Effective population and phenotype-genotype decoupling in cultural evolution

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Although the attempt of sociobiology to provide a unified account of human biological and cultural evolution foundered on the sheer plasticity of human behaviour, subsequent attempts to rescue the relevance of evolutionary biology for the study of cultural phenomena have proved fruitful. A—perhaps the—major driver of this success has been the development of dual inheritance models (Boyd and Richerson 1985) that explicitly acknowledge the operation of both genetic and non-genetic inheritance in human sociocultural evolution. The development of such models has come about through, on the one hand, a willingness to apply Darwinian "population thinking" to social and cultural phenomena and, on the other, the recognition that biological genetic evolution is but one specific example of a more general 'algorithm' applicable to several domain beyond biology (Hull, 1982; Dennett, 1995).

Nevertheless, there remains considerable debate about whether cultural change is an evolutionary process operating on the same kinds of functional entities (replicators, interactors and lineages), or whether it is simply an analogous process. A common refrain in the debate about the status of cultural change as an evolutionary process, voiced by biologists and social scientists (Gould, 1987), is that if cultural change is evolutionary then it is Lamarckian rather that Darwinian. None of the protagonists believe that cultural evolution is literally Lamarckian in the sense that acquired cultural characteristics might somehow become encoded in genetic material. Rather, the question arises out of uncertainty surrounding what is genotypic and what is phenotypic in purely cultural evolution (e.g. Lake 1998). Indeed, in the case of the evolution of material culture, objects are often conceived as phenotypic expressions of genotypic ideas, but there may well be circumstances in which they actually function as cultural genotypes or even conflate both functions (Lake 1998).

Although the genotype-phenotype distinction in material culture is philosophically interesting, the question we address in this paper is essentially pragmatic: does the uncertainty surrounding the physical permanence of material culture actually matter for the application of models derived from evolutionary biology? We seek to explore potential implications of this phenomena for the application of one particular model that has been widely adopted for the study of cultural evolution:the neutral allele theory (Kimura, 1983). Originally developed in population genetics, its flexible and broad mathematical basis can serve as a null model for a variety of applications, including circumstances where the frequency of cultural variants change as a function of innovation rate and unbiased copying processes. The latter implies that variants are

replicated without any particular selective pressure, and random events associated with sampling errors can lead to the spread or loss of knowledge.

Archaeological applications of this null hypothesis produced a variety of results. Some exhibit empirical patterns predicted by the neutral model (e.g. Bentley et al. 2004), while others suggest the effect of systematic social choices or biases (e.g. Shennan and Wilkinson 2001). Premo (2014) has however demonstrated that techniques developed to identify neutrality are not necessarily capable of identifying unbiased cultural transmission in samples collected from time-averaged archaeological assemblages.

In this paper we argue that there is potentially another problem with using the standard biological neutral model to detect the emergence of systematic preferences in the evolution of material culture, i.e the possibility that the effective population of cultural models is the number of artefacts in circulation rather than the number of people producing them. In addition, considering the differential durability of material culture, it is also possible that this number includes artefacts created by previous generations of producers. The first issue was noted by Shennan and Wilkinson (2001). As we are aware there have been explorations of the concept of memory in language evolution (Bentley et al. 2011), but there are no formal studies concerning the consequences of the persistence of material culture on the application of the neutral model.

In order to investigate this problem we develop a simulation model where standard unbiased cultural transmission has been modified to incorporate a 'production' and a 'persistence' bias. Rather than formalising knowledge transfer as an individual-to-individual process, we build a model where individuals update their 'genotype' by copying from objects produced by other agents. This slight change in the model introduces two new mechanisms: the expression of the phenotype might be affected by stochastic events ('production bias'), and objects might persist in the physical world for a given amount of time, potentially outliving their creator/genotype ('persistence bias'). We generate a series of artificial archaeological records to examine whether these two biases modify the result of tests commonly used to detect neutrality in cultural datasets (Slatkin's Exact test and Ewens-Watterson homozygosity test). Preliminary results suggest that this is the case, with the frequency of cultural variants showing significantly greater diversity than expected according to the standard neutral model. Our result thus indicates that in the presence of production and persistence bias there is a higher chance of incorrectly rejecting the null hypothesis of random copying/neutral cultural transmission.

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