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Natural Selection and Neanderthal Extinction in a Malthusian Economy

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Abstract

This study develops a Malthusian model with natural selection of human species. We explore how population dynamics of one group of humans may cause the extinction of another group. In our model, different groups of humans engage in hunting-gathering. The larger group of humans can occupy more land. Therefore, in a Malthusian economy, the expansion of one population causes the other population to shrink. Whether it causes the other population to become extinct depends on a structural parameter that is the elasticity of the relative share of land with respect to the relative population size. If this elasticity is below unity, then both populations converge to their positive steady-state levels. However, if the elasticity is equal to unity, then the population that has a lower fertility cost, stronger fertility preference, higher hunting-gathering productivity and higher labor supply converges to a positive steady-state level whereas the other population eventually becomes extinct.

JEL classification: O13, Q56
Keywords: Neanderthals, early modern humans, hunting-gathering, natural selection

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> "One of the biggest remaining mysteries is why modern humans were so successful in their expansion and why the Neanderthals and Denisovans went extinct after having adapted to a Eurasian environment for several hundred thousand years." The Nobel Assembly at Karolinska Institutet (2022)

1 Introduction

Modern humans, *Homo sapiens*, have lived on this planet for about 300,000 years.[1] During most of their existence, early modern humans shared this planet with other archaic humans, such as Neanderthals and Denisovans. Neanderthals lived in Eurasia and became extinct about 40,000 years ago,[2] whereas Denisovans lived in Asia and possibly became extinct as late as 20,000 years ago. These human species coexisted with *Homo sapiens* and only became extinct some time after the arrival of early modern humans, who migrated from Africa to Asia and Europe about 50,000 years ago.[3] One hypothesis for their extinctions is the competitive exclusion principle, according to which two species competing for limited resources cannot coexist and will lead to the extinction of one of them.

In this study, we develop a Malthusian model of hunting-gathering with natural selection of different human species. We use this model to explore the conditions under which population dynamics of one group of humans may cause the extinction of another group of humans. In our model, the two groups of humans engage in hunting-gathering activities in a given amount of land. The larger group of humans can occupy a larger area of land. Therefore, in a Malthusian economy, the expansion of one population causes the other population to shrink. Whether it causes the other population to become extinct depends on a structural parameter that is the elasticity of the relative share of land with respect to the relative population size. If this elasticity is less than unity, then the two populations converge to their steady-state levels, which are both positive. However, if the elasticity is equal to unity, then the population that has a lower fertility cost, a stronger fertility preference, a higher level of hunting productivity and a higher supply of labor converges to a positive steady-state population size whereas the other population eventually becomes extinct.

The above results have the following implications. Although "Neanderthals supposedly had superior bodily strength" relative to early modern humans,[4] Neanderthals also had a lower fertility rate according to Trinkaus (2011). Our study provides a formal economic model that shows how this lower fertility of the Neanderthals could be caused by a higher fertility cost[5] and/or a weaker fertility preference[6] (despite their potentially higher hunting

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[1] See Hublin *et al.* (2017) and Richter *et al.* (2017).

[2] See Higham *et al.* (2014).

[3] See Reich (2018).

[4] See Horan *et al.* (2005).

[5] For example, according to Trinkaus (1986), their relatively large pelvic dimensions are possible evidence that Neanderthals had a relatively long gestation length of at least 11 months.

[6] More precisely, a weaker fertility preference refers to a smaller weight on fertility relative to consumption in the utility function. Given their more muscular bodies and larger brain size than early modern

productivity) and give rise to their extinction when competing with early modern humans for limited resources.[7] In our model, early modern humans could afford higher fertility only by enduring a lower level of consumption, which is consistent with the observation that early modern humans had less robust skeletons/muscular bodies and a smaller brain size than Neanderthals.

This study relates to the literature on the economic modelling of natural selection in a Malthusian environment.[8] Recent contributions in this literature establish that the forces of natural selection that operated in the Malthusian epoch selected traits that were complementary to the growth process and contributed ultimately to the transition from pre-industrial stagnation to modern economic growth. In particular, Galor and Moav (2002) and Galor and Klemp (2019) demonstrate the selection of the growth-enhancing predisposition towards child quality during the Malthusian regime, Galor and Michalopoulos (2012) demonstrate the rise in the prevalence of entrepreneurial spirit, and Galor and Ozak (2016) highlight the emergence of future-oriented mindset.[9] This study complements the interesting studies in this literature by developing a Malthusian model with natural selection of human species (with differences in fertility cost, fertility preference, hunting productivity and labor supply) to explore human evolution.[10] As Galor (2020) writes, "[i]t is virtually impossible to understand human history without grasping the contributions of these undercurrents [the size and the composition of the human population] to human evolution".

This study also relates to the literature on mathematical models of Neanderthal extinction. Flores (1998) develops a mathematical biology model of two interacting species with the same fertility rate but different mortality rates, in which the higher mortality rate of Neanderthals gives rise to their eventual extinction.[11] Horan *et al.* (2005) develop an economic model of two interacting species with different degrees of biological efficiency (e.g., different levels of hunting-gathering productivity and labor supply), in which the species with a lower degree of biological efficiency eventually becomes extinct. Then, they introduce the division of labor and trade to their model and show that although early modern humans had a lower degree of biological efficiency than Neanderthals, the division of labor and trading among early modern humans enabled them to overcome their biological deficiencies and drive Neanderthals to extinction. A recent study by Degioanni

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humans, Neanderthals may have needed a higher level of food consumption; see Lagerlof (2007) who also argues that the relatively large bodies of Neanderthals had higher metabolism requirements.

[7] Banks *et al.* (2008) find that the Neanderthal extinction was preceded by a decrease in their geographic range due to competition with early modern humans and their expansion in geographic range.

[8] Earlier economic models of natural selection not in a Malthusian environment include Hansson and Stuart (1990) and Rogers (1994), who model natural selection of agents with different time preferences; see Robson (2001) for a survey on this earlier branch of the literature.

[9] See also Lagerlof (2007) on how small versus large human bodies affect the transition of an economy from pre-industrial stagnation to modern economic growth.

[10] See Galor (2005, 2011) for comprehensive reviews on unified growth theory and Ashraf and Galor (2018) for an overview of a more recent literature on the macrogenoeconomics of comparative development.

[11] Diamond (1992) also argues that the shorter lifespan of Neanderthals may have mitigated their ability to accumulate social capital. However, Trinkaus (2011) does not find any difference in the mortality rates across samples of early modern humans and Neanderthals.

et al. (2019) uses a matrix population model to show that a decline in the Neanderthals' fertility rate could have caused their extinction. Our study contributes to this literature by developing an economic model of Neanderthal extinction, in which fertility decisions are made by optimizing agents of each species. This microfoundation for the fertility rate enables us to explore how the fertility preference and the cost of fertility could dominate hunting-gathering productivity and labor supply in determining the endogenous fertility rates of different species and the possible extinction of some of them.

This study also relates to the literature on pre-industrial hunting-gathering economies; see Smith (1975), Locay (1989), Baker (2003, 2008), Bulte *et al.* (2006) and Chu (2022). Studies in this literature often focus on the evolution of human society from hunting-gathering to agriculture (i.e., the Neolithic Revolution); see Weisdorf (2005) for a survey. The model in this study extends Locay (1989) and Baker (2008) by introducing multiple human species in the hunting-gathering era. Complementing their interesting studies, we focus on the earlier transition from multiple human species to the dominance of early modern humans in the hunting-gathering Malthusian economy. One can reintroduce an agricultural production function as in Locay (1989) and Baker (2008) to model the subsequent transition from hunting-gathering to an agricultural economy, which would be identical to these previous studies once the hunting-gathering Malthusian era is left with early modern humans. As Galor (2022, p. 205-206) writes, "early agricultural civilisations typically used their larger populations and greater technological power either to displace hunter-gatherers, pushing some to remote corners while destroying others, or to integrate them."[12] Then, one can further introduce an industrial production function as in Chu (2022) to also model the transition from agriculture to a modern industrial economy, in addition to the Neolithic Revolution.

The rest of this study is organized as follows. Section 2 develops the model. Section 3 explores population dynamics under different conditions and discusses the relation of our results to existing hypotheses. Section 4 considers an extension with an arbitrary number of populations. Section 5 concludes.

2 A Malthusian model with natural selection

We consider a simple Malthusian model of hunting-gathering.[13] There are two groups of humans indexed by $i \in \{a, s\}$.[14] The human group s denotes *Homo sapiens*, whereas the human group a refers to a group of archaic humans, such as the Neanderthals. Both groups of humans are hunter-gatherers. There is a fixed amount of land Z, and the larger group of humans occupies a larger share of land. We use a parameter $\phi \in [0, 1]$ to capture how sensitive the relative share of land is to the relative population size.

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[12] If early modern humans experienced the transition from hunting-gathering to agriculture before the Neanderthal extinction, then the resource competition between agriculturalists and hunter-gatherers could be a potential and interesting hypothesis for the Neanderthal extinction, which however occurred up to 28,000 years before the Neolithic Revolution.

[13] The model is based on Ashraf and Galor (2011), extended to allow for multiple groups of humans.

[14] In Section 4, we extend the number of groups to $m \geq 2$ to confirm the robustness of our results.

2.1 Endogenous fertility

In each human group $i \in \{a, s\}$, there are N_t^i agents at time t. We consider overlapping generations of agents. Each agent lives for two periods. Each adult agent of group i at time t has the following utility function:[15]

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

where the parameter $\gamma^i \in (0, 1)$ measures her preference for fertility and n_{t+1}^i is the agent's number of children, who then become adults at time $t + 1$. Raising children is costly, and the level of consumption c_t^i net of the fertility cost is given by

$$c_t^i = y_t^i - \rho^i n_{t+1}^i, \tag{2}$$

where the parameter $\rho^i > 0$ determines the cost of fertility and y_t^i is the per capita level of food production in group i.

Substituting (2) into (1), we derive the utility-maximizing level of fertility n_{t+1} as

$$n_{t+1}^i = \frac{\gamma^i}{\rho^i} y_t^i \tag{3}$$

and $c_t^i = (1 - \gamma^i) y_t^i$. Each adult agent in group i has n_{t+1}^i children, and the number of adult agents at time t is N_t^i. Therefore, the law of motion for the adult population size of group i is

$$N_{t+1}^i = n_{t+1}^i N_t^i = \frac{\gamma^i}{\rho^i} y_t^i N_t^i, \tag{4}$$

and its growth rate at time t is

$$\frac{\Delta N_t^i}{N_t^i} \equiv \frac{N_{t+1}^i - N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i} y_t^i - 1, \tag{5}$$

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

2.2 Hunting-gathering

Total food production from hunting-gathering in human group $i \in \{a, s\}$ is given by

$$Y_t^i = \theta^i (l^i N_t^i)^\alpha (Z_t^i)^{1-\alpha}, \tag{6}$$

where $l^i N_t^i$ and Z_t^i are respectively the total amount of labor and land devoted to hunting-gathering by group i. Individual labor supply $l^i > 0$ is exogenous. The parameters $\theta^i > 0$

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[15] One can introduce subsistence consumption $\overline{c}^i$ in utility $u_t^i = (1 - \gamma^i) \ln(c_t^i - \overline{c}^i) + \gamma^i \ln n_{t+1}^i$. In this case, all our results are robust. Furthermore, an increase in $\overline{c}^i$ reduces the steady-state level of population i under $\phi \in [0, 1)$. Also, it raises the steady-state level of population j under $\phi \in (0, 1)$ and makes it more likely for population i to become extinct in the long run under $\phi = 1$. Derivations are available upon request. The author would like to thank Oded Galor for suggesting this interesting result.

and $\alpha \in (0,1)$ measure respectively the productivity and labor intensity of the hunting-gathering process. Each agent in group i receives y_t^i units of food production given by

$$y_t^i \equiv \frac{Y_t^i}{N_t^i} = \frac{\theta^i (l^i N_t^i)^\alpha (Z_t^i)^{1-\alpha}}{N_t^i} = \theta^i (l^i)^\alpha \left(\frac{Z_t^i}{N_t^i}\right)^{1-\alpha}, \tag{7}$$

which is decreasing in N_t^i due to the decreasing returns to scale in hunting-gathering labor.

2.3 Land division

We follow the literature on the macrotechnology of conflict to assume the presence of a conflict success function for resource competition and the division of land between the two groups of humans. Specifically, the amount of land occupied by human group i is specified as follows:

$$Z_t^i = \frac{\varphi(N_t^i)}{\varphi(N_t^i) + \varphi(N_t^j)} Z = \frac{(N_t^i)^\phi}{(N_t^i)^\phi + (N_t^j)^\phi} Z, \tag{8}$$

where the parameter $Z > 0$ denotes the total amount of land. The functional form $\varphi(N_t^i) = (N_t^i)^\phi$ is known as the ratio form in the literature,[16] and the parameter $\phi \in [0,1]$ is known as the decisiveness parameter.[17] If $\phi = 0$, then the amount of land is equally divided between the two groups, such that $Z_t^i = Z/2$. As ϕ increases, the ratio of land becomes more sensitive to the population ratio:

$$\frac{Z_t^i}{Z_t^j} = \left(\frac{N_t^i}{N_t^j}\right)^\phi, \tag{9}$$

which shows the advantage of the ratio form in which ϕ parameterizes the elasticity of the land ratio with respective to the population ratio. As we will show, this elasticity determines whether the Neanderthal extinction occurs or not.

3 Population dynamics

Given an initial level of population N_0^i, the population growth rate of human group i is

$$\frac{\Delta N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i} \theta^i (l^i)^\alpha \left[\frac{(N_t^i)^\phi}{(N_t^i)^\phi + (N_t^j)^\phi} \frac{Z}{N_t^i}\right]^{1-\alpha} - 1, \tag{10}$$

which uses (5), (7) and (8). There are three scenarios: $\phi = 0$, $\phi \in (0,1)$, and $\phi = 1$.

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[16] See Hirshleifer (2000) for a discussion.

[17] In general, ϕ can be greater than unity; however, in our dynamic model, the population dynamics would become unstable if $\phi > 1$.

3.1 Population dynamics without resource competition

First, we consider $\phi = 0$. In this case, the dynamics of the two populations becomes independent, and (10) simplifies to

$$\frac{\Delta N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha \left(\frac{Z}{2N_t^i}\right)^{1-\alpha} - 1. \tag{11}$$

Given any initial level N_0^i, the population size N_t^i converges to a unique and stable steady state:

$$N^i = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} \frac{Z}{2}, \tag{12}$$

which shows that the steady-state level of population i is decreasing in its fertility cost ρ^i but increasing in its fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the total amount of land Z. Here the positive effects of hunting productivity θ^i, labor supply l^i and land Z on fertility capture the Malthusian mechanism. Imposing $\Delta N_t^i = 0$ on (5) yields the steady-state level of food output per capita given by $y^i = \rho^i/\gamma^i$ and the steady-state level of consumption per capita given by $c^i = (1-\gamma^i)y^i = \rho^i(1-\gamma^i)/\gamma^i$. The steady-state levels of food output and consumption per capita are increasing in fertility cost ρ^i and decreasing in fertility preference γ^i due to their respective effects on the steady-state population size, which negatively affects output per capita given the decreasing returns to scale in hunting-gathering labor. We summarize all these results in the following proposition.

Proposition 1 *If $\phi = 0$, then the dynamics of the two populations is independent of each other. Given any N_0^i, the population size N_t^i converges to a unique and stable steady-state level, which is decreasing in fertility cost ρ^i but increasing in fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the amount of land Z. The steady-state levels of food output and consumption per capita are increasing in fertility cost ρ^i and decreasing in fertility preference γ^i.*

3.2 Population dynamics with resource competition

Second, we consider $\phi \in (0,1)$. In this case, the dynamics of the two populations depends on each other. Setting $\Delta N_t^i = 0$ in (10) yields

$$N^i = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} \frac{(N^i)^\phi}{(N^i)^\phi + (N^j)^\phi} Z, \tag{13}$$

which can be re-expressed as

$$N^j = \left\{\left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} \frac{Z}{(N^i)^{1-\phi}} - (N^i)^\phi\right\}^{1/\phi}. \tag{14}$$

Similarly, setting $\Delta N_t^j = 0$ yields

$$N^i = \left\{ \left[\frac{\gamma^j}{\rho^j} \theta^j (l^j)^\alpha \right]^{1/(1-\alpha)} \frac{Z}{(N^j)^{1-\phi}} - (N^j)^\phi \right\}^{1/\phi}. \tag{15}$$

Figure 1 plots (14) and (15) along with the dynamics of N_t^i and N_t^j in a phase diagram.

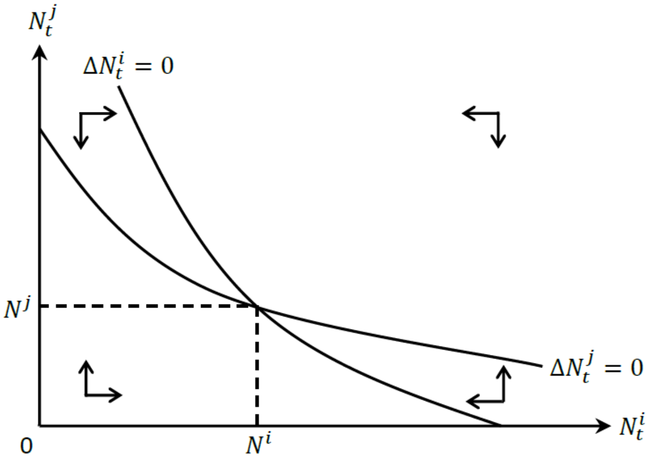

Figure 1: Phase diagram for $\phi \in (0, 1)$

Figure 1 shows that given any initial levels of population N_0^i and N_0^j, the population size N_t^i converges to a unique and stable steady-state value given by

$$N^i = \left[\frac{\gamma^i}{\rho^i} \theta^i (l^i)^\alpha \right]^{1/(1-\alpha)} \left[1 + \left(\frac{N^j}{N^i} \right)^\phi \right]^{-1} Z, \tag{16}$$

where the population ratio is given by

$$\frac{N^i}{N^j} = \left[\frac{\gamma^i \theta^i}{\gamma^j \theta^j} \left(\frac{l^i}{l^j} \right)^\alpha \frac{\rho^j}{\rho^i} \right]^{1/[(1-\alpha)(1-\phi)]}. \tag{17}$$

As before, the steady-state level of population i is decreasing in its own fertility cost ρ^i and increasing in its own fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the total amount of land Z. Interestingly, the steady-state level of population i is increasing in the other population's fertility cost ρ^j and decreasing in their fertility preference γ^j, hunting productivity θ^j and labor supply l^j. Intuitively, as the other population j becomes larger, the amount of land captured by population i becomes smaller, which in turn reduces its population size in this Malthusian economy. However, both populations continue to coexist in the long run. As before, we impose $\Delta N_t^i = 0$ on (5) to derive the steady-state level of food output per capita as $y^i = \rho^i / \gamma^i$ and the steady-state level of consumption per capita as $c^i = \rho^i (1 - \gamma^i) / \gamma^i$, which are both increasing in own fertility cost ρ^i and decreasing in own fertility preference γ^i for the same reason as before. We summarize all these results in the following proposition.

Proposition 2 *If $\phi \in (0,1)$, then the dynamics of the two populations depends on each other. Given any N_0^i and N_0^j, each population size N_t^i converges to a unique and stable steady-state level N^i, which is decreasing in its own fertility cost ρ^i but increasing in its own fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the total amount of land Z. The steady-state population level N^i is also increasing in the other population j's fertility cost ρ^j and decreasing in their fertility preference γ^j, hunting productivity θ^j and labor supply l^j. The steady-state levels of food output and consumption per capita are increasing in own fertility cost ρ^i and decreasing in own fertility preference γ^i.*

3.3 Population dynamics with population extinction

Third, we consider $\phi = 1$. In this case, (10) simplifies to

$$\frac{\Delta N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha \left(\frac{Z}{N_t^i + N_t^j}\right)^{1-\alpha} - 1, \tag{18}$$

which shows that

$$\frac{\Delta N_t^i}{N_t^i} > \frac{\Delta N_t^j}{N_t^j} \Leftrightarrow \frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha > \frac{\gamma^j}{\rho^j}\theta^j (l^j)^\alpha. \tag{19}$$

Without loss of generality, let's assume that $\gamma^i\theta^i(l^i)^\alpha/\rho^i > \gamma^j\theta^j(l^j)^\alpha/\rho^j$. Setting $\Delta N_t^i = 0$ in (18) yields

$$N^j = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} Z - N^i. \tag{20}$$

Similarly, setting $\Delta N_t^j = 0$ yields

$$N^i = \left[\frac{\gamma^j}{\rho^j}\theta^j (l^j)^\alpha\right]^{1/(1-\alpha)} Z - N^j. \tag{21}$$

Figure 2 plots (20) and (21) along with the dynamics of N_t^i and N_t^j in a phase diagram.

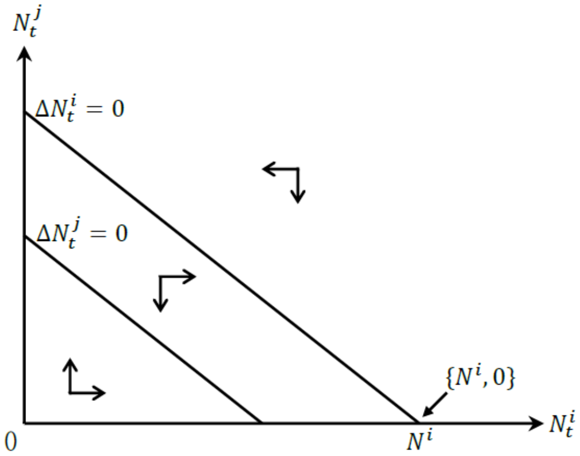

Figure 2: Phase diagram for $\phi = 1$

Figure 2 shows that given any initial levels of population N_0^i and N_0^j, the population sizes $\{N_t^i, N_t^j\}$ always converge to $\{N^i, 0\}$. Suppose $\Delta N_0^i / N_0^i > \Delta N_0^j / N_0^j > 0$ at the initial population levels $\{N_0^i, N_0^j\}$. Then, the two populations are both initially growing. As both N_t^i and N_t^j increase, their growth rates decrease over time. Eventually, $\Delta N_t^j / N_t^j$ becomes negative while $\Delta N_t^i / N_t^i$ remains positive. At this stage, the size N_t^i of population i keeps rising whereas the size N_t^j of population j shrinks over time. In the long run, the size N_t^j of population j shrinks towards zero at which point the size N_t^i of population i converges to the following steady state:

$$N^i = \left[\frac{\gamma^i}{\rho^i} \theta^i (l^i)^\alpha \right]^{1/(1-\alpha)} Z, \tag{22}$$

which as before is decreasing in the fertility cost ρ^i but increasing in fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the total amount of land Z.

The transition path of consumption per capita is given by

$$c_t^i = (1-\gamma^i) y_t^i = (1-\gamma^i) \theta^i (l^i)^\alpha \left(\frac{Z}{N_t^i + N_t^j} \right)^{1-\alpha}, \tag{23}$$

which is increasing in hunting productivity θ^i and labor supply l^i but decreasing in fertility preference γ^i. Given the survival of *Homo sapiens* and the extinction of other archaic humans, our model requires $\gamma^s \theta^s (l^s)^\alpha / \rho^s > \gamma^a \theta^a (l^a)^\alpha / \rho^a$. Evidence suggests that Neanderthals had more robust skeletons and muscular bodies, which may imply $\theta^a (l^a)^\alpha > \theta^s (l^s)^\alpha$. These two conditions together imply that γ^s / ρ^s must be significantly larger than γ^a / ρ^a in order for early modern humans to have a higher fertility rate than Neanderthals. In other words, the lower fertility of the Neanderthals could be caused by their higher fertility cost ρ^a and/or their weaker fertility preference γ^a despite their potentially higher hunting productivity $\theta^a (l^a)^\alpha$. However, early modern humans could afford higher fertility only by enduring lower consumption. Therefore, Neanderthals should have enjoyed a higher level of consumption than early modern humans before their extinction (i.e., $c_t^a > c_t^s$ for all t before $N_t^a \to 0$).

We summarize all the above results in the following proposition.

Proposition 3 *If $\phi = 1$, then the dynamics of the two populations depends on each other. Suppose $\gamma^i \theta^i (l^i)^\alpha / \rho^i > \gamma^j \theta^j (l^j)^\alpha / \rho^j$. Then, given any N_0^i and N_0^j, the size N_t^j of population j converges to zero whereas the size N_t^i of population i converges to a unique and stable steady-state level N^i, which is decreasing in its own fertility cost ρ^i but increasing in fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the total amount of land Z. Given N_t^i and N_t^j, the transition path of per capita consumption c_t^i is increasing in hunting productivity θ^i and labor supply l^i but decreasing in fertility preference γ^i. The population that has a larger $(1-\gamma^i)\theta^i(l^i)^\alpha$ enjoys a higher transition path of consumption until one of the populations becomes extinct.*

3.4 Discussion

In addition to the competitive exclusion principle, there are also other hypotheses of Neanderthal extinction. In this section, we discuss how our results relate to these hypotheses and how they can be demonstrated within our model. One hypothesis of Neanderthal extinction is that the arrival of early modern humans brought with them diseases that Neanderthals had no immunity to.[18] According to Higham *et al.* (2014), early modern humans and Neanderthals had an overlap of 2,600-5,400 years in Europe. Therefore, any potential diseases transmitted from early modern humans to Neanderthals did not rapidly cause a deadly epidemic but only gradually reduced the population growth rate of Neanderthals either via a higher mortality rate and/or a lower fertility rate. According to Trinkaus (2011), Neanderthals seemed to have a similar mortality rate but a lower fertility rate than early modern humans. In this case, an increase in the difficulty of fertility for the Neanderthals potentially caused by transmittable diseases can be captured by an increase in their fertility cost parameter in our model.

Another hypothesis is the lack of division of labor between the sexes of Neanderthals.[19] According to this hypothesis, both male and female Neanderthals engaged in hunting-gathering. In this case, their opportunity cost of fertility would be higher than that of early modern humans. Our model can also capture this scenario by assuming that Neanderthals had a larger fertility cost parameter than early modern humans.

Furthermore, the domestication of the dog by early modern humans may have improved their hunting efficiency.[20] This scenario can be captured by an increase in early modern humans' hunting productivity parameter in our model. Similarly, climate change

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[18] See Houldcroft and Underdown (2016).

[19] See Kuhn and Stiner (2006).

[20] See Shipman (2012).

or natural catastrophe (e.g., volcanic eruptions) that led to a decline in large mammals mainly eaten by the Neanderthals can be captured by a decrease in Neanderthals' hunting productivity parameter in our model. Early modern humans were less affected by this change as they seemed to be more capable of prey-shifting and hunting smaller preys, such as rabbits.[21]

Harsh climatic conditions caused the relatively small population of Neanderthals to isolate into even smaller groups and engage in inbreeding practices.[22] Inbreeding in turn led to reduced fertility and possibly extinction. This scenario can be captured by a decrease in the Neanderthals' fertility preference parameter in our model.

Another hypothesis is that violence or warfare between early modern humans and Neanderthals gave rise to the extinction of the latter.[23] Although our theoretical framework does not model violent competition, the parameter ϕ captures resource competition. If $\phi = 0$, then the two species do not compete with each other over natural resources. The larger the value of ϕ, the more intense the competition is. If $\phi = 1$, then the competition is so intense that the less fertile species (whether this lower fertility is due to weaker fertility preference, higher fertility cost, lower hunting productivity, lower labor supply, or any combination of them) would eventually become extinct. Therefore, although Neanderthals and early modern humans could have coexisted in the long run under $\phi < 1$, only one of the two species eventually survived when ϕ rose to unity for whatever reason.

Finally, there is also the hypothesis of Neanderthal extinction caused by interbreeding with early modern humans, which however seemed to be a minor contributor according to Timmermann (2020). In order for interbreeding to cause Neanderthal extinction, it must be the case that hybrids who carried more Neanderthal genes were significantly less fertile. Although our model does not capture interbreeding, one can think of this scenario as more Neanderthal genes translating to a higher fertility cost or a weaker fertility preference. As a result, those with more Neanderthal genes would produce less offsprings, and the percentage of Neanderthal genes in the human population would decline over time. A recent study estimates that the proportion of Neanderthal-derived DNA in modern humans outside Africa ranges from only 1.5% to 2.1%.[24]

4 Multiple groups of human species

In addition to Neanderthals and Denisovians, there were several other archaic humans, such as *Homo heidelbergensis* and *Homo erectus*, who likely coexisted with early modern humans. Furthermore, there is evidence that Neanderthals and Denisovians interacted with early modern humans.[25] Therefore, in this section, we extend the number of inter-

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[21] See Fa *et al.* (2013).

[22] See Rios *et al.* (2019) and Vaesen *et al.* (2019).

[23] See Longrich (2020).

[24] See Prufer *et al.* (2014).

[25] See Pennisi (2013).

acting groups from two to $m \geq 2$. In this case, the land-division rule in (8) becomes

$$Z_t^i = \frac{(N_t^i)^\phi}{\sum_{j=1}^m (N_t^j)^\phi} Z, \tag{24}$$

where $i \in \{1, ..., m\}$. Given (24), the population growth rate of group i in (10) becomes

$$\frac{\Delta N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha \left[\frac{(N_t^i)^\phi}{\sum_{j=1}^m (N_t^j)^\phi}\frac{Z}{N_t^i}\right]^{1-\alpha} - 1. \tag{25}$$

The rest of the model is the same as before. Once again, There are three scenarios to consider: $\phi = 0$, $\phi \in (0,1)$, and $\phi = 1$.

First, we consider $\phi = 0$. In this case, the dynamics of the m groups is independent of each other, and (25) simplifies to

$$\frac{\Delta N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha \left(\frac{Z}{mN_t^i}\right)^{1-\alpha} - 1. \tag{26}$$

Given any initial level N_0^i, the population size N_t^i converges to a unique and stable steady state:

$$N^i = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} \frac{Z}{m}, \tag{27}$$

which shows that N^i is decreasing in the number m of groups and fertility cost ρ^i but increasing in fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the amount of land Z. All these results are the same as before, except for the new finding that as the number m of groups increases, the steady-state population size of each group shrinks.

Second, we consider $\phi \in (0,1)$. In this case, the dynamics of the m populations depends on each other. Setting $\Delta N_t^i = 0$ in (25) yields

$$N^i = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} \frac{(N^i)^\phi}{\sum_{j=1}^m (N^j)^\phi} Z = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha\right]^{1/(1-\alpha)} \left[\sum_{j=1}^m \left(\frac{N^j}{N^i}\right)^\phi\right]^{-1} Z, \tag{28}$$

where the population ratio is given by

$$\frac{N^i}{N^j} = \left[\frac{\gamma^i\theta^i}{\gamma^j\theta^j}\left(\frac{l^i}{l^j}\right)^\alpha \frac{\rho^j}{\rho^i}\right]^{1/[(1-\alpha)(1-\phi)]}. \tag{29}$$

Given any initial levels N_0^i for $i \in \{1, .., m\}$, N_t^i converges to the unique and stable steady state N^i in (28). As before, N^i is decreasing in own fertility cost ρ^i and increasing in own fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the amount of land Z. Also, N^i is increasing in other groups' fertility cost ρ^j but decreasing in their fertility preference γ^j, hunting productivity θ^j and labor supply l^j. Interestingly, all m groups coexist even in the long run, which unfortunately is not the case in reality.

Third, we consider $\phi = 1$. In this case, (25) simplifies to

$$\frac{\Delta N_t^i}{N_t^i} = \frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha \left(\frac{Z}{\sum_{j=1}^m N_t^j} \right)^{1-\alpha} - 1. \tag{30}$$

Let's assume that $\gamma^i \theta^i (l^i)^\alpha / \rho^i > \gamma^j \theta^j (l^j)^\alpha / \rho^j$ for all $j \neq i$. In this case, given any N_0^j for $j \in \{1, .., m\}$, the population sizes $\{N_t^j\}$ for all $j \neq i$ converge to 0 whereas N_t^i converges to

$$N^i = \left[\frac{\gamma^i}{\rho^i}\theta^i (l^i)^\alpha \right]^{1/(1-\alpha)} Z, \tag{31}$$

which as before is decreasing in fertility cost ρ^i but increasing in fertility preference γ^i, hunting productivity θ^i, labor supply l^i and the amount of land Z. More importantly, only the population that has the largest $\gamma^i \theta^i (l^i)^\alpha / \rho^i$ survives in the long run and all other populations eventually become extinct. This scenario is consistent with the reality that *Home sapiens* is the only surviving human species.

5 Conclusion

In this study, we have developed a Malthusian model with natural selection of human species and applied this microfounded theoretical framework to explore the population dynamics of interacting human species. Given the scarcity of natural resources and the ability of the larger group of humans to capture more natural resources, the expansion of one population causes the other population to shrink in a Malthusian economy. However, the less fertile population does not necessarily become extinct. Whether the extinction of a species occurs depends on the elasticity of the relative share of land with respect to the relative population size, which captures the intensity of resource competition. If this elasticity is below unity, then the two populations coexist even in the long run. However, if the elasticity is equal to unity, then the less fertile population eventually becomes extinct due to the high intensity of resource competition.

References

[1] Ashraf, Q., and Galor, O., 2011. Dynamics and stagnation in the Malthusian epoch. *American Economic Review*, 101, 2003-2041

[2] Ashraf, Q., and Galor, O., 2018. The macrogenoeconomics of comparative development. *Journal of Economic Literature*, 56, 1119-1155.

[3] Baker, M., 2003. An equilibrium conflict model of land tenure in hunter-gatherer societies. *Journal of Political Economy*, 111, 124-173.

[4] Baker, M., 2008. A structural model of the transition to agriculture. *Journal of Economic Growth*, 13, 257-292.

[5] Banks, W., d'Errico, F., Peterson, A.T., Kageyama, M., Sima, A., and Sanchez-Goni, M.-F., 2008. Neanderthal extinction by competitive exclusion. *PLoS ONE*, 3, e3972.

[6] Bulte, E., Horan, R., and Shogren, J., 2006. Megafauna extinction: A paleoeconomic theory of human overkill in the pleistocene. *Journal of Economic Behavior & Organization*, 59, 297-323.

[7] Chu, A., 2022. From Neolithic Revolution to Industrialization. MPRA Paper No. 111835.

[8] Degioanni, A., Bonenfant, C., Cabut, S., and Condemi, S., 2019. Living on the edge: Was demographic weakness the cause of Neanderthal demise?. *PLoS ONE*, 14, e0216742.

[9] Diamond, J., 1992. *The Third Chimpanzee: The Evolution and Future of the Human Animal.* New York: Harper Collins.

[10] Fa, J., Stewart, J., Lloveras, L., and Vargas, J., 2013. Rabbits and hominin survival in Iberia. *Journal of Human Evolution*, 64, 233-241.

[11] Flores, J., 1998. A mathematical model for Neanderthal extinction. *Journal of Theoretical Biology*, 191, 295-298.

[12] Galor, O., 2005. From stagnation to growth: Unified growth theory. *Handbook of Economic Growth*, 1, 171-293.

[13] Galor, O., 2011. *Unified Growth Theory.* Princeton University Press.

[14] Galor, O., 2020. The journey of humanity: Roots of inequality in the wealth of nations. *Economics and Business Review*, 6, 7-18.

[15] Galor, O., 2022. *The Journey of Humanity: The Origins of Wealth and Inequality.* Dutton.

[16] Galor, O., and Klemp, M., 2019. Human genealogy reveals a selective advantage to moderate fecundity. *Nature Ecology & Evolution*, 3, 853-857.

[17] Galor, O., and Michalopoulos, S., 2012. Evolution and the growth process: Natural selection of entrepreneurial traits. *Journal of Economic Theory*, 147, 759-780.

[18] Galor, O., and Moav, O., 2002. Natural selection and the origin of economic growth. *Quarterly Journal of Economics*, 117, 1133-1191.

[19] Galor, O., and Ozak, O., 2016. The agricultural origins of time preference. *American Economic Review*, 106, 3064-3103.

[20] Hansson, I., and Stuart, C., 1990. Malthusian selection of preferences. *American Economic Review*, 80, 529-544.

[21] Higham, T., Douka, K., Wood, R., *et al.*, 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature*, 512, 306-309.

[22] Hirshleifer, J., 2000. The macrotechnology of conflict. *Journal of Conflict Resolution*, 44, 773-792.

[23] Horan, R., Bulte, E., and Shogren, J., 2005. How trade saved humanity from biological exclusion: An economic theory of Neanderthal extinction. *Journal of Economic Behavior & Organization*, 58, 1-29.

[24] Houldcroft, C.J., and Underdown, S.J., 2016. Neanderthal genomics suggests a Pleistocene time frame for the first epidemiologic transition. *American Journal of Physical Anthropology*, 160, 379-388.

[25] Hublin, JJ., Ben-Ncer, A., Bailey, S., *et al.*, 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of Homo sapiens. *Nature*, 546, 289-292.

[26] Kuhn, S., and Stiner, M., 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. *Current Anthropology*, 47, 953-981.

[27] Lagerlof, N.-P., 2007. Long-run trends in human body mass. *Macroeconomic Dynamics*, 11, 367-387.

[28] Locay, L., 1989. From hunting and gathering to agriculture. *Economic Development and Cultural Change*, 37, 737-756.

[29] Longrich, N., 2020. War in the time of Neanderthals: How our species battled for supremacy for over 100,000 years. *The Conversation*, November 2, 2020.

[30] Pennisi, E., 2013. More genomes from Denisova Cave show mixing of early human groups. *Science*, 340, 799.

[31] Prufer, K., Racimo, F., Patterson, N., *et al.*, 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature*, 505, 43-49.

[32] Reich, D., 2018. *Who We Are and How We Got Here: Ancient DNA and the New Science of the Human Past*. New York: Pantheon Books.

[33] Richter, D., Grun, R., Joannes-Boyau, R., *et al.*, 2017. The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle Stone Age. *Nature*, 546, 293-296.

[34] Rios, L., Kivell, T.L., Lalueza-Fox, C., *et al.*, 2019. Skeletal anomalies in the Neandertal family of El Sidron (Spain) support a role of inbreeding in Neandertal extinction. *Scientific Reports*, 9, 1697.

[35] Robson, A., 2001. The biological basis of economic behavior. *Journal of Economic Literature*, 39, 11-33.

[36] Rogers, A., 1994. Evolution of time preference by natural selection. *American Economic Review*, 84, 460-481.

[37] Shipman, P., 2012. Do the eyes have it? Dog domestication may have helped humans thrive while Neandertals declined. *American Scientist*, 100, 198-201.

[38] Smith, V., 1975. The primitive hunter culture, Pleistocene extinction, and the rise of agriculture. *Journal of Political Economy*, 83, 727-756.

[39] The Nobel Assembly at Karolinska Institutet, 2022. Scientific background: Discoveries concerning the genomes of extinct hominins and human evolution.

[40] Timmermann, A., 2020. Quantifying the potential causes of Neanderthal extinction: Abrupt climate change versus competition and interbreeding. *Quaternary Science Reviews*, 238, 106331.

[41] Trinkaus, E., 1986. The Neandertals and modern human origins. *Annual Review of Anthropology*, 15, 193-218.

[42] Trinkaus, E., 2011. Late Pleistocene adult mortality patterns and modern human establishment. *Proceedings of the National Academy of Sciences*. 108, 1267-1271.

[43] Vaesen, K., Scherjon, F., Hemerik, L., and Verpoorte, A., 2019. Inbreeding, Allee effects and stochasticity might be sufficient to account for Neanderthal extinction. *PLoS ONE*, 14, e0225117.

[44] Weisdorf, J., 2005. From foraging to farming: Explaining the Neolithic Revolution. *Journal of Economic Surveys*, 19, 561-586.