

# THE SPATIAL SCALE OF SOCIAL LEARNING AFFECTS CULTURAL DIVERSITY

L. S. Premo and Jonathan B. Scholnick

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*Sewall Wright's (1943) concept of isolation by distance is as germane to cultural transmission as genetic transmission. Yet there has been little research on how the spatial scale of social learning—the geographic extent of cultural transmission—affects cultural diversity. Here, we employ agent-based simulation to study how the spatial scale of unbiased social learning affects selectively neutral cultural diversity over a range of population sizes and densities. We show that highly localized unbiased cultural transmission may be easily confused with a form of biased cultural transmission, especially in low-density populations. Our results have important implications for how archaeologists infer mechanisms of cultural transmission from diversity estimates that depart from the expectations of neutral theory.*

*El concepto de Sewall Wright de aislamiento por distancia es relevante tanto en la transmisión cultural, como en la transmisión genética. Sin embargo, ha habido poca investigación sobre cómo la escala espacial de aprendizaje social—la extensión geográfica de la transmisión cultural—afecta a la diversidad cultural. Aquí, utilizamos simulaciones basadas en agentes para estudiar cómo la escala de aprendizaje social no sesgada, afecta la diversidad cultural no adaptativa bajo un rango de tamaños y densidades de poblaciones. Mostramos que la transmisión cultural no sesgada altamente localizada puede ser fácilmente confundida con una forma de transmisión cultural parcial, especialmente en poblaciones de baja densidad. Nuestros resultados tienen importantes implicaciones para la forma en que los arqueólogos infieren mecanismos de transmisión cultural, a partir de estimaciones de diversidad que se alejan de las expectativas de la teoría neutral.*

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In a series of influential papers, Sewall Wright (1938, 1940, 1943, 1946) explored how spatially mediated gene flow affects genetic variation in idealized populations. He started with the basic assumption that the likelihood of two individuals reproducing is inversely related to their spatial proximity—that individuals or subpopulations become reproductively *isolated by distance*. One of the central findings of Wright's (1943) work is that the degree of genetic similarity among (spatially defined) subpopulations decreases as the geographic distance between them increases. Another is that isolation by distance increases diversity at the level of the population while it decreases diversity at the level of the subpopulation.

Although the evolutionary forces that drive biological evolution, including drift, mutation, gene flow, and selection, have analogies in the cultural

sphere, there are significant differences between the mechanisms of genetic and cultural transmission (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). The most obvious difference is that novel cultural variants can be introduced through social learning, whereby individuals acquire cultural variants from people other than their biological parents through oblique and/or horizontal transmission. Furthermore, in the case of cultural transmission an individual can choose which teacher to learn from or which cultural variant to adopt, and this choice can be influenced by extrinsic factors (Boyd and Richerson 1985; Schiffer 2008). One possible strategy is to choose a teacher or a variant at random (unbiased transmission). An individual may also select the modal variant (conformist transmission) or the least common variant (anti-conformist transmission). Or one may

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choose to imitate a high-status individual (prestige-biased transmission) or experiment with a new variant (guided variation), among other strategies (see Boyd and Richerson 1985; Henrich and McElreath 2003).

Despite these differences between genetic and cultural transmission, there is good reason to believe that isolation by distance affects non-adaptive (i.e., selectively neutral) cultural diversity in the same way that it affects non-adaptive genetic diversity, at least with unbiased cultural transmission. Modifying the central assumption such that geographic distance affects the likelihood that cultural—rather than genetic—transmission occurs between two individuals does not diminish the utility of the isolation by distance model. The isolation by distance model provides clear predictions for the amount (and structure) of non-adaptive cultural diversity displayed by a population, given the spatial scale at which cultural traits are transmitted among individuals. Thus, archaeological inferences concerning mechanisms of cultural transmission stand to benefit from incorporating an understanding of how isolation by distance affects cultural diversity.

Our goal is to assess the extent to which the spatial scale of unbiased social learning affects the level of non-adaptive cultural diversity in a population. By controlling important variables like population size, population density, and cultural innovation rate, and by collecting data only when cultural diversity is at equilibrium, we are able to isolate the effect of the spatial scale of social learning on non-adaptive cultural diversity in artificial societies. We apply many of the same techniques used previously in estimating cultural diversity from empirical archaeological data (see Kohler et al. 2004; Neiman 1995; Shennan and Wilkinson 2001) to simulated data for which the spatial scale of social learning and the mechanism of cultural transmission are known.

We start with some background on neutral theory, including its central assumptions, and a brief review of some archaeological studies that have drawn from it. Next, we provide a short description of our agent-based model and the quantitative methods used to assess diversity in simulated data. Because the results show that highly localized unbiased social learning can cause departures from neutrality that may be mistaken for biased cultural

transmission, our discussion stresses the importance of employing independent lines of evidence to assess the spatial scale of social learning that characterized past communities.

## Background

Consider a constant, finite population of  $N$  individuals, each of whom displays a single (possibly unique) variant for a given non-adaptive culturally transmitted trait or behavior. This trait could be a design on a ceramic vessel, a style of dress or personal adornment, or any other culturally transmitted behavior that is selectively neutral. During each time step, every individual replaces its current variant with one that it “learns” socially (i.e., copies) from an individual chosen at random from the population. According to this unbiased form of cultural transmission, an individual retains its variant with probability  $1/N$  and adopts someone else’s variant with probability  $(N - 1)/N$ . Fraser Neiman (1995) illustrates how drift affects non-adaptive cultural diversity. In the case of cultural transmission, drift refers to the sampling error associated with randomly choosing a teacher in a finite population. In the absence of innovation, the total number of cultural variants,  $k$ , will eventually and inevitably drop to one due to drift (or, in other words, a single cultural variant will reach fixation in the population). The time required for the system to arrive at this strong attractor is positively correlated with  $N$ . The outcome is not so simple in the presence of innovation, an important point to which we will return later in the paper.

Population geneticists would quickly recognize the scenario described above as a Wright-Fisher model of reproduction, even though the replicators are cultural variants rather than genes. In its most basic form, the Wright-Fisher model assumes a constant and finite population size, random mating (i.e., panmixia), no selection, and non-overlapping generations (Wright 1931). Research that employs the Wright-Fisher model often assumes an infinite-allele model of mutation, which holds that each mutation results in an entirely new allele. Population geneticists have studied the degree to which drift and mutation affect non-adaptive genetic diversity under these idealized conditions. Their findings teach us that the “effective size” of a population ( $N_e$ )—roughly, the number of individuals

contributing to subsequent generations—can have a large effect on diversity (Crow and Kimura 1970). When the effective size of a population is relatively small, drift can be an important force even if the census size ( $N$ ) is large. Neutral theory research also provides quantitative tools for calculating the amount of non-adaptive diversity one would expect to see in an idealized population given only its effective population size and mutation rate (Crow and Kimura 1970); for estimating the amount of non-adaptive diversity displayed by a population from a sample (Ewens 1972, 1979); and for testing whether the amount of diversity observed in an empirical sample is statistically different from what one would expect in a sample from an idealized population (Slatkin 1994, 1996).

Adapting the findings of population genetic work on selectively neutral alleles to cultural traits, Neiman (1995:14) shows that, if innovation and drift are the only forces influencing the relative frequencies of non-adaptive cultural variants, then the amount of diversity ( $\theta$ ) displayed by a constant finite population at innovation-drift equilibrium is equal to twice the effective population size times the innovation rate ( $\mu$ ):

$$\theta = 2N_e\mu \quad (1)$$

Equation 1 assumes panmixia. In the context of cultural transmission, panmixia refers to the scenario in which a social learner is equally likely to learn from anyone in the population (including itself). Note that panmixia does not mean that every individual will serve as a teacher during each time step (see Neiman 1995:10; Shennan and Wilkinson 2001:581–582). The assumption of panmixia is satisfied only when the mechanism of cultural transmission is unbiased *and* the spatial scale of social learning is equivalent to the geographical extent of the study area—the scale we refer to as “global.” The assumption of panmixia is violated whenever cultural transmission is biased, either behaviorally or spatially, such that some teachers or variants are favored over others.

An obvious source of bias can come from the positive (or negative) biological fitness effects associated with a culturally transmitted behavior, and this is why the tenets of neutral theory apply only to non-adaptive traits. However, neutral theory is not necessarily applicable to every non-adaptive cultural trait just because it is selectively neutral. Unlike

genetic transmission, where offspring obviously cannot choose which alleles they receive from their parents, social learners can (and do) make choices about which individuals to learn from or which cultural variants to adopt. These choices can be biased by factors unrelated to biological fitness (Boyd and Richerson 1985; Henrich and McElreath 2003). Thus, biased forms of cultural transmission can strongly affect the frequencies of even non-adaptive cultural variants such that observed empirical estimates of diversity may depart from the theoretically derived expectation,  $\theta$ . This fact has not been lost on those interested in studying mechanisms of cultural transmission in the archaeological record.

Previous studies compare estimates of non-adaptive cultural diversity derived from empirical archaeological samples to theoretically derived estimates of  $\theta$ , which are obtained by substituting estimated values of effective population size and innovation rate into Equation 1. Differences between observed and expected levels of diversity are interpreted as a sign of biased cultural transmission. Shennan and Wilkinson (2001) analyze diversity in ceramic band-types collected from two contemporaneous and adjacent Neolithic sites in Germany. They invoke anti-conformist transmission to explain why they consistently find a higher degree of diversity in their archaeological material than predicted by  $\theta$  during the later phases of occupation. Conformist transmission is Kohler, VanBuskirk, and Ruscavage-Barz's (2004) preferred explanation for the lower-than-expected diversity observed in ceramic attributes at Late Coalition hamlets on the Pajarito Plateau in the U.S. Southwest. Difficulties associated with estimating prehistoric effective population sizes and innovation rates from archaeological data notwithstanding, the conclusions of these case studies are valid to the extent that the assumptions of the neutral model—constant population size, an infinite-variant model of innovation, “global” scale unbiased social learning, etc.—apply. Violating any of these assumptions may affect diversity such that empirical observations will depart from analytical expectations. While each of these assumptions deserves individual attention, here we concentrate on just one: the spatial scale of unbiased social learning.

Throughout prehistory cultural transmission was mediated in large part by geographic distance. Before the advent of modern forms of travel and

communication, long distances inhibited the transmission of cultural variants. Thus, isolation by distance holds important implications for the amount (and structure) of cultural diversity displayed by many prehistoric human societies. Here, we investigate how the spatial scale of unbiased social learning affects the amount of non-adaptive cultural diversity displayed by a population, and we assess whether it can cause departures from neutrality that might be mistaken for biased cultural transmission. We employ analytical models and computer simulation in our investigation.

### Methods

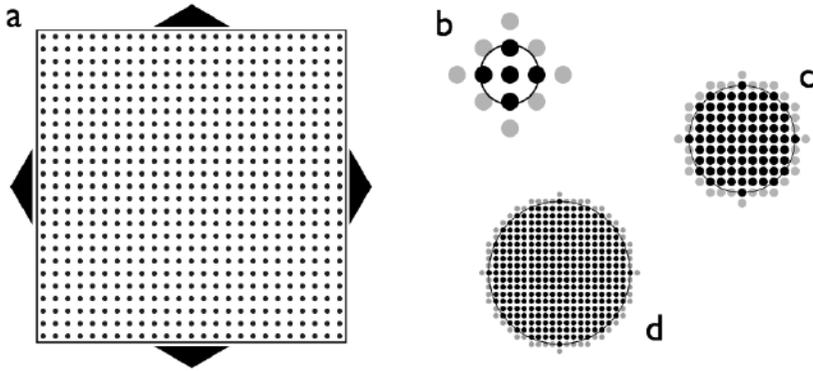
To date, there are two kinds of analytical models of neutral cultural evolution. We have already discussed the first (see Equation 1), which addresses unbiased transmission within a single population and provides predictions about diversity at equilibrium as a function of effective population size and innovation rate (see Kohler et al. 2004; Neiman 1995; Shennan and Wilkinson 2001). Unfortunately,  $\theta$  does not readily accommodate spatially explicit effects of social learning. A second type of analytical tool, the migration matrix model, considers multiple groups within a structured population and yields predictions about intergroup (or interassemblage) differences and diversity (see Neiman 1995). In migration matrix models, cultural transmission *within* groups is unbiased and cultural transmission *between* groups is determined by a matrix of intergroup transmission (or “migration”) rates. Although migration matrix models can be given a more explicitly spatial cast by stipulating that transmission rates scale with geographic distance between groups, they impose an arbitrary structure upon the population rather than allow one to emerge as a consequence of individuals’ locations and the spatial scale of social learning. For example, migration matrix models require mutually exclusive group membership; every individual can be a member of only one group at a time. Consequently, the number of groups is much lower than the number of individuals in the population. It is also worth noting that migration matrix models do not allow for innovation. Our aim is to assess whether a more realistic, continuous portrayal of spatial interaction and cultural transmission with innovation makes a difference in the amount of

diversity one would expect to see at different scales of social learning.

The agent-based modeling technique is specially suited to addressing archaeological research questions in which space plays an essential role (Brantingham 2003; Kohler and Gumerman 2000; Premo 2006, 2007, 2008, 2010). Here, we employ an agent-based simulation, called CTSIM,<sup>1</sup> of the Wright-Fisher model of cultural transmission described above. In CTSIM, each individual occupies a unique location in continuous space and has access to a unique spatial “neighborhood” for the purpose of social learning (Figure 1). The spatial scale of social learning refers to the length of the radius used to delineate each individual’s neighborhood. Any individual located within this spatial neighborhood (and this includes those whose Cartesian coordinates fall exactly on the limits of the neighborhood) may serve as a teacher for the individual located at its center. In other words, an individual cannot learn from those who reside outside of its spatially defined neighborhood. In CTSIM, unlike in migration matrix models, there are as many unique neighborhoods as individuals, and a single individual can be a member of many different neighborhoods at the same time. The extent to which individuals are members of multiple neighborhoods is a function of the degree to which neighborhoods overlap in space. The degree of overlap between spatial neighborhoods is a nonlinear function of both population density and the spatial scale of social learning.

In CTSIM, the spatial scale of social learning represents Euclidean distance, and its value can vary from one (highly localized) to “global” (the entire study area). In addition, population size and population density can vary between simulations. CTSIM also allows for two different mechanisms of cultural transmission: unbiased transmission (choose a teacher randomly from those in your spatial neighborhood) and conformist transmission (choose the most common variant in your neighborhood). Note that when the spatial scale of social learning is less than “global” or when the mechanism of cultural transmission is conformist, the simulation purposefully violates the assumption of panmixia.

Each simulation is initialized with a population of  $N$  individuals. Population size remains constant throughout each simulation run; individuals do not



**Figure 1.** A spatially explicit model of cultural transmission. (a) An example of the spatial configuration of social learners when population density = 1. The spatial scale of social learning defines the size of an individual’s neighborhood. Black dots represent members of the neighborhood and grey dots represent individuals that are not included in the neighborhood: (b) spatial scale = 1, neighborhood size = 5 individuals; (c) spatial scale = 5, neighborhood size = 81 individuals; and (d) spatial scale = 10, neighborhood size = 317 individuals. When the spatial scale of social learning is “global,” all individuals in the population are included in the neighborhood (a).

die or reproduce. Each individual has a unique coordinate in continuous Euclidean space. The opposing edges of the theoretical landscape are wrapped to avoid edge effects. Each individual displays a single variant of a non-adaptive cultural trait, which is represented by an integer. Upon initialization, every individual displays the same cultural variant ( $k = 1$ ). The simulation progresses in incremental time steps. During each time step, each individual experiences social learning and has the opportunity to innovate. With unbiased cultural transmission, an individual can learn from a teacher chosen randomly from the set of individuals (including itself) located within its spatial neighborhood. With conformist transmission, an individual adopts the modal variant displayed by the individuals located within its spatial neighborhood. Because we assume that a teacher must be physically present within the learner’s neighborhood in order to transmit cultural information, the results are particularly applicable to preliterate societies in which social learners habitually acquire variants by watching and/or listening to teachers directly or by studying their cultural material firsthand. Following social learning, each individual undergoes innovation with probability  $\mu = .001$ . Every innovation event results in a novel cultural variant (represented by a unique integer), one that has never before been seen in the population. Thus, CTSIM employs an infinite-variant model of innovation that is analogous to the infinite-allele model of mutation employed by population geneticists.

Some of the analytical tools we (and others) use to assess how well archaeological data match the expectations of neutral theory assume that cultural diversity is at equilibrium (Ewens 1972; Slatkin 1996). At equilibrium, cultural variants are lost to drift at the same rate that novel variants are introduced by innovation. When the assumptions of neutral theory apply, it can be shown that cultural diversity is at innovation-drift equilibrium in a population when the empirical estimate of homogeneity  $\hat{F}$  (Neiman 1995:Equation 5) is equal to its theoretically derived expectation (Neiman 1995:Equation 4), or more formally when:

$$\sum_{i=1}^k p_i^2 = \frac{1}{2N_e\mu + 1}, \quad (2)$$

where  $p_i$  is the relative frequency of the  $i$ -th cultural variant observed in a population,  $N_e$  is the effective population size, and  $\mu$  is the innovation rate. To quantify the effect of the spatial scale of social learning on cultural diversity in a spatially explicit setting, we set  $N_e = N$ . The actual value of  $N_e$  varies as a function of population density, the spatial scale of social learning and, when population density < 1, the unique spatial distribution of individuals. Making the simplifying assumption that  $N_e = N$  allows us to isolate the effect of the spatial scale of social learning on non-adaptive diversity.

With conformist transmission and population density = 1, equilibrium occurs at a much lower level of diversity than with unbiased transmission,

regardless of the spatial scale of social learning. Under these conditions, it can be shown that cultural diversity reaches equilibrium in a population when the empirical estimate of homogeneity ( $\hat{F}$ ) is equal to the probability of randomly drawing two individuals that display the same cultural variant, or when:

$$\sum_{i=1}^k p_i^2 = \frac{(1-\mu)(N - N\mu - 1)}{N - 1}, \quad (3)$$

where  $p_i$  is the relative frequency of the  $i$ -th cultural variant observed in a population,  $N$  is the census size of the population, and  $\mu$  is the innovation rate. To allow for the fact that both sides of Equations 2 and 3 may never be exactly equivalent in our stochastic simulations, we consider cultural diversity to be at equilibrium when the empirical estimate of  $\hat{F}$  (on the left) is within  $\pm 1$  percent of the theoretically derived expectation (on the right).

Not only does the agent-based simulation allow us to collect data from populations in which cultural diversity is known to be at equilibrium, but it also allows for complete knowledge of the cultural diversity displayed by a population. There are obvious advantages to dealing with data collected from a population rather than from a small—and, thus, potentially unrepresentative—sample of a population. However, because outside of simulation, experimental archaeology, and some ethnoarchaeological case studies, archaeologists do not have access to entire populations of culture material, representative samples must suffice. Thus, to make our analyses of simulated data comparable to empirical studies, we randomly sample one percent of the individuals in a simulated population during data collection.

There are techniques for estimating the amount of cultural diversity in a population from an empirical sample (see Neiman 1995; Shennan and Wilkinson 2001). We concentrate on two estimates that archaeologists have used previously:  $t_F$  and  $t_E$ . The first empirical estimate of  $\theta$  is designated with an  $_F$  to remind us that it incorporates the empirical estimate of homogeneity ( $\hat{F}$ ):

$$t_F = \frac{1}{\sum_{i=1}^k p_i^2} - 1. \quad (4)$$

It is important to note that when  $p_{(i,\dots,k)}$  represent the relative frequencies of variants observed in a *sample* rather than the actual relative frequencies of the *population*,  $t_F$  provides a biased estimator of  $\theta$  (see Neiman 1995). We apply Equation 4 to relative frequencies observed in small random samples. Thus, we employ  $t_F$  solely as a biased estimator. The second empirical estimate of  $\theta$ ,  $t_E$ , makes use of the Ewens sampling distribution. Ewens (1972) shows that, under the conditions of the neutral model, the expected number of unique variants,  $E(k)$ , in a small random sample of a population in which cultural diversity is at equilibrium is a function of the size of the sample,  $n$ , and  $\theta$ :

$$E(k) = \sum_{i=0}^{n-1} \frac{\theta}{\theta + i}. \quad (5)$$

Although there is no analytic solution for  $\theta$  in Equation 5, its value can be estimated numerically after substituting the number of variants observed in a sample for  $E(k)$  and the size of the sample for  $n$ . It is important to note that, unlike  $t_F$ ,  $t_E$  is not based on homogeneity ( $\hat{F}$ ). However, like  $t_F$ ,  $t_E$  is affected by sample size (see Neiman 1995).

The Ewens sampling distribution also serves as the basis for the exact test for neutrality (Slatkin 1994, 1996; see also Lansing et al. 2008). The exact test for neutrality requires a non-increasing ordered configuration of the quantities ( $r_1, \dots, r_k$ ) in which  $k$  unique variants are observed in a sample of size  $n$  (see Slatkin 1996:259). Here is an example of an ordered configuration in which  $k = 6$  variants are observed in a sample of  $n = 30$  individuals in the following quantities: (10, 8, 7, 3, 1, 1). Like  $t_F$  and  $t_E$ , the exact test for neutrality assumes that cultural diversity is at equilibrium in the population sampled.  $P_E$  provides the sum of the probabilities (provided by the Ewens sampling distribution) of all of the possible unordered configurations that are *less* likely to result under neutral conditions than the observed configuration. The exact test for neutrality is two-tailed. Given  $\alpha = .05$ ,  $P_E < .025$  indicate that the configuration of observed variants is more even (e.g., 7, 6, 5, 5, 4, 3) than would be expected under neutral conditions. This may signify the presence of anti-conformist cultural transmission. By contrast,  $P_E > .975$  indicate an overly uneven configuration, one in which just one or two variants dominate the assemblage while a few others appear

Table 1. Analytical and Empirical Estimates of Non-Adaptive Cultural Diversity and Results of the Exact Test for Neutrality under Unbiased Cultural Transmission at Different Spatial Scales in High-Density Populations of Different Size.

| Scale  | Density | <i>N</i> | $\theta$ | $t_F$ | $t_E$ | $t_F - t_E$ | $\theta - t_F$ | $\theta - t_E$ | $P_E < .025$ | $P_E > .975$ |
|--------|---------|----------|----------|-------|-------|-------------|----------------|----------------|--------------|--------------|
| 1      | 1       | 1024     | 2.05     | 1.80  | 1.97  | -.17        | .25            | .08            | 0            | 4            |
| 1      | 1       | 1521     | 3.04     | 2.35  | 3.30  | -.95        | .69            | -.26           | 0            | 2            |
| 1      | 1       | 2025     | 4.05     | 3.55  | 4.54  | -.99        | .50            | -.49           | 0            | 1            |
| 1      | 1       | 2500     | 5        | 4.28  | 5.93  | -1.65       | .72            | -.93           | 0            | 2            |
| 5      | 1       | 1024     | 2.05     | 1.77  | 1.61  | .16         | .28            | .44            | 0            | 1            |
| 5      | 1       | 1521     | 3.04     | 2.64  | 2.36  | .28         | .40            | .68            | 0            | 0            |
| 5      | 1       | 2025     | 4.05     | 3.14  | 2.93  | .21         | .91            | 1.12           | 1            | 0            |
| 5      | 1       | 2500     | 5        | 4.68  | 3.50  | 1.18        | .32            | 1.50           | 1            | 0            |
| 10     | 1       | 1024     | 2.05     | 2.25  | 1.65  | .60         | -.20           | .40            | 0            | 0            |
| 10     | 1       | 1521     | 3.04     | 2.64  | 2.49  | .15         | .40            | .55            | 1            | 0            |
| 10     | 1       | 2025     | 4.05     | 3.41  | 3.10  | .31         | .64            | .95            | 0            | 0            |
| 10     | 1       | 2500     | 5        | 4.36  | 3.87  | .49         | .64            | 1.13           | 0            | 0            |
| global | 1       | 1024     | 2.05     | 1.63  | 1.63  | 0           | .42            | .42            | 0            | 3            |
| global | 1       | 1521     | 3.04     | 2.42  | 2.42  | 0           | .62            | .62            | 0            | 1            |
| global | 1       | 2025     | 4.05     | 3.59  | 3.17  | .42         | .46            | .88            | 0            | 0            |
| global | 1       | 2500     | 5        | 4.10  | 3.74  | .36         | .90            | 1.26           | 0            | 0            |

Note: The values of  $t_F$ ,  $t_E$ ,  $t_F - t_E$ ,  $\theta - t_F$ , and  $\theta - t_E$  are geometric means (rounded to the second decimal place) of 20 unique simulation runs. Integers in the last two columns represent the number of simulations (out of 20) that provided significant  $P_E$  values.  $\theta = 2N_e\mu$ , where  $N_e = N$  and  $\mu = .001$ .

but rarely (e.g., 25, 1, 1, 1, 1, 1). An overly uneven configuration implies that conformist transmission may have shaped diversity. Given  $.025 < P_E < .975$ , one cannot reject the null hypothesis that the observed configuration is the result of strictly neutral processes, which in the case of cultural transmission refer to innovation and global scale unbiased social learning.

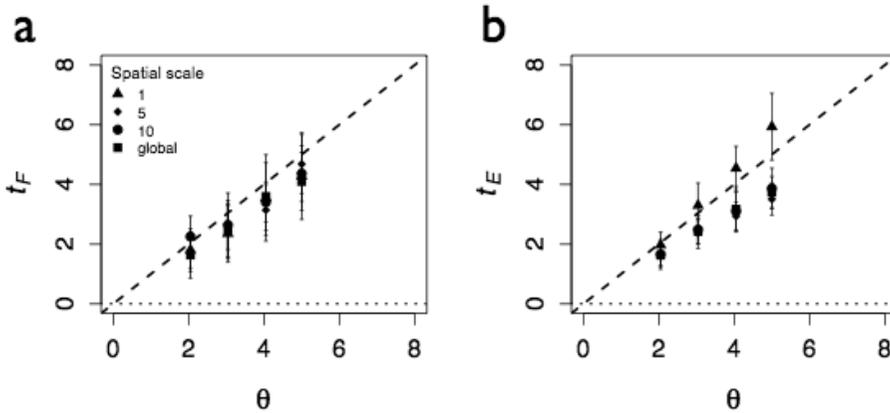
To calculate  $t_F$  for our simulated data, we collect the relative frequencies of the variants observed in a sample of  $n = N * .01$  individuals. Calculating  $t_E$  requires  $k$ , which we obtain by simply counting the number of unique variants observed in the sample. To calculate  $P_E$ , we collect an ordered configuration of the quantities of the cultural variants observed in the same sample of  $n$  individuals. All data are sampled from populations in which cultural diversity is known to be at equilibrium, according to Equation 2 or 3. Populations are simulated at different sizes, densities, and spatial scales of social learning. Twenty unique simulations are run at each parameter setting. We apply to simulated data the same methodology that has been applied to empirical archaeological data (Kohler et al. 2004; Neiman 1995; Shennan and Wilkinson 2001); we compare empirical estimates of cultural diversity ( $t_F$  and  $t_E$ ) with theoretically derived (and, in our case, known) expectations of cultural diversity ( $\theta$ ). To the best of our knowledge, this is the first application of

Slatkin’s (1996) exact test for neutrality to non-adaptive cultural diversity, simulated or otherwise.

### Results

Recall that we use the sum of the squared relative frequencies of variants in a population to identify when cultural diversity is at equilibrium and, thus, when to collect data from each simulation (Equations 2 and 3). Because  $t_F$  is also based on the sum of the squared relative frequencies of variants—though, in this case, the relative frequencies are known from a sample rather than the population (Equation 4)—the scale of social learning can have very little (if any) effect on  $t_F$  in our simulated data. By contrast,  $t_E$  is based on the richness of variants observed in a sample rather than their relative frequencies. Because  $t_E$  is independent of the method used to identify when cultural diversity has reached equilibrium in simulated populations, it shows the effects of the spatial scale of social learning on cultural diversity. Thus, if we (inappropriately, but purposefully) assume that the tenets of neutral theory apply to simulated populations in which the spatial scale of unbiased social learning is less than “global,” then  $t_E$  and, better yet, the difference,  $\theta - t_E$ , can indicate the effect of the spatial scale of unbiased social learning.

Table 1 provides some guide as to the values we



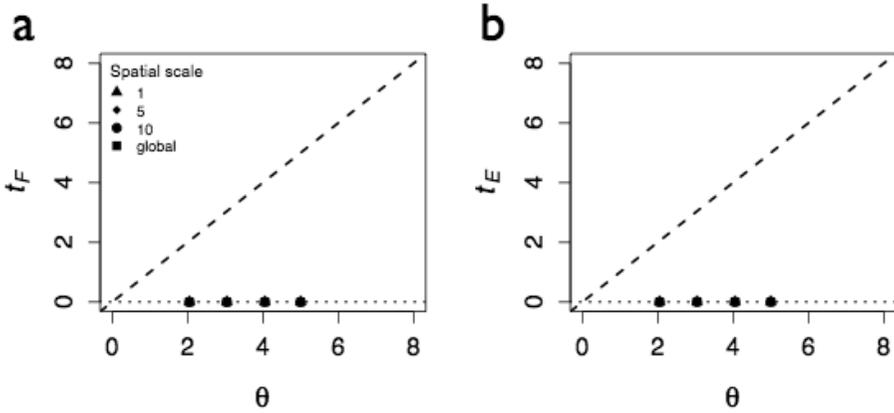
**Figure 2.** Empirical estimates—(a)  $t_F$  and (b)  $t_E$ —vs.  $\theta$  for high-density populations (population density = 1) with unbiased social learning at different spatial scales. *Note:* Each data point represents the mean  $\pm 1$  standard deviation of 20 unique simulation runs. The analytically derived expectations of diversity at equilibrium with unbiased (dashed line) and conformist (dotted line) cultural transmission for populations of different size are provided for reference.

should expect to see for  $t_E$  and the difference,  $\theta - t_E$ , under neutral model conditions. When the spatial scale of unbiased social learning is global,  $\theta - t_E$  is positive and increases with population size (Table 1). The magnitude of the effect of the spatial scale of unbiased social learning on non-adaptive cultural diversity can be measured by the extent to which the  $\theta - t_E$  values observed at nonglobal spatial scales deviate from the  $\theta - t_E$  values observed when social learning is global. For example, consider a population that maintains a greater number of variants than predicted by the neutral model as a result of unbiased social learning at a nonglobal spatial scale. Because this population will provide a higher  $t_E$  for a given  $\theta$ , the difference,  $\theta - t_E$ , will be lower than the values observed under global unbiased transmission for a population with the same size and innovation rate. Although  $\theta - t_E$  can indicate the effect of the spatial scale of social learning in the context of our simulation model, the exact test for neutrality provides a more formal statistical tool for identifying departures from the expectations of neutrality.

We begin by considering how the spatial scale of social learning affects non-adaptive cultural diversity when population density = 1 (i.e., individuals occupy all possible locations on the landscape [see Figure 1]). Figure 2 and Table 1 summarize the results of such populations simulated over different sizes and spatial scales of social learning. Here, we see that only highly localized unbiased social learning affects cultural diversity. When the spatial scale of social learning = 1,  $t_E$  is

greater and  $\theta - t_E$  lower than when the spatial scale of social learning is global in a population of the same size and innovation rate (Table 1). With highly localized unbiased cultural transmission, a population maintains a greater number of unique cultural variants than predicted by the neutral model. The results of the exact test weakly support the conclusion that highly localized unbiased social learning can cause non-adaptive diversity to depart from the expectation of neutrality when population density = 1 (Table 1).

Shennan and Wilkinson (2001:590–591) suggest that the mismatch between  $t_F$  and  $t_E$  may provide a reliable indicator of the mechanism of cultural transmission, with  $t_F < t_E$  implying conformist transmission and  $t_F > t_E$  anti-conformist transmission. The results from simulations in which population density = 1 provide an opportunity to investigate this claim. As expected,  $t_F$  and  $t_E$  are statistically indistinguishable under global scale unbiased cultural transmission (t-tests provide  $df = 38$ ,  $p > .15$  for each value of  $N$ ). However,  $t_F$  and  $t_E$  are significantly different for all but the smallest value of  $N$  (t-tests provide  $df = 38$ ,  $p < .01$  for  $N = 1521$ , 2025, and 2500) under highly localized unbiased social learning, resulting in  $t_F - t_E$  values that are less than zero (Table 1). It appears that *unbiased* cultural transmission can yield  $t_F < t_E$  when the spatial scale of social learning is highly localized. In addition,  $t_F$  and  $t_E$  are strikingly similar to each other in all simulations with conformist transmission (Figure 3 and Table 2). Thus, conformist transmission does not necessarily result in  $t_F < t_E$ , as



**Figure 3. Empirical estimates—(a)  $t_F$  and (b)  $t_E$ —vs.  $\theta$  for high-density populations (population density = 1) with conformist biased social learning at different spatial scales. *Note:* Each data point represents the mean  $\pm$  1 standard deviation of 20 unique simulation runs. Standard deviations fall within the symbols for the mean. The analytically derived expectations of diversity at equilibrium with unbiased (dashed line) and conformist (dotted line) cultural transmission for populations of different size are provided for reference.**

previously suggested. Clearly, the exact test for neutrality provides a more powerful test than  $t_F < t_E$  for recognizing departures caused by conformist transmission in our simulated data (Table 2).

One consequence of a “packed landscape” (i.e., population density = 1) is that every individual in the population has exactly the same number of potential teachers in its spatial neighborhood. Another is that every individual is connected (directly or indirectly) to every other individual—

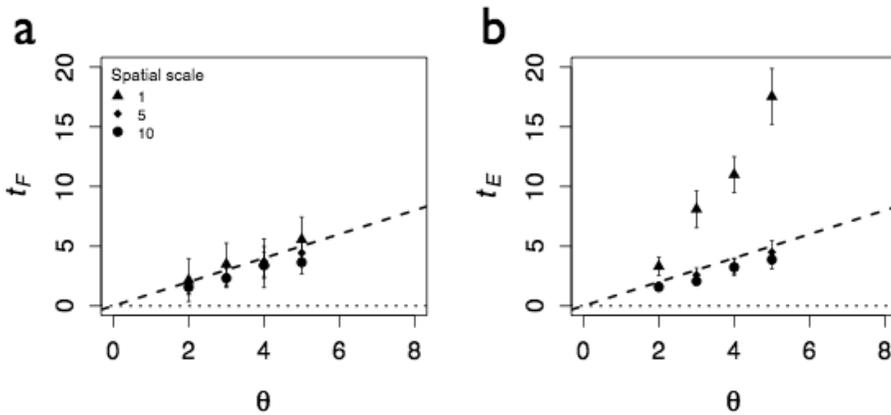
albeit by paths of varying length. This is due to the fact that, when all possible locations are occupied and the spatial scale of social learning  $\geq 1$ , every individual is a member of more than one neighborhood. This also explains why the spatial scale of social learning has no effect on diversity when cultural variants are passed via conformist biased transmission in a population with density = 1 (Figure 3b, Table 2).<sup>2</sup> However, human populations are rarely distributed so uniformly, and social networks

**Table 2. Analytical and Empirical Estimates of Non-Adaptive Cultural Diversity and Results of the Exact Test for Neutrality under Conformist Cultural Transmission at Different Spatial Scales in High-Density Populations of Different Size.**

| Scale  | Density | $N$  | $\theta$ | $t_F$ | $t_E$ | $t_F - t_E$ | $\theta - t_F$ | $\theta - t_E$ | $P_E < .025$ | $P_E > .975$ |
|--------|---------|------|----------|-------|-------|-------------|----------------|----------------|--------------|--------------|
| 1      | 1       | 1024 | 2.05     | 0     | 0     | 0           | 2.05           | 2.05           | 0            | 20           |
| 1      | 1       | 1521 | 3.04     | 0     | 0     | 0           | 3.04           | 3.04           | 0            | 20           |
| 1      | 1       | 2025 | 4.05     | 0     | 0     | 0           | 4.05           | 4.05           | 0            | 20           |
| 1      | 1       | 2500 | 5        | 0     | .01   | -.01        | 5              | 4.99           | 0            | 20           |
| 5      | 1       | 1024 | 2.05     | 0     | 0     | 0           | 2.05           | 2.05           | 0            | 20           |
| 5      | 1       | 1521 | 3.04     | .01   | 0     | .01         | 3.03           | 3.04           | 0            | 20           |
| 5      | 1       | 2025 | 4.05     | .01   | .01   | 0           | 4.04           | 4.04           | 0            | 20           |
| 5      | 1       | 2500 | 5        | 0     | 0     | 0           | 5              | 5              | 0            | 20           |
| 10     | 1       | 1024 | 2.05     | 0     | 0     | 0           | 2.05           | 2.05           | 0            | 20           |
| 10     | 1       | 1521 | 3.04     | 0     | 0     | 0           | 3.04           | 3.04           | 0            | 20           |
| 10     | 1       | 2025 | 4.05     | .01   | 0     | .01         | 4.04           | 4.05           | 0            | 20           |
| 10     | 1       | 2500 | 5        | 0     | .01   | -.01        | 5              | 4.99           | 0            | 20           |
| global | 1       | 1024 | 2.05     | 0     | 0     | 0           | 2.05           | 2.05           | 0            | 20           |
| global | 1       | 1521 | 3.04     | 0     | .01   | -.01        | 3.04           | 3.03           | 0            | 20           |
| global | 1       | 2025 | 4.05     | 0     | .01   | -.01        | 4.05           | 4.04           | 0            | 20           |
| global | 1       | 2500 | 5        | 0     | 0     | 0           | 5              | 5              | 0            | 20           |

*Note:* The values of  $t_F$ ,  $t_E$ ,  $t_F - t_E$ ,  $\theta - t_F$ , and  $\theta - t_E$  are geometric means (rounded to the second decimal place) of 20 unique simulation runs. Integers in the last two columns represent the number of simulations (out of 20) that provided significant  $P_E$  values.  $\theta = 2N_e\mu$ , where  $N_e = N$  and  $\mu = .001$ .

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**Figure 4.** Empirical estimates—(a)  $t_F$  and (b)  $t_E$ —vs.  $\theta$  for low-density populations (population density = .2) with unbiased social learning at different spatial scales. Note: Each data point represents the mean  $\pm 1$  standard deviation of 20 unique simulation runs. The analytically derived expectations of diversity at equilibrium with unbiased (dashed line) and conformist (dotted line) cultural transmission for populations of different size are provided for reference.

are rarely so regular. Whether because of the presence of physical obstacles (mountains, desert, sea, etc.), physical conduits (rivers, coastlines, resource-rich areas, etc.), or the vagaries of history (locations of previous settlements), human populations are more often distributed discontinuously. As a result, some individuals, groups, or villages will have access to a greater number of potential teachers given the same spatial scale of social learning. This can be included in the simulation by relaxing the assumption that social learners occupy all possible locations on the landscape. When population density  $< 1$ , some individuals will have a greater number of potential teachers in their neighborhood than others even though the spatial scale of social learning is the same for everyone.

We use two methods for simulating populations of different  $N$  when population density  $< 1$ . According to the first method, to increase  $N$  we simply increase the size of the study area while holding population density constant. We have already discussed the effect of the spatial scale of social learning on cultural diversity in populations of different size when population density = 1 (Figure 2 and Table 1). But we are also interested in the interaction between population size and the spatial scale of social learning in low-density populations. To investigate this, we rerun the entire set of simulations with population density = .2 (Figure 4 and Table 3). Although the densities of the populations differ between these two sets of simulations, their census sizes are nearly equivalent. Controlling for

population size, the effect of highly localized unbiased social learning on cultural diversity (as estimated by  $t_E$ ) is greater in the low-density population than the high-density population (compare Figures 2b and 4b or compare Tables 1 and 3). In addition, the results of the exact test strongly support the conclusion that highly localized social learning affects cultural diversity in the low-density population. The exact test recognizes a departure from neutrality in almost every case of highly localized unbiased transmission when population density = .2 (Table 3). However, there is little difference between the levels of cultural diversity observed in low- and high-density populations under “intermediate” spatial scales (5 and 10) of unbiased social learning. The degree to which spatial neighborhoods overlap in space at intermediate spatial scales of unbiased social learning is sufficient to avoid isolation by distance, even when just 20 percent of the possible locations are inhabited. These results suggest a complex relationship between population density and the spatial scale of social learning that is deserving of further study. For example, it is likely that the cultural diversity of simulated populations with very low densities (i.e., less than .2) would be affected by unbiased social learning at spatial scales larger than 1.

As we know from modern examples of rapid population growth around the world, population density usually increases with  $N$ . Thus, the second method calls for holding the size of the study area constant while simulating populations at different

Table 3. Analytical and Empirical Estimates of Non-Adaptive Cultural Diversity and Results of the Exact Test for Neutrality under Unbiased Cultural Transmission at Different Spatial Scales in Low-Density Populations of Different Size.

| Scale | Density | $N$  | $\theta$ | $t_F$ | $t_E$ | $t_F - t_E$ | $\theta - t_F$ | $\theta - t_E$ | $P_E < .025$ | $P_E > .975$ |
|-------|---------|------|----------|-------|-------|-------------|----------------|----------------|--------------|--------------|
| 1     | .2      | 1000 | 2        | 2.16  | 3.31  | -1.15       | -.16           | -1.31          | 0            | 19           |
| 1     | .2      | 1500 | 3        | 3.49  | 8.09  | -4.60       | -.49           | -5.09          | 0            | 20           |
| 1     | .2      | 2000 | 4        | 3.57  | 10.98 | -7.41       | .43            | -6.98          | 0            | 20           |
| 1     | .2      | 2500 | 5        | 5.55  | 17.52 | -11.97      | -.55           | -12.52         | 0            | 20           |
| 5     | .2      | 1000 | 2        | 1.55  | 1.68  | -.13        | .45            | .32            | 0            | 0            |
| 5     | .2      | 1500 | 3        | 2.44  | 2.59  | .15         | .56            | .41            | 0            | 0            |
| 5     | .2      | 2000 | 4        | 3.71  | 3.35  | .36         | .29            | .65            | 1            | 0            |
| 5     | .2      | 2500 | 5        | 4.43  | 4.49  | -.06        | .57            | .51            | 1            | 0            |
| 10    | .2      | 1000 | 2        | 1.57  | 1.58  | -.01        | .43            | .42            | 0            | 0            |
| 10    | .2      | 1500 | 3        | 2.32  | 2.06  | .26         | .68            | .94            | 0            | 0            |
| 10    | .2      | 2000 | 4        | 3.39  | 3.23  | .16         | .61            | .77            | 0            | 0            |
| 10    | .2      | 2500 | 5        | 3.65  | 3.87  | -.22        | 1.35           | 1.13           | 2            | 0            |

Note: The values of  $t_F$ ,  $t_E$ ,  $t_F - t_E$ ,  $\theta - t_F$ , and  $\theta - t_E$  are geometric means (rounded to the second decimal place) of 20 unique simulation runs. Integers in the last two columns represent the number of simulations (out of 20) that provided significant  $P_E$  values.  $\theta = 2N_e\mu$ , where  $N_e = N$  and  $\mu = .001$ .

$N$  (Figure 5 and Table 4). Again controlling for population size, highly localized social learning has a greater effect on non-adaptive cultural diversity (as estimated by  $t_E$ ) in populations with lower densities (compare Figures 4b and 5b or compare Tables 3 and 4). Under these conditions, the exact test recognizes departures from neutrality in some of the cases of unbiased cultural transmission when the spatial scale of social learning is highly localized (Table 4), though not as regularly as when population density is even lower (Table 3). As before, intermediate spatial scales of social learning (5 and 10) do not affect cultural diversity.

**Discussion**

This study explores the interaction between the spatial scale of social learning, population size and density, and different cultural transmission mechanisms. In the presence of highly localized unbiased social learning, simulated populations regularly display a greater number of cultural variants—and, thus, higher  $t_E$ —than predicted by neutral theory. Put simply, under highly localized unbiased social learning, populations maintain greater diversity than their size would allow under neutral conditions. This is not unexpected. Wright found that isolation by distance increased non-adaptive genetic diversity at the level of the population. Our data show that the same holds for non-adaptive cultural diversity, at least when cultural variants are transmitted via unbiased social

learning. Our results suggest that greater-than-expected cultural diversity estimates can result from highly localized unbiased cultural transmission.

Many of the same populations that display a greater number of variants than predicted by the neutral model due to highly localized unbiased social learning also display  $P_E > .975$ , a sign of conformist transmission. Why does the exact test for neutrality regularly identify highly localized unbiased social learning as conformist transmission in our simulated data? All else equal, the number of cultural variants that exist at very low frequencies—some displayed by just a single individual—increases as the spatial scale of unbiased social learning decreases. This effect is stronger in low-density populations. As a result, samples of populations in which unbiased social learning is highly localized will include a greater number of “singletons.” Recall that the exact test for neutrality does not require information about the size of the population or the rate of innovation, but rather only the quantities in which unique variants are observed in a sample. As a result, the exact test assigns an ordered configuration like (10, 1, 1, 1, 1) the highest possible  $P_E$  value of 1 regardless of whether the sample derives from a small, low-density population with highly localized unbiased cultural transmission; from a small population with “global” scale conformist transmission and a high innovation rate; or from a much larger population with “global” scale conformist transmission and a low innovation rate. This further illustrates the need for

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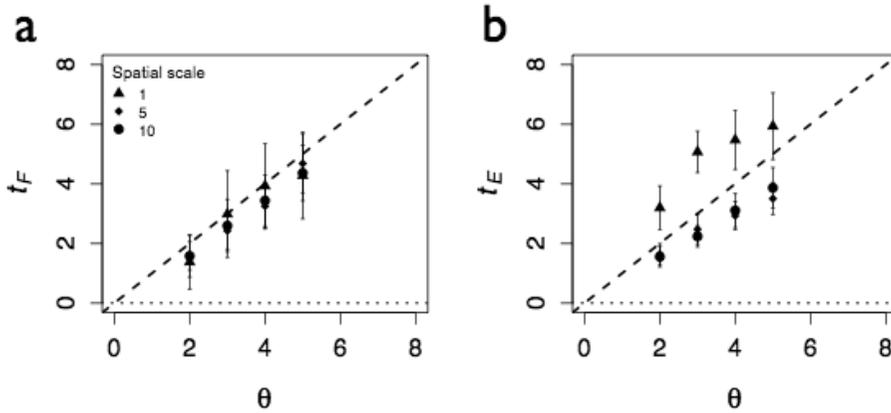


Figure 5. Empirical estimates—(a)  $t_F$  and (b)  $t_E$ —vs.  $\theta$  for populations in which density varies with  $N$  with unbiased social learning at different spatial scales. Note: Each data point represents the mean  $\pm$  1 standard deviation of 20 unique simulation runs. The analytically derived expectations of diversity at equilibrium with unbiased (dashed line) and conformist (dotted line) cultural transmission for populations of different size are provided for reference.

archaeologists to consult other lines of evidence, such as independent estimates of population size and the spatial scale of social learning, when inferring mechanisms of cultural transmission from archaeological assemblages.

Fortunately, archaeological assemblages provide material correlates that can indicate the spatial scale of social learning. Long-distance interactions can be inferred by the presence of exotic artifacts or non-local raw materials. Provenience studies can be used to study the scale of artifact circulation in a region, assuming the requisite raw material heterogeneity is present (Bishop et al. 1982). Evidence that artifacts or raw materials were

transmitted over a given distance raises the possibility that cultural variants (including ideas) were too. A conservative assumption would employ the spatial scale of artifact circulation (when available) as a proxy for the *minimum* spatial scale of social learning. The spatial scale of artifact circulation cannot provide a proxy for the *maximum* extent of social learning for the same reason that highly localized social learning cannot be inferred by the absence of nonlocal materials: people can apply ideas learned from afar to materials available closer to home. Consider the simple hypothetical scenario in which two geographically distant groups *A* and *C* interact with a third group *B*, but not with each

Table 4. Analytical and Empirical Estimates of Non-Adaptive Cultural Diversity and Results of the Exact Test for Neutrality under Unbiased Cultural Transmission at Different Spatial Scales in Populations of Different Densities and Sizes.

| Scale | Density | $N$  | $\theta$ | $t_F$ | $t_E$ | $t_F - t_E$ | $\theta - t_F$ | $\theta - t_E$ | $P_E < .025$ | $P_E > .975$ |
|-------|---------|------|----------|-------|-------|-------------|----------------|----------------|--------------|--------------|
| 1     | .4      | 1000 | 2        | 1.38  | 3.20  | -1.82       | .62            | -1.20          | 0            | 20           |
| 1     | .6      | 1500 | 3        | 2.99  | 5.07  | -2.08       | .01            | -2.08          | 0            | 10           |
| 1     | .8      | 2000 | 4        | 3.93  | 5.47  | -1.54       | .07            | -1.47          | 0            | 2            |
| 1     | 1       | 2500 | 5        | 4.28  | 5.93  | -1.65       | .72            | -.93           | 0            | 2            |
| 5     | .4      | 1000 | 2        | 1.57  | 1.64  | -.07        | .43            | .36            | 0            | 0            |
| 5     | .6      | 1500 | 3        | 2.43  | 2.47  | -.04        | .57            | .53            | 1            | 1            |
| 5     | .8      | 2000 | 4        | 3.25  | 2.93  | .32         | .75            | 1.07           | 1            | 0            |
| 5     | 1       | 2500 | 5        | 4.68  | 3.50  | 1.18        | .32            | 1.50           | 1            | 0            |
| 10    | .4      | 1000 | 2        | 1.58  | 1.55  | .03         | .42            | .45            | 0            | 0            |
| 10    | .6      | 1500 | 3        | 2.60  | 2.24  | .36         | .40            | .76            | 1            | 0            |
| 10    | .8      | 2000 | 4        | 3.44  | 3.11  | .33         | .56            | .89            | 0            | 0            |
| 10    | 1       | 2500 | 5        | 4.36  | 3.87  | .49         | .64            | 1.13           | 0            | 0            |

Note: The values of  $t_F$ ,  $t_E$ ,  $t_F - t_E$ ,  $\theta - t_F$ , and  $\theta - t_E$  are geometric means (rounded to the second decimal place) of 20 unique simulation runs. Integers in the last two columns represent the number of simulations (out of 20) that provided significant  $P_E$  values.  $\theta = 2N_e\mu$ , where  $N_e = N$  and  $\mu = .001$ .

other. Some of the non-adaptive cultural traits that originated in *A* can be transmitted to *C* (via *B*) in lieu of raw material or artifacts characteristic of *A*. There are many scenarios in which the spatial scale of cultural transmission is larger than the scale of artifact circulation.

Isolation by distance may be detected directly through a combination of settlement pattern analysis and interassemblage comparisons. Interassemblage distance measures between contemporary assemblages can indicate variation in the level of interaction between sampled locales. All else equal, groups in which individuals commonly learn from individuals in other groups will display greater diversity and lower interassemblage distances than more isolated groups (Neiman 1995). An important caveat is that detecting variation in cultural transmission rates between groups depends on both the scale of analysis (i.e., the spatial scale at which archaeologists define groups and/or assemblages) and the spatial scale of social learning. Our results suggest a complex relationship between cultural diversity and the spatial scale of unbiased social learning, as intermediate scales did not regularly generate skewed samples in the population densities we tested. This calls for a multiscale approach to estimating the spatial scale of social learning from measures of interassemblage differences.

### Conclusion

Controlled, reproducible simulation experiments of cultural transmission in spatially explicit artificial societies suggest that the spatial scale of unbiased social learning can have a profound effect on non-adaptive cultural diversity. Our results should not be taken as an argument against employing the tools provided by neutral theory to study cultural transmission in the archaeological record, *per se*. Nevertheless, the spatial scale of unbiased social learning may cause departures from the theoretically derived expectations of neutral theory, such that highly localized unbiased transmission may be easily confused with a form of biased transmission. In other words, the spatial scale at which cultural traits were habitually passed between individuals or villages via unbiased transmission can result in departures from neutrality. Thus, archaeologists should temper inferences of cultural transmission mechanisms with proxies of the spatial scale of

social learning drawn from the material record.

This simulation work also has broader implications for the application of neutral theory to the cultural diversity found in archaeological data. It raises the specter that violating one of the other assumptions of the neutral model (constant population size or infinite-variant model of innovation) or using  $t_F$  and  $t_E$  to estimate diversity for assemblages in which cultural diversity was not at innovation-drift equilibrium could also be responsible for observed departures from neutrality. These issues deserve the kind of individual attention we have given to the spatial scale of social learning. Resolving them will require addressing other difficult questions: What is the archaeological evidence for a constant population size? How valid is the assumption that each innovation event results in an entirely novel variant when we know from our own experience that “new” styles commonly borrow from the past (fashion is circular, as they say)? How can one demonstrate that cultural diversity was at equilibrium (and at what point?) from archaeological assemblages that conflate time?

In practice, comparing empirical estimates of non-adaptive cultural diversity to theoretically derived expectations as a means to infer past cultural transmission mechanisms may not be applicable to archaeological case studies in which population size fluctuated through time, innovation was not analogous to an infinite-allele model of mutation, or cultural diversity was not at equilibrium. At the very least, we need to be aware of how violating any of these fundamental assumptions, not just that of “global” scale unbiased social learning, could bias our interpretations of cultural transmission in archaeological data (also see Bettinger 2008). Although the application of the neutral model has limits, diversity metrics may still provide a means of inferring social learning mechanisms from culture material. Explicitly ruling out the alternative explanations for why archaeological data depart from the expectations of neutrality, such as highly localized unbiased social learning, will only strengthen archaeological inferences of cultural transmission mechanisms.

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## Notes

1. The fully documented source code, including a full model description, is freely available from the first author. CTSIM runs on NetLogo (Wilensky 1999), a popular, easy to use, and increasingly powerful agent-based modeling platform that can be freely downloaded from the World Wide Web (<http://ccl.northwestern.edu/netlogo/>).

2. It is highly likely that the spatial scale of conformist transmission would affect non-adaptive cultural diversity when population density < 1. As in the case of unbiased cultural transmission, we would expect to see greater-than-expected diversity at the level of the population with highly localized conformist biased social learning in low-density populations. This is worth investigating further.

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