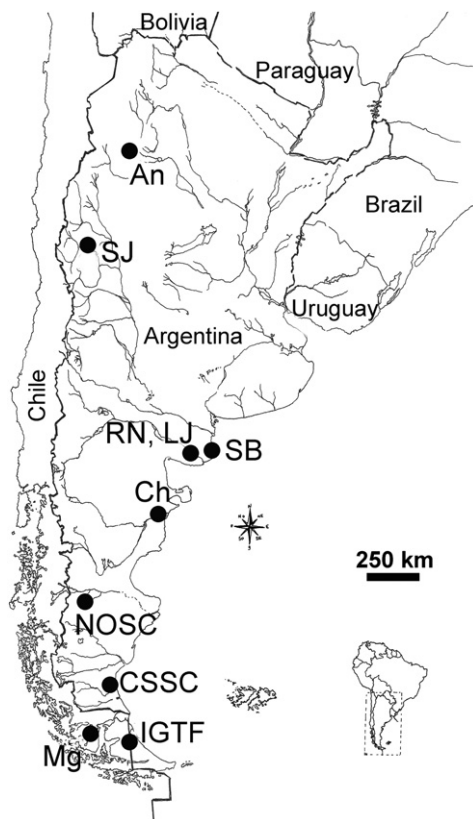


Figure 1. Map showing the geographic localization of the samples of crania analyzed. An: Andalgala, $N = 15$; SJ: San Juan, $N = 15$; RN: Río Negro Valley, $N = 21$; SB: San Blas, $N = 30$; LJ: Laguna del Juncal, $N = 20$; Ch: Chubut Valley, $N = 31$; NOSC: Northwest of Santa Cruz, $N = 16$; CSSC: Center-south of Santa Cruz, $N = 10$; IGTF: Isla Grande de Tierra del Fuego, $N = 11$; Mg: Magallanian region, $N = 11$. All samples are detailed in Bernal et al. (2006).

The relationship between PC1 and latitude (a good proxy for geographical distance in the region under study) shows morphometric similarity among neighboring populations (Fig. 3a). We explore the spatial structure of form variation using a spatial correlogram based on Moran's I autocorrelation coefficients (Sokal and Oden, 1978). The correlogram of PC1 score vs. Moran's I shows a cline affecting the entire distribution of the samples (Fig. 4), which can be explained by several processes (e.g., directional selection or gene flow). However, it is important to point out that PC1 values are similar among neighbor populations (ca. 200 km; Fig. 4), showing that, in this dataset, there is autocorrelation among them. We also note that other works show a great similarity among neighbor populations in southern South America (more similarity to each other than expected by chance alone, i.e., autocorrelation), probably as a consequence of genetic exchange and/or local environmental conditions (Perez, 2006; Perez et al., in press).

These analyses also show a strong relationship between PC1 and mean annual temperature in southern South America (Fig. 3b). The samples from southernmost Patagonia show more robust cranial features than those from northern Argentina and this is a result of the lower temperatures in Patagonia (for a more detailed morphometric results, see Bernal et al., 2006). Regression and Mantel correlation results are shown in Table 1. The OLS analysis confirms that temperature has a significant effect on the variation of robusticity patterns, described in the first PC score (Table 1). The slope value for temperature is highly significant: particularly robust crania are found in cooler regions (Fig. 3b). Moreover, this environmental variable explains 75% of the variation in form. The Mantel test also indicates that temperature has a significant effect on the patterns of robusticity variation, but for this analysis, temperature only explains 40% of form variation (Table 1).

We used both spatial regression techniques and partial Mantel correlation to test the association between PC1 and temperature, incorporating spatial structure into the analysis. To define the spatial structures for the spatial regression models, we calculated the weighting matrix (W) as the inverse of the geographic distance matrix, where the influence of one sample over the other decreases non-linearly with the increase of the geographical distance between the samples (Fig. 5). This generates a large decline in morphometric distances when geographical distance is between 0–300 km and shows a plateau with little distance change after 500 km (Fig. 5). This approach works under the assumption that the morphometric variation of a population is likely to resemble the variation of another population from the same area due to genetic exchange and/or local environmental conditions (Perez et al., 2009a). Alternatively, we calculated the first principal component of the geographic coordinates, which describes broad-scale geographic trends in this region on a north–south direction (the correlation between PC1 of the geographic coordinates and latitude was 0.836, $P = 0.003$). Using this PC score in the regression model, we assume that the clinal pattern of morphometric variation among populations was generated by processes such as migration from one side (Legendre and Legendre, 1998).

The results of GLS, SEVM, and TSA regression models are shown in Table 1. The GLS and SEVM models were calculated using the matrix W to define the spatial structure and showed, as did the OLS analysis, a significant effect of temperature over robusticity variation patterns—though with a lower significance value. However, the TSA model, calculated using the first principal component of geographic coordinates to define the spatial structure, showed no significant effect of temperature on PC1 score (Table 1). The partial Mantel test was calculated using the matrix of geographic distances among samples (the V matrix, which describes the broad-scale geographic trends in the region) to define the spatial structure, and also suggests that robusticity is not associated with temperature,

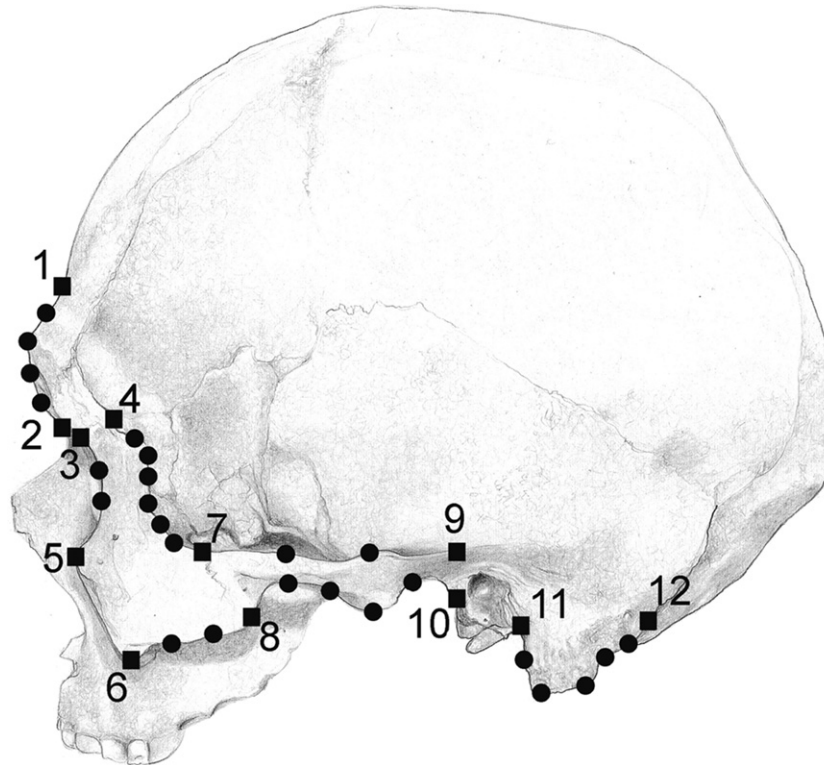


Figure 2. Allocated landmarks (squares) and semilandmarks (circles) on craniofacial structures. Landmarks: 1) frontex; 2) nasion; 3) frontomolare anterior; 4) frontomolare temporale; 5) infraorbitale; 6) zygomaxillare anterior; 7) the most superior point on the suture between the zygomatic process of the temporal bone and the temporal process of the zygomatic bone; 8) the most inferior point on the same suture as landmark 7; 9) auriculare; 10) the point on the lateral aspect of the inferior border of the root of the zygomatic process; 11) the most anterior point on the root of the mastoid process; 12) the most posterior point on the root of mastoid process. Drawing by Marina Perez.

showing a r^2 value of 0.06 and a P value of 0.141 (Table 1). Whereas the results of GLS and SEVM models shown here corroborate the previous works by Bernal et al. (2006) and Perez and Monteiro (2009), the partial Mantel test and the TSA model behaved as expected: they eliminate the relationship between robusticity variation and temperature after removing the linear relationship of both variables with geographic distance.

Discussion

Despite its popularity in biological anthropology, ordinary Mantel and partial Mantel tests show questionable performance when testing the association between morphological and environmental variables. In our example, the association between

morphological and environmental variables decreased when Mantel correlation was used (ca. 35% lesser association; Table 1). These results agree with previous ones, which have shown that the Mantel test has a low statistical power (Harmon and Glor, 2010). The reduced performance of the Mantel test could be partly a result of the fact that the vector data are converted to pairwise distances; therefore, the same set of distances could be obtained from two different vectors, and a single value in the original vector could have a cascading effect on distance matrix (Harmon and Glor, 2010). Based on our results, we suggest not converting vector data to pairwise distances in order to test the importance of environmental variables on morphological variation. In this way, Harmon and Glor (2010) recommended the use of Mantel tests only when absolutely necessary, i.e., when data cannot be expressed in any form other

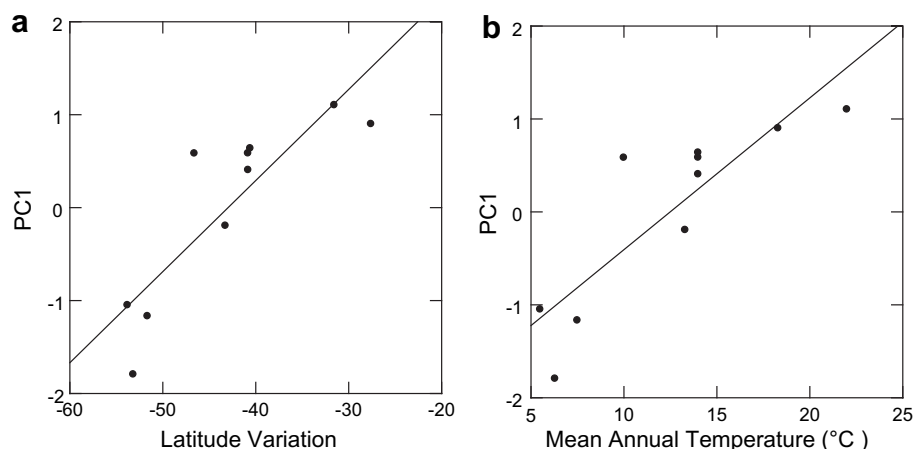


Figure 3. Plot of PC1 score vs. latitude variation (a) and mean annual temperature (b) among samples.

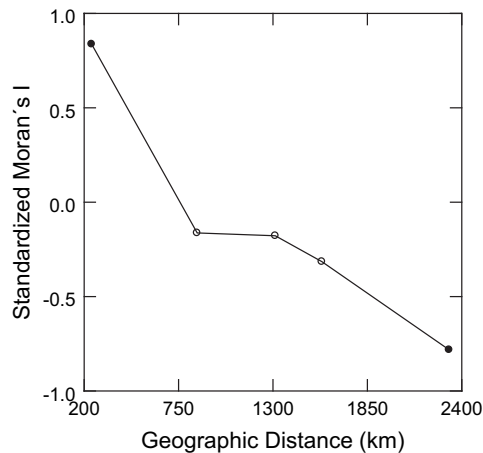


Figure 4. PC1 vs. Moran's *I* autocorrelation. Filled circles indicate significant autocorrelation coefficient values.

than pairwise distances. A better alternative would be to first convert this distance matrix to vectors using principal coordinate analysis (Mitteroecker and Bookstein, 2009), and then use an ordinary or spatial regression model. Additionally, in our example, the partial Mantel test "removed" the geographical variation and the effect of temperature (Oden and Sokal, 1992; Perez et al., 2009b). However, as noted above, temperature is a factor for which we have good reasons to believe that actually covaries with cranial variation in this dataset. The performance of the partial Mantel test could be due to the fact that it is designed to test the association between two variables (e.g., morphology and temperature) after removing their linear relationship with a third variable (e.g., geographic distance).

Spatial regression models are generally more powerful and flexible when testing for correlations between morphological and environmental variation in the presence of spatial dependence or autocorrelation in the dataset. This is because the partial Mantel correlation does not exactly work as spatial regression techniques, i.e., taking into account only spatial similarity among neighbor populations. This is particularly important in human population studies where, as a result of spatial structure, gene flow will be more frequent between nearby populations leading to some degree of genetic uniformity at smaller geographical scales, while greater distances restrict gene flow, leading to genetic differentiation by genetic drift (Cavalli-Sforza et al., 1994; Relethford, 2004b; Betti et al., 2010). Therefore, the partial Mantel test could be useful when our interest lies in eliminating broad-scale lineal trends or

Table 1

Results of the regression and Mantel analyses performed between PC1 score and the temperature variables.

Technique	<i>r</i>	<i>r</i> ²	Std. coeff. temp.	<i>P</i> value
<i>Standard models</i>				
Ordinary least-squares (OLS)	0.861	0.741	0.861	0.002
Mantel	0.632	0.399	–	0.001
<i>Spatial models</i>				
Generalized least-squares (GLS)	0.848	0.720	0.716	0.014
Spatial eigenvector mapping (SEVM) ^a	0.793	0.793	1.319	0.014
Trend surface analysis (TSA) ^a	0.877	0.769	0.634	0.085
Partial Mantel	0.258	0.066	–	0.141

^a The *r* and *r*² values show the predictor plus the spatial structure. Bold letters represent significant associations.

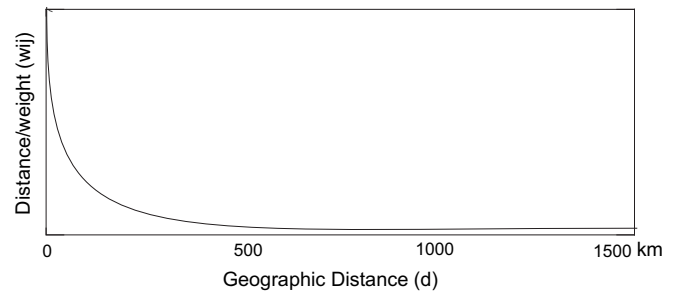


Figure 5. Plot of geographical distance (*d*) vs. distance/weight (*w_{ij}*).

spatial dependence out of a dataset, e.g., the geographic trends generated by an expansion or migration from a single direction (Sokal et al., 1989). However, given the problems found when converting vector data to pairwise distances (see above), we would rather incorporate the broad-scale lineal trends into the structure of a spatial regression model (e.g., into trend surface analysis, TSA; Diniz-Filho et al., 2009; Perez et al., 2009a).

Here, we stress the use of spatial regression techniques, but we could also incorporate genetic distance or phylogenetic relationships to test autocorrelation among populations, an approach known as the comparative phylogenetic method (for reviews, see Rohlf, 2001; Garland et al., 2005). In such cases, different evolutionary models (e.g., isolation-by-distance or phylogenetic trees) can easily be used to generate the **W** matrix, instead of geographical distances (Rohlf, 2001; Perez et al., 2009a). For example, Bernal et al. (2010) used a GLS model where **W** matrices were generated using a neighbor-joining tree, the inverse function of mtDNA distances, and the inverse function of geographical distance between human populations. Having a strong model for dependence and/or autocorrelation due to ecological or evolutionary processes in the dataset analyzed, will improve the ability of regression techniques to detect the association between a particular environment factor and a morphological variable.

Although anthropological studies generally apply correlation analyses to infer the importance that environmental variables have in shaping morphological differences among human populations, the use of quantitative genetic models to measure the magnitude of shape variation, and not only its pattern, could be a good complementary approach (Schluter, 2000; Roseman, 2004; Perez and Monteiro, 2009; Perez et al., in press). These techniques are useful for understanding the importance of ecological factors in shaping the patterns of morphological variation among populations in an explicit geographical context. However, neither tests for pattern nor magnitude is sufficient for determining if natural selection is the evolutionary process shaping morphological divergence among populations. Once the importance of an environmental variable has been detected with the appropriate method, further studies based on morphological, genetic, ecological, and evolutionary evidence are required in order to prove the existence of natural selection and adaptation (Losos, 2000).

Conclusions

The results obtained by partial Mantel tests should be treated with caution because these tests can sometimes remove the effect one is trying to detect, including the influence of environmental factors. Spatial regression techniques, on the other hand, could be used to provide more accurate statistical estimates of the association between morphological and ecological variables. The spatial and phylogenetic regression techniques are not new to interspecific research (Ives and Zhu, 2006; Bini et al., 2009), but they have been

underused in biological anthropology. In our view, spatial regression techniques are more flexible and they can incorporate similarity among populations (i.e., autocorrelation) as well as broad-scale geographic trends (i.e., spatial dependence) into the models, depending on how the data are modeled. We do not claim that previous studies aiming to test ecological factors are misguided, but we wonder if the use of more explicit spatial regression models could also be used to study the importance of ecological factors driving morphological variation among human populations.

Acknowledgments

We are deeply indebted to the Associate Editor who contributed greatly to improve the clarity of the manuscript.

References

- Beals, K.L., Smith, C.L., Dodd, S.M., 1984. Brain size, cranial morphology, climate, and time machines. *Curr. Anthropol.* 25, 301–330.
- Bernal, V., Perez, S.I., Gonzalez, P., 2006. Variation and causal factors of craniofacial robusticity in Patagonian late holocene hunter-gatherers. *Am. J. Hum. Biol.* 18, 748–765.
- Bernal, V., Perez, S.I., Gonzalez, P.N., Diniz-Filho, J.A.F., 2010. Ecological and evolutionary factors in dental morphological diversification among modern human populations from southern South America. *Proc. R. Soc. B* 277, 1107–1112.
- Betti, L., Balloux, F., Hanihara, T., Manica, A., 2010. The relative role of drift and selection in shaping the human skull. *Am. J. Phys. Anthropol.* 141, 76–82.
- Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., Aparicio, A., Araújo, M.B., Baselga, A., Beck, J., Bellocq, M.I., Böhning-Gaese, K., Borges, P.A.V., Castro-Parga, I., Khen Chey, V., Chown, S.L., De Marco Jr., P., Dobkin, D.S., Ferrer-Castán, D., Field, R., Filloy, J., Fleishman, E., Gómez, J.F., Hortal, J., Iverson, J.B., Kerr, J.T., Kissling, W.D., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Morales-Castilla, I., Moreno, J.C., Oberdorff, T., Olalla-Tárraga, M.A., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.A., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N.J., Terribile, L.C., Vetaas, O.R., Hawkins, B.A., 2009. Coefficients ships in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography* 32, 1–12.
- Cavalli-Sforza, L.L., Menozzi, P., Piazza, A., 1994. *The History and Geography of Human Genes*. Princeton University Press, Princeton, NJ.
- Diniz-Filho, J.A.F., Nabout, J.C., Campos Telles, M.P., Soares, T.N., Rangel, T.F.L.V.B., 2009. A review of techniques for spatial modeling in geographical, conservation and landscape genetics. *Genet. Mol. Biol.* 32, 203–211.
- Dormann, C.F., McPherson, J., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of distributional species data: a review. *Ecography* 30, 609–628.
- Felsenstein, J., 2002. Contrasts for a Within-Species Comparative Method. In: Slatkin, M., Veuille, M. (Eds.), *Modern Developments in Theoretical Population Genetics*. Oxford University Press, Oxford, pp. 118–129.
- Garland Jr., T., Bennett, A.F., Rezende, L., 2005. Phylogenetic approaches in comparative physiology. *J. Exp. Biol.* 208, 3015–3035.
- Griffith, D.A., Peres-Neto, P., 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87, 2603–2613.
- Harmon, L.J., Glor, R.E., 2010. Poor statistical performance of the mantel test in phylogenetic comparative analyses. *Evolution* 64, 2173–2178.
- Harvati, K., Weaver, T.D., 2006. Human cranial anatomy and the differential preservation of population history and climate signatures. *Anat. Rec. Part A* 288A, 1225–1233.
- Ives, A.R., Zhu, J., 2006. Statistics for correlated data: phylogenies, space, and time. *Ecol. Appl.* 16, 20–32.
- Katzmarzyk, P.T., Leonard, W.R., 1998. Climatic influences on human body size and proportions: ecological adaptations and secular trends. *Am. J. Phys. Anthropol.* 106, 483–503.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673.
- Legendre, P., Lapointe, F.-J., Casgrain, P., 1994. Modelling brain evolution from behavior: a permutational regression approach. *Evolution* 48, 1478–1499.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier, Amsterdam.
- Losos, J., 2000. Ecological character displacement and the study of adaptation. *Proc. Natl. Acad. Sci. U.S.A.* 97, 5693–5695.
- Manica, A., Amos, W., Balloux, F., Hanihara, T., 2007. The effect of ancient population bottlenecks on human phenotypic variation. *Nature* 448, U346.
- Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27, 209–220.
- Mitteroecker, P., Bookstein, F., 2009. The ontogenetic trajectory of the phenotypic covariance matrix, with examples from craniofacial shape in rats and humans. *Evolution* 63, 727–737.
- Mitteroecker, P., Gunz, P., 2009. Advances in geometric morphometrics. *Evol. Biol.* 36, 235–247.
- Oden, N.L., Sokal, R.R., 1992. An investigation of 3-matrix permutation tests. *J. Classif.* 9, 275–290.
- Perez, S.I., 2006. *El poblamiento holoceno del Sudeste de la Región Pampeana: Un estudio de morfometría geométrica craneofacial*. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Argentina.
- Perez, S.I., Monteiro, L.M., 2009. Nonrandom factors in modern human morphological diversification: a study of craniofacial variation in southern South American populations. *Evolution* 63, 978–993.
- Perez, S.I., Diniz-Filho, J.A.F., Bernal, V., Gonzalez, P.N., 2009a. Spatial statistical techniques for inter-population data: studying the relationships between morphological and ecological variation. *J. Evol. Biol.* 23, 237–248.
- Perez, S.I., Diniz-Filho, J.A.F., Rohlf, F.J., dos Reis, S.F., 2009b. Ecological and evolutionary factors in the morphological diversification of South American spiny rats. *Biol. J. Linn. Soc.* 98, 646–660.
- Perez, S.I., Lema, V., Diniz-Filho, J.A.F., Bernal, V., Gonzalez, P., Gobbo, D., Pucciarelli, H.M. The role of diet and temperature in shaping cranial diversification of South American human populations: an approach based on spatial regression and rate tests. *J. Biogeogr.*, in press, doi:10.1111/j.1365-2699.2010.02392.x.
- Relethford, J.H., 2004a. Global patterns of isolation by distance based on genetic and morphological data. *Hum. Biol.* 76, 499–513.
- Relethford, J.H., 2004b. Boas and beyond: migration and craniometric variation. *Am. J. Hum. Biol.* 16, 379–386.
- Roberts, D.F., 1953. Body weight, race and climate. *Am. J. Phys. Anthropol.* 11, 533–558.
- Rohlf, F.J., 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55, 2143–2160.
- Roseman, C.C., 2004. Detection of interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proc. Natl. Acad. Sci. U.S.A.* 101, 12824–12829.
- Schluter, D., 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Sokal, R.R., Oden, N.L., 1978. Spatial autocorrelation in biology. 1. Methodology. *Biol. J. Linn. Soc.* 10, 199–228.
- Sokal, R.R., Jacquez, G.M., Wooten, M.C., 1989. Spatial autocorrelation analysis of migration and selection. *Genetics* 121, 845–855.
- Smouse, P.E., Long, J.C., Sokal, R.R., 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst. Zool.* 35, 627–632.