A mathematical model for Neanderthal extinction

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A simple mathematical homogeneous model of competition is used to describe Neanderthal extinction in Europe. It considers two interacting species, Neanderthals and Early Modern Men, in the same ecological niche. Using paleontological data we claim that the parameter of similarity, between both species, fluctuates between 0.992 and 0.997. An extension of the model including migration (diffusion) is also discussed nevertheless, extinction of Neanderthal seems unavoidable. Numerical analysis of travelling wave solutions (fronts) confirms the extinction. The wave-front-velocity is estimated from linear analysis and numerical simulations confirm this estimation. We conjecture a mathematical formulation for the principle of exclusion between competitive interacting species (Gause).
Mathematical models for interaction and coexistence between species, yield non-linear equations which contain a number of rate constants. These constants are usually determined empirically in controlled experiments, or by observations in natural environments [1-5].

In this work we consider a system with competitive exclusion. We study the competition between Neanderthals and men with early modern structure. So, explicitly, we assume that Neanderthals did not evolve into Early Modern Men.

Neanderthals were very stable in Europe for more than 60,000 years nevertheless, 40,000 years before our epoch, they were replaced by Early Modern Men. This massive extinction was completed between 5,000 and 10,000 years depending on the region. It is not clear how modern men appear in Europe, but some evidence of coexistence in the Levant (see for instance [6] and [7]), suggests a diffusive process from that region. Moreover, whether the interaction was direct (war) or not (competition) remains unclear nevertheless, we assume the last possibility. So, we have two species competing for the same ecological niche composed of limited nutrient and territory. The principle of exclusion (Gause) [5,8] can be applied and then both species cannot coexist.

The following simplified non-linear mathematical model could describe this biological interaction. Let $N$ be the number of individual, at time $t$, with Neanderthal characters, and $C$ the one related to Early Modern Men.
Consider the pair of time-evolution equations

\[
\frac{\partial N}{\partial t} = N(F - \beta), \quad (1)
\]
\[
\frac{\partial C}{\partial t} = C(F - s\beta). \quad (2)
\]

In this way, we assume the same rate of birth \( F(N, C) \) for both species, and a tiny difference in the constant rate of mortality \( \beta \). Namely, we assume that the parameter of similarity \( s \) varies between \( 0 < s \leq 1 \), where \( s = 1 \) means complete similarity. Thus, species \( C \) is better adapted to survive. The limited nutrient reservoir and territory is modeled by the dependence of \( F \) on the variables \( N \) and \( C \) (see for instance[1]) :

\[
F = \alpha - \delta(N + C) \quad (3)
\]

where the growth rate \( \alpha \) and the interaction parameter \( \delta \) are positive numbers, and we assume \( \alpha > \beta > 0 \).

Equations (1-3) define a Malthusian-birth-death process with interaction, and obviously is a crude model. For instance, it does not consider the diffusion process due to the alleged migration of modern hominin. Moreover, one might expect the rate constant \( \alpha, \beta \) and \( \delta \) to be affected by changes of ecological nature (temperature, humidity, random fluctuations, amount of resources, and others). In fact, usually in population dynamics one deals with systems subjected to random environment [2,3] where, sometimes, the impact may be drastic (noise-induced transition). However, equations (1-3) are in accord with the principle of exclusion. Predictions related to the degree of similarity \( s \), between both species, will be conjectured.
The set (1-3) can be solved partially. The usual linear stability analysis
tell us that the point \((N, C) = (0, 0)\) is an unstable node; \((N, C) = (\frac{a-\beta}{\delta}, 0)\) is a saddle point (i.e. unstable); and finally \((N, C) = (0, \frac{a-s\beta}{\delta})\) is a stable node. All this in accord with Gause’s principle (figure 1). Moreover, a direct integration gives:

\[
\frac{N}{C} = A_0 e^{-\beta(1-s)t}
\]

(4)

where \(A_0\) is a constant of integration. As long as \(0 < s < 1\) (already assumed) the species \(N\) disappear, and the time of extinction \(\tau\) can be related to the parameters by

\[
\tau = \frac{1}{\beta(1-s)}.
\]

(5)

Using the above relationship, paleontological data for the extinction time \(\tau\) (i.e. 5000 < \(\tau\) < 10000, years), and the life-time for individual (30 < \(1/\beta\) < 40, years), then \(s\) fluctuates between 0.992 < \(s\) < 0.997. It is instructive to compare this result, for instance, with the parameter of similarity between man and chimpanzee [9] where \(s' \sim 0.975\). This last parameter is related to the sequence of nucleotides in DNA, and then not necessarily connected to \(s\). On the other hand, following Reef.[10], Neanderthal industry (silex-knife) did require about 111 percussions (4 stages) against 251 (9 stages) for Cro-Magnon. So the comparison of the number of percussion (for stage) gives \(s'' = \frac{111}{4}/\frac{251}{9} \sim 0.995\). A number curiously close of our parameter \(s\).

Turning to the two species model (1-3), a more realistic case requires
migration. This can be carried-up by adding a diffusive term onto (2), and
neglecting the mobility of \(N\) in a first approach. In a more quantitative form,
for instance, consider a migration term like to this one considered originally
by Volterra [1,2], i.e. adding up a positive constant \(m\) onto (2):

\[
\frac{\partial C'}{\partial t} = C(F - s\beta) + m,
\]

\((2')\)
the linear analysis of \((1,2')\) and \((3)\) shows that the only stable point is 
\((N, C) \sim \left(0, \frac{\alpha - S\beta}{\delta} + \frac{m}{\alpha}\right)\), corresponding to the extinction for the species \(N\). Nevertheless, a modification on the time of extinction \(\tau\) \((5)\) is expected in this case. So, a constant migration term does not stop Neanderthal extinction.

In a more realistic approach, we can consider a diffusive term like to 
\(D\partial_{xx}C\) added to \((2)\) and look for travelling wavefront solution. Namely we consider solutions like to \(N(x - vt)\) and \(C(x - vt)\) in the population variables where \(v\) is the velocity of propagation. In this case using the variable 
\(z = x - vt\) , the evolution equations become,

\[-v \frac{\partial N}{\partial z} = N (\alpha - \beta - \delta (N + C)) , \quad (6)\]

\[-v \frac{\partial C}{\partial z} = C (\alpha - s\beta - \delta (N + C)) + D \frac{\partial^2 C}{\partial z^2} . \quad (7)\]

The linear stability analysis tell us that the point \((N, C) = \left(\frac{\alpha - \beta}{\delta} , 0\right)\) is a saddle point with one stable manifold. Nevertheless, the condition

\[v^2 > 4D (1 - s) \beta \quad (8)\]

is necessary because any physical solution requires \(C \geq 0\). On the other hand the point \((N, C) = \left(0, \frac{\alpha - \beta}{\delta}\right)\) is an unstable node and, finally, the point \((N, C) = (0, 0)\) is always stable (figure 2). For this last point, the condition

\[v^2 > 4D (\alpha - s\beta) \quad (9)\]

must be imposed \((N, C \geq 0)\). Moreover, remark the invariance under velocity inversion \((v \rightarrow -v)\) and coordinate inversion \((z \rightarrow -z)\) in \((6,7)\). So, for any solution with velocity \(v\) we can found one other with velocity \(-v\).
From the above discussion, there is the possibility of travelling wave solutions connecting the point \( \left( \frac{\alpha - \beta}{\delta}, 0 \right) \) and \( \left( 0, \frac{\alpha - s\beta}{\delta} \right) \). Numerical calculations confirm this possibility. Figure 3 shows two front-expansion for species \( C \) and the backward motion for \( N \) is superposed. The stability of this wavefront solution was tested numerically using different extended initials conditions for \( N \). So, numerical solutions confirm the extinction. Remark, like to the Fisher equation \([5]\), we can use the inequality \((9)\), more stronger than \((8)\), to obtain a first estimation of the wavefront velocity, i.e. \( v \sim \sqrt{4D (\alpha - s\beta)} \). Numerical calculations confirm this estimation. Figure 4 shows the variation of the velocity wave front for different values of \( \sqrt{D} \). It was carried up assuming \( \int C(x, t) \, dx \propto vt \) after the transient producing the stable front (figure 3).

Finally, the deterministic model (1-3) with interaction is simple and similar to those proposed in [1]. Nevertheless, as long as we assume the validity of the exclusion principle (Gause), other deterministic models [2-4] cannot gives us very different results. Namely, the exclusion principle guaranties the extinction of species \( N \). In fact, from equations (1-3) we have the inequality

\[
\frac{1}{C} \frac{\partial C}{\partial t} > \frac{1}{N} \frac{\partial N}{\partial t}
\]

which tell us that no-equilibrium points exist like to \((N_0, C_0)\), where \( N_0 \neq 0 \) and \( C_0 \neq 0 \). Moreover, the above inequality (10) guaranties the instability of equilibrium points like to \((N_0, 0)\). In this way, the above inequality can be interpreted as a mathematical formulation of the exclusion principle, and then we can expect its validity for other deterministic models describing the interaction between \( N \) and \( C \).
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FIGURE CAPTIONS

Figure 1: A numerical sketch of competition between Neanderthal (N) and Early Modern Men (C). A simple mathematical model is described by equations (1-3). Species C fills gradually the ecological niche of N (arbitrary unities).

Figure 2: A linear stability analysis of equation (6-7) with a diffusive term. \((N, C) = (\alpha - \beta, 0)\) is a saddle point and \((N, C) = (0, \alpha - \beta)\) is a unstable node. In this way, there is a possible solution connecting these points. The point \((0, 0)\) is stable.

Figure 3: A typical numerical simulation of the solution of (1-3) with a diffusive term \(D\partial_x^2 C\) add to (2). The central pick corresponds to the expanding front for C. The other two, are related to Neanderthal backward motion \((0 < X < 1000)\). The stability of these wave-fronts have been tested numerically using different extended initial conditions for N (arbitrary unities).

Figure 4: A numerical calculation of the wave front velocity \(v\) for different diffusion coefficients \((\sqrt{D})\). The assumption, to obtain this graphic, is the number of total individual C grows like to \(vt\) after the transient (i.e. \(t \rightarrow \infty\)). This calculation confirms our estimation for the wave front velocity.