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Abstract

Early modern humans interbred with archaic humans. To explore this phenomenon, we develop a Malthusian growth model with hybridization in human evolution. Our hunting-gathering Malthusian economy features two initial human populations. We derive population dynamics and find that the more fertile population survives whereas the less fertile one eventually becomes extinct. During this natural-selection process, a hybrid human population emerges and survives in the long run. This finding explains why modern humans still carry DNA from archaic humans. A higher hybridization rate reduces long-run population size but raises long-run output per capita for the surviving populations in this Malthusian economy.

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1 Introduction

Homo sapiens emerged on this planet about 300,000 years ago. During most of this time, early modern humans not only shared this planet with archaic humans but also interbred with them. A prominent example of an archaic human species that interbred with early modern humans is *Homo neanderthalensis*, commonly known as the Neanderthals.[1] As a result of this hybridization in human evolution, most modern humans still carry some proportion of Neanderthal-derived DNA; for example, Prufer *et al.* (2017) report estimates of 2.3-2.6% of Neanderthal-derived DNA in East Asians and 1.8-2.4% in Western Eurasians.[2]

Given the importance of interbreeding between archaic and modern humans, what are its economic implications? To explore this question, this study develops a Malthusian growth model with different human species and provides a novel economic analysis on interbreeding between human species. In our Malthusian economy, there are initially two human populations (e.g., early modern humans and the Neanderthals), which engage in food production in the form of hunting-gathering. We analytically derive the population dynamics in this Malthusian economy. In the long run, the more fertile human population survives, whereas the less fertile one becomes extinct, capturing the Neanderthal extinction. During this process of natural selection, a hybrid human population emerges and survives in the long run if it continues to interbreed with the initial human population that survives. This finding may help explain why modern humans still carry Neanderthal DNA.[3]

An increase in the hybridization rate reduces the long-run population size but raises the long-run levels of food output per capita for both surviving populations. At the steady state, the hybrid population as a share of the total human population is increasing in the hybridization rate and the Malthusian potential of the hybrid population (which is increasing in its hunting-gathering productivity and degree of fertility preference but decreasing in the fertility cost). If the Malthusian potential of the hybrid human population is sufficiently high, it may even dominate the population as the only surviving human species, capturing the possibility that all modern humans are hybrid descendents of archaic and early modern humans.

This study relates to the literature on evolutionary growth theory, which explores natural selection in the Malthusian growth model. A seminal study in this literature is Galor and Moav (2002), who consider how natural selection and the quality-quantity tradeoff of children determine the endogenous transition of an economy from stagnation to growth. Subsequent studies in this influential literature include Lagerlof (2007), Galor and Michalopoulos (2012), Collins *et al.* (2014), Dalgaard and Strulik (2015), Galor and Ozak (2016) and Galor and Klemp (2019).[4] This study relates most closely to Chu (2023), who explores the Neanderthal extinction in a similar Malthusian economy.[5] The present study generalizes the analysis in Chu (2023) by introducing the interbreeding of human species to the model. Another recent study by Chu (2024) explores

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[1]Another example is the Denisovans, who also interbred with early modern humans; see Krause *et al.* (2010).

[2]An earlier scientific consensus is that only non-Africans carry Neanderthal DNA, but recent evidence suggests that Africans may also carry Neanderthal DNA of up to 0.3%; see Price (2020).

[3]Modern humans with Neanderthal DNA can be viewed as descendents of the hybrid population in our model, whereas those without Neanderthal DNA are non-hybrid descendents of the initial *Homo sapiens* population.

[4]See Ashraf and Galor (2018) for a survey of this literature.

[5]See also Horan *et al.* (2005) for an economic model of two interacting human species with different degrees of biological efficiency, in which extinction occurs to the species with a lower degree of biological efficiency unless trade is present and offsets these biological deficiencies.

the causes and consequences of human brain evolution also in the Malthusian growth model.[6]

This study also relates to the evolutionary biology literature on population genetics. A seminal model of population genetics is the Wright-Fisher model of genetic drift developed by Fisher (1922, 1930) and Wright (1931).[7] Subsequent studies extend the Wright-Fisher model with a fixed population size to capture interbreeding of human species; see for example, Neves and Serva (2012) and Serva (2015). We take a different approach in this study by using a microfounded Malthusian growth model with endogenous population growth to explore the economic implications of interbreeding between archaic and early modern humans.

2 A Malthusian model with human interbreeding

The Malthusian growth model is based on the seminal work of Malthus (1798).[8] In this section, we extend the canonical Malthusian growth model in Ashraf and Galor (2011) to consider two human populations as in Chu (2023) but incorporate the novel element of interbreeding that gives rise to a hybrid human population. There are two initial groups of humans,[9] who engage in hunting-gathering within a fixed area of land Z. These two initial species of humans are indexed by superscript $i \in \{a, s\}$. The human species s denotes *Homo sapiens*, whereas the human species a refers to an archaic human species, such as the Neanderthals. The hybrid human species that emerges as a result of interbreeding is indexed by superscript h.

2.1 Fertility and interbreeding

At time 0, there are N_0^i agents in each human group $i \in \{a, s\}$. Each agent lives for two periods, and each adult agent of group i at time t has the following utility function:

$$u_t^i = (1 - \gamma^i) \ln c_t^i + \gamma^i \ln n_t^i, \tag{1}$$

in which the parameter $\gamma^i \in (0, 1)$ determines human group i's preference for fertility, n_t^i is the number of children per adult agent in this group, and c_t^i is the agent's consumption level. The resource constraint faced by each adult agent in group i is given by

$$c_t^i + \rho^i n_t^i = y_t^i, \tag{2}$$

where the parameter $\rho^i > 0$ determines human group i's fertility cost and y_t^i is the per capita level of food production in this group. We substitute (2) into (1) to derive the utility-maximizing fertility rate n_t^i of group i as

$$n_t^i = \frac{\gamma^i}{\rho^i} y_t^i \tag{3}$$

and consumption as $c_t^i = (1 - \gamma^i) y_t^i$.

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[6]See also Chu and Xu (2024) on the Malthusian transition from the Neolithic Revolution to the Industrial Revolution and Chu *et al.* (2024) on the Malthusian transition from political fragmentation to unification.

[7]See Ishida and Rosales (2020) for a review on the intellectual origins of the Wright-Fisher model.

[8]See Ehrlich and Lui (1997) for a review on the intellectual origins of the Malthusian model.

[9]We consider $m \geq 2$ initial human groups in Appendix A, and our results remain robust.

The number of adult agents in group i at the beginning of time t is N_t^i. Each adult agent, who remains in group i, has n_t^i children; however, a share $\sigma^i \in (0,1)$ of the N_t^i adult agents leaves group i and engages in interbreeding with the other human population group j.[10] Therefore, the law of motion for the adult population size of group i is

$$N_{t+1}^i = n_t^i(1-\sigma^i)N_t^i = (1-\sigma^i)\frac{\gamma^i}{\rho^i}y_t^i N_t^i, \tag{4}$$

where the second equality uses (3). Then, the growth rate of N_t^i at time t is

$$\frac{\Delta N_t^i}{N_t^i} = (1-\sigma^i)\frac{\gamma^i}{\rho^i}y_t^i - 1, \tag{5}$$

which will be referred to as the population growth rate of group i.

At the beginning of time 0, the population size of the hybrid group is zero. However, $\sigma^s N_0^s + \sigma^a N_0^a$ agents from the two initial groups join the hybrid group h and give birth to $n_0^h(\sigma^s N_0^s + \sigma^a N_0^a)$ hybrid children.[11] We assume that all agents joining or being born in the hybrid group h have the same preference $u_t^h = (1-\gamma^h)\ln c_t^h + \gamma^h \ln n_t^h$. As a result, the fertility rate of the hybrid group h at time t is

$$n_t^h = \frac{\gamma^h}{\rho^h}y_t^h. \tag{6}$$

Then, the law of motion for the adult population size of the hybrid group at time t is

$$N_{t+1}^h = n_t^h\left(N_t^h + \sigma^s N_t^s + \sigma^a N_t^a\right) = \frac{\gamma^h}{\rho^h}y_t^h\left(N_t^h + \sigma^s N_t^s + \sigma^a N_t^a\right), \tag{7}$$

and its population growth rate at time t is

$$\frac{\Delta N_t^h}{N_t^h} = \frac{\gamma^h}{\rho^h}y_t^h\left(1 + \frac{\sigma^s N_t^s + \sigma^a N_t^a}{N_t^h}\right) - 1. \tag{8}$$

2.2 Hunting-gathering

Each agent in group $i \in \{s, a, h\}$ receives y_t^i units of food output from hunting-gathering given by

$$y_t^i = \theta^i(l^i)^\alpha\left(\frac{Z}{N_t}\right)^{1-\alpha}, \tag{9}$$

where the parameter $\theta^i > 0$ determines hunting-gathering productivity, the parameter $l^i > 0$ denotes hunting-gathering labor with intensity $\alpha \in (0,1)$, the parameter $Z > 0$ is the total amount of land, and $N_t = N_t^s + N_t^a + N_t^h$ is the total population size at time t. Therefore, Z/N_t is the amount of land per capita at time t.

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[10] We follow Neves and Serva (2012) to assume that "at each generation a number α of randomly extracted individuals from subpopulation 1 migrates to subpopulation 2". Our difference is that they join a hybrid population.

[11] The number of agents joining the hybrid group h from the two groups $i \in \{a, s\}$ do not have to be equal, as one agent can mate with multiple agents.

2.3 Population dynamics and hybridization in human evolution

Substituting (9) into (3) and (6) yields the rate of fertility in group $i \in \{s, a, h\}$ as

$$n_t^i = \frac{\gamma^i}{\rho^i} \theta^i (l^i)^\alpha \left(\frac{Z}{N_t}\right)^{1-\alpha} = \Omega^i \left(\frac{Z}{N_t}\right)^{1-\alpha}, \tag{10}$$

where we define the composite parameter $\Omega^i \equiv \gamma^i \theta^i (l^i)^\alpha / \rho^i$ as the Malthusian potential of group i. It is useful to note that this Malthusian-potential parameter Ω^i is increasing in hunting-gathering productivity θ^i, labor supply l^i and fertility preference γ^i but decreasing in fertility cost ρ^i. We substitute (10) into (4) to derive the population dynamics of group $i \in \{s, a\}$ as

$$N_{t+1}^i = (1 - \sigma^i) \Omega^i \left(\frac{Z}{N_t}\right)^{1-\alpha} N_t^i. \tag{11}$$

Similarly, we substitute (10) into (7) to derive the population dynamics of the hybrid group h as

$$N_{t+1}^h = \Omega^h \left(\frac{Z}{N_t}\right)^{1-\alpha} N_t^h \left(1 + \sigma^i \frac{N_t^i}{N_t^h} + \sigma^j \frac{N_t^j}{N_t^h}\right). \tag{12}$$

Combining (11) and (12) yields the relative population size between group $i \in \{s, a\}$ and the hybrid group h as

$$\frac{N_{t+1}^i}{N_{t+1}^h} = \frac{(1 - \sigma^i) \Omega^i / \Omega^h}{1 + \sigma^i \frac{N_t^i}{N_t^h} + \sigma^j \frac{N_t^j}{N_t^h}} \frac{N_t^i}{N_t^h}. \tag{13}$$

If we define $x_t^i \equiv N_t^i / N_t^h$ for $i \in \{s, a\}$, then (13) simplifies to

$$x_{t+1}^i = \frac{(1 - \sigma^i) \Omega^i / \Omega^h}{1 + \sigma^i x_t^i + \sigma^j x_t^j} x_t^i. \tag{14}$$

From (14), the growth rate of x_t^i is given by

$$\frac{\Delta x_t^i}{x_t^i} = \frac{(1 - \sigma^i) \Omega^i / \Omega^h}{1 + \sigma^i x_t^i + \sigma^j x_t^j} - 1. \tag{15}$$

At the steady state, the $\Delta x_t^i = 0$ locus can be expressed as

$$\Delta x_t^i = 0 \Rightarrow x^i = \frac{1}{\sigma^i} \left[\frac{(1 - \sigma^i) \Omega^i}{\Omega^h} - 1 - \sigma^j x^j\right]. \tag{16}$$

Similarly, the $\Delta x_t^j = 0$ locus can be expressed as

$$\Delta x_t^j = 0 \Rightarrow x^i = \frac{1}{\sigma^i} \left[\frac{(1 - \sigma^j) \Omega^j}{\Omega^h} - 1 - \sigma^j x^j\right]. \tag{17}$$

Then, we plot the phase diagram for the dynamics of x_t^i in (15)-(17) for $i \in \{s, a\}$ and assume $(1 - \sigma^s) \Omega^s > (1 - \sigma^a) \Omega^a$. We first consider the case $(1 - \sigma^s) \Omega^s > \Omega^h$ as our benchmark scenario.
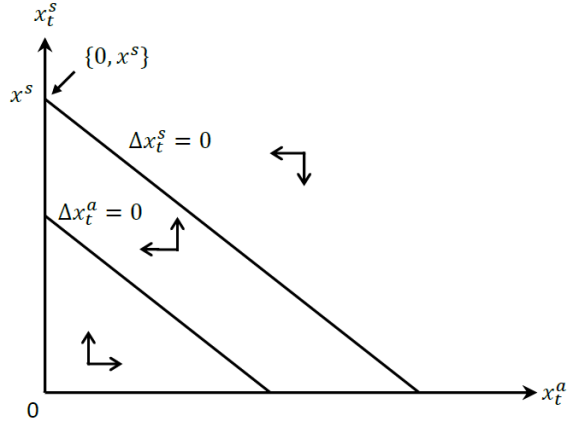
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Figure 1: Phase diagram

Figure 1 shows that $x_t^a \to 0$, implying the extinction of archaic humans, and $x_t^s \to x^s > 0$, implying the survival of early modern humans.[12] Given the parameter assumption $(1-\sigma^s)\Omega^s > \Omega^h$, the steady-state value of x_t^s is given by

$$x^s = \frac{(1 - \sigma^s)\Omega^s - \Omega^h}{\sigma^s \Omega^h}. \tag{18}$$

Equation (18) then implies that the steady-state population ratio N^h/N^s is given by[13]

$$\frac{N^h}{N^s} = \frac{\sigma^s \Omega^h}{(1 - \sigma^s)\Omega^s - \Omega^h}, \tag{19}$$

which is increasing in the hybridization rate σ^s and the hybrid human group's Malthusian potential Ω^h but decreasing in early modern humans' Malthusian potential Ω^s. The hybrid population survives despite its lower Malthusian potential due to its continued hybridization with early modern humans. From (11), the steady-state level of total population is given by

$$N = N^s + N^h = [(1 - \sigma^s)\Omega^s]^{1/(1-\alpha)}Z, \tag{20}$$

which is increasing in land supply Z and early modern humans' Malthusian potential Ω^s but decreasing in their hybridization rate σ^s. Although the long-run level of population N is decreasing in the hybridization rate due to the hybrid population h having a lower Malthusian potential than early modern humans (i.e., $\Omega^s > (1 - \sigma^s)\Omega^s > \Omega^h$), the long-run levels of food output per capita for both early modern humans s and the hybrid population h are increasing in the hybridization rate σ^s due to the Malthusian mechanism. To see this, substituting (20) into (9) yields

$$y^i = \frac{\theta^i (l^i)^\alpha}{(1 - \sigma^s)\Omega^s} \tag{21}$$

and $\partial y^i/\partial \sigma^s > 0$ for $i \in \{s, h\}$. We summarize the above results in Proposition 1.

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[12] See also Chu (2023) for a similar result. The novelty here is on the emergence of a hybrid population.

[13] Here, we assume that early modern humans continue to interbreed with the hybrid population after the archaic humans become extinct.

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Proposition 1 *Given $(1 - \sigma^s)\Omega^s > \max\{\Omega^h, (1 - \sigma^a)\Omega^a\}$, archaic humans (group a) eventually become extinct, whereas early modern humans (group s) and hybrid humans (group h) survive in the long run. The steady-state total population size N is decreasing in the hybridization rate σ^s, whereas the steady-state levels of food output per capita for both early modern humans s and hybrid humans h are increasing in the hybridization rate σ^s.*

Before concluding, we also discuss the other case $\Omega^h > \max\{(1 - \sigma^s)\Omega^s, (1 - \sigma^a)\Omega^a\}$ as an alternative scenario. In this case, the population growth rate of the hybrid group h from (8) is

$$\frac{\Delta N_t^h}{N_t^h} = \Omega^h \left(\frac{Z}{N_t}\right)^{1-\alpha} \left(1 + \frac{\sigma^i N_t^i + \sigma^j N_t^j}{N_t^h}\right) - 1, \tag{22}$$

whereas the population growth rate of human group $i \in \{s, a\}$ from (5) is

$$\frac{\Delta N_t^i}{N_t^i} = (1 - \sigma^i)\Omega^i \left(\frac{Z}{N_t}\right)^{1-\alpha} - 1. \tag{23}$$

Equations (22) and (23) show that $\Delta N_t^h/N_t^h > \Delta N_t^i/N_t^i$ even when $N_t^i = N_t^j = 0$ given $\Omega^h > \max\{(1 - \sigma^s)\Omega^s, (1 - \sigma^a)\Omega^a\}$. Therefore, it must be the case that the hybrid population dominates the entire human population in the long run such that[14]

$$N_t^h \to N = (\Omega^h)^{1/(1-\alpha)} Z, \tag{24}$$

which is increasing in the supply of land Z and hybrid humans' Malthusian potential Ω^h. Finally, the long-run level of food output per capita for the hybrid population h is given by

$$y^h = \frac{\theta^h (l^h)^\alpha}{\Omega^h} = \frac{\rho^h}{\gamma^h}, \tag{25}$$

which depends on fertility preference γ^h and cost ρ^h. We summarize the results in Proposition 2.

Proposition 2 *Given $\Omega^h > \max\{(1 - \sigma^s)\Omega^s, (1 - \sigma^a)\Omega^a\}$, both early modern humans (group s) and archaic humans (group a) eventually become extinct, whereas hybrid humans (group h) survive in the long run. The steady-state population size is given in (24), whereas the steady-state level of food output per capita is given in (25).*

3 Conclusion

In this study, we have developed a Malthusian growth-theoretic framework to explore interbreeding between archaic and early modern humans. We have analytically derived population dynamics and shown that the archaic human group becomes extinct whereas the group of early modern humans survives. More importantly, a hybrid human group emerges and also survives in the human population due to the continued hybridization with early modern humans. This finding may help explain the fact that modern humans still carry some Neanderthal-derived DNA.

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[14]In this case, the vertical intercepts of both $\Delta x_t^s = 0$ and $\Delta x_t^a = 0$ loci in Figure 1 would be below zero, implying that $\{x_t^s, x_t^a\} \to 0$.

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Appendix A

In this appendix, we consider an arbitrary number $m \geq 2$ of initial human groups $i \in \{1, ..., m\}$, along with the subsequent emergence of a hybrid human group h. The rest of the model is the same as before. In this case, the relative population size between group $i \in \{1, ..., m\}$ and the hybrid group h in (13) becomes

$$\frac{N_{t+1}^i}{N_{t+1}^h} = \frac{(1 - \sigma^i)\Omega^i/\Omega^h}{1 + \sum_{j=1}^m \sigma^j \frac{N_t^j}{N_t^h}} \frac{N_t^i}{N_t^h}. \tag{A1}$$

Defining $x_t^i \equiv N_t^i/N_t^h$ for $i \in \{1, ..., m\}$ as before yields

$$x_{t+1}^i = \frac{(1 - \sigma^i)\Omega^i/\Omega^h}{1 + \sum_{j=1}^m \sigma^j x_t^j} x_t^i. \tag{A2}$$

Then, the growth rate of x_t^i is given by

$$\frac{\Delta x_t^i}{x_t^i} = \frac{(1 - \sigma^i)\Omega^i/\Omega^h}{1 + \sum_{j=1}^m \sigma^j x_t^j} - 1, \tag{A3}$$

which shows that the human group i with the largest $(1 - \sigma^i)\Omega^i > (1 - \sigma^j)\Omega^j$ for all $j \neq i$ would have the highest growth rate $\Delta x_t^i/x_t^i$ at all time t. Therefore, as $\Delta x_t^i/x_t^i \to 0$, the growth rates of all other groups $j \neq i$ would become negative (i.e., $\Delta x_t^j/x_t^j < 0$), implying that $x_t^j \to 0$ for all $j \neq i$. In this case, the initial human group i with the largest $(1 - \sigma^i)\Omega^i$ survives in the long run, and so does the hybrid human group h. Let's use s to denote the surviving initial human group. In this case, the steady-state value x^s is the same as (18), and the steady-state population ratio N^h/N^s is the same as (19), which implicitly assumes $(1 - \sigma^s)\Omega^s > \Omega^h$.

Suppose $\Omega^h > (1 - \sigma^i)\Omega^i$ for all $i \in \{1, ..., m\}$ instead. Then, we compare (23) with the modified version of (22) given by

$$\frac{\Delta N_t^h}{N_t^h} = \Omega^h \left(\frac{Z}{N_t}\right)^{1-\alpha} \left(1 + \sum_{i=1}^m \frac{\sigma^i N_t^i}{N_t^h}\right) - 1, \tag{A4}$$

which shows that $\Delta N_t^h/N_t^h > \Delta N_t^i/N_t^i$ even when $N_t^i = 0$ for all $i \in \{1, ..., m\}$. In this case, the hybrid human group h dominates the entire human population in the long run, as before; i.e., $N_t^h \to N = (\Omega^h)^{1/(1-\alpha)} Z$.