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# A Malthusian Model of Hybridization in Human Evolution

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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 the conditions for a hybrid human population to emerge and survive in the long run, which 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. A sufficiently high hybridization rate may even cause the hybrid human population to dominate the population as the only surviving human species. This result captures the probable scenario that all modern humans are hybrid descendants of archaic and early modern humans and provides the following novel insight: modern humans, which emerged from interbreeding, may have caused the extinction of archaic humans and non-hybrid early modern humans. Finally, we also use the Malthusian model to shed some light on the proportion of Neanderthal DNA in the modern human population.

*JEL classification:* O13, Q56, N10

*Keywords:* Ancient human interbreeding, natural selection, Malthusian model

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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.<sup>1</sup> 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.

Given the importance of interbreeding between archaic and early 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. This finding may help explain why modern humans still carry Neanderthal DNA. In this case, modern humans with Neanderthal DNA can be viewed as descendants of the hybrid population in our model; furthermore, if there are modern humans without any Neanderthal DNA, they would be non-hybrid descendants of the initial early modern humans.

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 hybridization rate or the Malthusian potential of the hybrid human population is sufficiently high, it may even dominate the population as the only surviving human species. This result provides a novel insight that the hybrid human population, which emerges as a result of interbreeding, may give rise to the extinction of the initial non-hybrid populations. This scenario captures the probable case that all modern humans are hybrid descendants of archaic and early modern humans. An earlier scientific consensus is that only non-Africans carry Neanderthal DNA, but recent evidence suggests that Africans also carry Neanderthal DNA of up to 0.3%; see Price (2020). Finally, we also use the Malthusian model to shed some light on the proportion of Neanderthal DNA in the modern human population.

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

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

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).<sup>2</sup> This study relates most closely to Chu (2023), who explores the Neanderthal extinction in a similar Malthusian economy.<sup>3</sup> The present study generalizes the analysis in Chu (2023) by introducing the interbreeding of human species to the model and shows that the new hybrid human species may give rise to the extinction of early human species. Another recent study by Chu (2025a) explores the causes and consequences of human brain evolution also in the Malthusian growth model.<sup>4</sup>

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).<sup>5</sup> 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 how interbreeding between archaic and early modern humans affects their survival in a Malthusian economy and show how the hybridization rate affects the size of population and the level of output per capita in the economy.

The rest of this paper is organized as follows. Section 2 presents the Malthusian model. Section 3 explores two scenarios on the survival and extinction of early modern humans. Section 4 concludes.

## 2 A Malthusian model with human interbreeding

The Malthusian growth model is based on the seminal work of Malthus (1798).<sup>6</sup> 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,<sup>7</sup> 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

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<sup>2</sup>See Galor (2005, 2011, 2022) and Ashraf and Galor (2018) for a survey of this literature.

<sup>3</sup>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.

<sup>4</sup>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 political unification. Chu (2025b) provides a book treatment of these studies.

<sup>5</sup>See Ishida and Rosales (2020) for a review on the intellectual origins of the Wright-Fisher model.

<sup>6</sup>See Ehrlich and Lui (1997) for a review on the intellectual origins of the Malthusian model.

<sup>7</sup>We consider  $m \geq 2$  initial human groups in Section 4, and our results remain robust.

species, such as the Neanderthals. The hybrid human species that emerges as a result of interbreeding is indexed by superscript  $h$ . It is useful to note that we treat the hybrid human species as a homogeneous group, without considering fully the continuous nature of genetic mixing, in order to focus on the heterogeneity across the three human groups: early modern humans, archaic humans, and hybrid humans.<sup>8</sup>

## 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:

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

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

$$c_t^i + \rho^i n_t^i = y_t^i, \quad (2)$$

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

$$n_t^i = \frac{\gamma^i}{\rho^i} y_t^i \quad (3)$$

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

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  $j$ .<sup>9</sup> Therefore, the law of motion for the adult population size of group  $i$  is

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

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

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

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

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<sup>8</sup>Considering the hybrid humans as a group of heterogeneous agents would complicate our analysis substantially.

<sup>9</sup>We follow Neves and Serva (2012) to assume that "at each generation a number  $\alpha$  of randomly extracted individuals from subpopulation 1 migrates to subpopulation 2". Our difference is that they join a hybrid population.

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.<sup>10</sup> 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

$$n_t^h = \frac{\gamma^h}{\rho^h} y_t^h. \quad (6)$$

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

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

and its population growth rate at time  $t$  is

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

## 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

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

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  $t$ .

## 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

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

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  $\Omega^i$  is increasing

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<sup>10</sup>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.

in hunting-gathering productivity  $\theta^i$ , labor supply  $l^i$  and fertility preference  $\gamma^i$  but decreasing in fertility cost  $\rho^i$ . We substitute (10) into (4) to derive the population dynamics of group  $i \in \{s, a\}$  as

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

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

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

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

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

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

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

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

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

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

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

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

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

In the next section, we will plot the phase diagram for the dynamics of  $x_t^i$  in (15)-(17) for  $i \in \{s, a\}$  and assume  $(1 - \sigma^s) \Omega^s > (1 - \sigma^a) \Omega^a$ .

### 3 Survival and extinction of early modern humans

In this section, we consider two possible scenarios. Section 3.1 considers the survival of early modern humans. Section 3.2 considers the extinction of early modern humans.

### 3.1 Survival of early modern humans

We consider the case  $(1 - \sigma^s)\Omega^s > \Omega^h$  as our first scenario, which arises when the hybridization rate  $\sigma^s$  or the Malthusian potential  $\Omega^h$  of the hybrid human population is low. Figure 1 shows that  $x_t^a \rightarrow 0$ , implying the extinction of archaic humans, and that  $x_t^s \rightarrow x^s > 0$ , implying the survival of early modern humans.<sup>11</sup> Given the parameter assumption  $(1 - \sigma^s)\Omega^s > \Omega^h$ , the steady-state value of  $x_t^s$  is given by

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

Equation (18) then implies that the steady-state population ratio  $N^h/N^s$  is given by<sup>12</sup>

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

which is increasing in the hybridization rate  $\sigma^s$  and the hybrid human group's Malthusian potential  $\Omega^h$  but decreasing in early modern humans' Malthusian potential  $\Omega^s$ . The hybrid population survives despite its lower Malthusian potential due to its continued hybridization with early modern humans. This scenario captures the possibility that modern humans with Neanderthal DNA can be viewed as descendants of the hybrid population in our model; furthermore, if there are modern humans without any Neanderthal DNA, they would be non-hybrid descendants of the initial early modern humans.

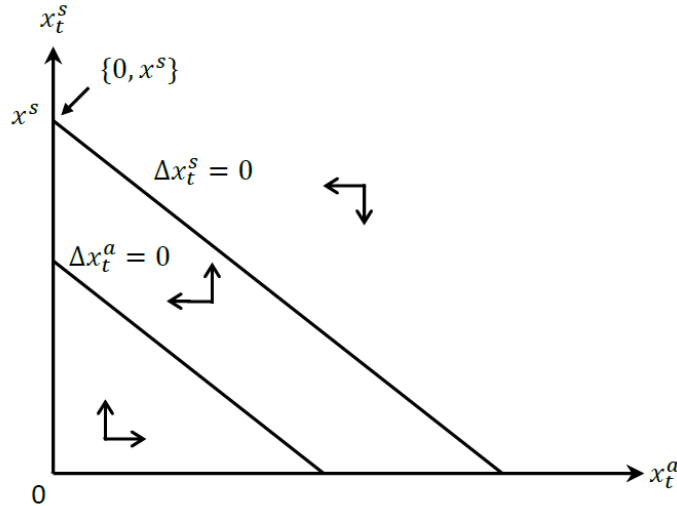


Figure 1: Survival of early modern humans

<sup>11</sup>See also Chu (2023) for a similar result. The novelty here is on the emergence of a hybrid population.

<sup>12</sup>Here, we assume that early modern humans continue to interbreed with the hybrid population after the archaic humans become extinct.

From (11), the steady-state level of total population is given by

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

which is increasing in land supply  $Z$  and early modern humans' Malthusian potential  $\Omega^s$  but decreasing in their hybridization rate  $\sigma^s$ . 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  $\sigma^s$  due to the Malthusian mechanism. To see this, substituting (20) into (9) yields

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

and  $\partial y^i / \partial \sigma^s > 0$  for  $i \in \{s, h\}$ . We summarize the above results in Proposition 1, which nests the result in Chu (2023) as a special case with  $\sigma^s = 0$  under which the hybrid population  $h$  does not emerge. The next section considers another parameter space in which the hybrid population  $h$  not only emerges but also gives rise to the extinction of both archaic humans and early modern humans.

**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  $\sigma^s$ , 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  $\sigma^s$ .*

### 3.2 Extinction of early modern humans

We now discuss the other case  $\Omega^h > (1 - \sigma^s)\Omega^s$  as the second scenario, which arises when the hybridization rate  $\sigma^s$  or the Malthusian potential  $\Omega^h$  of the hybrid human population is high. In this case, the population growth rate of the hybrid group  $h$  from (8) is

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

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

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

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  $\Omega^h > (1 - \sigma^s)\Omega^s > (1 - \sigma^a)\Omega^a$ . Therefore, it must be the case that the hybrid population dominates the entire human population in the long run. 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  $\{x_t^s, x_t^a\} \rightarrow 0$  as in Figure 2. This scenario captures the possibility that all modern humans are hybrid descendants of archaic and early modern humans, which seems to be the more likely scenario given the presence of Neanderthal DNA in all modern humans, both within and outside Africa.

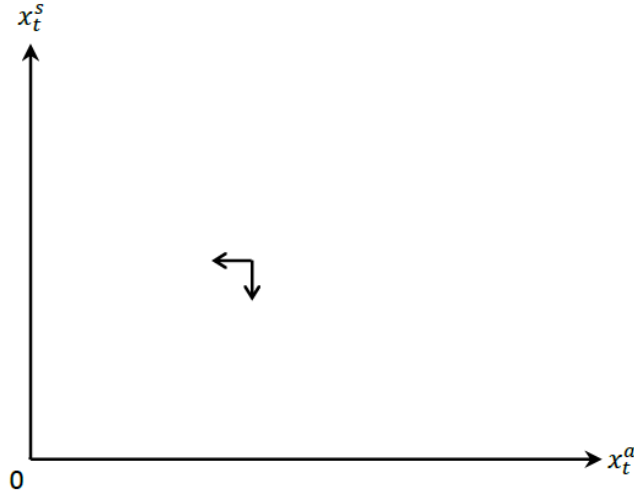


Figure 2: Extinction of early modern humans

In this case, the total level of human population converges to

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

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

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

which depends on fertility preference  $\gamma^h$  and fertility cost  $\rho^h$ . We summarize the results in Proposition 2.

**Proposition 2** *Given  $\Omega^h > (1 - \sigma^s)\Omega^s > (1 - \sigma^a)\Omega^a$ , 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).*

### 3.3 Proportion of Neanderthal DNA in the modern population

In this section, we explore the proportion of Neanderthal DNA in the modern population. Although our Malthusian model is not designed as a quantitative model of genetic mixing, we can shed some light on this issue by assuming that the proportion of Neanderthal DNA in the population is determined by the proportion of Neanderthal descendants in the hybrid population. Given this assumption, the population share (and also genetic share)  $s_T^a$  of archaic humans in the hybrid population at time  $T \geq 1$  is given by

$$s_T^a = \frac{\sum_{t=0}^{T-1} \left( \prod_{\tau=t}^{T-1} n_\tau^h \sigma^a N_t^a \right)}{\sum_{t=0}^{T-1} \left( \prod_{\tau=t}^{T-1} n_\tau^h \sigma^a N_t^a \right) + \sum_{t=0}^{T-1} \left( \prod_{\tau=t}^{T-1} n_\tau^h \sigma^s N_t^s \right)}, \quad (26)$$

where  $\prod_{\tau=t}^{T-1} n_\tau^h \sigma^a N_t^a$  is the hybrid descendants at time  $T > t$  of the Neanderthal population  $\sigma^a N_t^a$  who joins the hybrid population at time  $t$ . Due to the Neanderthal extinction,  $N_t^a$  eventually converges to zero.

In the case of the survival of early modern humans, the population size of the non-hybrid descendants  $N_t^s$  of the initial early modern humans remains positive for all time  $t$ , whereas the population size of the non-hybrid Neanderthal descendants  $N_t^a$  becomes zero after a certain point in time due to their extinction. Therefore, the genetic share of Neanderthal DNA in the hybrid human population eventually becomes zero as more and more descendants of non-hybrid early modern humans join the hybrid population.

In the case of the extinction of early modern humans, the population size of the non-hybrid descendants  $N_t^s$  of the initial early modern humans also becomes zero after a certain point of time. In this case, the genetic share of Neanderthal DNA in the hybrid population remains positive and depends on the final population size of the non-hybrid early modern humans and the final population size of the non-hybrid Neanderthals. If non-hybrid early modern humans remain in the human population for a much longer time than non-hybrid Neanderthals, then the proportion of Neanderthal DNA in the modern hybrid human population would be small but remain positive indefinitely. This implication is consistent with the fact that all modern humans carry a small but non-negligible proportion of Neanderthal DNA.

## 4 An arbitrary number of initial human groups

In this section, we consider an arbitrary number  $m \geq 2$  of initial human groups  $i \in \{1, \dots, m\}$ , 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  $i \in \{1, \dots, m\}$  and the hybrid group  $h$  in (13) becomes

$$\frac{N_{t+1}^i}{N_{t+1}^h} = \frac{(1 - \sigma^i) \Omega^i / \Omega^h}{1 + \sum_{j=1}^m \sigma^j \frac{N_t^j}{N_t^h}} \frac{N_t^i}{N_t^h}. \quad (27)$$

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

$$x_{t+1}^i = \frac{(1 - \sigma^i)\Omega^i/\Omega^h}{1 + \sum_{j=1}^m \sigma^j x_t^j} x_t^i. \quad (28)$$

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

$$\frac{\Delta x_t^i}{x_t^i} = \frac{(1 - \sigma^i)\Omega^i/\Omega^h}{1 + \sum_{j=1}^m \sigma^j x_t^j} - 1, \quad (29)$$

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  $\Delta x_t^i/x_t^i \rightarrow 0$ , 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  $x_t^j \rightarrow 0$  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  $(1 - \sigma^s)\Omega^s > \Omega^h$ . We summarize the results for this case in the following proposition.

**Proposition 3** *Given  $(1 - \sigma^s)\Omega^s > \max\{\Omega^h, (1 - \sigma^j)\Omega^j\}$  for all  $j \neq s$ , all archaic human groups  $j$  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 given in (20) and decreasing in the hybridization rate  $\sigma^s$ , whereas the steady-state levels of food output per capita for both early modern humans  $s$  and hybrid humans  $h$  are given in (21) and increasing in the hybridization rate  $\sigma^s$ .*

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

$$\frac{\Delta N_t^h}{N_t^h} = \Omega^h \left( \frac{Z}{N_t} \right)^{1-\alpha} \left( 1 + \sum_{i=1}^m \frac{\sigma^i N_t^i}{N_t^h} \right) - 1, \quad (30)$$

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  $i \in \{1, \dots, m\}$ . In this case, the hybrid human group  $h$  has the highest population growth rate and dominates the entire human population in the long run, as before; i.e.,  $N_t^h \rightarrow N = (\Omega^h)^{1/(1-\alpha)}Z$ . We summarize these results in Proposition 4.

**Proposition 4** *Given  $\Omega^h > (1 - \sigma^i)\Omega^i$  for all  $i \in \{1, \dots, m\}$ , early modern humans (group  $s$ ) and all other archaic humans groups 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).*

## 5 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 archaic humans become extinct whereas early modern humans may or may not survive. More importantly, a hybrid human group emerges and always survives in the human population. This finding helps explain the fact that modern humans still carry some Neanderthal-derived DNA and provides a novel insight that modern humans emerging as a result of interbreeding between archaic and early modern humans may have given rise to the extinction of these early humans. Finally, our Malthusian growth model with endogenous population growth also enables us to explore the economic implications of ancient human interbreeding, which affects population size and output per capita in the long run.

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