An ecocultural model predicts Neanderthal extinction through competition with modern humans

William Gilpin[a], Marcus W. Feldman[b,1], and Kenichi Aoki[c]

[a]Department of Applied Physics, Stanford University, Stanford CA 94305; [b]Department of Biology, Stanford University, Stanford CA 94305; and [c]Organization for the Strategic Coordination of Research and Intellectual Properties, Meiji University, Tokyo 164-8525, Japan

Archaeologists argue that the replacement of Neanderthals by modern humans was driven by interspecific competition due to a difference in culture level. To assess the cogency of this argument, we construct and analyze an interspecific cultural competition model based on the Lotka−Volterra model, which is widely used in ecology, but which incorporates the culture level of a species as a variable interacting with population size. We investigate the conditions under which a difference in culture level between cognitively equivalent species, or alternatively a difference in underlying learning ability, may produce competitive exclusion of a comparatively (although not absolutely) large local Neanderthal population by an initially smaller modern human population. We find, in particular, that this competitive exclusion is more likely to occur when population growth occurs on a shorter timescale than cultural change, or when the competition coefficients of the Lotka−Volterra model depend on the difference in the culture levels of the interacting species.

Lotka−Volterra | cultural evolution | Paleolithic | feedback | replacement

Neanderthals are a human species (or subspecies) that went extinct, after making a small contribution to the modern human genome (1, 2). Hypotheses for the Neanderthal extinction and their replacement by modern humans, in particular as recorded in Europe, can be classified into those emphasizing competition with modern humans and those arguing that interspecific competition was of minor relevance. Among the latter are the climate change (3) and epidemic/endemic (4) hypotheses. However, an ecocultural niche modeling study has shown that Neanderthals and modern humans exploited similar niches in Europe (5), which, together with a recent reassessment of European Paleolithic chronology showing significant spatiotemporal overlap of the two species (6), suggests a major role for interspecific competition in the demise of the Neanderthals.

Replacement of one species (or population) by another is ultimately a matter of numbers. One competing species survives while the other is reduced to, or approaches, zero in size. In the classical Lotka−Volterra model of interspecific competition, this process is called competitive exclusion (7). If Neanderthals were indeed outcompeted by modern humans, the question arises: Wherein lay the advantage to the latter species? Many suggestions have been made, including better tools (8), better clothing (9, 10), and better economic organization (11). These hypotheses share the premise that modern humans were culturally more advanced than the coeval Neanderthals.

The purpose of our paper is threefold. First, we extend the Lotka−Volterra-type model of interspecific competition by incorporating the "culture level" of a species as a variable that interacts with population size (12, 13). Here, culture level may be interpreted as the number of cultural traits, toolkit size, toolkit sophistication, etc. Although, as noted above, many anthropological and archaeological discussions invoke interspecific cultural competition, there is, to the best of our knowledge, no mathematical theory of this ecocultural process. A mechanistic resource competition model is difficult to justify at present, because there is a

limited understanding of "what the species are competing for... [or] how they compete" (14). Second, we use our interspecific cultural competition model to explore, analytically and numerically, the possibility that a difference in culture level, or in underlying learning ability, may produce competitive exclusion of a comparatively (although not absolutely) large regional (Neanderthal) population by an initially smaller (modern human) one. Third, we assume the competition coefficients of the Lotka−Volterra model to depend explicitly on the difference in the culture levels of the interacting species (rather than to be constants) and ask how this modification affects the invasion and subsequent dynamics.

Dependence of the culture/technology level of a human population on its size has been the focus of many theoretical (15–21) as well as psychological (22–24), archaeological (25, 26), and ethnological (27–30) studies. However, the coupled dynamics of population size and culture level, where both quantities are treated as variables, has received less theoretical attention (12, 13, 31, 32).

Taking refs. 12 and 13 as the point of departure, we extend previous treatments by introducing two such populations in direct competition with each other in the Lotka−Volterra framework. The two populations are described in terms of their size, N_i (≥ 0), their culture level z_i (≥ 0), i (=1, 2), and parameters to be defined below. We ask whether a population can be replaced by an initially smaller one, which has an advantage in culture level or in learning ability. This ecological perspective on the competition between "size−culture profiles" may inform ongoing debate on the replacement of Neanderthals by modern humans.

Significance

Ecocultural niche modeling and radiocarbon dating suggest a causal role for interspecific competition in the extinction of Neanderthals. Most archaeologists argue that the advantage to modern humans lay in a higher culture level (a sizable minority dispute this view). Competition between the two species may have occurred when a modern human propagule entered a region occupied by a larger Neanderthal population. We present a model for this replacement, stressing the importance of the founder effect. Our findings shed light on the disappearance of the Neanderthals, showing that endogenous factors such as relative culture level, rather than such extrinsic factors as epidemics or climate change, could have caused the eventual exclusion of a comparatively larger population by an initially smaller one.

EVOLUTION

ANTHROPOLOGY

Theoretical Model

Our model is a four-variable system of coupled differential equations,

$$\dot{N}_i = r_i N_i \left(1 - \frac{N_i + b_{ij} N_j}{M_i(z_i)} \right); \qquad [1]$$

$$\dot{z}_i = -\gamma_i z_i + \delta_i N_i, \qquad [2]$$

where $i = 1, 2$, $j \neq i$, and the super dot indicates differentiation with respect to time.

Eq. 1 entails logistic growth of population i subject to competition from population j, where b_{ij} (>0) is the competition coefficient. Population i has carrying capacity $M_i(z_i)$, which is assumed to be a monotone nondecreasing function of the culture level (see below; Eq. 1 with $M_i(z_i)$ constant reduces to the Lotka–Volterra model). Eq. 2 was originally introduced in ref. 12 as a minimal model for the effect of population size on culture level. Parameter δ_i (>0) measures the per capita input rate of innovations that upgrade culture level (i.e., make z_i more positive); the total innovation rate is therefore proportional to population size. Parameter γ_i (>0) gives the decay rate of culture level due to the infidelity of social learning (and random drift). Larger values of δ_i and smaller values of γ_i indicate higher learning ability. The timescales of demographic and cultural change are determined by r_i and γ_i, respectively.

For the carrying capacity of population i, we assume the step function

$$M_i(z_i) = \begin{cases} K_i & z_i < z_i^* \\ K_i + D_i & z_i \geq z_i^*, \end{cases} \qquad [3]$$

where $K_i > 0$ and $D_i > 0$. That is, $M_i(z_i)$ undergoes a discontinuous jump when culture level crosses a critical value z_i^* (>0). Eq. 3 can be made slightly more general by interpolating a gradual continuous transition between the lower carrying capacity, K_i, and the higher one, $K_i + D_i$. We call this a "ramp" function, and it is analyzed in *SI Text*.

Results

Equilibrium Properties. We formulate the question of replacement of Neanderthals by modern humans in terms of the instability of an equilibrium involving the size−culture profile of the former to an invading propagule of the latter that may be smaller in numbers but more advanced culturally or in underlying learning ability. Equilibria of the model are obtained by setting Eqs. 1 and 2 to zero. Local stability can be determined from the Jacobian. We introduce the shorthand notation $\hat{M}_i = M_i(\hat{z}_i)$ to denote the carrying capacity of population i at equilibrium, which equals either K_i or $K_i + D_i$ for the step function (Eq. 3). Here, we summarize the kinds of equilibria and their local stability conditions for general parameter values when the competition coefficients are constants. Later, we consider the case where b_{ij} is a function of $z_j - z_i$.

First, an internal (i.e., coexistence) equilibrium $\hat{N}_1 > 0$, $\hat{N}_2 > 0$, $\hat{z}_1 (\neq z_1^*) > 0$, $\hat{z}_2 (\neq z_2^*) > 0$ (given that it exists) is locally stable if

$$b_{12} b_{21} < 1, \qquad [4]$$

as shown in *Local Stability with Constant Competition Coefficients*. In the Lotka−Volterra model, this condition ensures global stability of the (unique) coexistence equilibrium. Second, an edge equilibrium $\hat{N}_i = \hat{M}_i > 0$, $\hat{N}_j = 0$, $\hat{z}_i (\neq z_i^*)$, $\hat{z}_j = 0$ (given that it exists) is locally stable if

$$\hat{M}_i b_{ji} > \hat{M}_j, \qquad [5]$$

which is also shown in *Local Stability with Constant Competition Coefficients*. Finally, the corner equilibrium $\hat{N}_1 = 0$, $\hat{N}_2 = 0$, $\hat{z}_1 = 0$,

$\hat{z}_2 = 0$ always exists but is necessarily unstable because $r_i > 0$ by assumption.

Case of Equal Parameter Values. We first investigate the equilibrium properties of the model (Eqs. 1–3) assuming cognitive equality of Neanderthals and modern humans. Suppose that the populations are equivalent with respect to the cognition parameters, $\gamma_1 = \gamma_2 = \gamma$ and $\delta_1 = \delta_2 = \delta$, and, with respect to the competition and growth parameters, $b_{12} = b_{21} = b$, $r_1 = r_2 = r$, and $M_1(z_1) = M_2(z_2) = M(z_i)$. In particular, this assumption entails that both populations have equivalent learning abilities. Under these assumptions, full characterization of the point equilibria and their stability properties is possible.

There are three different kinds of internal equilibria. If $\hat{z}_1 \leq \hat{z}_2 < z^*$ (alternatively, $\hat{z}_2 \leq \hat{z}_1 < z^*$), Eq. 3 entails $\hat{M}_1 = \hat{M}_2 = K$. Hence, solving the simultaneous equations $\hat{N}_1 + b\hat{N}_2 = K$, $b\hat{N}_1 + \hat{N}_2 = K$ yields

$$\hat{N}_1 = \hat{N}_2 = K/(1 + b). \qquad [6]$$

Then, from Eq. 2, we have $\hat{z}_1 = \hat{z}_2 = (\delta/\gamma) K/(1 + b)$, and the consistency requirement $\hat{z}_1 \leq \hat{z}_2 < z^*$ entails that this "low" symmetrical internal equilibrium exists only if $(\gamma/\delta) z^* > K/(1 + b)$. Inequality 4 entails local stability of this equilibrium if $b < 1$ (and instability if $b > 1$).

Similarly, a "high" symmetrical internal equilibrium

$$\hat{N}_1 = \hat{N}_2 = (K + D)/(1 + b), \qquad [7]$$

where $z^* < \hat{z}_1 \leq \hat{z}_2$ exists if $(\gamma/\delta) z^* < (K + D)/(1 + b)$, and is locally stable if $b < 1$ (unstable if $b > 1$). Explicit values of $\hat{z}_1 = \hat{z}_2$ can again be obtained using $\hat{z}_i = (\delta_i/\gamma_i) \hat{N}_i$ from Eq. 2.

The third kind of internal equilibrium is asymmetrical. Suppose, without loss of generality, $\hat{z}_1 < z^* < \hat{z}_2$, which entails $\hat{M}_1 = K$, $\hat{M}_2 = K + D$. Then,

$$\hat{N}_1 = \frac{K - b(K + D)}{1 - b^2}, \quad \hat{N}_2 = \frac{K + D - bK}{1 - b^2}. \qquad [8]$$

Using the consistency requirement and the condition $\hat{N}_2 > \hat{N}_1 > 0$, this equilibrium exists and is locally stable if

$$\frac{K - b(K + D)}{1 - b^2} < \frac{\gamma z^*}{\delta} < \frac{K + D - bK}{1 - b^2} \qquad [9]$$

$$b < K/(K + D). \qquad [10]$$

In addition, another locally stable asymmetrical internal equilibrium with $\hat{N}_1, \hat{z}_1$ and $\hat{N}_2, \hat{z}_2$ interchanged—the symmetrically placed counterpart to Eq. 8—will exist when inequalities 9 and 10 are satisfied. Thus, four stable coexistence equilibria are possible in this special case of our model. Moreover, they may exist and be locally stable at the same time.

The edge equilibria can also be identified. The "low" edge equilibrium,

$$\hat{N}_1 = K, \hat{N}_2 = 0, \quad \hat{z}_1 = (\delta/\gamma) K, \hat{z}_2 = 0 \qquad [11]$$

and its counterpart

$$\hat{N}_1 = 0, \hat{N}_2 = K, \quad \hat{z}_1 = 0, \hat{z}_2 = (\delta/\gamma) K \qquad [12]$$

both exist if $(\gamma/\delta) z^* > K$. From inequality 5, both are locally stable if $b > 1$. Similarly, the "high" edge equilibrium,

$$\hat{N}_1 = K+D, \hat{N}_2 = 0, \quad \hat{z}_1 = (\delta/\gamma)(K+D), \hat{z}_2 = 0 \qquad [13]$$

and its counterpart

$$\hat{N}_1 = 0, \hat{N}_2 = K+D, \quad \hat{z}_1 = 0, \hat{z}_2 = (\delta/\gamma)(K+D) \qquad [14]$$

both exist if $(\gamma/\delta)z^* < K+D$, and are locally stable if inequality **10** is reversed.

Thus, the equilibrium structure of our model is quite complex. An edge equilibrium corresponds to the presence of just one of the populations (population 1, say), and is (locally or globally) stable in the absence of the other (i.e., population 2) (13). However, it may or may not be stable when population 2 is introduced. In the replacement problem, we equate populations 1 and 2 with Neanderthals and modern humans, respectively. We show in *Numerical Analysis with Equal Parameter Values* that the subsequent dynamics could result in coexistence or in competitive exclusion of population 1, either of which can happen when the initial value of $N_2(\equiv N_2^0)$ is large enough relative to, but still smaller than, the initial value of $N_1(\equiv N_1^0)$. The more stringent conditions for competitive exclusion are of particular interest, because these are the conditions that predict the phenomenon that we are trying to explain, namely the replacement of a resident Neanderthal population by invading modern humans.

Numerical Analysis with Equal Parameter Values. To illustrate the dynamics of competition between the size−culture profiles of Neanderthals and modern humans, we carry out a numerical analysis under the above simplifying assumptions. We assume the step function model with equal parameter values in the two populations. Because the dynamical system in Eqs. **1−3** is four-dimensional, it is difficult to generate a simultaneous 2D pictorial representation of the basins of attraction for all of the equilibria described above. For simplicity, we focus on the case where the system is initially at the low edge equilibrium (Eq. **11**), corresponding to our premise that the Neanderthals in isolation would have formed a comparatively small population at a relatively low culture level. Figs. 1 and 2 illustrate the basins of attraction in the (N_2^0, z_2^0) plane of initial conditions for population 2 (N_2^0 on the horizontal axis, z_2^0 on the vertical axis) (33). They show how these basins of attraction depend on deviations of the initial culture levels, z_2^0, from the "quasi-equilibrium" values, $(\delta/\gamma)N_2^0$ (Eq. **2** with $\dot{z}_2 = 0$).

Positive deviations $[z_2^0 > (\delta/\gamma)N_2^0]$ may arise if population 2 is a propagule derived from an equilibrium population of large size at a high culture level (e.g., Eq. **14**) but whose culture level has not yet declined to a value commensurate with its reduced size. Using a "serial founder effect" model, it has been argued that such a propagule may be about 0.09–0.18 the size of the parental population (34). Figs. 1 and 2 show that population 1 can be competitively excluded by an initially smaller population 2, provided the latter maintains an advantage in culture level.

Each colored region in Figs. 1 and 2 corresponds to the basin of attraction for a distinct equilibrium. Seven equilibria exist given the parameter values in Fig. 1. The values of the parameters K and D in the numerical analysis do not represent known carrying capacities; rather, they should be regarded as being measured in some unspecified units. The two symmetrical coexistence equilibria (Eqs. **6** and **7**) and the two high edge equilibria (Eqs. **13** and **14**), are locally stable, but only two of these—Eqs. **6** and **14**—are attractors from the initial conditions considered here. The low edge equilibrium **11**, representing the state of the system before the introduction of population 2, is unstable. Hence, population 2 will necessarily invade, and the question is whether convergence occurs to equilibrium **6**, resulting in coexistence, or to equilibrium **14**, resulting in competitive exclusion. The purple and blue regions in Fig. 1B denote the basins of attraction of the low symmetrical coexistence equilibrium **6** and the high edge equilibrium **14**, respectively.

To the left of the white broken line in Fig. 1B, population 2 is initially smaller than population 1. Fig. 1B shows that competitive exclusion of population 1 by population 2 is possible even when the latter is initially smaller than the former. For example, convergence to the high edge equilibrium **14** (black disk in the upper right-hand corner) can occur from an initial population ratio of $N_2^0/N_1^0 = 0.9$ and an initial culture level of $z_2^0 = \delta(K+D)/\gamma$ (right-hand white cross). If population 2 is initially even smaller, e.g., $N_2^0/N_1^0 = 0.7$ (left-hand white cross in Fig. 1B), then convergence to the low symmetrical internal equilibrium **6** (black disk in the lower left-hand corner) results. Importantly, our ecocultural model—in contrast to the standard Lotka−Volterra model—predicts the simultaneous existence of locally stable internal and edge equilibria, where the former may act as "traps" hindering competitive exclusion. Fig. 1A shows the corresponding trajectories.

Fig. 1 *A* and *B* illustrates the default case where the timescales of demographic and cultural change are equal, specifically $r = \gamma = 1$. Fig. 1B suggests that N_2^0 must be of the same order of magnitude as N_1^0 for competitive exclusion to occur in this case. Fig. 1C shows
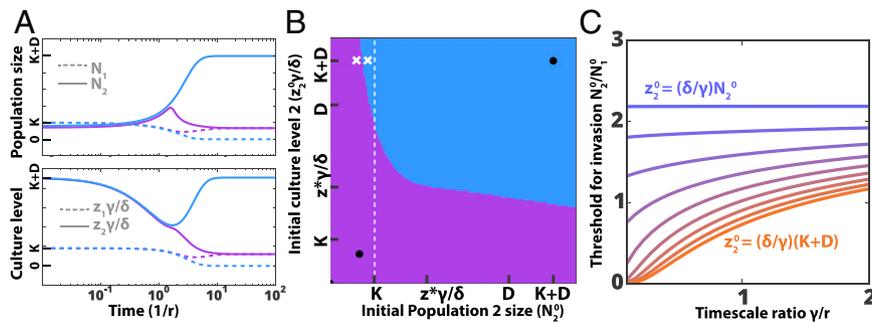

Fig. 1. Modern human invasion of a Neanderthal population. (*A*) Trajectories for invasion with the modern humans (solid traces) starting at a lower initial population size than the Neanderthals (dashed traces), but with an initially higher culture level. (*Top*) Population sizes versus time and (*Bottom*) the culture levels. Purple traces correspond to $N_2^0/N_1^0 = 0.7$, which is too low for replacement, whereas blue traces indicate replacement when $N_2^0/N_1^0 = 0.9$. (*B*) Basins of attraction to coexistence (purple; final population sizes are equal and nonzero) and replacement (blue; final size of population 1 is zero). The initial conditions for population 2 in *A* are marked by white crosses in *B*, and the equilibria are marked by black disks. (*C*) The effect of varying the timescale ratio, γ/r, on the threshold initial population ratio, N_2^0/N_1^0, necessary for replacement. The different lines correspond to different initial culture levels for the invading population. In this figure, $K_1 = K_2 = K = 10$, $D_1 = D_2 = D = 40$, $b_{12} = b_{21} = b = 0.5$, $z_1^* = z_2^* = z^* = 10$, and $r_1 = r_2 = r = 1$. For *A* and *B*, $\gamma_1 = \gamma_2 = \gamma = 1$ and $\delta_1 = \delta_2 = \delta = 1/2.2$. Initial values are $N_1^0 = K = 10$ and $z_1^0 = (\delta/\gamma)K = 10/2.2$.
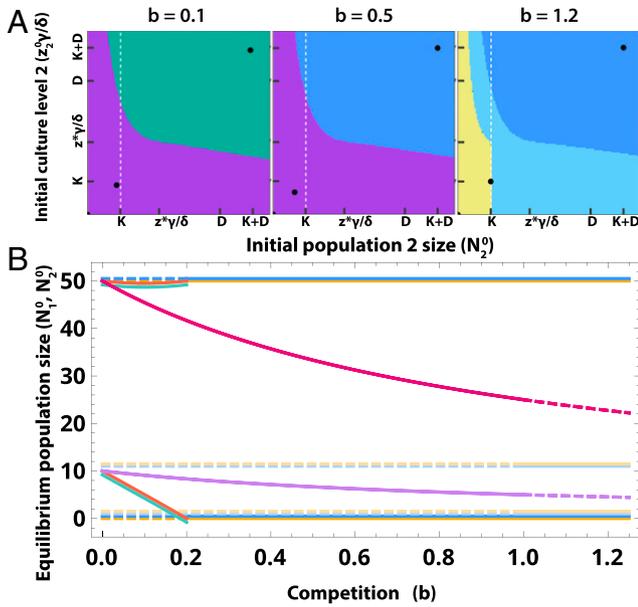
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Fig. 2. Effect of increasing competition on invasion. (*A*) The basins of attraction in the (N_2^0, z_2^0) plane for three values of the competition coefficient *b*. For low enough competition (*Left*), asymmetric coexistence (green) and symmetric coexistence (purple) occur and are locally stable. As competition increases (*Middle*), the asymmetric coexistence solutions become exclusion solutions (blue). With even larger *b* (*Right*), low symmetric coexistence becomes a pair of low exclusion equilibria (light yellow and light blue), both locally stable. Invasion cannot occur in the light yellow region. (*B*) A bifurcation diagram showing how equilibrium sizes of the two populations vary with *b* (stable equilibria, solid lines; unstable equilibria, dashed lines). All other parameter and initial values are as in Fig. 1.

that the minimum N_2^0/N_1^0 required for competitive exclusion is sensitive to our assumptions regarding these timescales. Here, we set $r = 1$ and vary γ and δ together, subject to the constraint $\gamma/\delta = 2.2$. By keeping γ/δ constant, the existence and stability conditions are unaffected and only the basins of attraction may change. Low rates of cultural decay (and innovation) relative to population growth appear to facilitate competitive exclusion by an initially smaller population with an initial cultural advantage. For example, if $\gamma = 0.2$ and $r = 1$, a ratio as low as $N_2^0/N_1^0 = 0.1$ may suffice.

Fig. 2 shows the effects of varying the competition coefficient, *b*. Fig. 2*A* (*Middle*) is equivalent to Fig. 1*B*. For low values of *b* satisfying inequality **10**, the two asymmetrical internal equilibria, **8** and its counterpart, exist and are locally stable. Thus, all nine corner, edge, and internal equilibria exist for the parameter values in Fig. 2*A* (*Left*). However, only two attractors are found, and the green region of Fig. 2*A* (*Left*) denotes the basin of attraction of the asymmetrical internal equilibrium **8** (where $\hat{N}_2 > \hat{N}_1$); for the parameter values assumed here, $\hat{N}_2 \approx 49$ and $\hat{N}_1 \approx 5$, which is close to replacement. As *b* increases, the asymmetrical coexistence equilibria undergo transcritical bifurcation into the high edge exclusion equilibria, as shown in the bifurcation diagram Fig. 2*B*.

Eventually, at even larger values of *b*, as in Fig. 2*A* (*Right*), all four coexistence equilibria are eliminated, while the four edge equilibria become locally stable. Here, the attractors are the low edge equilibria **11** and **12**, and the high edge equilibrium **14**; the basins of attraction are colored in light yellow, light blue, and blue, respectively. The light yellow region corresponds to non-invasion, whereas the light blue and blue regions both correspond to competitive exclusion of population 1 by population 2. The sizes of the populations at equilibrium, $\hat{N}_1, \hat{N}_2$, also vary with *b*, as shown in Fig. 2*B*.

Difference in Learning Ability. The jury is still out on whether or not Neanderthals and modern humans differed in cognition (35, 36). Aspects of cognition incorporated into our model are the infidelity of social learning, γ_i, and the upgrade innovation rate δ_i. Assume again that the two populations are equivalent with respect to the competition and growth parameters $b_{ij}, r_i, M_i(z_i)$. However, we now assume that they differ in the ratio γ_i/δ_i, smaller values of which indicate higher learning ability. Specifically, we take

$$(\gamma_2/\delta_2)z^* < K/(1+b) < K + D < (\gamma_1/\delta_1)z^*. \qquad [15]$$

As shown in *Effect of a Large Difference in Learning Ability*, inequality **15** together with

$$K/(K+D) < b < 1$$

imply that the high edge equilibrium

$$\hat{N}_1 = 0, \hat{N}_2 = K + D, \hat{z}_1 = 0, \hat{z}_2 = (\delta_2/\gamma_2)(K+D)$$

is the sole locally stable equilibrium. Moreover, if cyclical solutions can be ruled out, as the numerical analysis suggests, this equilibrium is globally stable, entailing competitive exclusion of population 1 (Neanderthals) by population 2 (modern humans) from all initial conditions. We can interpret this result to mean that, no matter how small an invading population of modern humans, given this large advantage in learning ability, they could replace a resident population of Neanderthals, no matter how large. The less stringent inequality obtained by setting $b = 0$ in **15** ensures a globally stable small population−low culture level equilibrium for population 1 in isolation and a globally stable large population−high culture level equilibrium for population 2 in isolation (13).

Feedback of Culture Level on Competition. Ecological competition coefficients between populations with different culture levels may be functions of this difference, rather than simple constants. We return to our assumption that the two populations are equivalent with respect to the cognition, competition, and growth parameters $[\gamma_1 = \gamma_2, \delta_1 = \delta_2, r_1 = r_2, M_1(z_1) = M_2(z_2)]$. However, we now assume that the competition coefficients, b_{ij}, are not constant but depend on the instantaneous culture levels of the two populations. A simple version of this sets

$$b_{ij} = b_0(1 + \epsilon(z_j - z_i)), \qquad [16]$$

where b_0 and ϵ are positive constants, and $z_j - z_i$ is the signed difference in the culture levels of populations *i* and *j* ($i = 1, 2$, $j \neq i$). For Eq. **1** to be meaningful, ϵ must be chosen small enough that b_{12} and b_{21} both remain positive.

In Eq. **16**, $b_{ij} > b_{ji}$ if and only if $z_j > z_i$; that is, the population with the higher culture level has a linear competitive edge. Introduction of Eq. **16** into Eq. **1** induces positive feedback, whereby a population (2, say) that enjoys a small initial cultural advantage (i.e., $z_2 > z_1$) is able to compound that advantage by first competing more strongly (because $b_{12} > b_{21}$), which then increases its population size (N_2), and in turn increases its culture level via Eq. **2**, which in turn further increases its competitive edge. Hence, we expect and find that this feedback enhances the effect of an initial cultural advantage (Fig. 3*A*).

The feedback model has the same edge and symmetric coexistence equilibria as occur in the model without feedback. The conditions for the existence of these equilibria are unchanged. The conditions for their local stability are given in *Local Stability with Feedback*. Fig. 3*A* shows that the minimum N_2^0/N_1^0 necessary for competitive exclusion decreases as ϵ increases. Fig. 3*B* is a phase diagram illustrating when different solutions exist and are
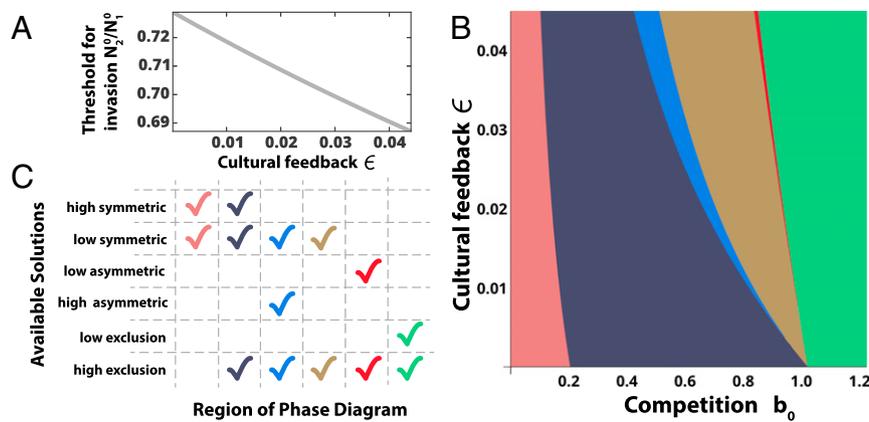
Fig. 3. Effect of competition feedback on coexistence. (*A*) The ε dependence of the ratio N_2^0/N_1^0 necessary for population 2 with culture level $z_2^0 = (\delta/\gamma)(K + D)$ to exclude population 1 at the low edge equilibrium 11. (*B*) An analytic phase diagram of the effect of the feedback ε and competition amplitude b_0 on existence and local stability of each equilibrium in the feedback model. (*C*) A legend showing the stable equilibria available in each of the six regions, listed from left to right with matching colors. All parameters except ε and b_0 are as given in Fig. 1.

stable for different values of (b_0, ϵ). The contours demarcating the various regions are determined analytically by the maximum eigenvalues of the Jacobian matrix associated with these equilibria. In general, as ε or b_0 increases, feedback causes coexistence solutions to become unstable in favor of exclusion. This includes the classical Lotka−Volterra case ($\epsilon = 0$, horizontal axis in Fig. 3*B*) where coexistence becomes unstable when $b_0 > 1$.

Somewhat surprising is the existence and stability of a new class of asymmetrical internal equilibria. These equilibria occur in pairs, either both above or below the step ($\hat{z}_1 < \hat{z}_2 < z^*$ and $\hat{z}_2 < \hat{z}_1 < z^*$, or $z^* < \hat{z}_1 < \hat{z}_2$ and $z^* < \hat{z}_2 < \hat{z}_1$). *Asymmetrical Internal Equilibria with Feedback* derives analytical conditions for their existence and reports a perturbation analysis suggesting that existence implies local stability. However, determination of local stability proves difficult in general, and we check for local stability by numerically obtaining the eigenvalues of the characteristic polynomial. We find that these solutions are, in fact, locally stable whenever they exist (at least for the parameter values assumed in Fig. 3*B*, blue and red regions).

Discussion

It is likely that Neanderthals went extinct and were replaced by modern humans due to interspecific competition for overlapping resources. Modern humans are believed to have gradually expanded their range into areas inhabited by Neanderthals (and other archaic humans) by a process of iterative propagule formation. This serial founder scenario receives support from a genetic study showing a regular reduction in heterozygosity with distance from a putative origin in Africa (37). The size of each such propagule may have been about 0.09–0.18 that of the parental population (34). These considerations suggest that a modern human group would have been smaller than a Neanderthal one at initial contact. Our paper reports the theoretical conditions under which such a numerical disadvantage could have been more than compensated by an advantage in culture level or learning ability. Note that in ref. 5, the term "ecocultural" refers to the relationship between environmental niches occupied by Neanderthals and modern humans, overlap in which may have led to competition.

In deriving these theoretical conditions, we have made two critical assumptions, which we now discuss. First, we have assumed that the culture level of the invading modern human population at first contact would have shown systematic positive deviations from the quasi-equilibrium value. Specifically, we assume that propagule formation does not entail a significant loss of cultural traits due to the founder effect, as it may for genetic variation. The fundamental difference between genetic and cultural transmission in

humans is that an individual inherits only a small subset of the genetic variation present in the population into which he/she is born (unless that population is highly inbred), but there is no such intrinsic limitation on the acquisition of cultural traits (38).

A caveat that immediately comes to mind here is division of labor. However, division of labor may not be pronounced in hunter−gatherer societies except between the sexes, and a viable propagule that comprises both reproductive males and females should initially lack few of the cultural traits in its parental population, and its culture level may therefore approximate that of the parental population. This situation may be maintained if time between propagule formation and first contact is short. (Eventually, quasi-equilibrium will be reached according to Eq. **2**, but, by then, the propagule will also have grown in size.) On the other hand, expert makers of sophisticated artifacts are likely few, so the cultural founder effect (and hence random cultural drift) cannot be completely neglected (39).

Second, we have assumed that the timescales of demographic and cultural change may differ, specifically that the potential rate of population growth may be an order of magnitude higher than the potential rate of cultural change. Richerson et al. suggest that this may be true for the Late Pleistocene and most of the Holocene (32). In extant hunter−gatherers, the intrinsic growth rate (r_i in our model) is of the order of 1% per year (40, 41). The realized growth rate during the Paleolithic, however, was likely much lower (42). We know of no direct evidence bearing on the cultural decay rate (γ_i) or the per capita upgrade innovation rate (δ_i) in hunter−gatherers. Here we cite two observations relevant to our assumption. One is the so-called "Tasmanian effect" in which a small isolated population loses many valuable skills and technologies. Because the reduction in the culture level of the eponymous Tasmanian hunter−gatherers occurred over a period of 5,000 y during the Holocene (16), we infer that the realized rate of cultural change was low. However, in the framework of our model, it is not clear whether this was because cultural decay was partially balanced by countervailing innovation—i.e., the first and second terms on the right-hand side of Eq. **2** were perhaps large but of similar magnitude—or because the cultural decay rate itself was small.

The other observation concerns the variation in Acheulean handaxe dimensions produced (by hominids ancestral to both Neanderthals and modern humans) over a time span of 1.2 million years. Based on a simulation model, Kempe et al. suggest that this is consistent with a copying error rate of 0.17% per generation, which is low compared with the intrinsic population growth rate and supports our assumption (43). The error rate associated with

simple social learning has been estimated in laboratory transmission chain experiments (with extant humans as subjects). In one such experiment (43), each participant in a transmission chain was tasked to view and faithfully reproduce, on an iPad screen, the size of a handaxe image made by the previous participant. The estimated error rate was of the order of 3% per act of copying. Kempe et al. suggest possible reasons for this major discrepancy; for example, unlike the Paleolithic knappers, the experimental subjects could not actually handle their artifacts and thereby reduce the copying error rate.

These assumptions (minimal cultural founder effect, different timescales of demographic and cultural change) were not invoked in our analysis of a difference in learning ability. We found that replacement of Neanderthals by modern humans was assured, given a large advantage in learning ability to the latter (inequality **15**) and provided an auxiliary condition was also met. However, it may be unrealistic to assume an innate cognitive difference of this magnitude between these two closely related species. A smaller difference in learning ability may be sufficient to drive the replacement process, if the assumptions on cultural dynamics discussed immediately above apply even partially.

Although our model defined by Eqs. **1–3** is simple, it preserves the qualitatively important features arising from the interaction between population size and culture level that are seen in more detailed models (13). However, two other assumptions also made in the interest of simplicity require comment here. First, we have neglected cultural/technological transfer between the competing populations. Acculturation of European Neanderthals by modern humans has been a hotly debated issue (44, 45), and, in eastern Eurasia, there is strong evidence for archaeological continuity, perhaps due to the reverse acculturation of incoming modern humans by the resident archaic humans (46, 47). Second, we have ignored the demographic and cultural consequences of interbreeding. Introgression of Neanderthal genes is small in scale (1, 2) but may have affected male fertility (48). Clearly, these considerations must be kept in mind.

The replacement process predicted by our ecocultural model can be "self-perpetuating." That is, given moderate competition ($b_{12} = b_{21} = b \approx 0.5$), a modern human population that has replaced a regional Neanderthal population will be large and at a high culture level (e.g., Fig. 2A, *Middle*). Hence, it will be in a position to generate a new propagule to invade the next area still occupied by Neanderthals. The resulting spatial effects could also have important consequences.

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