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Comparative Methods for Studying Cultural Trait Evolution: A Simulation Study

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Anthropologists and archaeologists increasingly use phylogenetic methods to test hypotheses involving cross-cultural traits, but the appropriateness of applying tree-based methods to analyze cultural traits is unclear. The authors developed a spatially explicit computer simulation model to investigate trait evolution in relation to phylogeny and geography and used the simulation to assess the sensitivity of two comparative methods (independent contrasts and partial Mantel tests) to different degrees of horizontal transmission. Simulation results show that (a) the method of independent contrasts is sensitive to even small amounts of horizontal transmission in cultural data sets, (b) Mantel tests fail to cleanly discriminate between datasets characterized by different levels of horizontal and vertical trait transmission, and (c) partial Mantel tests do not produce markedly improved statistical performance when testing for associations among traits (as compared to independent contrasts). The results highlight the need for empirical estimates of

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horizontal transmission and extinction rates in cross-cultural datasets.

Keywords: *comparative methods; cultural trait evolution; phylogeny; simulation study*

Comparison is fundamental to anthropology, for it is only through informed comparison that a general framework for understanding cultural trait evolution can be developed (Campbell, 1988). Thus, the comparative method has played a central role in anthropology (C. R. Ember & Ember, 1998; M. Ember & Ember, 2000). Key results include the finding that residence patterns are correlated with patterns of warfare (M. Ember & Ember, 1971), that son-biased inheritance and bride wealth are associated with polygyny (Hartung, 1982), that dowry is found with monogamy (Gaulin & Boster, 1990), that women's labor contributions decline with agricultural intensification (Burton & White, 1984), and that states generally emerge in conditions of political and geographic circumscription (Carneiro, 1970). More recently, cross-cultural comparison has been used to investigate life history correlates of disease diversity (Guegan, Thomas, Hochberg, de Meeus, & Renaud, 2001) and the functional basis of variation in dietary preferences (Billing & Sherman, 1998; for other examples, see Bentley, Jasienska, & Goldberg, 1993; Hill & Hurtado, 1996).

One potential constraint on the comparative analysis of cultural traits is that the data points representing societies are linked differentially through historical effects and the movement of traits among societies. In other words, the data points in a comparative analysis are not necessarily independent of one another (Borgerhoff Mulder, 2001; Burton & Reitz, 1981; Dow, 1989; Dow, Burton, White, & Reitz, 1984; Mace & Pagel, 1994). Sir Francis Galton recognized this problem in his 1889 evaluation of E. B. Tyler's comparative work, and as "Galton's problem," it has engaged comparativists ever since (e.g., Naroll & Cohen, 1970).

A number of methods have been developed to deal with Galton's problem (Dow et al., 1984; Murdock & White, 1969; Smouse & Long, 1992; Sokal, 1988). In recent years, cultural anthropologists have borrowed methods from biology to study the evolution of cultural traits (e.g., Borgerhoff Mulder, George-Cramer, Eshleman, & Ortolani, 2001), and some anthropologists have collaborated with evolutionary biologists to address questions in cultural evolution using tools developed for biological systems (e.g., Mace & Pagel, 1994). These "phylogenetic comparative methods" have been used in biology to deal with the nonindependence of species values by incorporating information on the branching evolutionary tree (phylogeny) that links the species under consideration (Felsenstein, 1985; Harvey & Pagel, 1991). Evolutionary biologists have applied these methods to address questions across species involving correlated trait change (Felsenstein, 1985; Harvey & Pagel, 1991), patterns of speciation and extinction (Nee, Holmes, May, & Harvey, 1994; Nee, May, & Harvey, 1994), and rates of phenotypic evolution (Martins, 1994; Martins & Hansen, 1997).

The application of phylogeny-based methods to study cultural data is based on three assumptions: (a) relationships among human societies can be represented as a branching pattern (a phylogenetic tree), (b) cultural traits are spread vertically from ancestral to descendent societies on this tree, and (c) models of biological trait evolution are appropriate for studying cultural traits (Borgerhoff Mulder et al., 2001; Cowlishaw & Mace, 1996; Mace & Holden, 2005; Mace & Pagel, 1994, 1997). Regarding (c), for example, one commonly used model in biology assumes that traits exhibit "Brownian motion" change, in which trait change is pulled from a normal distribution with a mean of zero and variance proportional to time (Felsenstein, 1988). Such assumptions have proved highly contentious, given that the emergence and diversification of human societies are not well understood and that cultural traits are often transmitted horizontally among societies through trade, teaching, or conquest (Cavalli-Sforza & Feldman, 1981; Guglielmino, Viganotti, Hewlett, & Cavalli-Sforza, 1995).

The extent to which the evolution of culture is analogous to biological evolution is still debated (Boyd, Borgerhoff Mulder, Durham, & Richerson, 1997; Cavalli-Sforza, Menozzi, & Piazza, 1994; Durham, 1990, 1992; Gray & Atkinson, 2003; Mace & Holden, 2005; Mesoudi, Whiten, & Laland, 2004; J. H. Moore, 1994; Pagel & Mace, 2004; Shennan, 2000). According to the model of phylogenesis, cultural evolution takes the form of descent with modifi-

cation through a successive subdivision of cultural assemblages (Gray & Jordan, 2000; Holden, 2002; Kirch, 1984). With ethnogenesis, cultural evolution occurs through the borrowing and blending of ideas and practices and through the trade and exchange of objects among contemporary societies (Terrell, Hunt, & Gosden, 1997). Much of this debate has been theoretical, and the limited quantitative data currently available (reviewed in Collard, Shennan, & Tehrani, in press) reveal great variation in the extent to which cultural traits are transmitted vertically and/or horizontally among societies. There is certainly some good evidence of phylogenetic signal in cultural data sets, determined either through cladistic analyses (e.g., Rexová, Frynta, & Zrzavý, 2003, using Indo-European language as a cultural trait) or through correlations between language (an indicator of shared history) and cultural traits (Holden, 2002; C. C. Moore & Romney, 1994, 1996; White, Burton, & Dow, 1981). But there is also evidence that the phylogenetic signature of history can be weak (e.g., Moylan, Borgerhoff Mulder, Graham, Nunn, & Håkansson, in press, who look at East African cultural traits), and examples exist in which blending appears to be more important than branching (Jordan & Shennan, 2003, focusing on Californian Indian basketry).

Given uncertainty regarding the transmission of cultural traits between parent-daughter and sister-sister populations, it is timely to evaluate the performance of phylogenetic comparative methods for testing correlated cultural trait change in the context of horizontal trait transmission. As a first step toward this goal, we focus on the most commonly used phylogenetic comparative method, namely, independent contrasts (Felsenstein, 1985; Garland, Harvey, & Ives, 1992; Nunn & Barton, 2001). Independent contrasts are calculated as differences in trait values between species or higher taxonomic units (i.e., reconstructed values on nodes deeper in the phylogeny; Figure 1a). As differences, these contrasts represent evolutionary change since two species last shared a common ancestor; thus, these contrasts deal with the nonindependence of species values. Contrasts are standardized using information on branch lengths to deal with the fact that more evolutionary change is usually found when greater amounts of time separate two species or nodes on the phylogeny.

It is also important to investigate the performance of an alternative general approach that has been used to examine the geographical distribution of genes and cultural traits, including languages (Dow, Cheverud, & Friedlaender, 1987; Smouse & Long, 1992;
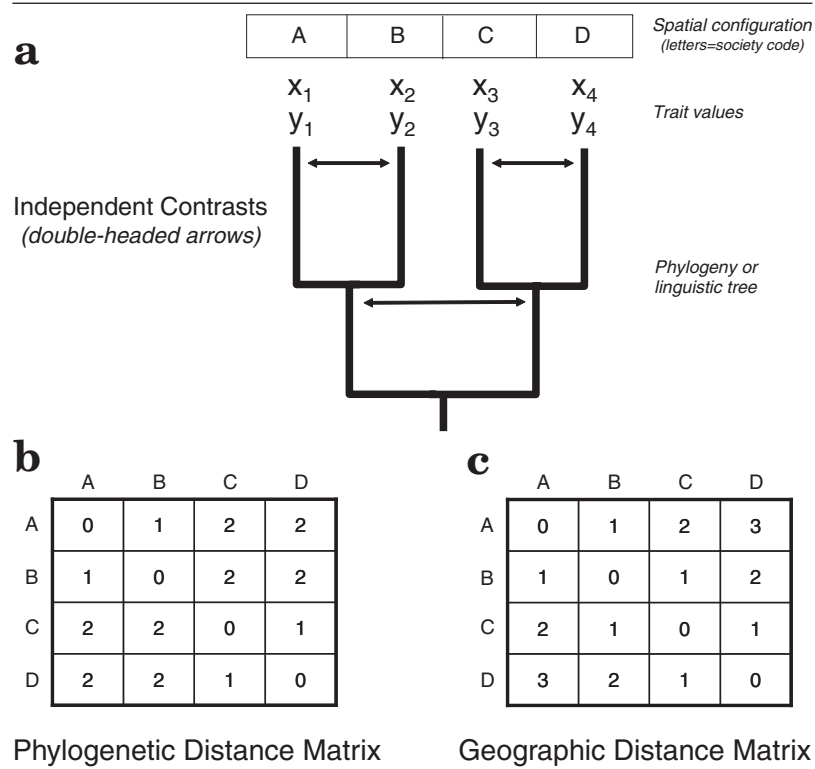
	A	B	C	D	
					Spatial configuration (letters=society code)

a

x_1 x_2 x_3 x_4 *Trait values*
y_1 y_2 y_3 y_4

Independent Contrasts
(double-headed arrows)

Phylogeny or linguistic tree

b

	A	B	C	D
A	0	1	2	2
B	1	0	2	2
C	2	2	0	1
D	2	2	1	0

Phylogenetic Distance Matrix

c

	A	B	C	D
A	0	1	2	3
B	1	0	1	2
C	2	1	0	1
D	3	2	1	0

Geographic Distance Matrix

Figure 1:   Statistical Procedures Investigated Using the Simulation Model

NOTE: Calculation of independent contrasts (a) requires information on the spatial configuration of societies (in this case, a single row), trait values, and a tree (branch lengths = 1 unit) that represents relatedness among the societies. Independent contrasts are calculated as differences in species values or reconstructed values at higher nodes, and these contrasts are typically standardized for branch length (evolutionary time). The tree is further used to construct a phylogenetic distance matrix (b), and the spatial configuration of the societies is used to construct a geographic distance matrix (c). These distance matrices, along with a distance matrix for the traits (not shown), can be examined with geographic methods such as the Mantel test and partial Mantel test.

Sokal, 1988). This other approach is based on distance matrices that incorporate information on the phylogenetic and geographical distribution of societies using Mantel tests (Mantel, 1967). After constructing matrices representing differences in trait values, phylogenetic distances (Figure 1b), and geographic distances (Figure 1c), one can investigate which of these matrices are correlated.

In addition, it is possible to assess correlations among traits while controlling for geographic distances, phylogenetic distances, or both. A permutation procedure is used to judge statistical significance (quadratic assignment procedure represents a generalization of the basic Mantel approach [Burton, Moore, Whiting, & Romney, 1996; Dow & Cheverud, 1985; Hubert, 1987]). Although these methods can be criticized for having no explicit underlying evolutionary model, their power in identifying vertical from horizontal transmission may compensate for this shortcoming. Furthermore, with respect to comparative studies, partial Mantel tests (e.g., Smouse, Long, & Sokal, 1986) may provide a means to assess the association between traits while controlling for phylogenetic and geographic distances simultaneously.

Ideally, a comparative method for studying multiple cultural traits should be able to address two questions. First, to what extent do the traits lack independence as a result of shared history or borrowing among neighbors? Second, are the traits correlated with one another? To evaluate comparative methods in the context of these questions, we developed a spatially explicit simulation approach to investigate trait evolution in relation to phylogeny and geography. Phylogeny in this case refers to the historical relationships among societies, such as a branching pattern indicated with a linguistic tree, whereas geography is measured as a matrix representing geographical distances among societies. A phylogeny can also be represented as a distance matrix, with the distance for a pair of species equal to the sum of the branches separating them (Figure 1b). Our simulation approach derives from previous simulation protocols that have been used to test phylogenetic comparative methods in biology (Harvey & Rambaut, 1998; Martins & Garland, 1991; Nunn, 1995; Purvis, Gittleman, & Luh, 1994). We augmented this basic procedure with a stochastic model of the diversification and extinction of societies in a spatial context that also allows for horizontal transmission of the simulated traits. Following previous approaches in biology, we compare methods that incorporate phylogenetic and/or geographic information to analyses that do not take this information into account. We refer to the latter analyses as nonhistorical tests.

This simulation model was used to evaluate the statistical properties (Type I and II error rates) of phylogeny-based and matrix-based methods (independent contrasts and Mantel tests, respectively). First, we examined the statistical performance of independent contrasts in simulations that varied the probability of

horizontal transmission. We predicted that the performance of this phylogeny-based method would decline as the probability of horizontal transmission increases (Prediction 1). Next, we investigated methods based on matrices that incorporate information on the geographical and phylogenetic distances among societies. We predicted that the phylogenetic distance matrix would account for greater variation in the data at low levels of horizontal transmission using Mantel tests, whereas the geographic distance matrix would account for greater variation as horizontal transmission rates increase (Prediction 2). Finally, we examined the performance of the partial Mantel test in assessing the association between traits while controlling for phylogenetic and geographic distances. We expected that a method incorporating both phylogenetic and geographic distance matrices would provide improved statistical performance when both vertical and horizontal transmission of traits occurs (Prediction 3).

METHOD

THE SIMULATION MODEL

We constructed a spatially explicit model of cultural trait evolution using the computer package MATLAB (Version 6.5). The model examines the evolution of a pair of continuously varying traits, represented here as X and Y. In relation to previous simulation work, the model can be viewed as a metapopulation model represented as a two-dimensional lattice. In this model, space and time are discrete, that is, with nonoverlapping generations (discrete time) and each cell of the lattice treated as a distinct society (discrete space). The model also has similarities to cellular automata models used to address ecological questions (e.g., Bascompte & Solé, 1996; Dytham, 1994).

The simulation begins with an empty matrix and a single society on the left-most column in the middle row of the matrix (e.g., row 2, column 1, in Figure 2). Extinction, colonization of empty cells, horizontal trait donation, and trait evolution occur sequentially and stochastically in discrete generations, with all simulations reported here based on 60 generations.

Step 1: Extinction. Societies can go extinct, or if they survive, they can colonize one or more adjacent empty neighboring cells
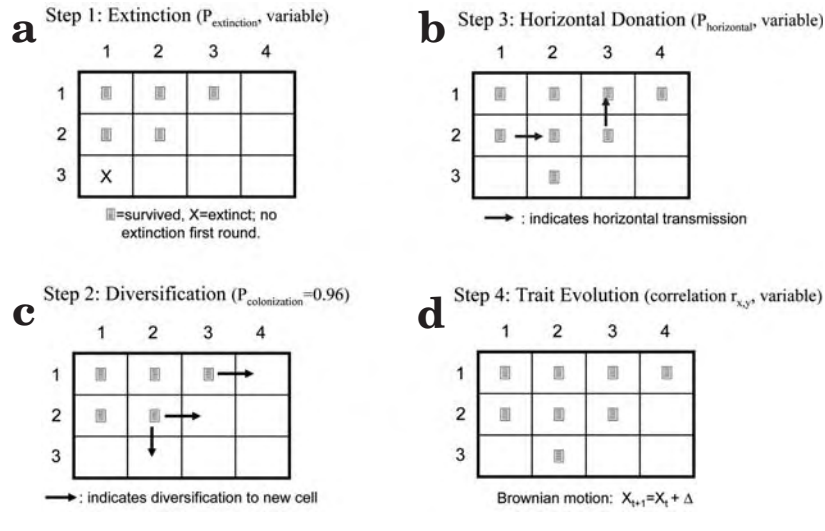
Figure 2:   Simulation Procedure

NOTE: A simplified version of the simulation procedure using a three-row-by-four-column spatial matrix partway through a simulation run. The following stochastic processes occur in sequence for each generation in the simulation: (a) extinctions of filled cells, (b) diversification of societies (and their traits) to new cells, (c) horizontal transmission among neighboring societies, and (d) Brownian motion trait evolution. Empty cells indicate unfilled niches in the spatial model. Table 1 provides the parameters that were used in the simulation. If the matrix is fully filled after the final iteration (= 60 for all results), statistical tests are conducted with the output; otherwise, the process is reinitiated; see text for details.

(Figure 2). We varied the probability of extinction ($P_{extinction}$, Table 1), with higher extinction rates increasing the number of empty cells and thus rates of cladogenesis, as indicated by increased diversification close to the tips of the tree (Figure 3). This corresponds to the "pull of the present" in lineage through time plots of biological systems, in which an apparent increase in the number of lineages occurs near the tips of a tree constructed from extant societies (Nee, Holmes, et al., 1994). As a simplifying assumption, we view extinction as the death of all individuals in a given cell. For cultural data, extinction may also occur when a society abandons its culture, either as a result of adopting the cultural traits of another society or through the forced imposition of the traits of another group as a result of conquest, migration, or political force (Durham, 1991). To avoid the possibility of an entirely empty matrix, the probability of extinction was set to zero when only one

TABLE 1
Parameters Varied in the Simulations

Parameter	Number of Parameter Values Simulated	Parameter Values
Dimensions of matrix	3	36 societies in three Row × Column configurations: 1×36, 3×12, and 6×6
Probability that a society goes extinct ($P_{extinction}$)	3	0.02, 0.08, and 0.32 per generation
Probability that a society donates a trait to an adjacent society ($P_{horizontal}$)	21	increments of 0.004 from 0 (vertical transmission only) to 0.06, increments of 0.01 from 0.07 to 0.10, and 0.15 per generation
Correlations between X and Y traits (r)	3	0, 0.3, 0.6

cell of a matrix was occupied, including the first generation of a simulation run.

Step 2: Colonization. Neighboring cells available for colonization were identified as empty cells on the "flat" sides of a given society's cell (rather than cells attached by their corners). Thus, a society may possess a maximum of four neighbors, with societies on the edges of the matrix having fewer neighbors. Societies that colonize adjacent cells are treated as distinct societies in the next generation. As societies colonize neighboring cells, their evolutionary relationships are recorded as a bifurcating tree. The program updated branch lengths by one unit in each generation of the simulation (extinction resulted in the elimination of a branch in Step 1). When a society colonized more than one cell in a generation, the relationship among societies was randomly resolved with short branch lengths (= 0.001; several examples can be found in Figure 3). We held colonization rates constant at 0.96 in all simulations.
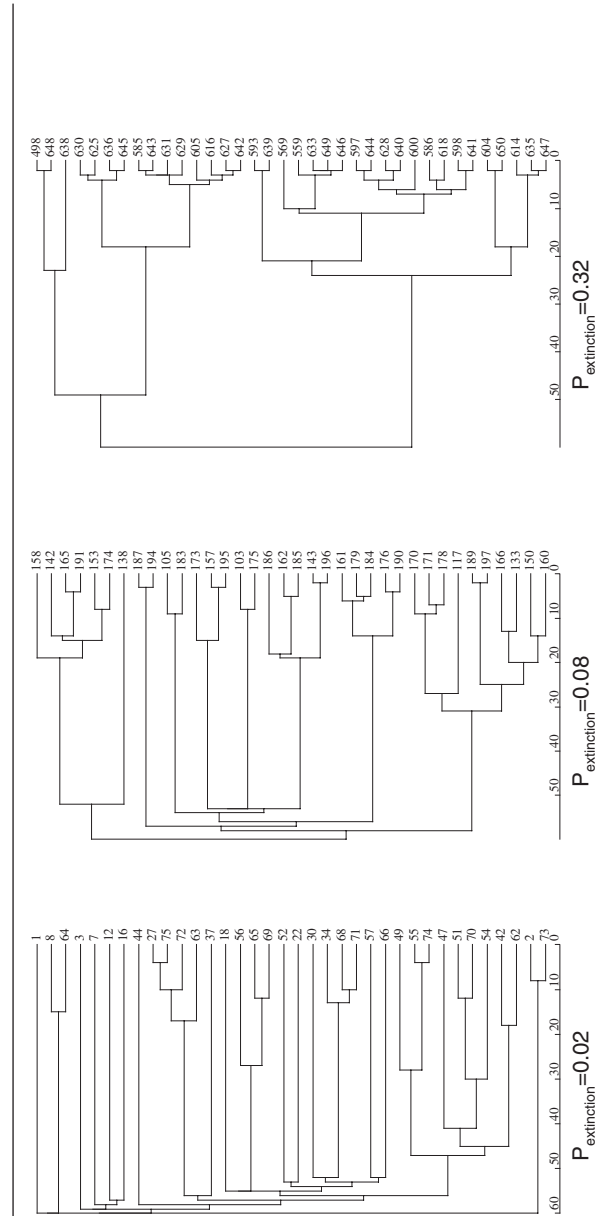
Figure 3: **Extinction Probability ($P_{extinction}$) and Example Trees From Simulation**

NOTE: Panels show three trees resulting from simulations based on 36 societies simulated across 60 generations, with no extinction allowed in the final generation. The probability that a society would colonize an empty cell was set at 0.96. Branch lengths are proportional to time. Nodes with polytomies (i.e., spread of a society to more than one cell in a generation) are randomly resolved with branches of length 1/1000 generation. As $P_{extinction}$ increases, nodes are shifted toward the tips of the tree, which increases the similarity of sister species (i.e., phylogenetic signal), because they more recently shared a common ancestor. A 4×9 grid was used as the spatial configuration for these simulations. Similar patterns between mean node age and $P_{extinction}$ are found with the other spatial configurations. Numbers at the tips represent identification codes for different societies, numbered sequentially starting with 1 and incremented as societies diversify to new cells.

Step 3: Horizontal trait donation. Trait values spread among neighbors based on a user-defined probability that a society donates traits to one of its neighbors ($P_{horizontal}$). The values of traits in the recipient are replaced by values from the donor. We focused on results with traits transmitted as a pair during horizontal transmission (i.e., if X moves, so does Y), applying the probability of trait donation to the paired movement of traits rather than independently for each trait. The assumption in this case is that correlated traits will be borrowed as a pair, but for some tests, we also investigated patterns when traits were transferred independently (i.e., with the same probability of donation per trait, calculated separately for each trait). These assumptions serve as a first step toward investigating possible models of horizontal trait transmission in simulation models. Extensions of this approach are considered in the discussion, including making the probability that both traits transfer contingent on the magnitude of the correlation. Transfers of traits among all societies in the matrix were implemented simultaneously in a given generation, meaning that transfers were identified but then occurred only after all cells were examined for possible trait transfer. The implications of simultaneous transfer are that a trait could be transmitted only to neighboring cells in a single generation, and two societies could effectively "swap" traits.

For a society with more than one neighbor, the possibility exists that more than one horizontal donation takes place in a single generation when a given cell has multiple neighbors. To deal with this possibility, the probability that at least one transmission event takes place for a potential recipient society was calculated using the binomial theorem based on the number of neighbors. If the condition for trait donation was met for a recipient society, the society donating the trait was randomly assigned from among the neighbors of the recipient society.

We simulated 21 parameters for the probability of trait donation ($P_{horizontal}$) to neighbors (Table 1). Most of our simulations were concentrated with a range of donation probabilities from 0 to 0.06 (see Table 1), with the midpoint representing a per-generation probability of horizontal transfer = 0.11 for societies that have four neighbors. By simulating evolution with $P_{horizontal} = 0$, only vertical transmission occurs; thus, under this parameter setting, phylogeny-based methods were expected to produce results that match previous simulation studies that have investigated the statistical properties of independent contrasts (Harvey & Rambaut, 1998; Mar-

tins & Garland, 1991; Purvis et al., 1994). At the highest probability of horizontal donation ($P_{horizontal} = 0.15$) and four neighbors, the probability of horizontal trait transmission in a given generation equals 0.48. Although such high rates are unlikely in most real-world data sets, we used this high rate as an upper bound for extrapolating to cases of extremely high rates of horizontal transmission, such as the spread of horses among New World peoples (Roe, 1955) or the spread of Islam across many parts of West (Trimmingham, 1970) and East Africa (Ensminger, 1997).

The spatial configuration of societies will affect the overall level of horizontal transmission by influencing the number of connections among societies and the number of societies on outer edges of the matrix. The average number of neighbors per cell in a matrix will be lower for a long and narrow arrangement, as compared to societies that are arranged in a square. We investigated the effects of different configurations of available niches by varying the three column × row dimensions, with one square matrix (6×6) and two rectangular matrices (1×36 and 3×12; see Table 1). The linear model (1×36) has the advantage of allowing better understanding of the transmission process, because traits can only spread in two directions, but it has the disadvantage of being unlike most real-world data sets. As expected, we found a significant difference in the number of recorded horizontal transmission events in different configurations in our simulations ($F_{2, 564} = 57.2, p < 0.0001$), with a markedly lower rate of recorded horizontal transmission events in the 1×36 configuration (mean of 0.051 recorded events per society per generation) as compared to the other two configurations (means of 0.119 and 0.131 for 3×12 and 6×6 matrices, respectively; recorded events are those in which the traits are actually transferred, and we used simulations with low extinction rates to maintain relatively filled matrices). Spatial configuration also influences the total number of empty cells, with, on average, more empty cells in the 1×36 configuration because of fewer neighbors available to colonize empty cells, which, in turn, influences observed patterns of horizontal transmission and extinction events.

Step 4: Trait evolution. Evolutionary change in traits *X* and *Y* occurs at the end of each generation. Trait evolution is modeled using Brownian motion (Felsenstein, 1988; Martins & Garland, 1991), with the user identifying variance in trait change per generation (constant in all simulations presented here). For correlated

trait evolution, per-generation changes in X and Y traits were drawn from a bivariate normal distribution that reflected trait correlations of 0, 0.3, or 0.6 (Table 1). These changes were calculated for each society and added to existing trait values. Vertical transmission occurs when descendent societies inherit trait values of their ancestors during colonization of new cells and across generations.

STATISTICAL PROPERTIES OF COMPARATIVE METHODS

The trait data that result from one run of the simulation reflect different degrees of horizontal transmission, vertical transmission, extinction, and correlated trait evolution, all occurring in the context of an adaptive radiation in a defined geographical area. The output from this program, run for 1,000 simulations that iterated the steps above for 60 generations in each run of the simulation, were analyzed using independent contrasts and Mantel tests calculated within the MATLAB program (see Figure 1). This process was repeated for each parameter combination listed in Table 1.

For simulations run with uncorrelated traits ($r = 0$), we calculated the Type I error rate, which is the probability of rejecting a true null hypothesis of no association between X and Y. Specifically, Type I error rate was calculated as the proportion of simulations with a given set of parameters (and $r = 0$) in which a significant association between the two traits was detected. We set our significance level at $\alpha = 0.05$, thus predicting a Type I error rate of 5% when the statistical and evolutionary assumptions were met.

For simulations of correlated trait evolution ($r = 0.3$ or 0.6; see Table 1), we calculated the statistical power to detect correlated change ($1 - $ Type II error rate). Power was calculated as the proportion of simulations with a given set of parameters and $r > 0$ in which a significant association was found. Statistical power depends on several variables, but by maintaining a constant number of societies, we compared statistical power for different methods across parameters simulated in Table 1. Because the process of colonization is stochastic, it is possible for some cells in the matrix to be empty at the end of the simulation when a society goes extinct but the cell remains unfilled in the final generation of the simulation. Thus, to maintain a constant sample size in assessing statisti-

cal power, we required that matrices were fully filled at the end of the last generation in each simulation. Simulations with unfilled matrices were discarded. As expected, the total number of unfilled matrices per batch of 1,000 simulations varied according to the probability of extinction and the geographic configuration of the societies. For $P_{extinction}$ = 0.02 or 0.08, the mean number of unfilled matrices was 0.013 per simulation (SD = 0.0021). With $P_{extinction}$ = 0.32, the mean increased to 7.89 per simulation (SD = 10.4).

Information on phylogeny, recorded in Steps 1 and 2 above, was used to calculate independent contrasts standardized by time. In addition to independent contrasts, we investigated the statistical properties of Mantel tests. Mantel tests were implemented by applying standard multiple regression approaches to vectorized distance matrices, which represent dissimilarity in trait values, geographical distance and or phylogenetic distance (Legendre, Lapointe, & Casgrain, 1994). Because the cells of a distance matrix are not independent of one another, the rows (and corresponding columns) of the geographic and trait matrices were randomly permuted to obtain statistical significance levels (Manly, 1997; Smouse et al., 1986; Smouse & Long, 1992). Significance levels were based on 500 permutations. In calculating distance matrices, we used Euclidean distances for geographic matrices and the sum of branch lengths connecting two societies for phylogenetic matrices (see examples in Figure 1).

In analyzing the statistical output, we used multivariate methods to distinguish independent effects of $P_{horizontal}$, $P_{extinction}$, and spatial configuration. In some analyses, we also included the correlation of trait changes (r) as a covariate or analyzed data restricted to r = 0 (for Type I error rates) or r = 0.3 or 0.6 (for analyses of statistical power). In these multivariate models, spatial configuration was treated as a categorical variable, whereas other variables were continuous. Statistical significance was assessed in two-tailed tests using a significance criterion of p = 0.05. In running these analyses, we log-transformed the data when assumptions were obviously broken based on residual plots, which was common for the effect of $P_{horizontal}$. In some analyses, we also included $P_{horizontal}$ as a squared term to deal with the occurrence of nonlinearity that remained even after transformation of the data. In the end, however, use of different transformations or predictor variables had little effect on the conclusions drawn from the statistical analyses.

RESULTS

PREDICTION 1: INDEPENDENT CONTRASTS, NON-HISTORICAL ANALYSES, AND HORIZONTAL TRAIT TRANSMISSION

When transmission of traits was entirely vertical ($P_{horizontal} = 0$), independent contrasts returned expected Type I error rates of approximately 5% (gray bars in Figure 4). Across the nine sets of simulations with $r = 0$ and no horizontal transmission, the mean Type I error rate for independent contrasts was not significantly different from the expected value of 5% ($M = 0.051$, $t_8 = 0.31$, $p = 0.77$, two-tailed). By comparison, results for nonphylogenetic analyses (Figure 4) produced inflated Type I error rates ($M = 0.305$, $t_8 = 4.74$, $p = 0.0015$). In a two-way analysis of variance of Type I error rates from nonhistorical analyses, the Type I error rate increased with increasing probability of extinction ($F_{1, 5} = 93.1$, $p = 0.0002$), whereas the spatial configuration of societies had no statistically detectable effect on Type I error rates ($F_{2, 5} = 0.15$, $p = 0.86$). The positive association between Type I error rates and the probability of extinction probably reflects more recent common ancestry (and thus more similar trait values) among the simulation endpoints that occur when extinction rates are higher (see Figure 3).

The method of independent contrasts assumes that traits are transmitted vertically. We therefore investigated the extent to which increasing probability of horizontal transmission reduces the statistical performance of independent contrasts (Prediction 1). With increasing probability of horizontal transmission, Type I error rates increased (Figure 5; multivariate model including $P_{horizontal}$, $P_{horizontal}^2$, spatial configuration, and $P_{extinction}$; results for $P_{horizontal}$, $b = 3.46$, $F_{1, 183} = 884$, $p < 0.0001$). Type I error rates in nonhistorical analyses also increased with increasing probability of horizontal trait transmission (multivariate model including the same variables; results for $P_{horizontal}$, $b = 1.65$, $F_{1, 183} = 278$, $p < 0.0001$). In these multivariate models, Type I error rates also increased with $P_{extinction}$ (e.g., for contrasts, $b = 0.097$, $F_{1, 183} = 15.2$, $p = 0.0001$), and Type I error rates were lower in the 1×36 configuration than in the 6×6 or 3×12 configurations (see Figure 5).

We investigated the effect of horizontal transmission on statistical power by repeating the simulations shown in Figures 4 and 5 with $r = 0.3$ and $r = 0.6$ (Figure 6). In a multivariate model that controlled for spatial configuration and $P_{extinction}$, the power increased
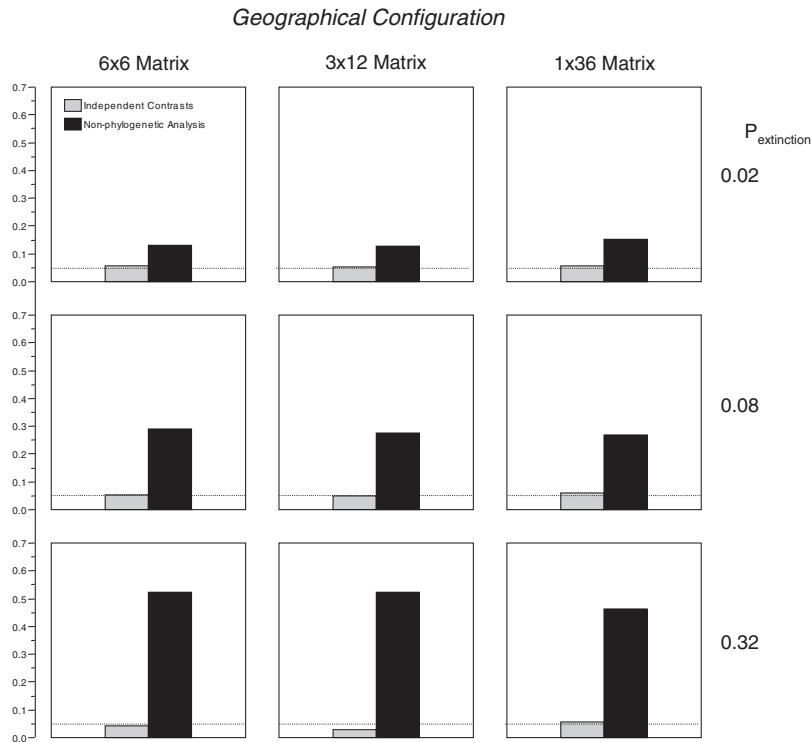
Figure 4:   Type I Error Rates as a Function of Spatial Configuration and Probability of Extinction

NOTE: Dotted horizontal line indicates expected Type I error rate ($\alpha = 0.05$). Bars are the proportion of results in a given simulation run ($N = 1,000$ iterations) in which a significant association was found between two traits that were simulated with $r = 0$.

with increasing horizontal transmission when $r = 0.3$ (nonhistorical, $b = 0.48$, $F_{1, 183} = 163$, $p < 0.0001$; independent contrasts, $b = 0.86$, $F_{1, 183} = 278$, $p < 0.0001$), but statistical power decreased with increasing horizontal transmission at the higher correlation of $r = 0.6$ (nonhistorical, $b = -0.44$, $t_{183} = 10.7$, $p < 0.0001$; independent contrasts, $b = -0.84$, $t_{183} = -15.2$, $p < 0.0001$). Spatial configuration and $P_{extinction}$ were generally significant, too, with the direction of the effect for $P_{extinction}$ following the direction of $P_{horizontal}$ (with the
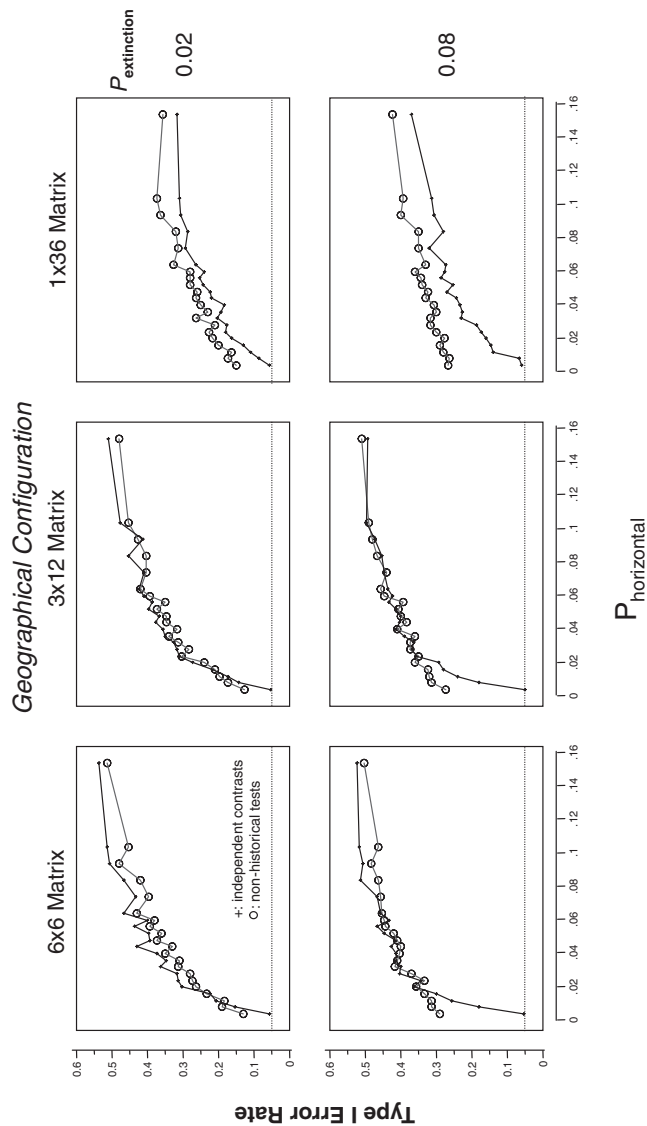
Figure 5:   Type I Error Rates and Horizontal Transmission

NOTE: Horizontal dotted line indicates expected Type I error rate ($\alpha = 0.05$). Plots show how $P_{horizontal}$ affects Type I error rates for independent contrasts ($+$) and in nonhistorical analyses (circles). There was no correlation between X and Y trait changes in these simulations ($r = 0$). Different plots reflect different combinations of spatial configuration and probability of extinction, and values plotted reflect the proportion of results in a given simulation run ($N = 1,000$) in which a significant association was found between traits x and y.
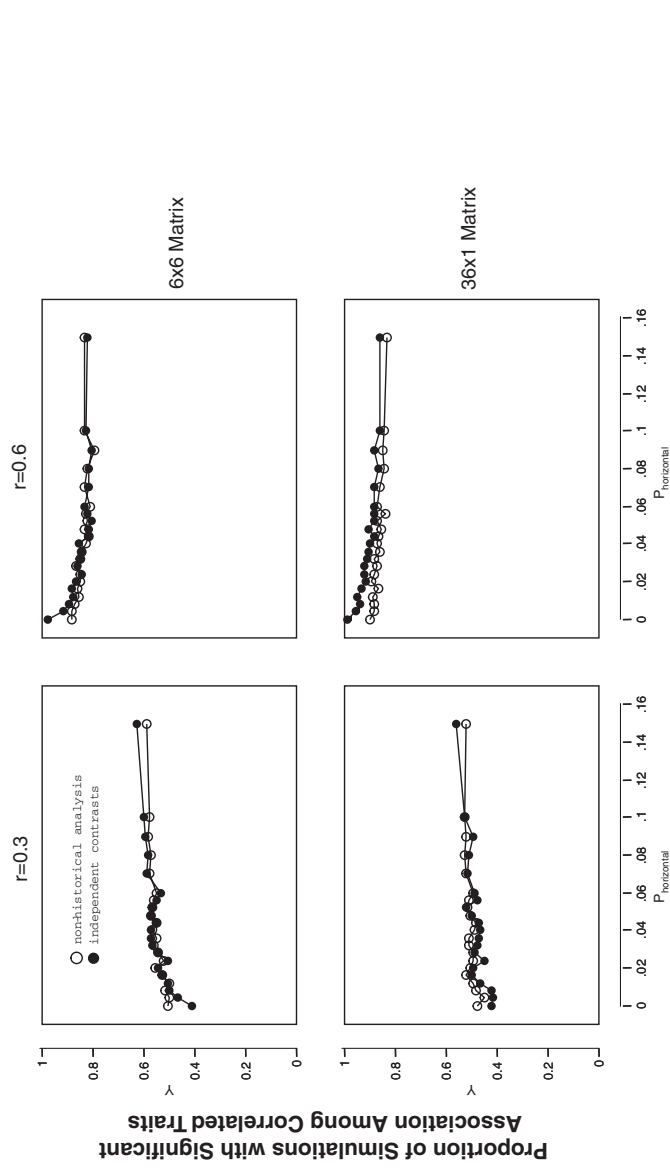
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Figure 6: Statistical Power and Horizontal Transmission

NOTE: Plots show proportion of simulation results ($N = 1,000$) in which a significant result was obtained in analyses of independent contrasts (filled circles) and nonhistorical analyses (open circles) under different levels of $P_{horizontal}$ and a correlation among the traits ($r = 0.3$ or 0.6). In the results shown here, $P_{extinction} = 0.08$.

exception of $P_{extinction}$ when using independent contrasts with $r = 0.6$, which was nonsignificant, $t_{183} = -1.19$).

PREDICTION 2: DETECTING PATTERNS OF TRAIT TRANSMISSION FROM DISTANCE MATRICES

We predicted that the phylogenetic distance matrix would correlate more strongly with the trait matrix at low levels of horizontal transmission (i.e., mainly vertical transmission), with the correlation between geographic distance and trait distance increasing as horizontal transmission rates increase (Prediction 2). Here we are concerned with the correlation between traits and geographical and phylogenetic distance matrices, and we have no reason to expect that the correlation between the two traits (r) would affect associations between a matrix of trait distances and a matrix representing spatial or phylogenetic distances. In support of this expectation, the correlation among traits was not a significant predictor of variation in geographical or phylogenetic distance matrices in bivariate and multivariate models. Thus, we combined results from simulations run with different values for correlated change in X and Y traits.

We found general support for our prediction. In a multivariate model with $P_{horizontal}$, $P_{extinction}$, and spatial configuration as independent variables, all variables were significant predictors of the probability of detecting a significant correlation between trait distance matrices and matrices representing geographical and phylogenetic distances (Table 2). As shown in Figure 7, the probability of horizontal transmission was significantly positively associated with the association between trait and geographic distances. A pattern in the opposite direction was found with phylogenetic distance, with increasing horizontal transmission reducing the association between phylogenetic distances and trait distances. Increasing $P_{extinction}$ increased the proportion of simulations in which geographic or phylogenetic distance matrices accounted for variation in trait matrices, and distance matrices were generally less often significant predictors of trait distances in the 1×36 spatial configuration.

Although our prediction was supported, the majority of tests detected significant associations between distance matrices. Even at the highest levels of horizontal trait transmission ($P_{horizontal} = 0.15$), for example, the phylogenetic distance matrix was found to

TABLE 2

Associations Between Trait Distances and Geographic or Phylogenetic Distances

	$P_{horizontal}$		$P_{extinction}$		Spatial Configuration	
	Slope	*F statistic*	*Slope*	*F statistic*	*Highest*	*F statistic*
Model a: Trait distance and geographic distance[a]	1.29	443.1	0.68	1600	6×6	19.5
Model b: Trait distance and phylogenetic distance	−1.38	166.2	0.64	474.7	3×12	15.1

NOTE: Table provides slopes and *F* statistics for two multivariate models that investigated as dependent variables the association between trait distance and geographic distance (Model a) and between trait distance and phylogenetic distance (Model b), measured as the percentage of tests significant. Independent variables in this model were $P_{horizontal}$, $P_{extinction}$, and the spatial configuration of societies. Thus, we were testing how these parameter settings influenced the associations between trait distance and (a) geographic or (b) phylogenetic distances. The degrees of freedom were (1, 562) for $P_{horizontal}$ and $P_{extinction}$ and (2, 562) for spatial configuration, as this was a three-part categorical variable. All results were statistically significant at $p < 0.001$. For spatial configuration, *highest* refers to the configuration in which significance was most commonly detected.

a. Results for geographic distance indicated the presence of some nonlinearity that was difficult to remove through transformation of the data. We also ran the analyses separately for each of the three levels of extinction, as this variable appeared to account for much of the nonlinearity in the overall model, and this produced similar results for the other variables.
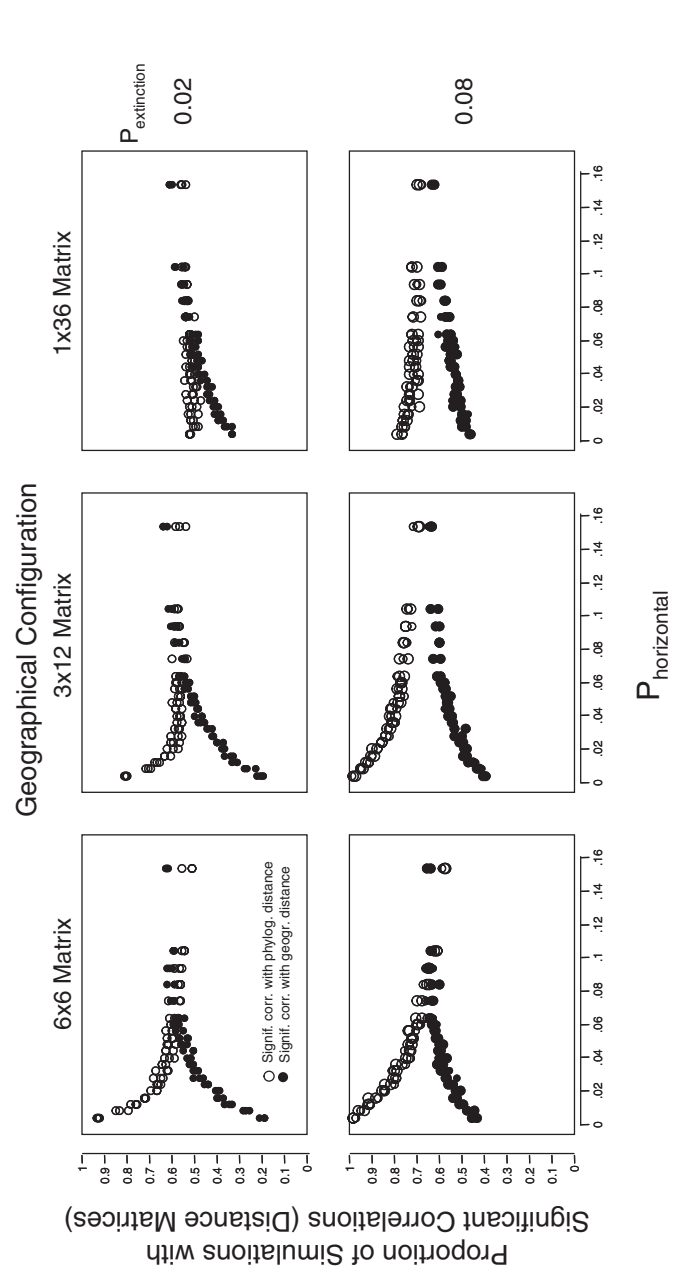
20

Figure 7: Statistical Power to Detect Trait Correlations with Phylogenetic and Geographic Distance Matrices

NOTE: Plots show the probability of detecting a significant association between the trait matrix (trait X) and the phylogenetic distance matrix (open circle) or geographic distance matrix (closed circle) under different spatial configurations and probabilities of extinction. Multiple data points for each value of $P_{horizontal}$ in each analysis represent the three trait correlations (r = 0, 0.3, and 0.6) used in the simulations. Results for $P_{extinction}$ = 0.32 are not shown.

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be significantly associated with trait distance in 63.5% of the simulations. At the opposite extreme, with $P_{horizontal} = 0$, the geographic distance matrix was significantly correlated with the trait matrix in 45.7% of the simulations. In part, this reflects that geographic and phylogenetic distance matrices were highly correlated in most cases, with these matrices significantly associated in more than 99% of the simulations. Thus, although it is generally true that use of geographic matrices provides relatively greater statistical power with increasing horizontal transmission, and phylogenetic matrices perform better at low levels of horizontal transmission, the ability of the Mantel test to differentiate between the two models of trait transmission appears to be relatively crude and imprecise, at least under the model implemented here and with information that is commonly available (or more typically unavailable) for comparative data sets, especially data on extinction rates and other evolutionary parameters.

PREDICTION 3: PARTIAL MANTEL TESTS

We next investigated Type I error rates and statistical power when using partial Mantel tests to incorporate information on both geographic and phylogenetic distance matrices (Prediction 3). With $P_{horizontal} = 0$ and $r = 0$, Type I error rates for tests of the association between X and Y were significantly higher than the expected value of 5% when controlling for phylogenetic distance alone ($M = 0.159$, $t_8 = 4.33$, $p = 0.0025$) or both phylogenetic and geographic distances ($M = 0.155$, $t_8 = 4.49$, $p = 0.002$; see Figure 8, open circles in left panel with $r = 0$). In simulations with all values of $P_{horizontal}$, a multivariate model that included $P_{horizontal}$, $P_{extinction}$, and spatial configuration revealed that all three traits had a significant effect on the Type I error rate (Table 3). $P_{horizontal}$ and $P_{extinction}$ tended to increase Type I error rates, and the lowest error rates were found in the 1×36 spatial configuration.

We also compared the statistical performance of independent contrasts to performance of a partial Mantel test that used both geographic and phylogenetic distance matrices. Independent contrasts tended to produce higher Type I error rates ($r = 0$, left panel of Figure 8) and higher statistical power ($r = 0.3$ or 0.6, right panels of Figure 8) at most levels of horizontal transmission. The difference in the proportion of tests significant in independent contrasts and partial Mantel tests was affected by the probability of
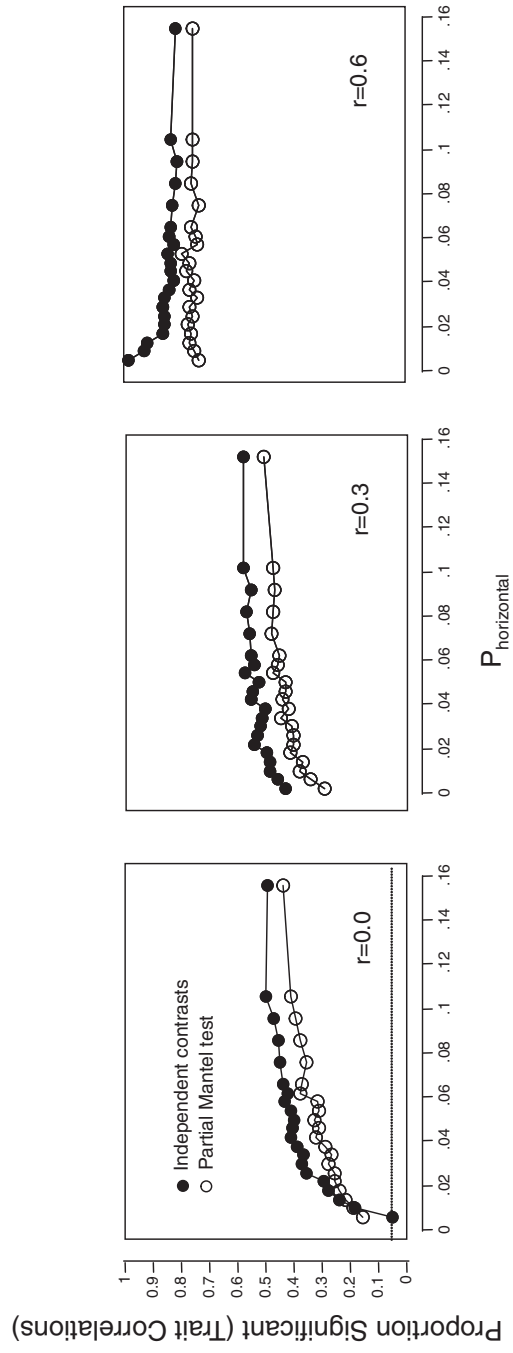
Figure 8: **Proportion of Simulations Producing a Significant Association Among Traits *X* and *Y* in Independent Contrasts and Partial Mantel Tests**

NOTE: Partial Mantel tests were used to control for both spatial distance and phylogenetic distances and independent contrasts examined evolutionary change on the tree recorded during a run of the simulation. Plots show results for a 3×12 spatial configuration and $P_{extinction} = 0.08$.

TABLE 3

Type I Error Rates[a] for Trait Correlations, Controlling for Geographic and Phylogenetic Distances

	$P_{horizontal}$		$P_{extinction}$		Spatial Configuration	
	Slope	*F statistic*	*Slope*	*F statistic*	*Lowest*	*F statistic*
Model a: Controlling for geographic distance	3.05	281.0	1.60	834.5	1×36	146.1
Model b: Controlling for phylogenetic distance	4.57	516.2	1.07	306.8	1×36	236.7
Model c: Controlling for both geographic and phylogenetic distance	4.13	485.2	1.07	353.4	1×36	223.1

NOTE: Table shows results for three multivariate models (a, b, and c) from simulations with $r = 0$. Dependent variable was the percentage of tests that were statistically significant (Type I error rate), based on partial Mantel tests, for the association between X and Y trait distances when controlling for (a) geographic distance, (b) phylogenetic distance, or (c) both geographic and phylogenetic distances. Independent variables for Models a and b included $P_{horizontal}$, $P_{extinction}$, and spatial configuration, with probabilities $\log_{10}$ transformed to deal with nonlinearities in the untransformed full model. Table gives slopes and F statistics based on $df(1, 183)$ for $P_{horizontal}$ and $P_{extinction}$ and $df(2, 183)$ for spatial configuration. For spatial configuration, data show lowest Type I error rates. All results were statistically significant at $p < 0.0001$.

a. Percentage of tests in which association between X and Y was incorrectly identified as significant, given that the correlation between X and Y was set to zero ($r = 0$).

horizontal donation ($b = -0.15, F_{1,\,561} = 5.53, p = 0.02$), with stronger effects for the correlation between x and y ($b = 0.15, F_{1,\,561} = 246, p < 0.0001$), $P_{\text{extinction}}$ ($b = -0.08, F_{1,\,561} = 20.4, p < 0.0001$), and spatial configuration (lowest in the $1 \times 36, F_{2,\,561} = 9.17, p = 0.0001$).

DISCUSSION

Analyses of the simulated data revealed that the method of independent contrasts is sensitive to increasing rates of horizontal transmission (Prediction 1), that Mantel tests fail to cleanly discriminate between data sets characterized by different levels of horizontal and vertical trait transmission (Prediction 2), and that partial Mantel tests fail to produce markedly improved statistical performance when testing for associations among two traits while controlling for geographic and/or phylogenetic distances (Prediction 3). These results therefore confirm that phylogeny-based comparative methods, such as independent contrasts, are appropriate for addressing questions in cultural anthropology but only under restrictive conditions when the traits in question are transmitted vertically. Although there are no measures of rates of horizontal transmission in human cultures, it is known that for language, massive influxes of new words can occur almost instantaneously (e.g., in the case of the infusion of Norman French words into English); in other instances, borrowing can be very gradual. Accordingly, we suggest that even though there are obvious parallels and strong analogies to be made between the processes involved in the evolution of cultural and biological traits (e.g., Mesoudi et al., 2004; Pagel & Mace, 2004), standard phylogenetic comparative methods are not an ideal way for dealing with the issues of independence once horizontal transmission moves above a zero rate ($P_{\text{horizontal}} > 0$).

We also investigated the performance of methods to control for the probability of horizontal transmission ($P_{\text{horizontal}}$) of traits among neighboring societies. Surprisingly, the Mantel test that we employed did not provide a means to readily identify the mechanism of trait transmission (Prediction 2). This failure arises because it appears to be difficult to distinguish horizontal from vertical trait transmission at fine levels using Mantel tests based on geography, when diversification occurs only to neighboring cells, and when geographical and historical distance matrices are highly correlated. Replacing our simple, untransformed Euclidean dis-

tances as the measure of potential for horizontal transmission with other measures, ranging from a simple coding of whether societies are neighbors to more complicated metrics gauging the probability of a trait moving across the matrix or identifying past contacts (for example, through proportions of shared loan words), may provide lower error rates (see also White et al., 1981). Thus, it may be possible to develop alternative distance metrics that increase the statistical power of Mantel tests, provided that they can be measured empirically in real-world data sets. In addition, the ability of the Mantel test to detect associations with geography depends on the linkage between these traits during horizontal transmission. Thus, when we repeated simulations with traits that were unlinked (i.e., X and Y were not transferred as a pair, even when $r > 0$), statistical power declined with increasing probability of horizontal transmission, regardless of the correlation simulated (compare to Figure 6, where the results depended on the correlation coefficient used). This pattern arises because horizontal transmission of only one trait breaks the association between the trait correlations that are established during trait change.

Future studies should consider more complicated models of trait transmission, focusing in particular on the possibility that traits are more likely to be transferred jointly to another society when the magnitude of their correlation is higher (M. Burton, personal communication, 2005). Developing a more realistic model of cultural trait evolution and transfer adds another dimension of complexity to the core model presented here, and our approach has been to investigate this basic model before developing more complicated scenarios of trait transmission within and across societies. Nonetheless, the issue of joint trait transfer is a clear area for future extensions on our research.

The partial Mantel test also failed to produce markedly improved statistical performance in testing for associations among traits (Prediction 3). Thus, the choice of using a Mantel test versus independent contrasts, even when the vertical transmission assumption of independent contrasts is violated, depends on preference for lower Type I or II error rates. If Type I error rates are more of a concern, then the partial Mantel test outperforms independent contrasts in most cases, with the exception of zero horizontal transmission (Figure 8, left panel with $r = 0$). If Type II error rates are a concern, then independent contrasts provides better statistical performance (i.e., higher statistical power; Figure 8, panels in which $r > 0$).

Our results also point to the importance of considering the effects of extinction rates when using phylogenetic comparative methods to test hypotheses using cultural data sets. High rates of extinction emphasize the signal of vertical transmission in comparative data (see Figures 3 and 7; Nee, Holmes, et al., 1994). Although little is known about rates of extinctions in human societies, estimated language extinction rates (since 1600) are higher (4.5%) than those observed for birds and mammals (Sutherland, 2003), and cultural group extinction (in warfaring sectors of New Guinea) ranges from 1.6% to 31.3% per generation (Soltis, Boyd, & Richerson, 1995). Thus, during some junctures in human history, cultural extinction is likely to have been a significant evolutionary force and to have inflated signals of vertical transmission.

As a related point, our results suggest that investigators need to be aware of how sensitive their estimates of horizontal and vertical transmission might be to the various strategies they use to sample human cultures. Cultural groups not sampled are effectively "extinct" to the phylogenetic analysis, although the nodes representing common ancestors may not be as close to the tips of the tree as occurs when true extinction takes place with subsequent diversification of societies into empty niches (e.g., Figure 3). Thus, broadly drawn samples representative of world regions (or, indeed, the entire globe) may be more likely to show evidence of vertical transmission than small-scale regional studies, where the sampling strategy is more complete. Computer simulations could be used to investigate the effect of sampling biases on the statistical properties of comparative methods in cultural data sets (see Ackerly, 2000, for a similar study relevant to biological data).

We focused on continuous traits in this study, although many of our results may also apply to discrete traits, which are common in anthropological, ethnographic, and archaeological sources (Borgerhoff Mulder et al., 2001; Jordan & Shennan, 2003; Welsch, Terrell, & Nadolski, 1992). Our program, or a similar approach, is suitable for investigating methods for analysis of discrete data. More important, our simulation program also can be used as a stepping stone to develop clear alternative models for human cultural evolution at macroecological scales (Nettle, 1999). Computer simulation forces the investigator to produce an explicit model of trait evolution. Thus, simulation studies of cultural evolution are likely to lead to further refinement of methods and underlying models, expanding our understanding of empirical patterns in the process.

In conclusion, our study reveals that phylogeny-based methods are appropriate in restrictive conditions in which cultural traits have spread vertically and that basic implementations of the Mantel test fail to finely resolve the predominant mode of cultural transmission. There is tremendous need for anthropologists, archaeologists, and linguists to design studies that determine rates of horizontal transmission from empirical data and how these rates differ across different kinds of traits. Here, we focused on conventional tools for detecting the mode of trait transmission. Different statistical approaches are likely to be needed in the future, and development of these tools offers great opportunities for collaboration between cultural anthropologists and evolutionary biologists.

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