

Cultural niche construction and human evolution

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Abstract

Organisms frequently choose, regulate, construct and destroy important components of their environments, in the process changing the selection pressures to which they and other organisms are exposed. We refer to these processes as niche construction. In humans, culture has greatly amplified our capacity for niche construction and our ability to modify selection pressures. We use gene-culture coevolutionary models to explore the evolutionary consequences of culturally generated niche construction through human evolution. Our analysis suggests that where cultural traits are transmitted in an unbiased fashion from parent to offspring, cultural niche construction will have a similar effect to gene-based niche construction. However, cultural transmission biases favouring particular cultural traits may either increase or reduce the range of parameter space over which niche construction has an impact, which means that niche construction with biased transmission will either have a much smaller or a much bigger effect than gene-based niche construction. The analysis also reveals circumstances under which cultural transmission can overwhelm natural selection, accelerate the rate at which a favoured gene spreads, initiate novel evolutionary events and trigger hominid speciation. Because cultural processes typically operate faster than natural selection, cultural niche construction probably has more profound consequences than gene-based niche construction, and is likely to have played an important role in human evolution.

Introduction

The relationship between genetic evolution and culture raises two causal issues. The first, which addresses the extent to which contemporary human cultures are constrained or directed by our biological evolutionary heritage, has been subject to intense investigation, and has spawned disciplines such as human sociobiology, human behavioural ecology, and evolutionary psychology. The second, which concerns whether hominid genetic evolution has itself been influenced by cultural activities and has received much less attention. Yet empirical data and theoretical arguments suggest that

human cultural activities have influenced human genetic evolution by modifying sources of natural selection and altering genotype frequencies in some human populations (Bodmer & Cavalli-Sforza, 1976; Durham, 1991; Feldman & Laland, 1996). Cultural traits such as the use of tools, weapons, fire, cooking, symbols, language and trade may also have played important roles in driving hominid evolution in general, and the evolution of the human mind in particular (Holloway, 1981; Dunbar, 1993; Aiello & Wheeler, 1995).

Here we use evolutionary models to explore the interactions between biological and cultural change. Our analyses are designed to address issues such as the circumstances under which the cultural transmission of traits can overwhelm prior natural selection, affect the rate of biological evolution, initiate novel evolutionary scenarios and trigger speciation events. Relative to many

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other organisms, hominids had an extraordinary capacity to modify their local selective environments. Their ability to learn relevant skills and knowledge from others may have left hominids particularly prone to influencing their own evolution. Cultural processes typically operate faster than natural selection, which is also likely to have amplified the impact of hominids on their environments. This analysis leads us to the conclusion that the significance of evolutionary theory to the human sciences cannot be fully appreciated without a more complete understanding of how human beings and their ancestors modified significant sources of natural selection in their environments, thereby codirecting subsequent biological evolution.

Niche construction

It is increasingly recognized that countless organisms across all known taxonomic groups significantly modify their local environments (Lewontin, 1983; Hansell, 1984; Odling-Smee, 1988; Jones *et al.*, 1994, 1997; Laland *et al.*, 1996, 1999; Odling-Smee *et al.*, 1996). Organisms regularly choose and consume resources, generate detritus, construct and destroy important components of their own environments (such as nests, holes, burrows, paths, webs, pupal cases and chemical environments), and choose, protect and provide 'nursery' environments for their offspring (Lewontin, 1983; Odling-Smee, 1988). We have referred to these processes as 'niche construction' (Odling-Smee, 1988; Laland *et al.*, 1996, 1999; Odling-Smee *et al.*, 1996) but they are elsewhere described as 'ecosystem engineering' (Jones *et al.*, 1994, 1997). Following Lewontin (1983), we argue that organisms not only adapt to environments but in part also construct them. They may also do so across a huge range of temporal and spatial scales stretching, for example, from a hole bored in a tree by an insect to the contribution of cyanobacteria to the earth's oxygen atmosphere, as a consequence of millions of years of photosynthesis (Odum, 1989). Niche construction is of evolutionary significance because, through their niche construction, organisms modify the natural selection pressures to which they and their descendants are exposed (Laland *et al.*, 1996, 1999).

Niche construction by both past and present generations may influence a population's selective environment. For instance, spider's webs and insect pupal cocoons modify the selective environments of the constructors themselves, whereas bird's nests or female insect's oviposition site choices, also influence the environment of the constructor's descendants. The latter cases are examples of ecological inheritance, where an organism experiences a modified functional relationship between itself and its environment as a consequence of the niche-constructing activities of either its genetic or ecological ancestors (Odling-Smee, 1988). Related theoretical work on cultural inheritance, maternal inheri-

tance and indirect genetic effects support the suggestion that ecological inheritance is likely to be of evolutionary interest (Feldman & Cavalli-Sforza, 1976; Kirkpatrick & Lande, 1989; Moore *et al.*, 1997).

Our earlier investigations of niche construction were not human orientated and did not explicitly investigate the consequences of cultural niche construction, but rather of niche construction in general. We used two-locus population genetics models, explored the joint evolutionary dynamics of environment-altering niche-constructing traits and other traits whose fitness depends on feedback from natural selection in environments affected by the niche construction. We began with the simplest case in which the frequency of a resource in the environment depended exclusively on the niche-constructing activities of a population as represented by the frequencies of alleles at a first locus, and this resource influenced selection acting on the population through the selection of alleles at a second locus (Laland *et al.*, 1996). We extended this analysis with a model that allowed the frequency of the resource to be influenced by varying mixes of both the population's niche-constructing activities and other independent environmental processes, which are partly responsible for the renewal or depletion of the same resource (Laland *et al.*, 1999). Together, these analyses suggest that the changes the organisms bring about in their own selective environments may substantially modify natural selection pressures and can generate some novel evolutionary outcomes. For example, niche construction can cause evolutionary inertia and momentum, lead to the fixation of otherwise deleterious alleles, support stable polymorphisms where none are expected and eliminate what would otherwise be stable polymorphisms.

Although niche construction is a general process, few species have modified their selective environment to the same extent as humans. It is now well recognized that phenotypic plasticity can play an instrumental role in the evolutionary process (Schlichting & Pigliucci, 1998) and that the human capacity for niche construction has been further amplified by culture (West-Eberhard, 1987; Bateson, 1988; Plotkin, 1988; Wcislo, 1989). Human innovation and technology has had an enormous impact on the environment: it has made many new resources available via both agriculture and industry; it has influenced human population size and structure via hygiene, medicine and birth control; it is drastically reducing bio-diversity; and it may already have resulted in the degradation of large areas of our global environment. These are all potential sources of modified natural selection pressures. Thus cultural processes that precipitate niche construction might be expected to have played a critical role in human evolution for many thousands, perhaps millions of years.

Culture works on the basis of various kinds of transmission systems (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985) that collectively provide

humans with an extra-genetic 'knowledge-carrying' inheritance system. If the cultural inheritance of an environment-modifying human activity persists for enough generations to generate a stable natural selection pressure, it will be able to influence human genetic evolution. The culturally inherited traditions of pastoralism provide an example. The persistent domestication of cattle and the associated dairying activities may have altered the selective environments of some human populations for sufficient generations to select for genes which today confer greater adult lactose tolerance (Aoki, 1986; Feldman & Cavalli-Sforza, 1989; Durham, 1991).

Gene-culture coevolution

Several evolutionary biologists have previously stressed that culture frequently does affect the evolutionary process through modifying natural selection pressures. This has led to the development of mathematical and conceptual models of gene-culture coevolution that involve descriptions not only of how human genetic evolution influences culture but also of how human culture can drive at least some genetic changes in human populations (Feldman & Cavalli-Sforza, 1976; Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Durham, 1991; Feldman & Laland, 1996). Genetic and cultural transmission systems frequently cannot be treated as independent because what an individual learns may depend on its genotype and the selection acting on genes may be generated or modified by the spread of a cultural practice. Models of this dual transmission have been employed to examine the adaptive advantages of learning and culture, investigate the processes of cultural change, partition the variance in complex human behavioural and personality traits and address specific cases in human evolution in which there is an interaction between genes and culture (see Feldman & Laland, 1996 for a review). Gene-culture coevolutionary models have also established the plausibility of a cultural group selection hypothesis (Cavalli-Sforza & Feldman, 1973; Boyd & Richerson, 1985). The common element among these cases is that cultural processes change the human selective environment and thereby affect which genotypes survive and reproduce.

To-date, all gene-culture coevolutionary models have assumed that the selection generated by cultural activities is a simple function of the frequency of the cultural trait in the population. Most commonly, it is assumed that the intensity of selection is directly proportional to the frequency of the cultural trait. Whereas this is generally a reasonable assumption for those systems to which the models have been applied, there are some obvious cases in which the assumption is violated. For example, in Kwa-speaking yam cultivators of West Africa, the frequency of an allele of the haemoglobin locus that causes sickle-cell disease increased as a result of the indirect effects of yam cultivation. These people

traditionally cut clearings in the rainforest, creating more standing water and increasing the breeding grounds for malaria-carrying mosquitoes. This, in turn, intensifies selection for the sickle-cell allele because of the protection offered by this allele against malaria in the heterozygous condition (Durham, 1991). Here the causal chain is so long that simply plotting the prevalence of the cultural trait of yam cultivation against the frequency of the sickle-cell allele would be insufficient to yield a clear relationship between the cultural trait and allele frequencies (Durham, 1991). The crucial variable is probably the amount of standing water in the environment caused by the yam cultivation, but standing water is an ecological variable and not a cultural variable and partly depends on factors (i.e. rainfall) that are beyond the control of the population. So here the simplifying assumption of a direct link between cultural and genetic inheritance distorts reality too much to allow their interaction to be modelled in the standard way. The two human inheritance systems interact via an intermediate, abiotic and ecological variable which is required to complete the model (Laland *et al.*, 2000). This example is unlikely to be an exception, both because human modification of water conditions often also affects the transmission of various parasitic diseases (malaria, schistosomiasis, river blindness, etc.) that may exert selective pressures on the genes coding for functions of the immune system (Combes, 1995; Klein, 1997), and because there are countless other ways in which humans have modified their selective environments.

Given that cultural inheritance can result in patterns of trans-generation transmission that differ from genetic inheritance and may operate on different time-scales, it is pertinent to ask how culturally generated niche construction may affect genetic evolution. Here we present the results of two gene-culture coevolutionary models that explore the evolutionary consequences of culturally transmitted niche construction. The two models presented here are gene-culture analogues of the simple genetic model (Laland *et al.*, 1996) and the more complex genetic and ecological model (Laland *et al.*, 1999) that we have previously developed to explore the evolutionary consequences of gene-based niche construction.

Models

Consider a population of humans or human ancestors capable of the cultural transmission of information from one generation to the next. Individuals express a culturally transmitted trait, which we call **E**, with two states *E* and *e*, representing the presence or absence (or greater or lesser impact) of a socially learned niche-constructing behaviour. We assume that the population's capacity for cultural niche construction is a function of the frequencies of individuals expressing cultural trait *E* or *e*. This cultural niche constructing behaviour affects the amount of a resource, *R*, in the environment. Thus the frequency

Table 1 Fitnesses of individuals with cultural traits E or e , and genotypes AA , Aa and aa .

	E (α_1)	e (α_2)
AA (η_1)	$w_{11} = \alpha_1\eta_1 + \varepsilon R$	$w_{12} = \alpha_2\eta_1 + \varepsilon R$
Aa (1)	$w_{21} = \alpha_1 + \varepsilon\sqrt{R(1-R)}$	$w_{22} = \alpha_2 + \varepsilon\sqrt{R(1-R)}$
aa (η_2)	$w_{31} = \alpha_1\eta_2 + \varepsilon(1-R)$	$w_{32} = \alpha_2\eta_2 + \varepsilon(1-R)$

of R (where $0 < R < 1$) is a function of the amount of cultural niche construction over n generations (i.e. the frequency of cultural trait E), as well as other independent processes of resource recovery or resource dissipation. Genotypes at locus **A** (with alleles A and a) have fitnesses that are functions of the frequency with which the resource R is encountered by organisms in their environment. The three genotypes and two cultural states can be found in six possible combinations, namely, AAE , AAe , AaE , Aae , aaE , aae , which have frequencies z_1 - z_6 , respectively and fitnesses w_{ij} (given in Table 1). We shall use p to denote the frequency of allele A , and x that of trait E , where $p = z_1 + z_2 + (z_3 + z_4)/2$ and $x = z_1 + z_3 + z_5$. We assume that the population is isolated from other population, and that individuals mate randomly (i.e. independently of their genotype or cultural trait).

As in our earlier treatments, fitnesses are assumed to be functions of a fixed viability component and a frequency-dependent viability component. The fixed components (given by the α_i and η_i terms) represent selection from the external environment, i.e. independent of cultural niche construction. These are analogous to the fitnesses of genotypes in the standard two-locus multiplicative viability model (Bodmer & Felsenstein, 1967; Karlin & Feldman, 1970). The frequency-dependent components of the contribution to fitness of genotypes AA , Aa and aa are again functions of R , $\sqrt{R(1-R)}$ and $1-R$, respectively, chosen so that allele A will be favoured by this component of selection when the resource is common and allele a when it is rare. The coefficient of proportionality (ε) determines the strength of the frequency-dependent component of selection relative to the fixed-fitness component, with $-1 < \varepsilon < 1$. Positive values of ε represent cases where an increase in the amount of resource results in an increment in the fitness of genotypes containing allele A , whereas negative values of ε represent cases where an increase in R favours a . In this framework niche construction perturbs the standard multiplicative population genetic model and allows us to analyse and describe its effects relative to a comparatively well analysed body of theory.

As before, we define *positive* niche construction as phenotypic activities that increase the fitness of the niche-constructing organism, whereas negative niche construction refers to niche-constructing activities that

reduce an organism's fitness (Laland *et al.*, 1999). In our models, positive and negative niche construction, respectively, refer to processes that increase and deplete the frequency of a valuable resource, R . Positive niche construction corresponds to cases where $\lambda_2 > 0$ and $\gamma = 0$ in equation 1b, below and negative niche construction refers to cases where $\lambda_2 = 0$ and $\gamma > 0$ in eqn (1b). Model 1 will consider the simple case in which the amount of the resource is proportional to the amount of cultural niche construction over the previous n generations, or

$$R = (1/n) \sum_{j=t-n+1}^t x_j \quad (1a)$$

where x_j is the frequency of E in generation j . Model 2 considers a more complex and realistic R function, for which, in each generation, the amount of the resource at time t is given by

$$R_t = \lambda_1 R_{t-1} (1 - \gamma x_t) + \lambda_2 x_t + \lambda_3 \quad (1b)$$

where λ_1 is a coefficient that determines the degree of independent depletion (if $\lambda_1 = 1$, there is no independent depletion), λ_2 is a coefficient that determines the effect of positive niche construction (if $\lambda_2 = 0$, there is no positive niche construction influencing the amount of the resource), λ_3 is a coefficient that determines the degree of independent renewal (if $\lambda_3 = 0$, there is no independent renewal), and γ is a coefficient that determines the effect of negative niche construction (if γ is 0, there is no negative niche construction influencing the amount of the resource). We assume $0 < \lambda_1, \lambda_2, \lambda_3, \gamma < 1$, that $\lambda_1 + \lambda_2 + \lambda_3 = 1$ and that $\lambda_1, \lambda_2, \lambda_3$, and γ are constrained so that R lies between 0 and 1. For simplicity, we also assume that if $\lambda_2 > 0$ then $\gamma = 0$, and vice-versa, i.e. there is either positive or negative niche construction acting, but not both. The term $\lambda_1 R_{t-1}$ represents the proportion of the resource that remains from the previous generation after independent depletion, whereas $(1 - \gamma x_t)$ represents any further decay in R because of negative niche construction.

Vertical cultural transmission occurs according to standard rules (Cavalli-Sforza & Feldman, 1981), given in Table 2. In the following analyses we will focus on three special cases of cultural transmission. The first is unbiased transmission (given by $b_3 = 1$, $b_2 = b_1 = 0.5$,

Table 2 Cultural transmission parameters giving the probability that matings between individuals with cultural traits E or e will give rise to E or e offspring.

Matings	Offspring	
	E	e
$E \times E$	b_3	$1 - b_3$
$E \times e$	b_2	$1 - b_2$
$e \times E$	b_1	$1 - b_1$
$e \times e$	b_0	$1 - b_0$

$b_0 = 0$) where offspring adopt traits in direct proportion to their parents' cultural trait, and where transmission would not by itself change the frequency of the traits in the population. The second is biased transmission (given by $b_3 = 1$, $b_2 = b_1 = b$, $b_0 = 0$, with $b \neq 0.5$), where the offspring of mixed matings (i.e. father and mother exhibit different traits) preferentially adopt one of the traits over the other. The third we call incomplete transmission (given by $b_3 = 1 - \delta$, $b_2 = b_1 = b$, $b_0 = \delta$, where $\delta > 0$), where only some of the offspring of parents with the same trait adopt that trait.

Following reproduction, cultural transmission and selection six (pheno-genotype) recursions that describe the frequency of each combination of cultural trait and genotype in terms of their frequencies in the previous generation. However, for analytical convenience, these can be reduced to a more-tractable system of four allelo-phenotype recursions which give the frequency of alleles A and a among E and e individuals. The allelo-phenotype frequencies of AE , aE , Ae , ae are u_1 – u_4 , respectively, in the present generation, with u_1' – u_4' the corresponding frequencies in the next generation, and

$$\begin{aligned} W_{u_1'} &= [u_1^2 b_3 + u_1 u_3 (b_1 + b_2) + u_3^2 b_0] w_{11} \\ &\quad + [u_1 u_2 b_3 + (u_1 u_4 + u_2 u_3)(b_1 + b_2)/2 + u_3 u_4 b_0] w_{21} \\ W_{u_2'} &= [u_1 u_2 b_3 + (u_1 u_4 + u_2 u_3)(b_1 + b_2)/2 + u_3 u_4 b_0] w_{21} \\ &\quad + [u_2^2 b_3 + u_2 u_4 + (b_1 + b_2) + u_4^2 b_0] w_{31} \\ W_{u_3'} &= [u_1^2 (1 - b_3) + u_1 u_3 (2 - b_1 - b_2) + u_3^2 (1 - b_0)] W_{12} \\ &\quad + [u_1 u_2 (1 - b_3) + (u_1 u_4 + u_2 u_3)(2 - b_1 - b_2)/2 \\ &\quad + u_3 u_4 (1 - b_0)] W_{22} \\ W_{u_4'} &= [u_1 u_2 (1 - b_3) + (u_1 u_4 + u_2 u_3)(2 - b_1 - b_2)/2 \\ &\quad + u_3 u_4 (1 - b_0)] W_{22} + [u_2^2 (1 - b_3) + \\ &\quad u_2 u_4 (2 - b_1 - b_2) + u_4^2 (1 - b_0)] W_{32} \quad (2a-d) \end{aligned}$$

where W is the sum of the right-hand sides of Eqns (2a–d) (Feldman & Zivovotzky, 1992). The frequency of the cultural trait E , is now given by $x = (u_1 + u_2)$ the frequency of allele A is given by $p = (u_1 + u_3)$, and the interaction between the gene and the cultural trait can be specified by the quantity $D = u_1 u_4 - u_2 u_3$. In the special cases where $w_{11} = w_{12}$, $w_{21} = w_{22}$, $w_{31} = w_{32}$, and with unbiased transmission ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$) we can write useful recursions for x , p and D . These can be seen in the appendix.

Results

To provide a baseline for the subsequent analysis, we first describe the behaviour of the models when there is no external source of selection (i.e. independent of the cultural niche construction), then consider selection that favours one of the alleles or one of the cultural traits and finally focus on the effects of cultural niche construction when the external selection generates overdominance at

the \mathbf{A} locus. We use the notation \hat{R} to indicate equilibrium values of the resource R . We note that whether the amount of this resource is exclusively a function of cultural niche construction (model 1) or also partly dependent on independent processes of renewal and depletion (model 2) the models generate consistent findings. Consequently, in the following section it can be assumed that the reported results apply to both models unless otherwise stated.

1. No external selection: $\alpha_1 = \eta_1 = \alpha_2 = \eta_2 = 1$

(i) *Unbiased cultural transmission* ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$)

Model 1 behaves exactly like our original genetic model (Laland *et al.*, 1996), with the same characteristic curve of E -frequency equilibria (Fig. 1a), the formal details of which are given in appendix 1 of Laland *et al.* (1996). If there is no statistical association between the cultural trait and allele frequencies, i.e. $D = 0$, then from eqn (A1) of the appendix, x and the amount of the resource are constant, and given by the frequency of E . As under such circumstances R is now unaffected by n , eqn (1a) simplifies to the $n = 1$ case. Numerical analysis reveals that gene-culture association breaks down after a small number of generations ($D \rightarrow 0$), and is rarely sufficiently consequential to drive meaningful change in the frequency of the cultural trait. However, the cultural niche construction does generate selection that changes the frequency of alleles at locus \mathbf{A} . If ε is positive, then in the selective environment characterized by high frequencies of E (i.e. $x > 0.5$), analysis of eqn (A2) of the appendix reveals that allele A will be favoured, whereas in the selective environment provided by low frequencies of E (i.e. $x < 0.5$) allele a will be favoured. The reverse is true if ε is negative.

Model 2 also behaves like the equivalent genetic model (Laland *et al.*, 1999), generating a curve of polymorphic equilibria at $\hat{R} = 0.5$. With only positive niche construction ($R_t = \lambda_1 R_{t-1} + \lambda_2 x_t + \lambda_3$, $\gamma = 0$), for frequencies of trait E from $x = 0$ to $x = 1$, the corresponding values of R range between 0 and 1, depending on λ_1 , λ_2 , λ_3 . The equilibrium resource value, \hat{R} , is given as a function of the equilibrium frequency of E , \hat{x} by

$$\hat{R} = \frac{\lambda_3 + \hat{x}\lambda_2}{1 - \lambda_1}. \quad (3a)$$

With only negative niche construction ($R_t = \lambda_1 R_{t-1} (1 - \gamma x_t) + \lambda_3$ and $\lambda_2 = 0$), for values of x increasing from 0 to 1, R decreases in an interval of values contained in 0–1, depending on the values of λ_1 , λ_3 and γ . The equilibrium value of R for any given value of \hat{x} is given by

$$\hat{R} = \frac{\lambda_3}{1 - \lambda_1 (1 - \gamma \hat{x})}. \quad (3b)$$

The direction of selection on the gene generated by the resource, and in part influenced by cultural niche

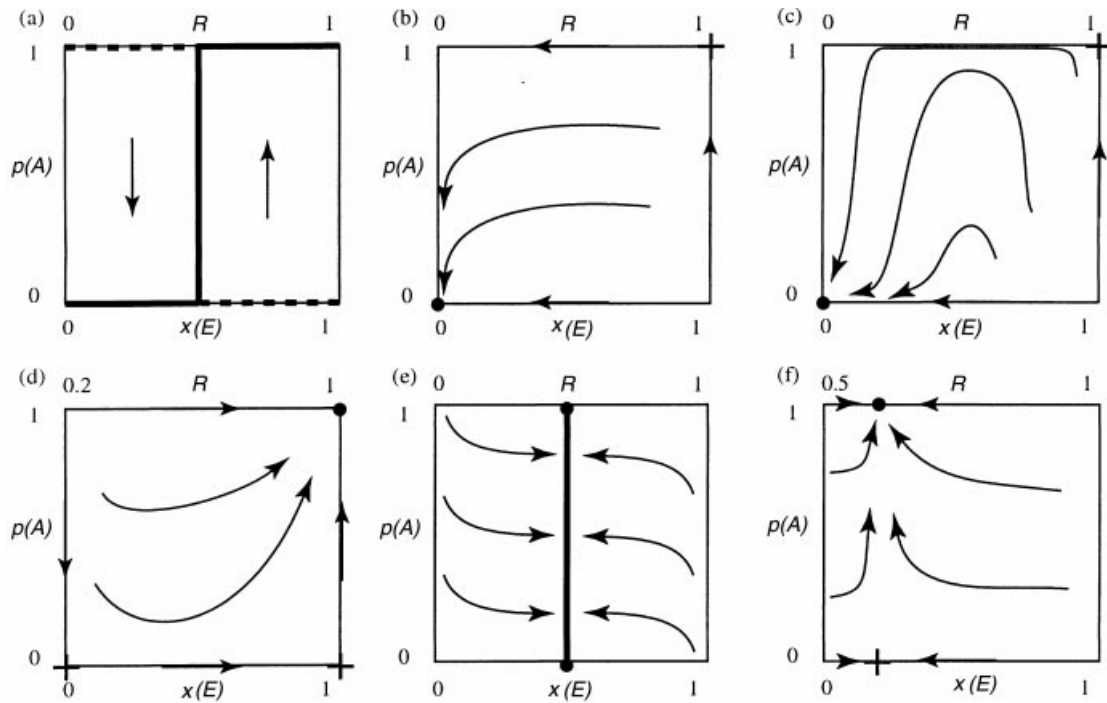


Fig. 1 Dynamics (arrows), stable equilibria (thick lines, filled circles) and unstable equilibria (dashed thick lines, pluses) for system with no external selection ($\alpha_1 = \eta_1 = \alpha_2 = \eta_2 = 1$, $\varepsilon = 0.3$). Model 1 with (a) unbiased cultural transmission ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$), (b) strongly biased cultural transmission ($b_3 = 1$, $b_2 = b_1 = 0.25$, $b_0 = 0$) and (c) weakly biased cultural transmission ($b_3 = 1$, $b_2 = b_1 = 0.49$, $b_0 = 0$); (d) model 2 with biased cultural transmission ($\lambda_1 = 0.5$, $\lambda_2 = 0.4$, $\lambda_3 = 0.1$, $\gamma = 0$, $\varepsilon = 0.3$, $b_3 = 1$, $b_2 = b_1 = 0.55$, $b_0 = 0$); (e) model 1 with incomplete transmission ($b_3 = 0.9$, $b_2 = b_1 = 0.5$, $b_0 = 0$); (f) model 2 with incomplete transmission ($\lambda_1 = 0.8$, $\lambda_2 = 0.1$, $\lambda_3 = 0.1$, $\gamma = 0$, $\varepsilon = 0.3$, $b_3 = 0.9$, $b_2 = b_1 = 0.25$, $b_0 = 0.1$). Note, as R is a variable dependent on x , on the top axis of each figure we present the value of R that corresponds to the value of x given on the bottom axis, where x ranges from 0 to 1.

construction, switches at $R = 0.5$. For positive values of ε , selection favours a when $R < 0.5$, A when $R > 0.5$, with no selection on A when $R = 0.5$. For negative values of ε the reverse is true.

(ii) *Biased transmission* ($b_3 = 1$, $b_2 = b_1 = b$, $b_0 = 0$)
Biased transmission results in an increase in the frequency of cultural trait E if $b > 0.5$ and in e if $b < 0.5$. If $b < 0.5$, so that cultural trait e is favoured and with the exception of populations on the $x = 1$ boundary, cultural trait E is lost. If ε is positive, there is fixation on ae if $R < 0.5$ at $x = 0$ (e.g. Fig. 1b, c), and on Ae if $R > 0.5$ at $x = 0$, and there is a neutrally stable curve of values of p stable at $x = 0$ for $R = 0.5$. With strong transmission bias in favour of e , populations rapidly converge on the $x = 0$ boundary as a result of cultural transmission and then the selection from the cultural niche construction fixes one or other allele (Fig. 1b). With weak transmission bias in favour of e ($b < 0.5$) and an initial value of $R > 0.5$, p initially increases (if ε positive) before cultural transmission may take populations into the range ($R < 0.5$) where the selection generated by the cultural niche construction favours a (Fig. 1c). Under such circumstances when the frequency of A is transiently large, in populations of

small size the a allele might be lost by random drift. Similarly, if $b > 0.5$, cultural transmission bias favours E , and with the exception of the $x = 0$ boundary, e is lost. If ε is positive, there is fixation on aE if $R < 0.5$ at $x = 1$, on AE if $R > 0.5$ at $x = 1$ (Fig. 1d) and with all values of p stable at $x = 1$ for $R = 0.5$. The reverse is true if ε is negative. These findings apply to both models.

(iii) *Incomplete transmission* ($b_3 = 1 - \delta$, $b_2 = b_1 = b$, $b_0 = \delta$)

For model 1 with $D = 0$, if $\delta > 0$ and $b \neq 0.5$, all populations remain polymorphic for the cultural trait (Cavalli-Sforza & Feldman, 1981) and there is convergence on a line of gene-frequency equilibria with the frequency of E given by

$$\hat{x} = \frac{1 + 2\delta - 2b - \sqrt{1 - 4b + 4\delta^2 + 4b^2}}{2(1 - 2b)}. \quad (4)$$

When $b = 0.5$, there is convergence to a neutral curve at $\hat{x} = 0.5$ (Fig. 1e). If $b \neq 0.5$ the value of R determines the stability of the equilibria, with (for positive ε) A fixed for $R > 0.5$ at \hat{x} (see Fig. 1f), a fixed for $R < 0.5$ at \hat{x} and all values of \hat{p} possible for $R = 0.5$ at \hat{x} (Fig. 1e). Again, we may substitute allele A for a if ε is negative. It is worthy of

note that if oscillations in the frequency of the cultural trait are imposed on this system they could generate cycles of selection alternately favouring A or a , dependent on whether the maximum and minimum values of R are greater than or less than 0.5, respectively (Cavalli-Sforza & Feldman, 1981).

2. External selection at the A locus only: $\alpha_1 = \alpha_2 = 1$, $\eta_1 \neq 1$, $\eta_2 \neq 1$

(i) *Unbiased cultural transmission* ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$)

From eqn (A1) in the appendix, if $D = 0$ at equilibrium, x remains constant. By summing eqns (2a) and (2c), we derive a recursion for the frequency p of A , whose equilibria are given by $\hat{p} = 0$, $\hat{p} = 1$, and the polymorphism

$$\hat{p} = \frac{1 + \varepsilon\sqrt{R(1-R)} - \eta_2 - \varepsilon(1-R)}{2 + 2\varepsilon\sqrt{R(1-R)} - \eta_1 - \eta_2 - \varepsilon}, \quad (5)$$

which is formally equivalent to expression (4) in Laland *et al.* (1999). The $\hat{p} = 1$ boundary is stable for $w_{1i} > w_{2i}$ ($i = 1, 2$), and we may rewrite this inequality in terms of R , and derive the range or ranges of R -values compatible with the stability of $\hat{p} = 1$, namely

$$R < \frac{2(1 - \eta_1) + \varepsilon - \sqrt{4(1 - \eta_1)(\eta_1 + \varepsilon - 1) + \varepsilon^2}}{4\varepsilon}, \quad (6a)$$

and

$$R > \frac{2(1 - \eta_1) + \varepsilon + \sqrt{4(1 - \eta_1)(\eta_1 + \varepsilon - 1) + \varepsilon^2}}{4\varepsilon}. \quad (6b)$$

A similar analysis for $\hat{p} = 0$, when $w_{3i} > w_{2i}$ ($i = 1, 2$), yields

$$R > \frac{3\varepsilon - 2(1 - \eta_2) + \sqrt{4(1 - \eta_2)(\eta_2 + \varepsilon - 1) + \varepsilon^2}}{4\varepsilon}, \quad (6c)$$

and

$$R < \frac{3\varepsilon - 2(1 - \eta_2) - \sqrt{4(1 - \eta_2)(\eta_2 + \varepsilon - 1) + \varepsilon^2}}{4\varepsilon}. \quad (6d)$$

These inequalities are identical to those in the genetic system, namely inequalities (5a–d) in Laland *et al.* (1999). As the system behaves identically to the genetic models, it will not be discussed further, but an illustration of the dynamics is given in Fig. 2a. Full details can be found in Laland *et al.* (1996, 1999).

(ii) *Biased transmission* ($b_3 = 1$, $b_2 = b_1 = b$, $b_0 = 0$)

With bias in cultural transmission there are no curves of equilibria. With cultural transmission favouring cultural trait E ($b > 0.5$), the final equilibrium for all initially polymorphic populations depends upon the value of R at $\hat{x} = 1$. For $\varepsilon > 0$, as positive niche construction increases the amount of the resource, cultural transmission favouring E reduces the likelihood that R will be sufficiently small for niche construction to generate

selection that counters the external selection favouring A . However, cultural transmission favouring e ($b < 0.5$) increases this likelihood, and stronger the bias in cultural transmission (the smaller the value of b) broader the parameter space over which ae eventually becomes fixed (cf. Fig. 2a,b). For ε negative, there are three possible equilibria at $\hat{x} = 1$, with AE fixed if (6a) or (6b) is satisfied, aE fixed if (6c) or (6d) is satisfied, or an equilibrium polymorphic for A and a (Fig. 2c) if (6a–d) are not satisfied, with \hat{p} given by (5). As when ε is negative, high values of \hat{x} are required for the polymorphic equilibrium to be stable, cultural transmission favouring E increases the parameter space over which populations will converge on such polymorphic equilibria, whereas transmission favouring e reduces it.

For ε positive, negative niche construction decreases the amount of the resource, and hence cultural transmission favouring E increases the likelihood that R will be sufficiently small for cultural niche construction to generate counter-selection to the a fixation boundary (Fig. 2d). As a result, the parameter space in which this counter selection is generated is considerably enlarged, relative to unbiased transmission. The effects of cultural transmission favouring e depend similarly on the value of R at $\hat{x} = 0$. For ε negative, there are three possible stable equilibria at $\hat{x} = 0$, with Ae fixed if (6a) or (6b) are satisfied, ae fixed if (6c) or (6d) are satisfied, or an equilibrium polymorphic for A and a if (6a–d) are not satisfied, at which \hat{p} is given by (5).

(iii) *Incomplete transmission* ($b_3 = 1 - \delta$, $b_2 = b_1 = b$, $b_0 = \delta$)

If $\delta > 0$, the cultural trait is polymorphic, and there is convergence to \hat{x} given by (4). Here, the value of R only partly determines the stability of the equilibria, which is also dependent on the external selection. If ε is positive, there are only two possible stable equilibria with A or a fixed at \hat{x} (Fig. 2e). Low values of R generate counter-selection that takes populations below the separatrix to the a fixation equilibrium. The position of the separatrix is affected by n , the number of generations of cultural niche construction influencing the amount of the resource (see legend, Fig. 2e). With ε negative, fully polymorphic equilibria are possible when R is large, as the line of equilibria characteristic of unbiased transmission collapses to a single equilibrium point at \hat{x} (Fig. 2f), with \hat{p} given by (5).

3. Selection of the cultural trait: $\alpha_1 \neq 1$, $\alpha_2 \neq 1$, $\eta_1 = \eta_2 = 1$

(i) *Unbiased cultural transmission* ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$)

Here both models behave exactly like the equivalent genetic model (Laland *et al.*, 1996, 1999).

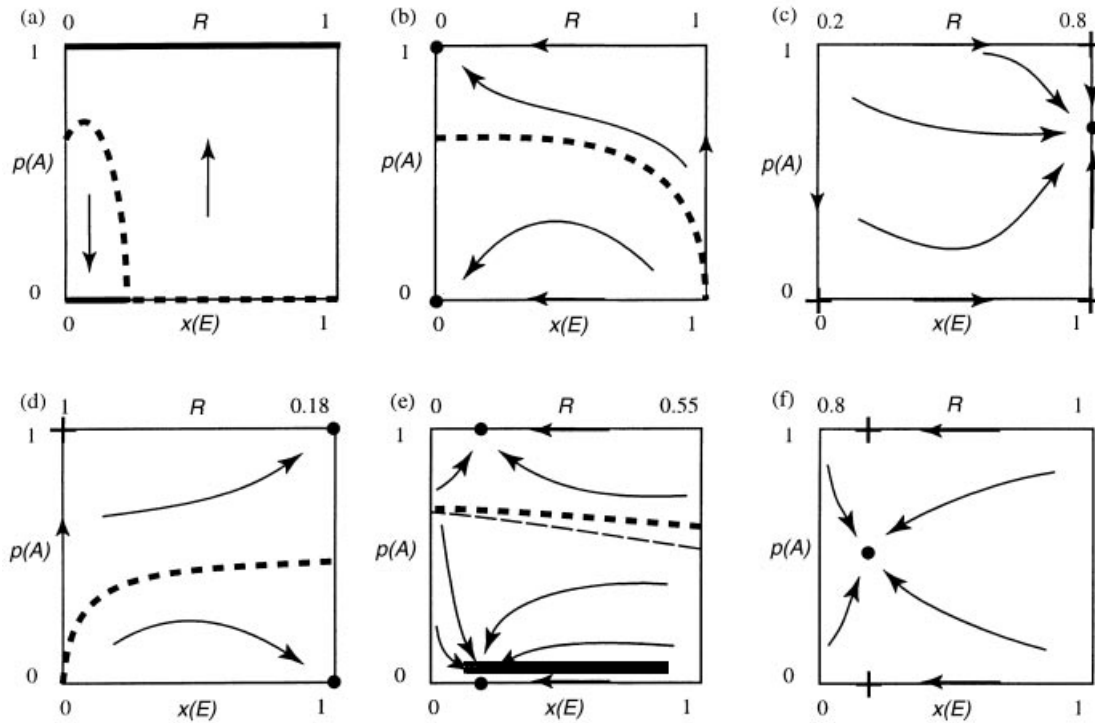


Fig. 2 Dynamics (arrows), stable equilibria (thick lines, filled circles) and unstable equilibria (dashed thick lines, pluses) for system with external selection at the **A** locus ($\alpha_1 = \alpha_2 = 1$, $\eta_1 = 1.1$, $\eta_2 = 0.9$). Model 1 with (a) unbiased cultural transmission with ε positive ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$, $\varepsilon = 0.3$) and (b) biased transmission with ε positive ($b_3 = 1$, $b_2 = b_1 = 0.25$, $b_0 = 0$, $\varepsilon = 0.3$). Model 2 with biased cultural transmission ($b_3 = 1$, $b_2 = b_1 = 0.75$, $b_0 = 0$) and (c) positive niche construction with ε negative ($\lambda_1 = 0.5$, $\lambda_2 = 0.3$, $\lambda_3 = 0.1$, $\gamma = 0$, $\varepsilon = -0.3$), and (d) negative niche construction with ε positive ($\lambda_1 = 0.9$, $\lambda_2 = 0$, $\lambda_3 = 0.1$, $\gamma = 0.5$, $\varepsilon = 0.3$). Model 2 with incomplete transmission ($b_3 = 0.9$, $b_2 = b_1 = 0.25$, $b_0 = 0.1$) and positive niche construction, with (e) ε positive ($\lambda_1 = 0.5$, $\lambda_2 = 0.275$, $\lambda_3 = 0$, $\gamma = 0$, $\varepsilon = 0.3$), and (f) ε negative ($\lambda_1 = 0.75$, $\lambda_2 = 0.05$, $\lambda_3 = 0.2$, $\gamma = 0$, $\varepsilon = -0.3$). In (e) the thick dashed line represents the separatrix for $n = 1$ and the thin dashed line that for $n = 25$. On the top axis of each figure we present the value of R that corresponds to the value of x given on the bottom axis.

(ii) *Biased transmission* ($b_3 = 1$, $b_2 = b_1 = b$, $b_0 = 0$)
 With bias in cultural transmission and selection on E , there are now two processes influencing the frequency of the cultural trait. When E is favoured either by natural selection ($\alpha_1 > 1 > \alpha_2$) or by cultural transmission ($b > 0.5$), positive values of ε result in fixation of AE , whereas negative values cause the fixation of aE . When e is favoured either by natural selection ($\alpha_1 < 1 < \alpha_2$) or by cultural transmission ($b < 0.5$), positive values of ε result in fixation of ae and negative values cause the fixation of Ae . Where these two processes reinforce each other in favouring E or e , the same fixation points are reached as when one or other acts alone, although the approach to equilibrium is faster. When they are in conflict then the final fixation point depend on the relative strength of the two processes. In some cases cultural transmission may take E or e to fixation in the face of natural selection favouring the other trait (e.g. $\alpha_1 = 1.1$, $\alpha_2 = 0.9$, $b = 0.25$).

(iii) *Incomplete transmission* ($b_3 = 1 - \delta$, $b_2 = b_1 = b$, $b_0 = \delta$)

If $\delta > 0$, there will be a polymorphism in the cultural trait, with either allele A or a fixed, and if there is no natural selection, \hat{x} is given by eqn (4). If there is natural selection, the frequency of the cultural trait at gene-fixation equilibria is given by a solution to the cubic

$$x^3[(w_{i1} - w_{i2}(1 - 2b)] + x^2[2(w_{i1} - w_{i2})(b - \delta) - w_{i1}(1 - 2b)] + x(w_{i2} - w_{i1})(1 - \delta) + w_{i1}(1 - 2b + 2\delta)] - \delta w_{i1} = 0, \quad (7)$$

where $i = 1$ at $\hat{p} = 0$ and $i = 3$ at $\hat{p} = 1$. Note that the frequency of the cultural trait typically differs at the two genetic fixation states, although this difference is small for realistic parameter values. The difference occurs because $w_{11}/w_{12} \neq w_{31}/w_{32}$ when $R \neq 0.5$.

As in the genetic models, for $n > 1$, we see timelags in the response to selection at the **A** locus, following the spread of a niche constructing trait. Typically, the timelags are shorter than in the case of the purely genetic system, principally because the cultural trait reaches equilibrium faster than an analogous genetic

trait. This is, firstly, because there are only two cultural states compared with three genotypes, analogous to a haploid genetic system, so that disadvantageous cultural traits are not shielded from selection as deleterious alleles are in heterozygotes and consequently rare cultural traits take less time than rare alleles, to be eliminated by selection. Second, cultural transmission is typically faster than natural selection in multicellular organisms. It is only if there is no selection and a weak transmission bias that we see timelags of the order seen in the genetic model. With a weak bias, and strong selection generated by the cultural niche construction, the *A* allele may reach fixation before *E*. Moreover, with a weak bias, allele *A* may reach very low frequencies (i.e. $p < 10^{-7}$) before it is selected towards fixation and in small populations might be lost. If $\delta > 0$, *E* does not go to fixation, but, provided $b > 0.5$, *A* will eventually fix. In general, a cultural niche-constructing trait only has to spread through the population enough to increase the frequency of the resource $R > 0.5$, before it can generate selection that will fix *A*.

4. Overdominance at the **A** locus: $\eta_1 < 1$, $\eta_2 < 1$

(i) *Unbiased cultural transmission* ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$)

We now consider the effects of cultural niche construction when there is heterozygote advantage at the **A** locus. With unbiased cultural transmission, the models behave differently from our earlier genetic models, because in this case, there is no selection on the cultural trait but there is external overdominant selection on the gene. Polymorphic equilibria at the **A** locus are possible, provided the selection generated by the resource does not overcome the external source of selection to negate the heterozygote advantage. Provided *R* is not so small that *a* may become fixed or so large that *A* may become fixed, there may be a line of fully polymorphic cultural equilibria. At equilibria polymorphic for **A**, the frequency of *A* is given by (5), the values of *R* at $\hat{p} = 1$ are given by (6a,b) and the values of *R* at $\hat{p} = 0$ are given by (6c,d). The curve (5) giving equilibrium values of *A*, can have some interesting features. For instance, with $\alpha_1 = \alpha_2 = 1$, $\eta_1 = 0.95$, $\eta_2 = 0.9$, $\varepsilon = -0.3$, as *x* increases the frequency of *A* increases, then decreases, then increases again.

(ii) *Biased transmission* ($b_3 = 1$, $b_2 = b_1 = b$, $b_0 = 0$)

With bias in cultural transmission, these curves of equilibria are no longer stable and initially polymorphic populations converge on a single stable equilibrium. The bias in cultural transmission takes *E* or *e* to fixation, with the frequency of *A* given by (5).

(iii) *Incomplete transmission* ($b_3 = 1 - \delta$, $b_2 = b_1 = b$, $b_0 = \delta$)

If $\delta > 0$ and $D = 0$ there is convergence on a single equilibrium where \hat{x} is given by (4) and \hat{p} by (5).

As with the genetic model, the selection generated by the resource can shift the position of polymorphic equilibria. The direction of the shift is in favour of *a* when ε is positive and $R < 0.5$ and also when ε is negative and $R > 0.5$, and in favour of *A* when ε is positive and $R > 0.5$ and also when ε is negative and $R < 0.5$. The selection generated by the resource is strongest when *R* is close to 0 or 1, and weakest at $R = 0.5$. By influencing the amount of the resource, cultural niche construction can significantly change the position of the equilibrium and may change the direction of selection resulting from *R*.

Discussion

The analysis provides ample evidence that cultural niche construction could plausibly affect human genetic evolution in a multitude of ways.

With the exception of the case of overdominance at the **A** locus, the gene-culture niche construction models with unbiased cultural transmission simplify to the equivalent purely genetic niche-construction models. The exception occurs because, under our framework, there is no pattern of frequency-independent natural selection that can maintain polymorphism in a two-trait cultural transmission system (unless cultural transmission is incomplete). Here the case of unbiased cultural transmission with overdominance at the **A** locus, has some interesting features: for example, curves of stable fully polymorphic equilibria are found that exhibit complex relationships between the frequencies of the cultural trait and the alleles at the **A** locus, similar to those found with the purely genetic models when selection operates at the **A** locus (Laland *et al.*, 1999). Such curves might represent situations like that of the effect of yam cultivation (the cultural niche-constructing trait, or *E*) on the frequency of the sickle-cell allele (the allele maintained through overdominance, or *A*) and illustrate the sensitivity of allele frequencies to cultural niche construction.

Biased cultural transmission can increase the range of parameter space over which niche construction has an impact. For instance, in the face of external selection favouring allele *A*, cultural transmission may generate counter selection that increases the likelihood of fixation on *a*, if cultural transmission favours trait *e* and *a* decrease in the amount of the resource results in a decrement in the fitness of genotypes containing *A* (ε is positive). Similarly, cultural niche construction will increase the chance of convergence to equilibria polymorphic for *A* and *a*, if cultural transmission favours *E* when an increase in the amount of the resource results in a decrement in the fitness of genotypes containing *A* (ε is negative). In both cases cultural niche construction is driving genetic evolution. Biased cultural transmission can also reduce the range of parameter space over which niche construction has an impact, if cultural transmission

favours E when ε is positive, or e when ε is negative. This means that if there is external selection at the **A** locus, the effect of biased transmission is that cultural niche construction is likely to have either a much smaller or a much bigger effect than that resulting from both unbiased transmission and purely gene-based niche construction. Note that because cultural processes typically operate on a faster timetable than natural selection, biased cultural transmission is likely to have a much greater influence on the consequences of niche construction than would natural selection on **E**. These findings illustrate processes by which cultural niche construction may have played an instrumental and active role in hominid evolution, initiating novel evolutionary events through the creation of novel selection pressures, and changing the direction of evolution by modifying established selection pressures. Moreover, they confirm the hypothesis that the hominid capacity for niche construction is likely to have been greatly enhanced by, and coevolved with, a capacity for cultural transmission.

There are at least two reasons why biased cultural transmission might be expected to sweep E or e to fixation more rapidly than natural selection. First, there are only two cultural states, compared with three genotypes, so rare cultural traits take less time to be eliminated by selection than rare alleles. Second, cultural transmission is typically faster than the natural selection of human genes, with b much more likely to deviate substantially from 0.5 (indicative of a significant bias in cultural transmission) than α_1 and α_2 are to deviate substantially from 1 (indicative of strong natural selection). This means that niche construction resulting from culture is more likely to cause dramatic changes in the frequency of the key resource, R , than niche construction resulting from genes. If, as we have assumed, niche construction has its greatest impact when R is large or small, by taking E or e to fixation, biased transmission will result strengthening of selection generated by cultural niche construction.

Weak transmission biases favouring a cultural niche-constructing behaviour can also generate interesting evolutionary scenarios. For instance, if transmission bias results in a change in frequency of cultural niche-constructing traits, then selection at the **A** locus may be modified or even reversed, as R may have increased or decreased beyond the $R = 0.5$ switch point. In the case of weak biases, there may be many more generations of selection favouring one of the alleles at the **A** locus than would be the case for strong biases before selection switches to favour the other allele, and as a consequence one or other allele may reach a very low frequency before increasing in frequency again. In reality, we anticipate that small populations that follow this trajectory because they are exposed to a weak cultural transmission bias, may lose genetic variation at the **A** locus before selection could favour the allele that had

previously been selected against. This type of process could easily create and maintain genetic differences between semi-isolated populations, and in hominids may have played a role in biological speciation events.

If cultural transmission and natural selection on **E** conflict, there are circumstances under which cultural transmission can overwhelm selection. If the two processes act in concert, cultural transmission accelerates the rate at which the cultural trait spreads.

Incomplete cultural transmission maintains variation in the cultural trait, even when there is directional natural selection at the **E** locus. This means that oscillations in the frequency of E could lead to corresponding fluctuations in A . It also means that a single fully polymorphic equilibria is more likely to be found when there is overdominance at the **A** locus. Under such circumstances, the gene-culture models with incomplete transmission most closely resemble the purely genetic models with overdominance.

When the amount of the resource is a function of more than one generation of niche construction ($n > 1$), we find timelags at the **A** locus in response to a change in selection pressures at the **E** locus. Typically, the timelags are shorter than in the case of the purely genetic systems, principally because the cultural trait reaches equilibrium faster than an analogous genetic trait. It is only if there is no selection and weak transmission bias that we see timelags of the order seen in the genetic models. With incomplete transmission, neither E nor e goes to fixation, but provided a cultural transmission bias favours trait E ($b > 0.5$), A will eventually fix. Thus a cultural niche-constructing trait only has to spread through the population enough to increase the frequency of the resource R above 0.5, before it can generate selection that will fix A .

As with gene-based niche construction (Laland *et al.*, 1996, 1999), these models demonstrate that cultural niche construction will commonly generate counter selection that compensates for, or counteracts a natural selection pressure in the environment. A reasonable inference from such findings would be that competent niche constructors should be more resistant to genetic evolution in response to autonomously changing environments than less able niche constructors. As culture enhances the capacity of humans to alter their niches, it would seem plausible to infer that hominid niche construction in general has been more flexible than that of other mammals.

This finding can be used to develop a number of predictions about human evolution (Laland *et al.*, 2000). For instance, we would expect hominids to show less of an evolutionary response in morphology to fluctuating climates than other mammals, assuming that the latter must have been less well equipped than the former to invest in counteractive niche construction. Similarly, we would expect more technologically advanced hominids to exhibit less of a response to climates than less technologically advanced hominids. Bergmann's and

Allen's rules suggest that populations in warmer climates will be smaller bodied and have bigger extremities than those in cooler climates. Hominids should show less correspondence these rules than other mammals and later hominids should exhibit less correspondence than earlier hominids. Moreover, it should also be possible to reverse this inference and use the fossil record to draw conclusions about the niche-constructing capabilities of animals, including hominids. Here we suggest that greater the phenotypic (as opposed to extended-phenotypic) response to environmental change by hominids, the more restricted must have been their capacity for niche construction.

If hominids have evolved more in response to self-constructed selection pressures than other mammals and less in response to selection pressures that stem from independent factors in their environment, then hominid populations may have become increasingly divorced from local ecological pressures. Support for this line of reasoning comes from Guglielmino *et al.*'s (1995) study of variation in cultural traits among 277 contemporary African societies in which most traits examined correlated with cultural (e.g. linguistic) history rather than ecology. Moreover, in the light of our findings, the view that modern human populations are adapted to an ancestral Pleistocene habitat or Environment of Evolutionary Adaptedness, is likely to be misleading because it treats humans as passive victims of selection rather than as potent niche constructors. Our recent evolutionary history may well reflect our capacity continuously to create solutions to self-imposed problems caused by prior niche construction. This adaptability may mean that rather than being adapted to a particular environment, humans adapted to a broad range of potential environments that they and their ancestors were involved in modifying.

In conclusion, a cursory glance at Figs 1 and 2 reveals that there is no simple function that relates the frequency of the cultural niche-constructing activity (x) to the frequency of the populations genes (p). Gene-culture models that do not treat the resource as an independent variable are forced to assume that a simple relationship exists between the incidence of cultural activity in the present generation and the resulting selection imposed on genes. In those situations referred to in the introduction, where the selection pressures acting on a human or hominid population are partly dependent on niche construction and partly on independent processes (as for model 2), or where niche construction generates an ecological inheritance with the activities of past generations affecting selection on contemporary populations (as in models 1 and 2), it is natural to treat the resource as a variable. The models presented here suggest the possibility of making estimates of gene frequencies given knowledge of cultural activity, or vice-versa. For instance, in the case of the yam cultivating peoples that modify selection pressures by increasing the amount of

standing water, it might be possible to use information about levels of rainfall or water surplus in different regions, together with the level of slash-and-burn agriculture in that region, to predict the frequency of the sickle-cell allele among those peoples. In this example, a cultural practice has left a measurable genetic signature, in the form of a different allele frequency. In theory, it is possible that genetic signatures left by other cultural practices, evident in archaeological or ethnographic records, could be identified and used as evidence for the presence or absence of the cultural trait in particular populations, or to trace the diffusion of the cultural practice across geographical regions. The preceding analyses suggest that there are likely to be rich opportunities to explore the impact of cultural niche construction in human evolution.

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References

- Aiello, L.C. & Wheeler, P. 1995. The expensive-tissue hypothesis. *Current Anthropol.* **36**: 199–221.
- Aoki, K. 1986. A stochastic model of gene-culture coevolution suggested by the 'culture historical hypothesis' for the evolution of adult lactose absorption in humans. *Proc. Natl. Acad. Sci., USA* **83**: 2929–2933.
- Bateson, P.P.G. 1988. The active role of behaviour in evolution. In: *Evolutionary Processes and Metaphors* (M. W. Ho & S. Fox, eds), pp. 191–207. Wiley, Chichester.
- Bodmer, W.F. & Cavalli-Sforza, L.L. 1976. *Genetics, Evolution and Man*. Freeman, Sanfransisco.
- Bodmer, W.F. & Felsenstein, J. 1967. Linkage and selection: theoretical analysis of the two locus random mating model. *Genetics* **57**: 237–265.
- Boyd, R. & Richerson, P.J. 1985. *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.
- Cavalli-Sforza, L.L. & Feldman, M.W. 1973. Models for cultural inheritance I. Group mean and within-group variation. *Theoret. Population Biology* **4**: 42–55.
- Cavalli-Sforza, L.L. & Feldman, M.W. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press, Princeton, NJ.
- Combes, C. 1995. *Interactions Durables. Ecologie et Evolution du Parasitisme*. Masson, Paris.
- Dunbar, R.I.M. 1993. Coevolution of neocortical size, group size and language in humans. *Behav. Brain Sciences* **16**: 681–735.
- Durham, W.H. 1991. *Coevolution: Genes, Culture and Human Diversity*. Stanford University Press, Stanford, CA.
- Feldman, M.W. & Cavalli-Sforza, L.L. 1976. Cultural and biological evolutionary processes, selection for a trait under complex transmission. *Theoret. Population Biology* **9**: 238–259.
- 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* (M. W. Feldman, ed.), pp. 145–173. Princeton University Press, Princeton, NJ.
- Feldman, M.W. & Laland, K.N. 1996. Gene-Culture Coevolutionary Theory. *Trends in Ecology & Evolution* **11**: 453–457.
- Feldman, M.W. & Zhivotovsky, L.A. 1992. Gene-culture coevolution: toward a general theory of vertical transmission. *Proc. Natl. Acad. Sci., USA* **89**: 11935–11938.
- Guglielmino, C.R., Viganotti, C., Hewlett, B. & Cavall-Sforza, L.L. 1995. Cultural variation in Africa: role of mechanisms of transmission and adaptation. *Proc. Natl. Acad. Sci., USA* **92**: 7585–7589.
- Hansell, M.H. 1984. *Animal Architecture and Building Behaviour*. Longman, New York.
- Holloway, R.L. 1981. Culture, symbols and human brain evolution: a synthesis. *Dialect Anthropologist* **5**: 287–303.
- Jones, C.G., Lawton, J.H. & Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.
- Jones, C.G., Lawton, J.H. & Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**: 1946–1957.
- Karlin, S. & Feldman, M.W. 1970. Linkage and selection: Toward locus symmetric viability model. *Theor. Pop. Biol.* **1**: 39–71.
- Kirkpatrick, M. & Lande, R. 1989. The evolution of maternal characters. *Evolution* **43**: 485–503.
- Klein, J. 1997. *Immunology*, 2nd edn. Blackwell Science, Oxford.
- Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. 1996. On the evolutionary consequences of Niche construction. *J. Evol. Biol.* **9**: 293–316.
- Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. 1999. Evolutionary consequences of Niche construction and their implications for ecology. *Proc. Natl. Acad. Sci., USA* **96**: 10242–10247.
- Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. 2000. Niche construction, biological evolution and cultural change. *Behav. Brain Sciences* **23**: 131–175.
- Lewontin, R.C. 1983. Gene, organism, and environment. In: *Evolution from Molecules to Men* (D. S. Bendall, ed.), pp. 273–285. Cambridge University Press, Cambridge, UK.
- Moore, A.J., Brodie, E.D. III & Wolf, J.B. 1997. Interacting phenotypes and the evolutionary process: I. direct and indirect genetic effects of social interactions. *Evolution* **51**: 1352–1362.
- Odling-Smee, F.J. 1988. Niche constructing phenotypes. In: *The Role of Behaviour in Evolution* (H. C. Plotkin, ed.), pp. 73–132. MIT, Cambridge, MA.
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. 1996. Niche Construction. *Am. Naturalist*. **147**: 641–648.
- Odum, P.E. 1989. *Ecology and Our Endangered Life-Support Systems*. Sinauer, Sunderland, MA.
- Plotkin, H.C. 1988. Learning and evolution. In: *The Role of Behavior in Evolution* (H. C. Plotkin, ed.), pp. 133–164. MIT Press, Cambridge, MA.
- Schlichting, C.D. & Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer, Sunderland, MA.
- Wcislo, W.T. 1989. Behavioural environments and evolutionary change. *Ann. Rev. Ecol. Syst.* **20**: 137–169.
- West-Eberhard, M.J. 1987. Flexible strategy and social evolution. In: *Animal Societies: Theories and Facts* (Y. Brown & J. Kikkawa eds), pp. 35–71. Japanese Social Science Press, Tokyo.

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Appendix

Recursions for x , i.e. the frequency of the cultural trait E , p , or the frequency of allele A , and the gene-culture interaction, D , in the special case where $w_{11} = w_{12}$, $w_{21} = w_{22}$, $w_{31} = w_{32}$, and with unbiased transmission ($b_3 = 1$, $b_2 = b_1 = 0.5$, $b_0 = 0$).

$$Wx' = Wx + D[pw_{11} + qw_{21} - pw_{21} - qw_{31}], \quad (\text{A1})$$

$$Wp' = p[pw_{11} + qw_{21}], \quad (\text{A2})$$

and

$$W^2D' = D \left[\frac{p^2w_{11}w_{21}}{2} + pqw_{11}w_{31} + \frac{q^2w_{21}w_{31}}{2} \right], \quad (\text{A3})$$

where

$$W = p^2w_{11} + 2pqw_{21} + q^2w_{31}.$$