

Research

Descent with modification and the archaeological record

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Recent years have seen major advances in our understanding of the way in which cultural transmission takes place and the factors that affect it. The theoretical foundations of those advances have been built by postulating the existence of a variety of different processes and deriving their consequences mathematically or by simulation. The operation of these processes in the real world can be studied through experiment and naturalistic observation. In contrast, archaeologists have an 'inverse problem'. For them the object of study is the residues of different behaviours represented by the archaeological record and the problem is to infer the microscale processes that produced them, a vital task for cultural evolution since this is the only direct record of past cultural patterns. The situation is analogous to that faced by population geneticists scanning large number of genes and looking for evidence of selection as opposed to drift, but more complicated for many reasons, not least the enormous variety of different forces that affect cultural transmission. This paper reviews the progress that has been made in inferring processes from patterns and the role of demography in those processes, together with the problems that have arisen.

Keywords: meme's eye-view; cultural drift; functional and neutral variation; transmission of complex technologies; demography and cultural complexity; archaeological record

1. INTRODUCTION

Over the last 30 years, the idea that the processes producing cultural stability and change are analogous in important respects to those of biological evolution has become increasingly popular. On this view, just as biological evolution is characterized by changing frequencies of genes in populations through time as a result of such processes as natural selection, so cultural evolution refers to the changing distributions of cultural attributes in populations, likewise affected by processes such as natural selection but also by others that have no analogue in genetic evolution. Since the presentation of the fundamental mathematically based theory by Cavalli-Sforza & Feldman [1] and Boyd & Richerson [2], the development of what has come to be called 'dual inheritance theory' or 'geneculture coevolution theory' has continued (e.g. [3,4]) and it has been accompanied by a slowly growing number of empirical case studies, applying the ideas to understanding patterned variation in cultural data (e.g. [5]).

The processes involved are complex and subtle. In the case of culture, the inheritance mechanism is social learning. Of course, the routes through which culture is inherited are much more diverse than those for genes and different routes have different consequences for the patterning of cultural change

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through time [1]. Variation in what is inherited is generated by innovations. These may be unintended copying errors, but they can also be intentional changes, perhaps arising from trial-and-error experimentation, which leads an individual to stop doing what they had previously learned and to start doing it differently, or even to do something different altogether. Whether this will be widely adopted depends on a range of selection and bias mechanisms, many of which have no equivalent in genetic evolution but whose existence and importance have formed the subject of major developments in the theory of cultural evolution over the last 30 years.

Natural selection in the narrowest sense affects humans as it does members of all other species. However, natural selection can also act on cultural attributes, in the sense that those individuals who inherit or acquire certain cultural attributes may have a greater probability of surviving and/or reproducing than those who do not; as a result those cultural attributes will become increasingly prevalent. For example, it is clear that in many parts of the world adopting an agricultural rather than a hunting-and-gathering way of life led to greater reproductive success; as a result, the cultural traits that characterize agriculture spread and, in some cases, subsequently influenced genetic evolution (e.g. the ability to digest lactose [6]). An analogous process of cultural selection can also operate if individuals with certain cultural traits are more likely to be taken as models for imitation than others, by virtue of those traits, and these in turn become successful models as a result. The traits

concerned will become more prevalent even if they have no bearing on reproductive success whatsoever, and indeed, even if they are deleterious to it. This is because if an attribute is passed on other than by parents to children there is no reason for its success to depend on the reproductive success of the individuals concerned. For example, if celibate priests are more likely than other adults to be teachers and if, as a result of what they teach, their pupils are more likely to become celibate priests and teachers, then the values they teach will increase in frequency relative to others [2, ch. 6].

In addition to these selection mechanisms, it has been shown that a number of 'bias' processes can affect what is transmitted; these refer to factors that affect what and who people try to copy when they are learning from others [2,3]. Thus, 'results bias' refers to the situation where people look at what other people do, for example, the crops they plant, compare the results with what they are doing themselves, and then change what they do because the other way of doing things seems to be more effective. 'Content biases' are affected by features of transmissible phenomena that make them intrinsically more or less memorable for reasons relating to the structure of the mind or the strong reactions they provoke; examples might be fairy tales or so-called urban myths. 'Context biases' are aspects of the context of learning that affect what is transmitted; thus, something may be copied simply because the person initially doing it is prestigious ('prestige bias') or because it is what most people locally do ('conformist bias'). In these latter two cases, whether a particular cultural attribute or practice becomes more prevalent in a population has nothing to do with its intrinsic properties but only with the context of learning.

Finally, there is the cultural equivalent of genetic drift [1, ch. 3]. In other words, the frequencies of particular cultural attributes can change for essentially chance reasons not involving any preference for a particular attribute. Who or what you copy may simply be a random choice dependent on who or what you meet. Thus, variants that occur more frequently in a population will have a greater chance of being copied purely by virtue of their greater frequency, but in any finite population there will also be an element of chance in what specific variants are copied, and when populations are small the role of chance will be important. If there is no innovation, the outcome will be that a single variant becomes fixed; the time taken for this depends on the population size.

2. THE 'MEME'S EYE-VIEW'

However, as just described, all these processes focus on the people involved in the processes. This is obviously an extremely important perspective but it is not the only one. It is also important to look at the processes from the meme's eye-view [7,8], the perspective of the cultural attributes themselves. This perspective matters because these culturally transmitted features are the only data accessible to archaeologists, and often all that anthropologists have as well. In fact, they are the only direct data about past cultural traditions and the forces affecting them that we have available. Moreover, the agent-centred cultural evolutionary processes described above are microscale ones: they occur at short time scales, at most a human generation but very often on a virtually day-to-day basis, and between individuals or small groups. The question then becomes, to what extent is it possible to identify the action of the various cultural evolutionary processes outlined above on the basis of distributions of through-time variation in the past, given the often poor temporal resolution of the archaeological record and the enormous range of complex processes that have affected it? This is a classic 'inverse problem' of a type very familiar to archaeologists: inferring the microscale processes producing a pattern from the pattern itself, as opposed to carrying out designed experiments or making naturalistic observations of processes in the field and examining their consequences. The problems are analogous to those faced by population geneticists in identifying the operation of selection and other processes given the evidence of gene distributions, but in that case the problems are less complex, the amounts of data available are now enormous and very powerful methods have been developed with a strong and well-justified theoretical background. However, as with the development of the theoretical models that created the basis for the field of cultural evolution, the existence of these methods is something from which empirical cultural evolutionary studies can benefit.

In fact, even to demonstrate that a pattern of contemporary variation or one of continuity through time results from the operation of a cultural inheritance process (i.e. is a 'meme'), as opposed to being a contingent response to local environmental conditions, is not straightforward. Going on to make inferences about the processes acting on the cultural lineages identified is even more difficult, and they look different from the 'meme's' perspective than from the agent's. Thus, in a recent paper on the evolution of Polynesian canoes, Rogers & Ehrlich [9] refer to the process acting on those canoe traits that have a functional significance as natural selection, and so it is from the perspective of the traits themselves, in that particular traits survive and are copied preferentially as a result of their greater functional effectiveness (cf [10])—something that could in principle be tested experimentally. What the results do not do as they stand is distinguish between natural selection operating on human agents via cultural traits, and thus on the future frequency of those traits and results bias, as defined above. In other words, the process could have operated as a result of the makers and users of ineffective canoes drowning more frequently, thus leading to the demise of those designs, while groups with better-designed canoes, perhaps different communities, survived and colonized new islands. Alternatively, it could have worked through people observing the performance of different canoe designs and preferentially copying those they perceived as more effective. The latter would potentially be far faster and the implied timescale difference could provide a basis for distinguishing between the two processes. Making this sort of distinction is actually at the root of some of the most

long-standing debates in archaeology, for example, whether the spread of farming into Europe was a process of indigenous adoption (involving results bias) or demographic expansion and extinction (natural selection acting on the bearers of cultural traditions). Note that despite the numerous attacks on the idea of memes as replicators encouraging their own reproduction, it is emphatically the case in both the above scenarios that whether or not people reproduce particular traits depends on the specific characteristics of the traits themselves.

In fact, the basic procedures of an evolutionary archaeology of cultural traditions are now clear [11]. It is necessary to identify the histories of transmission to show that an ancestor-descendant relationship exists, if indeed it does [12], and then attempt to understand the forces shaping it, all on the basis of patterned variation in the archaeological record. In practice, however, these two operations, identifying a transmission history and characterizing the forces affecting it, are not necessarily sequential, and the information to make the distinctions required may simply not exist. Thus, if a particular cultural attribute, for example, the sharpness of a lithic cutting edge, is very strongly determined by its function, then it will contain no signal of its transmission history as a particular technique of stone tool production, even though it is likely that it had one (as opposed to being discovered anew by every novice flint knapper through trial-and-error learning).

Clearly, transmission implies continuity but continuity does not necessarily imply transmission. It might arise, for example, from the continuity of environmental conditions or of a particular function. In practice, probably the most important method for characterizing transmission in archaeology has been seriation. This is a very well-known technique developed in the late nineteenth and early twentieth centuries for the purpose of building artefact chronologies in the absence of absolute dates; it involves putting phenomena in a sequential order on the basis of some measure of their similarity to one another [12,13]. If we have independent evidence of the chronological order, we can test whether the phenomena that are most similar to one another are indeed closest to one another in time. To the extent that they are, continuity is implied. Thus, if successive pottery assemblages linked by transmission, characterized by counts of different ceramic types, are put in order, then the changing frequencies of the types will show a characteristic pattern of first appearance, increasing popularity and decline. Ultimately, however, our conviction that cultural transmission is the predominant force accounting for the pattern is also based on other knowledge, for example, that the making of pottery is an activity acquired by social learning. Other situations are a priori less clear cut. Thus, Huester-Plogmann and colleagues [14] showed graphically that through-time fluctuations in the proportional and absolute frequencies of wild and domestic animal bones at Neolithic sites in Switzerland probably did not relate to changing cultural preferences for hunting or keeping domestic animals but to climatic fluctuations, because hunting became predominant

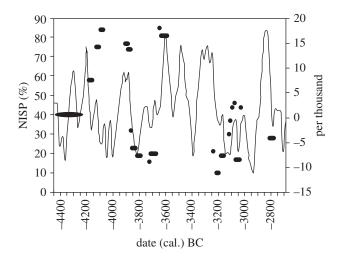


Figure 1. Fluctuations in the proportion of wild animals through time in faunal assemblages (filled circles) from the Swiss Neolithic between 4400 and 2800 cal. BC. Percentage of number of identified specimens (left-hand axis), against a climatic indicator, the delta ¹⁴C value (right-hand axis); higher values indicate cooler, wetter conditions. Adapted from Huester-Plogmann *et al.* [14, fig. 1].

at times of a cool, wet climate, which could be demonstrated by independent evidence (figure 1).

3. CHARACTERIZING CULTURAL DRIFT

The main single topic on which the characterization of processes has focused in archaeology is the identification of cultural drift and departures from it. The idea that cultural phenomena could be subject to drift processes goes well back into the mid-twentieth century and before (e.g. [15]). In his early expositions of evolutionary archaeology, Dunnell (e.g. [10]) suggested that the attributes of material culture assemblages could be divided into those influenced by selection (functional attributes) and those that were not (stylistic attributes). However, the key development in linking material culture attributes to evolutionary theory was Neiman's [16] demonstration of the way the mathematics of the neutral theory of evolution could be used to generate quantitative expectations of what a distribution of artefact frequencies should look like if drift and innovation were the only factors affecting it, rather than simply making a priori judgements about what is likely to have been functional and what stylistic, as previous authors had done.

Specifically, he made use of the fact that at mutation/innovation-drift equilibrium, when the mutation rate is very low, the homogeneity of a population made up of variants whose distribution is only affected by drift and innovation is proportional to twice the effective population size times the innovation rate $(2N_e\mu)$ [16]. As this quantity (designated θ) increases, the homogeneity of the population decreases. This may be compared with the value of θ obtained from a given set of data:

$$\theta = \frac{1}{\sum_{i} p_i^2} - 1,$$

where p_i is the relative frequency of the *i*th member of a population of k variants.

However, as Neiman pointed out, there is a preliminary issue that needs to be taken into account if we are to use our archaeological data for this purpose. We cannot necessarily assume that the frequency of decorative types in an archaeological assemblage corresponds to the frequency of variants in the past population; it will have been governed, among other things, by discard rates. Nevertheless, Neiman showed by simulation that where assemblages are the product of multiple transmission episodes and multiple discard events, then the assemblage frequency distribution of types/variants will closely correspond to that of the frequency of the variants in the population from which the assemblage is drawn.

However, we still need to obtain an estimate of the neutral expected variation in a sample of a given size. For this Neiman made use of an equation from Ewens [17] who showed that, if the neutrality assumption holds, then the expected number of different variants in a sample (E(k)) is a function of the sample size (n) and the parameter θ , based on the effective population size and the mutation rate, presented above [16, eqn (9)]:

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

Since in a given case we know the observed number of variants (k) and the sample size (n), we can use this equation to obtain an estimate of θ [16].

Following the logic of genetic drift, cultural drift variation is the result of random copying of cultural attributes, with some possibility of innovation, and the results of the process depend solely on the innovation rate and the effective population size, itself dependent on the scale of interaction. It is very unlikely that any individual act of copying, for example, of a ceramic decorative motif, will be random in terms of the model copied, but if everyone has their own reasons for copying one person rather than another, the result will be that there are no directional forces affecting what or who is copied. Neiman's original case study indicated that patterning in the rim attributes of eastern North American Woodland period pottery was a result of drift, and on this basis he was able to go on to argue that the Woodland period was one of large-scale human interaction, a view that had been held by earlier scholars but had subsequently been rejected, for reasons that Neiman was able to show were erroneous. In contrast, Shennan & Wilkinson [18] showed that patterning in the frequency through time of decorative attributes of Early Neolithic pottery from a small region of Germany indicated a more even distribution of variants than expected under drift, in the later phases of the sequence studied; i.e. there was an 'anti-conformity' bias, with many different types being relatively frequent (figure 2). Conversely, Kohler et al. [19] in a case study of decorative designs on pottery from the southwest USA, were able to show a departure in the direction of conformity. Thus, these methods do provide a potential basis for distinguishing some of the transmission forces outlined above, although the

statistical methods used to test for departures from drift in these cases were very weak.

The above studies followed Neiman in using an assemblage diversity measure to identify drift. Subsequently, Bentley and colleagues [20] took another aspect of predictions of the neutral theory as their focus, the proportion of variants having a given frequency, and used computer simulation to explore the implications of the neutral model in terms of the relative frequency distribution of individual variants accumulated over time. They showed that the result was a power law, with a small number of the variants attaining very high frequencies but most occurring only very few times, so long as $N\mu$ is not too large. Clearly, if the mutation rate is high then no variant is going to achieve high frequencies because variants are constantly being replaced.

They explored the implications of this model by analysing a number of datasets, including the distribution of baby names represented in the 1990 US census and in a series of sample datasets for each decade of the twentieth century. They found an extremely good fit to a power law distribution in all cases, although this was not statistically tested, and therefore suggested that the distributions were governed by a process of random copying. In such cases, although one can predict that a small number of variants will attain very high frequencies, it is impossible to predict which ones.

Mesoudi & Lycett [21] took this approach further by simulating the frequency distributions produced by biased transmission processes distinct from the drift model of random copying. They showed that conformist and anti-conformist transmission produced log-log frequency distributions with markedly distinctive features different from those produced by random copying, and confirmed Bentley & Shennan's [22] result that if copying is independent of the frequency of the models available to be copied then the distribution of frequencies will be exponential. However, they also showed that processes of 'frequencydependent trimming', in which there is a bias against copying either the most popular or the least popular variants, are not easy to distinguish from simple random copying. However, in no case did they attempt to test statistically the extent of the departure from random copying that would be required to reject this model.

All these studies addressed the frequencies of discrete traits. Eerkens & Lipo [23] developed a similar approach to the characterization of neutral variation in continuous measurements and the measurement of departures from it. Studies of drift in discrete attributes have not addressed the processes that generate variation in those attributes, whether copying error or the intentional creation of, e.g. new decorative motifs, but have simply explored the effects of different innovation rates. In contrast, in the case of variation in continuous attributes there has been a focus on precisely what is involved in the generation of small errors and what the consequences are for the outcome of those errors over repeated transmission episodes, because in this case we have some knowledge about what the relevant processes are. Specifically, psychological studies have shown that below a certain

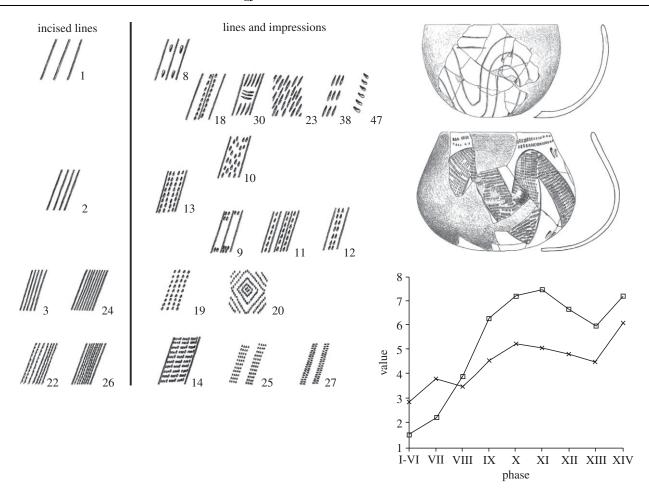


Figure 2. Plot of actual diversity (squares) and neutral predicted diversity (crosses) of the decorative variation on Early Neolithic ceramic vessels from a site in Germany against the sequence of chronological phases from the site (lower right). From phase IX onwards the diversity values are greater than those predicted by the neutral model. Examples of Early and Late vessels (upper right). The diversity values were calculated on the basis of the frequencies of the decorative motifs shown on the left. Adapted from Shennan & Wilkinson [18, fig. 4c]; Luening, J. & Stehli, P. 1994 Die bandkeramik im Merzbachtal auf der Aldenhovener platte. Bonn: Habelt, plates 6.3 and 29.7, pp. 207–394; Frirdich, C. 1994 kulturgeschichtliche betrachtungen zur bandkeramik im Merzbachtal, fig. 10, respectively.

threshold (the so-called Weber fraction), people are incapable of distinguishing differences in physical dimensions; the threshold is relative to the scale of the dimension. Thus, lines that are within 3 per cent of each other in terms of their length cannot be distinguished [23]. Over multiple transmission episodes, and assuming that no other processes are operating, the errors generated by this sub-perceptual copying error will accumulate, although the accumulation rate will gradually slow down (figure 3a). On the other hand, if individuals tend to conform to the mean of the population at any given transmission episode then the variation in the measurement concerned will reach an equilibrium level, with a range dependent on the strength of the conformity (figure 3b). Prestige bias also acts to reduce variation over repeated transmission episodes but its effects will vary depending on the proportion of individuals that are taken to be prestigious for the attribute in question [23]. The authors applied the theory to explaining variation in projectile point dimensions in the western US Owens Valley and in Illinois Woodland ceramic vessel diameters. They showed that drift was sufficient to explain the variation in projectile point thickness, but base width showed less variation than expected, so

some biasing process leading to a reduction in variation over time must have been operating while, in the case of the pottery vessel diameters, variation increasing mechanisms were at work.

Lycett & von Cramon-Taubadel [24] have recently also explored the use of continuous measurements to explore questions of drift. In just the same way as recent results have shown that genetic variation in modern human populations declines in a regular fashion with distance from east Africa as a result of serial bottle-necking or founder effects [25], they postulated that there should be similar effects on variation in the dimensions of Acheulean handaxes if the main factor affecting them was drift as populations of handaxe uses spread out of Africa. Their results indicated that handaxe variation did indeed decrease in the manner predicted.

Recently, Hamilton & Buchanan [26] have used both these approaches in an analysis of the role of drift in affecting variation in the dimensions of the projectile points of early hunter—gatherers in North America. They showed that over time accumulated copying error (ACE) in a given dimension as a result of the Weber fraction will lead to a decrease in the mean of the dimension concerned because smaller

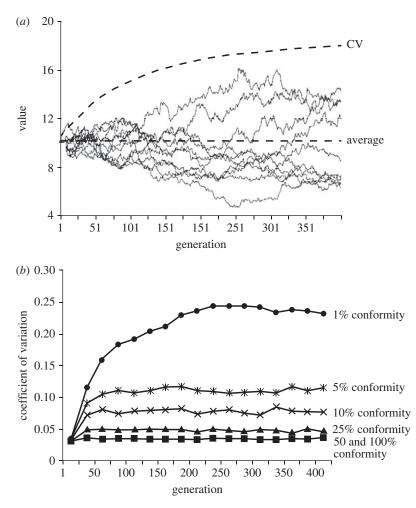


Figure 3. (a) Results of simulations of 10 transmission chains of a continuous measurement with sub-perceptual error at each transmission step, under conditions of unbiased transmission, showing the mean and the coefficient of variation (CV). (b) The effect of different intensities of conformist transmission. Here, the data points represent average CV values calculated over 10 simulations. Adapted from Eerkens & Lipo [23, figs 1 and 2].

values will be copied with less error, as the errors are proportional rather than absolute, while larger values will be copied with greater error and sometimes that error will be in the direction of smaller values; the variance, however, will increase through time in a linear fashion. They then investigated the effect of introducing biased transmission into the system, for example, that generated by copying the most prestigious individual available or conformist copying of the local mean. They show that whereas these biases and ACE have no effect on the mean, which still decreases with the number of copying episodes, they do have an effect on the variance, which increases to a limit determined by the strength of the bias and then stabilizes. They went on to examine the role of both founder effects, indicated as above by changes in within-assemblage variation, and ACEs in accounting for variation in the sizes of Clovis-type projectile points through time. Time was measured by using radiocarbon dates.

They found no evidence of multiple founder effects in this case but did find that the mean size of projectile points decreased through time and that the variance in size was constant, suggesting that the key factor affecting the size of the points was strongly biased transmission with ACE. They noted that a decrease in mean point size over time greater than that expected by drift, or any increase in size, would be indicative of directional selection.

Clearly, in all these studies, the key issue is to have strong methods for distinguishing the effects of different processes and few if any of the studies described above have really attempted to do this in a rigorous fashion. This point has been developed in a recent paper by Steele et al. [27]. In the case of the discrete trait drift models, for example, they point out that if the standard methods are being used it is important to be sure that the system being studied is at mutation-drift equilibrium, otherwise it cannot be assumed that apparent departures from drift are real. More generally, they argue that simply comparing an empirical to a theoretically based frequency distribution is insufficient even when it is done using an appropriate statistical test, and earlier work by and large has not even done that. It is necessary, they argue, to go further and consider the effects of other variables that there are grounds for thinking might be having at least some influence on the distribution in question. The authors develop this argument through an analysis of the factors affecting the frequency distribution of different rim shapes in ceramic bowls from the Hittite Bronze Age capital of Bogazkov. They found that although statistical tests on the diversity of rim types did not indicate a departure

from neutrality, in fact the frequency of different types was affected by the functionally significant variable of ware type—the coarseness of the vessel fabric—which was influencing potters' decision making. They also found a trend in bowl sizes that did not correspond to the ACE model described above. This was not revealed by simply testing for the departure of the bowl rim frequency distribution from neutrality, which did not produce a statistically significant result.

This example brings home the point that the real issue in most cases of trying to understand the factors affecting variation in archaeological assemblages is less likely to be the question of whether the variation is neutral or not, but what is the relative importance of various selective and stochastic factors in accounting for it. The way this can be done has been shown by Brantingham [28] using the Price equation, on the basis of a study of variation in the relative frequency of ceramic decoration in an artificial dataset where different households in a village decorate their ceramics with different frequencies. He distinguishes payoff-correlated from payoffindependent variations, corresponding to 'functional' and 'stylistic' variation, respectively, where the functional aspect of decoration could refer, for example, to social benefits to be gained by conforming to the usage of the local majority or penalties for not conforming. Stylistic, or non-functional, variation might arise, on the other hand, as a result of copying errors in producing the correct proportion of decorated vessels, or individual experimentation.

As Brantingham describes, on the assumption that any real process of change potentially involves an aspect related to payoffs and an aspect that is payoff independent, an equation can be written bringing the two together. Thus, in the case of his artificial example,

$$p_i^t z_i^t = p_i rac{W_i}{W} (z_i + \delta_i),$$

where p_i is the proportion of all vessels made by household i in the previous time step, z_i is the relative frequency of ceramic decoration in household i, w_i is the payoff to household i, given ceramic decoration at proportional frequency z_i , w is the mean payoff to all households given a mean proportion of ceramic decoration, δ_i is the stochastic fluctuation in the frequency of decoration in household i, the equation states that the contribution of household i to the new frequency of ceramic decoration at the next time step, depends on change in its contribution to the total number of vessels from the previous step, which is payoff related, and in the frequency with which the vessels are decorated. He goes on to show that the general formula for the total evolutionary change in the frequency of ceramic decoration (Δz) corresponds to the sum of payoff-related and payoff-independent variations as given by the Price equation:

$$\Delta z = ext{COV}\Big(rac{w_i}{w}, z_i\Big) + E(\delta_i),$$

where COV $(w_i/w, z_i)$ is the covariance between the relative payoffs and relative frequency of decorated ceramics, the functional variation and $E(\delta_i)$ is the expected value of stochastic fluctuations in the relative frequency of ceramic variation, the stylistic variation.

As Brantingham points out, this formulation, in which change in any given attribute over time can be affected to different degrees by both functional and stylistic variation, contradicts Dunnell's argument that style and function are mutually exclusive.

The implications of the approach are then illustrated by analysis of a simulated dataset made up of 50 households, with 2000 pottery-making generations, a small positive payoff to decorating vessels (β = 0.005) and a very slight tendency ($\mu = 0.0001$) for the variation introduced in each generation to increase the proportion of decorated vessels, the two relevant parameters for the Price equation. Analysis of the frequency patterns in the data generated by the simulations recovered the known payoff value and the value for novel variation introduced in each generation with a high degree of accuracy, confirming the potential for inferring the strength and nature of functional and stylistic processes from real archaeological data. The Price equation method has now been taken further by Brantingham & Perreault [29].

4. THE EVOLUTION OF COMPLEX TECHNOLOGIES

The examples above have been largely concerned with distinguishing drift from other evolutionary forces in the case of situations where we have very little information about the specific goals the makers and users of the artefacts were trying to achieve and the relevant constraints, except for our knowledge of the Weber fraction and its implications in the case of continuous measurements. In cases where we know a lot more about these goals and constraints, hypotheses can be more closely framed and at least in principle more readily tested. Recently, Charlton and colleagues [30,31] have taken an evolutionary approach to understanding ironsmelting technology in a case study from northwest Wales. Here, there can be no doubt about the goal (at least in general terms) and the conditions required to successfully smelt iron are well understood, arising as they do from universal properties of the materials involved.

Once again though, the issue is first to identify patterns of cultural descent in the methods used and to distinguish variation arising from transmission from that relating, for example, to the local ore or fuel type; and then to characterize the forces affecting that variation, in a situation where, by the very nature of the process there are only a limited number of successful solutions. The most informative source of information on the processes involved in past episodes of early iron production is chemical variation in the slags produced as a waste product. In this case then the data are quantitative variations in the chemistry of chronologically ordered slag deposits and the inverse problem is as above: can we establish whether or not there is a signal of cultural descent in the chemical variation; if so, what can we infer about the factors affecting transmission processes that produced it?

Charlton [30] showed convincingly that a transmission signal could be identified. In terms of the forces acting on the technical knowledge and practices passed on from one iron producer to another, it is easy to imagine that there might be some more or less

random variation in exactly what was done each time. It is also likely that there would be strong selection for those practices that were successful, though, given the complexity of the process and its many stages, it would not necessarily be easy to identify precisely what produced a successful smelt on any given occasion. From the point of view of the agents, it is thus likely that transmission would be affected by results bias; from the point of view of the smelting recipes, this would be a process of natural selection, since recipes would be differentially reproduced depending on their ability to successfully smelt iron. The results of Charlton et al. [31] showed that all changes related to furnace operation could be accounted for by a drift process but that at a certain point a second effective procedure was more or less accidentally discovered and a decision was taken to use make use of the two distinct procedures, visible in different slag signatures (figure 4). At the same time, there were clear trends in the use of manganese-rich ores with better fluxing capabilities, and evidence of decreased variability in reducing conditions related to results bias: that is to say the iron makers consistently reproduced the airflow conditions that gave the best results for a given recipe. Ore variability, on the other hand, did not decrease through time and probably simply reflects the properties of the bog ore available.

5. DRIFT, DEMOGRAPHY AND THE ADAPTIVE **ROLE OF CULTURE**

Most of the work described above has focused on looking for evidence of pure drift or departures from it, and considering the implications for the processes believed to be operating in particular cases, but there has been another strand of more theoretical work which has considered the implications of drift or sampling processes under different demographic conditions. Even in cases where selection or bias are strong in principle they can be overwhelmed by the effects of chance if the effective size of the relevant population is very small. If some functionally useful knowledge, for example, is only held by a small number of old men and they all die suddenly in a disease outbreak, the knowledge will be lost regardless of its usefulness. This phenomenon has been known since the earlier twentieth century [32].

Shennan [33] suggested that this sort of process might be relevant to explaining why so-called modern human symbolic culture might have taken so long to appear on a large scale after the emergence of anatomically modern humans ca 200 ka. Some of its characteristics appear and disappear sporadically in Africa over a long period but it does not appear to take off on a large scale anywhere until after 50 ka, when there is both genetic and archaeological evidence for major population increase. Shennan argued that this was a result of population levels being kept low by adverse climate conditions in Africa. On the basis of a genetic model [34], modified to include oblique transmission of cultural traits, he showed by simulation that larger populations can evolve to a higher average fitness than smaller ones because they carry a smaller drift load of deleterious cultural traits. Subsequently, Powell et al. [35] used an analytical model created by Henrich [36] to address the same issue

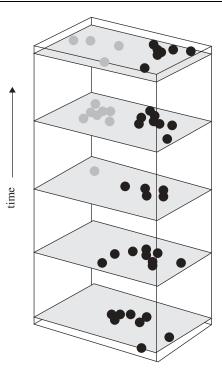


Figure 4. Chemistry of slags from the medieval Welsh ironsmelting site of Llwyn Du projected into PC space and arranged in stratigraphic order. Group 1 slag is plotted in dark grey and group 2 slag is plotted in light grey. The two groups are close to two distinct optima for successful iron production under different smelting conditions. Adapted from Charlton et al. [31, fig. 4].

(figure 5). On this model, individuals learn a new skill by attempting to copy the best individual of the senior generation in their group. Most people are not as good as the best, reflected in the group modal value for the skill. However, there will always be some random variation between the individuals in their attempts to innovate and occasionally someone may exceed the current best. This will then become the example to follow, and as a result, even though most people are not as good as the best, the modal value will be pulled in a positive direction. However, the probability of exceeding the current best depends on the cultural effective population size. If population size decreases then no one in the new generation may even match the current best so the maximum level of achievement will decline. Powell et al.'s simulation based on this model showed that greater population densities or increased migration rates between groups would lead to the kind of cultural accumulation that modern human symbolic culture represents (cf [37]; figure 6). Kline & Boyd [38] have shown that there is ethnographic evidence for the predictions of this model in Polynesia, with larger/well-connected islands having more complex technologies than smaller ones (though contrast [39]).

6. DISCUSSION

It has taken a long time to start developing methods of empirical data analysis to solve the inverse problem of making inferences from archaeological frequency distributions in order to arrive at explanations of their form and inter-relationships in terms of cultural

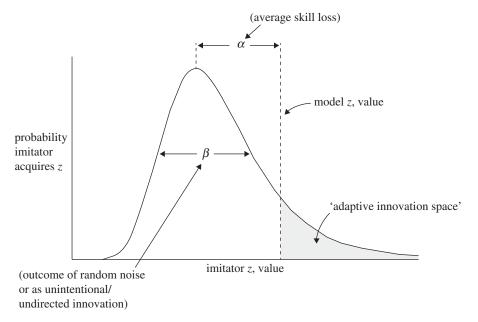


Figure 5. Henrich's model for result-biased transmission with error using the Gumbel distribution. Adapted from Henrich [36, fig. 1].

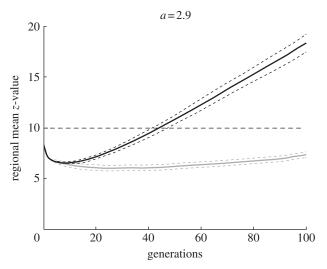


Figure 6. Simulated regional mean z-values (averaged over 100 iterations) over 100 generations in a world containing randomly distributed groups at a given density, divided into two halves, one with a high and one with a low migration rate, but with no barrier between them. The 95% CI for each region are given as dotted lines. Msd is the migratory range expressed as a proportion of the mean nearest neighbour distance. Black line, Msd = 1; light grey line, Msd = 0.1. Adapted from Powell $et\ al.\ [35, fig.\ S2].$

evolutionary processes, and it seems reasonable to suggest that the work has barely begun. For example, it can be argued that the methods described here are much more appropriate for cases where a reasonably high degree of chronological resolution is available, likely to be more frequent in more recent periods. Thus, Richerson & Boyd [40] have expressed some doubt about attempting to fit micro-evolutionary models of process to archaeological data given their normally coarse chronological resolution and the lack of information available for parametrizing such models, and in particular about using a 'null' model of drift as a starting point, since other more complex models might well give the same result. They point

out that what appears as drift may simply be the result of short-term selection pressures that push in opposite directions from one short time period to the next, and thus are not resolvable. This is certainly true but it is questionable how much distinguishing 'real' drift from 'pseudo' drift matters, certainly when data are available that have a human-generation level of resolution. What matters is identifying the presence of selection/bias forces pushing the choices people make in some consistent direction over time, and attempting to explain them. Similarly, they argue that it is better to build models incorporating theoretical concepts, for example, 'neophilia', a preference for things that are slightly different, in the stylistic sphere. However, there are dangers in rather vague concepts like this, whose values could potentially be finetuned to fit whatever pattern we find. The view taken here is that we are better off obtaining estimates of innovation rates from our data. As always, it is certainly true that the more information we have in any given case and the more we have independent grounds for inferring the probable selection pressures operating, as in the case of iron production, the better our models are likely to be. Equally, the cumulative development of the methods described in this paper offers increasing potential for distinguishing the role of different evolutionary forces. Finally, it is becoming increasingly clear that demographic factors play an important role in the processes discussed in this paper and that if we can obtain independent evidence of prehistoric demographic patterns we will be in a much better position to build models that are appropriate for particular cases.

REFERENCES

- 1 Cavalli-Sforza, L. L. & Feldman, M. W. 1981 *Cultural transmission and evolution: a quantitative approach.* Princeton, NJ: Princeton University Press.
- 2 Boyd, R. & Richerson, P. J. 1985 Culture and the evolutionary process. Chicago, IL: University of Chicago Press.

- 3 Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. Evol. Anthropol. 12, 123-135. (doi:10. 1002/evan.10110)
- 4 Henrich, J., Boyd, R. & Richerson, P. J. 2008 Five misunderstandings about cultural evolution. Hum. Nat. 19, 119-137. (doi:10.1007/s12110-008-9037-1)
- 5 Bettinger, R. L. & Eerkens, J. 1999 Point typologies, cultural transmission, and the spread of bow-and-arrow technology in the prehistoric Great Basin. Am. Antiq. 64, 231-242. (doi:10.2307/2694276)
- 6 Feldman, M. W. & Cavalli-Sforza, L. L. 1989 On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In Mathematical evolutionary theory (ed. M. W. Feldman), pp. 145-173. Princeton, NJ: Princeton University Press.
- Dawkins, R. 1976 The selfish gene. Oxford, UK: Oxford University Press.
- Dennett, D. C. 1995 Darwin's dangerous idea: evolution and the meanings of life. London, UK: Allen Lane.
- Rogers, D. S. & Ehrlich, P. R. 2008 Natural selection and cultural rates of change. Proc. Natl Acad. Sci. USA 105, 3416-3420. (doi:10.1073/pnas.0711802105)
- Dunnell, R. C. 1978 Style and function: a fundamental dichotomy. Am. Antiq. 43, 192–202. (doi:10.2307/279244)
- Shennan, S. J. 2008 Evolution in archaeology. Annu. Rev. Anthropol. 37, 75-91. (doi:10.1146/annurev. anthro.37.081407.085153)
- 12 O'Brien, M. J. & Lyman, R. L. 2000 Applying evolutionary archaeology. New York, NY: Plenum.
- 13 Lyman, R. L. & O'Brien, M. J. 2006 Seriation and cladistics: the difference between anagenetic and cladogenetic evolution, 2006. In Mapping our ancestors: phylogenetic approaches in anthropology and prehistory (eds C. P. Lipo, M. J. O'Brien, M. Collard & S. J. Shennan), pp. 65-88. New Brunswick, NJ: AldineTransaction.
- 14 Huester-Plogmann, H., Schibler, J. & Steppan, K. 1999 The relationship between wild mammal exploitation, climatic fluctuations, and economic adaptations. A transdisciplinary study on Neolithic sites from Lake Zurich region, Southwest Germany and Bavaria. In Historia animalium ex ossibus. Festschrift für Angela von den Driesch (eds C. Becker, H. Manhart, J. Peters & J. Schibler), pp. 189-200. Rahden, Germany: Verlag Marie Leidorf.
- 15 Binford, L. R. 1963 'Red Ocher' caches from the Michigan area: a possible case of cultural drift. Southwest 7. Anthropol. 19, 89–108.
- 16 Neiman, F. D. 1995 Stylistic variation in evolutionary perspective: inferences from decorative diversity and inter-assemblage distance in Illinois Woodland ceramic assemblages. Am. Antiq. 60, 7-36. (doi:10.2307/282074)
- 17 Ewens, W. J. 1972 The sampling theory of selectively neutral alleles. Theor. Popul. Biol. 3, 87-112. (doi:10. 1016/0040-5809(72)90035-4)
- 18 Shennan, S. J. & Wilkinson, J. R. 2001 Ceramic style change and neutral evolution: a case study from Neolithic Europe. Am. Antiq. 66, 577-593. (doi:10.2307/ 2694174)
- 19 Kohler, T. A., VanBuskirk, S. & Ruscavage-Barz, S. 2004 Vessels and villages: evidence for conformist transmission in early village aggregations on the Pajarito Plateau, New Mexico. J. Anthropol. Archaeol. 23, 100-118. (doi:10. 1016/j.jaa.2003.12.003)
- 20 Bentley, R. A., Hahn, M. W. & Shennan, S. J. 2004 Random drift and culture change. Proc. R. Soc. Lond. B 271, 1443-1450. (doi:10.1098/rspb.2004.2746)
- 21 Mesoudi, A. & Lycett, S. J. 2009 Random copying, frequency-dependent copying and culture change. Evol. Hum. Behav. 30, 41-48. (doi:10.1016/j.evolhumbehav. 2008.07.005)

- 22 Bentley, R. A. & Shennan, S. J. 2003 Cultural evolution and stochastic network growth. Am. Antiq. 68, 459-485. (doi:10.2307/3557104)
- 23 Eerkens, J. W. & Lipo, C. P. 2005 Cultural transmission, copying errors, and the generation of variation in material culture in the archaeological record. J. Anthropol. Archaeol. 24, 316-334. (doi:10.1016/j.jaa.2005.08.001)
- 24 Lycett, S. J. & von Cramon-Taubadel, N. 2008 Acheulean variability and hominin dispersals: a model-bound approach. J. Archaeol. Sci. 35, 553-562. (doi:10.1016/j. jas.2007.05.003)
- 25 Liu, H., Prugnolle, F., Manica, A. & Balloux, F. 2006 A geographically explicit genetic model of worldwide human-settlement history. Am. J. Hum. Genet. 79, 230-237. (doi:10.1086/505436)
- 26 Hamilton, M. J. & Buchanan, B. 2009 The accumulation of stochastic copying errors causes drift in culturally transmitted technologies: quantifying Clovis evolutionary dynamics. J. Anthropol. Archaeol. 28, 55-69. (doi:10.1016/j.jaa.2008.10.005)
- 27 Steele, J., Glatz, C. & Kandler, A. 2010 Ceramic diversity, random copying, and tests for selectivity in ceramic production. J. Archaeol. Sci. 37, 1348-1358. (doi:10.1016/j.jas.2009.12.039)
- 28 Brantingham, P. J. 2007 A unified evolutionary model of archaeological style and function based on the Price equation. Am. Antiq. 72, 395-416. (doi:10.2307/ 40035853)
- 29 Brantingham, P. J. & Perreault, C. 2010 Detecting the effects of selection and stochastic forces in archaeological assemblages. J. Archaeol. Sci. 37, 3211-3225. (doi:10. 1016/j.jas.2010.07.021)
- 30 Charlton, M. F. 2009 Identifying iron production lineages: a case-study in north-west Wales. In Pattern and process in cultural evolution (ed. S. J. Shennan), pp. 133-144. Berkeley, CA: University of California Press.
- 31 Charlton, M. F., Crew, P., Rehren, T. & Shennan, S. J. 2010 Explaining the evolution of ironmaking recipesan example from northwest Wales. J. Anthropol. Archaeol. **29**, 352–367. (doi:10.1016/j.jaa.2010.05.001)
- 32 Rivers, W. H. R. 1926 Psychology and ethnology. London, UK: Kegan Paul, Trench, Trubner.
- 33 Shennan, S. J. 2001 Demography and cultural innovation: a model and some implications for the emergence of modern human culture. Camb. Archaeol. J. 11, 5-16.
- 34 Peck, J. R., Barreau, G. & Heath, S. C. 1997 Imperfect genes, Fisherian mutation and the evolution of sex. Genetics 145, 1171-1199.
- 35 Powell, A., Shennan, S. J. & Thomas, M. G. 2009 Late Pleistocene demography and the appearance of modern human behavior. Science 324, 1298-1301. (doi:10. 1126/science.1170165)
- 36 Henrich, J. 2004 Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. Am. Antiq. 69, 197-214. (doi:10. 2307/4128416)
- 37 d'Errico, F. & Stringer, C. B. 2011 Evolution, revolution or saltation scenario for the emergence of modern cultures? Phil Trans R. Soc. B 366, 1060-1069. (doi:10. 1098/rstb.2010.0340)
- 38 Kline, M. A. & Boyd, R. 2010 Population size predicts technological complexity in Oceania. Proc. R. Soc. B 277, 2559–2564. (doi:10.1098/rspb.2010.0452)
- Collard, M., Buchanan, B., Morin, J. & Costopoulos, A. 2011 What drives the evolution of hunter-gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. Phil. Trans. R. Soc. B 366, 1129–1138. (doi:10.1098/rstb.2010.0366)
- 40 Richerson, P. J. & Boyd, R. 2008 Response to our critics. Biol. Phil. 23, 301-315. (doi:10.1007/s10539-007-9084-8)