

# Cosmopolitan ancestors: Simulations calibrated with genetic and ethnographic data show that prehistoric populations were not small and isolated

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September 2009

## Abstract

The traditional view about our ancestors is that they lived in closed worlds where the interactions were limited to just a small number of relatives or lifelong close associates. However, using the extent of genetic differentiation (Wright's  $F_{ST}$ ) in populations which are likely to have had population structures and characteristics similar to our ancestors it is shown that this idea seems to be incorrect. Under idealized assumptions in which only random migration and small group size are at work, we show that the observed  $F_{ST}$  values could be produced by small and isolated populations. However, when we introduce different deviations to the idealized situation -reproductive skew, population crashes, recolonization processes, lineage-based group fission and non-random migration in order to reflect some of the conditions in the Pleistocene our simulations show that the  $F_{ST}$  values could not be produced by small and isolated populations but by large and cosmopolitan ones.

Keywords: Human prehistoric populations, effective population size, migration rate, genetic differentiation value.

## Introduction

The prehistoric populations of humans are an important source of information to analyze some aspects of the modern human societies. Thinking about the human ancestors it is important because it is possible to understand some of the characteristics of humans nowadays. For instance, human behavior or languages structures are some of the elements that could be studied by looking to human evolution. This explains why it is necessary to understand the population dynamics of our ancestors.

The common view of human prehistoric populations is that they were small and isolated. How Dawkins (2006) said: "Throughout most of our prehistory, ... most of your fellow band members would have been kin, more closely related to you than members of other bands. . . plenty of opportunities for kin altruism to evolve. And... you would tend to meet the same individuals again and again throughout your life-ideal conditions for the evolution of reciprocal altruism. Those were also the ideal conditions for building reputations for altruism and the very same ideal conditions for advertising conspicuous generosity" How the general though this quote is basically suggesting that

our ancestors lived in small groups with low migration rates between them, where one individual just interact with a few number of people through his/her life. However how is this idea supported? Is it really correct?

In order to answer these questions it is possible to use the value of genetic differentiation between groups. This value was introduced by Sewall Wright and is noted like  $F_{ST}$ . In a model of populations with hierarchical structure the  $F_{ST}$  value is defined as the extent to which two individuals in the same subpopulation are more likely to be genetically similar than two individuals drawn from the entire population (Bowles 2006). In the hierarchical structure the entire population known as the metapopulation is composed of groups which are composed of demes. A deme is a collection of people reproductive semi-isolated. Many demes with the same ethno-linguistic, historical, geographical or other unit conform a group (Figure 1). For this reason there is a collection of F-statistics associated to different levels for the  $F_{ST}$ . All corresponding to the ratio of the genetic variance between units at a lower level to the total genetic variance in a unit at a higher level there are three F-statistics (Bowles 2006):  $F_{DT}$  for demes into the total,  $F_{GT}$  for groups into the total and  $F_{DG}$  for demes into the groups.

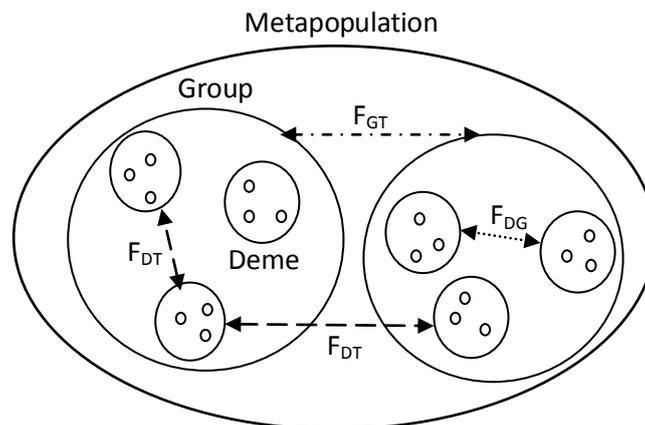


Figure 1. Hierarchical population structure and F-statistics.

$F_{ST}$  is very useful because the way that it is defined allow to capture the effect of many process associated to the population dynamics. For instance, this value is product of migratory flows, reproductive inequalities, selection pressures, fissioning, group size and environmental shocks between others elements of population dynamics. The genetic differentiation between groups could describe in a very good way the elements associated to population dynamics because it depends on the following two variables: The effective population size and the migration rate between groups. The effective population size is defined as the number of individuals in a theoretically ideal population having the same magnitude of random genetic drift as the actual population (Hartl and Clark 1989). In this sense this value is going to be inverse to the value of genetic differentiation because the effect of genetic drift which tends to differentiate populations will be greater when the effective size is small. About the migration rate, it tends to homogenize the populations. For that reason as low is the migration rate as high is the genetic differentiation between groups. If one metapopulation is evolving in the long run, the opposite effects of genetic drift due to small size and migration will be equilibrated at some value of genetic differentiation. This value is the  $F_{ST}$  and could

be expressed using an equation including the effective size and the migration rate. How this is a model with diploid individuals this equation is (Wright 1935):

$$F_{ST} = \frac{1}{1 + 4N_e m} [1]$$

Note that  $N_e m$  is a composite measure of the migration rate and the group size. This number will be denoted by  $M^*$  and represent the number of migrants per generation in each deme.

The empirical  $F_{ST}$  value has been calculated for modern populations of hunter-gatherers with similar characteristics to ancestral humans. Although these populations are not exact replicas of human prehistoric populations some of them could be a good approach because they have similar population structures and live in similar places. In other words, it is possible to find modern populations with a high resemblance to ancestral humans. The average value of genetic differentiation in these populations is 0.076 ( $\pm 0.013$ ) and it will be taken as the empirical  $F_{ST}$  (Bowles 2006).

Under idealized assumptions in which only random migration and small group size are at work, it is possible to calculate the migration rate expected using estimations about the size of the prehistoric populations and the empirical  $F_{ST}$ . Looking to the ethnographic record Marlowe (2005) estimated that the average census size could be 37 which imply that  $N_e=12.3$  if it is assumed that just one third of the population is in reproductive age (Cavalli-Sforza and Bodmer 1970). Using the equation [1] it is possible to conclude that  $M^*=3.03$  in order to have the observed value of genetic differentiation which means that  $m=0.24$ . Then, in the ideal situation the values for group size and migration rate are according to not cosmopolitan populations but to small and isolated ones. However the assumptions behind the ideal situation are completely unlikely in the Pleistocene. It is necessary to include many deviations to this model to make an approach to the real conditions in this period. Mating practices, natural disasters, warfare and massacres, splitting and fragmentation of communities, non random patterns of migration and social changes are just some of the aspects that it is necessary to take into account to really think about ancestral humans. As we will show under these deviations the effective population size and the migration rate are smaller than the observed values which basically mean that the  $F_{ST}$  will be greater than the observed value. In this sense, in a scenario close to the real situation in the Pleistocene a value of 0.076 for the  $F_{ST}$  could not be produced by small and isolated populations but by large and cosmopolitan ones. The objective of this work is to model five of all the possible deviations to the ideal situation and figured out their effect on the  $F_{ST}$ . This would allow us to suggest a possible value for  $M^*$  in a more realistic situation.

## Simulations

All the simulations work using an initial metapopulation which evolves according to certain parameters for a set number of generations. In a metapopulation there are  $V$  groups and  $M$  demes ( $M/V$  demes per group) each one with  $N_I$  individuals. Each individual is characterized using a vector with five components which include a tag, the group and the deme of the individual, the sex (0 for female and 1 for male) and the genetic information. These simulations are based in a model of 2 alleles with diploid individuals each one with 5 loci. Here is an example of one possible agent who is tagged 25, belongs to the deme 3 in the group 2 and is female:

{25,2,3,0,{{1,0},{0,1},{0,0},{1,1},{1,0}}}

### Migration and reproduction

These simulations are based on the Wright Fisher model of reproduction which is a model of non-overlapping generations (e.g. every generation after reproduction the entire population produce a new population and is replaced by it). In this sense, every generation each deme is filled with the sons of NI couples of parents selected according to certain probabilities from the overall population. More specifically if there is a deme  $x$  which is in a group  $G$  each one of its members has a probability  $1-m-m_2$  of having parents which in the previous generation were in the deme  $x$ , a probability  $m$  of having parents which in the previous generation were in other deme in the group  $G$  and a probability  $m_2$  of having parents which in the previous generation were in a deme outside the group  $G$  where  $m$  and  $m_2$  are the migration rates between demes in the same group and demes in different groups respectively. Then basically in one deme a fraction  $m$  of the individuals are migrants from others demes in the same group, a fraction  $m_2$  are migrants from demes in other groups and a fraction  $1-m-m_2$  is from the same deme.

### Mutation

There is a mutation rate  $\mu$  to avoid allele fixation because this is a 2-alleles model. In order to this rate not to affect the  $F_{ST}$  values,  $\mu \ll m$ . Then every generation each locus of an individual has a probability  $\mu$  of mutate which means that one of its two alleles change.

### $F_{ST}$ calculation

In the hierarchical model presented it is possible to calculate three values for  $F_{ST}$ :  $F_{DT}$  which accounts for the differentiation among demes in the metapopulation,  $F_{DG}$  for the average differentiation among demes in each one of the groups and  $F_{GT}$  for the differentiation among groups in the metapopulation. Suppose that there is a locus with two alleles (A,a), with  $M$  demes,  $V$  groups and  $U$  demes per group. These values are defined by (Bowles 2006):

$$F_{DT} = \frac{\sum_{i=1}^M (p_i - p)^2}{M(p(1-p))} [2]$$

$$F_{GT} = \frac{\sum_{j=1}^V (p_j - p)^2}{V(p(1-p))} [3]$$

$$F_{DG} = \frac{\sum_{j=1}^V \frac{\sum_{i=1}^M (p_{ij} - p_j)^2}{U(p_j(1-p_j))}}{V} [4]$$

Where  $p_i$ ,  $p_j$  and  $p$  denote the fraction of individuals bearing the allele A in demes, groups and in the metapopulation respectively;  $p_{ij}$  is the fraction of individuals in deme  $i$  in group  $j$  that is A.

## Parameters

How a first approach to simulate the Pleistocene conditions the following parameters are used:

$V = 1$  (which implies  $m_2 = 0$ ),  $M = 10$

However how it is going to be showed it is necessary to work with bigger scale simulations.

To select  $N_I$  and  $m$  the Marlowe's estimates about population size were used. How it is supposed that one third of the population is in reproductive age and Marlowe suggest a census size around 30 in these simulations  $N_I = 10$ . The migration rate was fixed in order to get the empirical  $F_{ST}$  value obtained in modern populations of hunter-gatherers (0.076). In this sense  $m = 0.3$  to have

$$\frac{1}{1 + (4 * 10 * 0.3)} = 0.076 \cdot$$

Using these parameters a metapopulation is created in the first generation. The genetic information for every individual is randomly chosen. This metapopulation evolves for a fixed number of generations according some rules depending on the specific simulated situation.

## Ideal situation

A model of the ideal situation was implemented to test the simulation. How there are no deviations included the expected value was 0.076. Besides, to simulate this situation is useful to analyze the results of including the deviations into the model.

## DEVIATIONS

### Reproductive skew

The effect of reproductive skew is basically to introduce variance in the expected number of progeny per individual. This is going to increase the  $F_{ST}$  values because it implies a reduction in the effective size of the population which is given by (Kimura and Crow 1963):

$$N_e = \frac{2N}{1 + \frac{\sigma^2}{k}} \quad [5]$$

where  $N$  is the generation size,  $\sigma^2$  is the variance in the number of progeny produced and  $k$  is the mean number of progeny produced. Note that in these simulations  $k = 2$  due to there is sexual reproduction and the population size is constant every generation. Besides, note that for the ideal situation -where the expected number of progeny is identical across individuals- there is a Poisson distribution for the number of progeny per individual which implies that it is expected to found that  $\sigma^2 = k = 2$  and that  $N_e = N$ . Indeed, the actual variance in reproductive success in the simulation of the ideal situation is around 2.

This deviation was introduced by changing the way of picking individuals for reproduction. Instead of doing a random selection process, in this simulation there is a vector  $\{k_1, \dots, k_{N_I}\}$  where  $k_i$  is the probability for the individual  $i$  of being chosen for reproduction. This vector is different for each

sex because in general the variance in the reproductive success is higher in males than in females. These two vectors are the same for every deme in the metapopulation.

This simulation was calibrated with data of the Ache hunters from Paraguay (unpublished data provided by Frank Marlowe). There is one study which recovered information in this population during 20 years about the number of offspring per individual discriminating between female and male (Figure 2). Looking at the distributions, it is found that for females  $\frac{\sigma^2}{k} = 1.52$  and for males  $\frac{\sigma^2}{k} = 2.99$ . These values were used to calibrate the simulation because the ratio between the variance and the mean of the number of progeny produced is what is going to affect the effective population size, which determines the  $F_{ST}$  [1].

It was previously mentioned that in these simulations  $k = 2$ , which implies that in order to obtain the ratios found for Ache hunters,  $\sigma^2_{female} \approx 3$  and  $\sigma^2_{male} \approx 6$ . Then, the vectors for introduce reproductive skew to the simulation were constructed to generate these variances in the reproductive success for males and females.

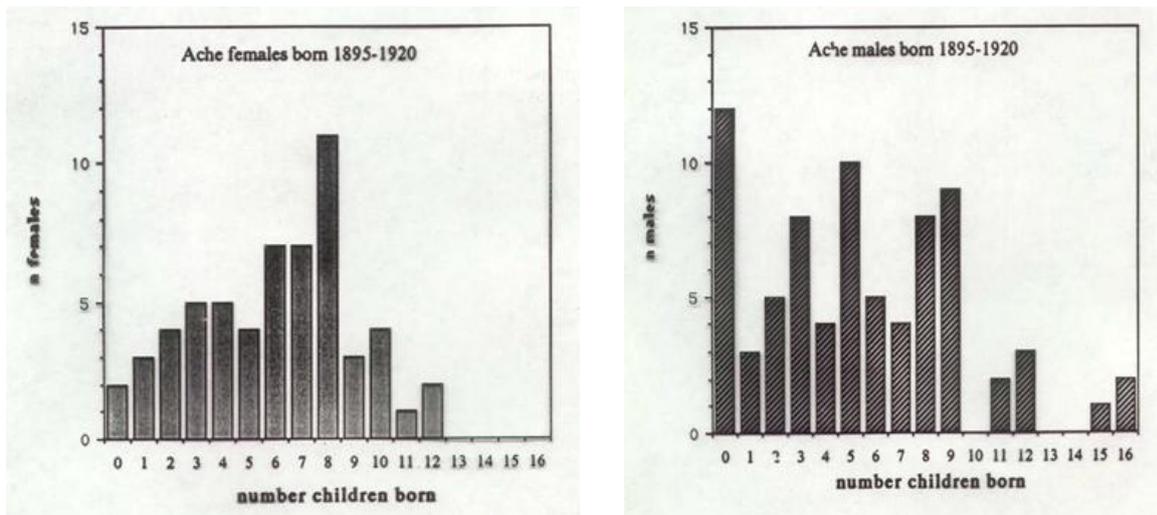


Figure 2. Distribution of number of children per females and males for the Ache hunters in Paraguay (Unpublished data provided by Frank Marlowe).

### Population Crashes

It is undeniable that in the Pleistocene the prehistoric populations were exposed to several environmental shocks. Ice-core evidence for instance shows that temperature was so variable in the late Pleistocene changing in some cases in  $10^{\circ}\text{C}$  in just two centuries (Figure 3). Population crashes generated by these environmental conditions cause a reduction in the effective population size. Indeed it has been proven that when the census size has different values over time the effective population size is the harmonic mean of those numbers rather than the arithmetic mean, which is higher than the first one. Returning to the equation [1] this basically implies an increasing in the  $F_{ST}$  value.

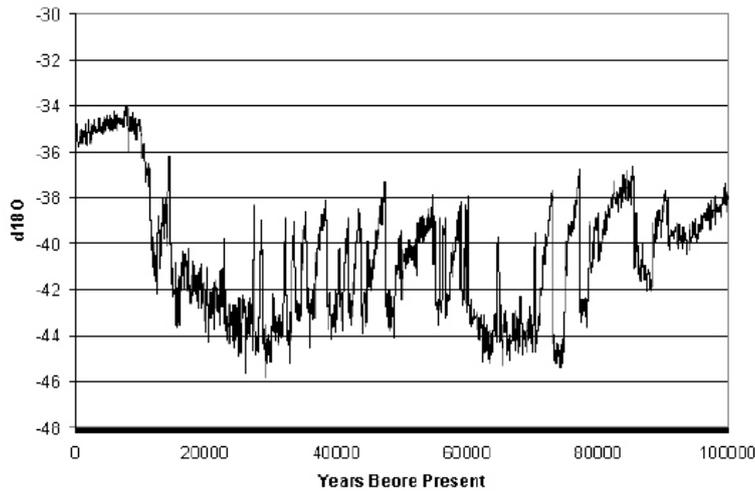


Figure 3. Variation in temperature in the late Pleistocene measured by the concentration of one oxygen isotope. One unit in the concentration of this element is associated with 1.2 degrees centigrade (from [http://www.glaciology.gfy.ku.dk/ngrip/index\\_eng.htm](http://www.glaciology.gfy.ku.dk/ngrip/index_eng.htm) and described in (North Greenland Ice Core Project members 2004)).

This deviation was simulated using two parameters: The magnitude, which is the fraction of the population dying in a crash and the frequency, which is the probability per deme of crashing in one generation. These values were calibrated using data from an island in the Pacific called Tristan da Cunha because this is maybe the only isolated society with a long term demographic record. Although this society disappeared in 1960 because of a volcano eruption, there is information about the population size since 1820 (Figure 4). The ratio between the harmonic and arithmetic mean was used in order to calibrate the simulation.

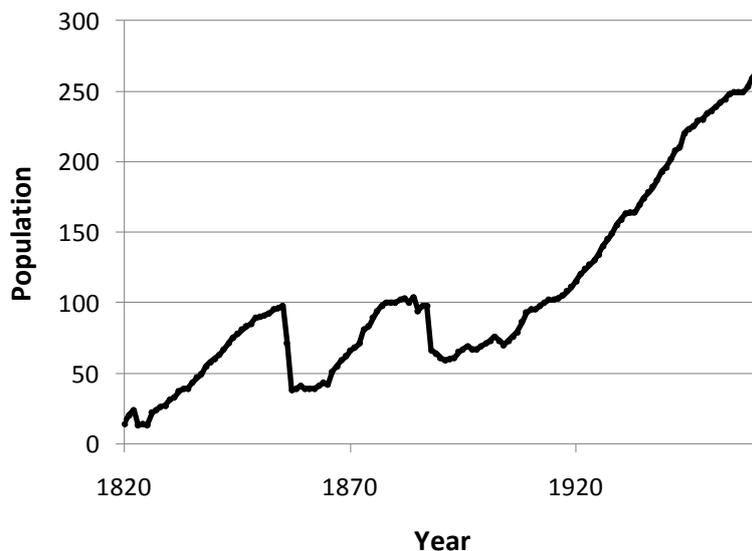


Figure 4. Variation in the census size for the population of the island Tristan da Cunha over 140 years (Roberts 1968)

### *Recolonization and fissioning*

It has been observed in modern populations of hunter-gatherers that small propagules of close related people in one deme tend to go away and colonize other places. This process increases the values of genetic differentiation because the allele frequencies for all loci are different between a population and a small group of related people in it. There are two possible reasons for moving of propagules. First, when there is a group conflict one small propagule of the winner group recolonizes the place of the other group. Second, when one group gets so large, small propagules of it tend to move to other places. In general these places are available because the extinction of other demes due to climate and environmental conditions. One of the mainly differences between these two phenomena is that in contrast to fissioning by large size which increases the number of demes, in general recolonization by group conflict does not modify it. However, because in this model the number of demes and its size are constant the process of recolonization and fissioning are going to be simulated together.

There are three parameters associated with this simulation: The probability of a fission event per deme (caused by any of the two reasons previously mentioned) in each generation, the fraction of the deme which goes away after splitting and the degree of relatedness between the members of the propagule. In order to establish the relatedness between members in the propagule one individual is randomly selected in the deme. Using the genetic information of this individual his relatedness with every people in the deme is calculated by averaging the values of relatedness for all loci. These relatedness values are organized in a vector from the highest to the lowest value. Then, with a probability  $p$ , which is the third parameter of the simulation, the individual takes the closest person to him who has not been taken so far and with a probability  $1-p$  he takes a randomly selected individual in the entire deme. This process of selection continue until get the value fixed by the fraction of the people which go away after fissioning.

To calibrate this deviation data about the frequency of recolonization and fissioning was taken of Yanomano tribes in the Amazonian forest. About the fraction of the deme which goes away after splitting based in estimations of Wade and McAuley (1988) a value of one third was used. Finally, the degree of genetic relatedness was fixed in 0.8 in order to express that close kin goes together which is a phenomenon observed in a great majority of the modern societies of hunter-gatherers.

### *Non-random migration*

This deviation is the only one that acts on the migration rate instead of in the effective size. How was mentioned previously the effect of migration in the metapopulation is to homogenize the demes which implies a reduction in the  $F_{ST}$  values. In this sense, migration will not going to have the same effect if one deme does not receive migrants with the same probability for all demes but with a higher probability just of few ones. If migration is not a random process then its effect is going to be reduced implying an increase in the genetic differentiation between demes.

After one generation it is possible to generate a vector for each deme with  $M-1$  positions corresponding to the number of migrants received of the others demes. Although the first generation the migration is completely random the next generation this vector is transformed in a vector of probabilities of receiving a migrant of each one of the other  $M-1$  demes. Then if the vector

is  $\{a_1, \dots, a_{M-1}\}$ , it is transformed using the following replacement rule  $a_i \rightarrow 1 + (a_i * k)$  where  $k$  is a parameter which allows to set the degree of non randomness for migration. Once the vector has been transformed this is normalized in order to have a vector of probabilities. This basically means that if there are two demes A and B the probability of migration from A to B depends on the number of migrants which was sent from A to B in the previous generation which also depends on the value of this number in the previous generation.

Data from the Aland islanders of Finland was used to calibrate this deviation. In these populations has been estimated that the effective migration rate when there is non-random migration is a half of the observed one (Rogers and Jorde 1987). In other words, the  $F_{ST}$  values produced when migration is non random are the ones produced by a migration rate which is half of the observed rate. How the migration rate in these simulations is 0.3, the value of  $k$  was calibrated in order to obtain the  $F_{ST}$  value produced when the migration rate is 0.15.

### Simulation results and discussion

Under the idealized assumptions, an effective size of 10 and a migration rate of 0.3, the  $F_{ST}$  obtained was  $0.076(\pm 0.017)$  which is the empirical value for modern populations of hunter-gatherers. This implies that the way to implement the simulation using the parameters of size and migration is according to the meaning of these values in a real situation. Besides, the results obtained show that the  $F_{ST}$  is the equilibrium of the effect of the forces related to the genetic differentiation in a metapopulation (Figure 5).

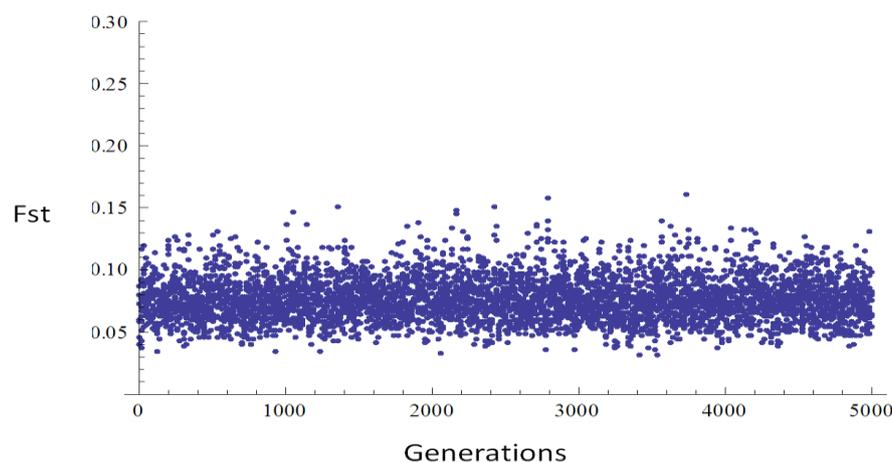


Figure 5.  $F_{ST}$  values for a metapopulation along 500 generations under the idealized assumptions.

How theoretical analyses have showed previously all the deviations introduced increase the value of genetic differentiation in the metapopulation (Bowles 2006). For each deviation it was possible to produce almost any value for  $F_{ST}$ , even 1 in some cases. However all the  $F_{ST}$  values presented are product of the simulations calibrated with empirical information how was explained before.

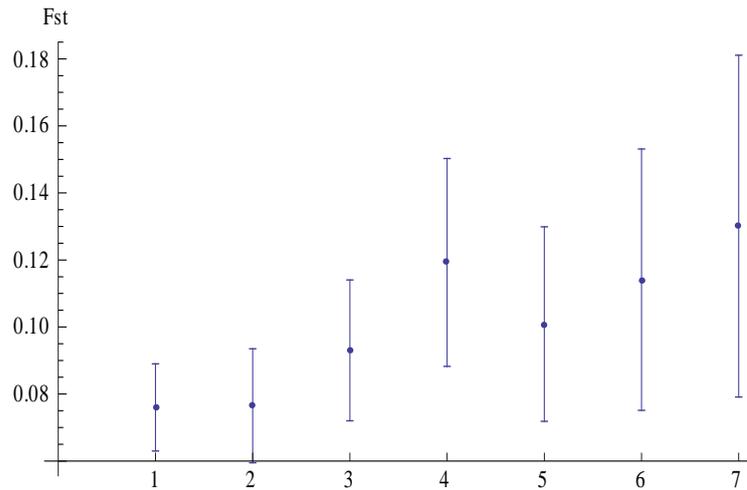


Figure 6.  $F_{ST}$  values for 1- Modern populations of hunter-gatherers and the simulations implemented: 2- Idealized situation, 3- Reproductive skew, 4- Population crashes, 5- Recolonization and fissioning, 6- Non random migration, 7- All the deviations working together.

What this suggests is that it is not probably that a  $F_{ST}$  value of 0.076 could be produced by small and isolated populations under the Pleistocene conditions. We should look especially to the case of all the deviations together which is the closest one to the real situation. The simulations results for this case are showed in the Figure 7. This figure show not just that when all the deviations work together for an effective size of 10 and a migration rate of 0.3 it is almost unlikely to have an  $F_{ST}$  value of 0.076 but also that in order to obtain this value for  $F_{ST}$  it is necessary to have  $M^*=8$  which means an effective size of 20 and a migration rate of 0.4. The value of  $M^*$  in order to have that  $F_{ST}=0.076$  was evaluated for each one of the deviations introduced (Table 1).

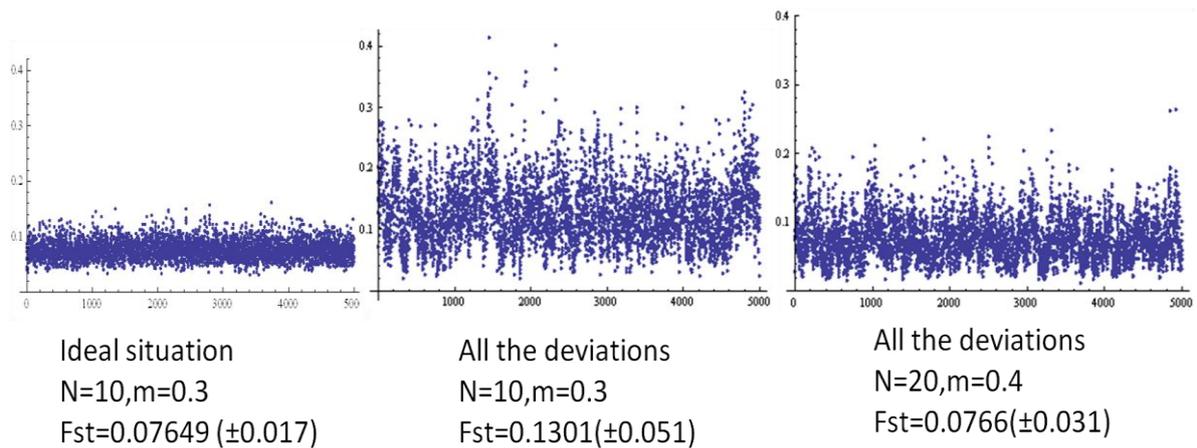


Figure 7. Simulation results for the ideal situation and for all the deviations working together with  $M^*=3$  (center) and with  $M^*=8$  (right).

Table 1. Percentage of increase of the  $F_{ST}$  value for each one of the deviations introduced from the idealized situation. The value of  $M^*$  ( $N_e m$ ) is the number of migrants per generation in each deme in order to obtain a  $F_{ST}$  value of 0.076.

| Population structure assumptions | Fst                   | % of increase | $M^*$ |
|----------------------------------|-----------------------|---------------|-------|
| 1. Estimated from genetic data   | 0.076 ( $\pm 0.013$ ) | -             | 3     |
| 2. Ideal situation               | 0.076 ( $\pm 0.017$ ) | 0             | 3     |
| 3. Reproductive skew             | 0.093 ( $\pm 0.021$ ) | 22.4          | 3.69  |
| 4. Population Crashes            | 0.12 ( $\pm 0.031$ )  | 56.9          | 4.88  |
| 5. Recolonization and fissioning | 0.10 ( $\pm 0.029$ )  | 32.7          | 4.04  |
| 6. Non random migration          | 0.11 ( $\pm 0.039$ )  | 50.1          | 4.64  |
| 7. All the deviations            | 0.13 ( $\pm 0.051$ )  | 71.2          | 8     |

The other conclusion of the results obtained with these simulations is that the combined effect of all the deviations put it together is subadditive. It is possible to conclude this looking not just to the  $F_{ST}$  value but also to  $M^*$ . For both measures the value expected in the case of additive or multiplicative effects is greater than the value obtained with the simulations. Besides, the other aspect to take into account is that the variance for the  $F_{ST}$  value when the five deviations work together is product of the cumulative effect of the variance for each one of the deviations taking alone (Figure 6). For this reason, this variance is greater than the one for the estimates with genetic data. It was expected to find that the deviations have a subadditive effect because they mask one to another. For instance, deviations where either a fraction or the entire deme die –like population crashes or recolonization and fissioning- are likely to diminish the effect on the genetic differentiation of other deviations.

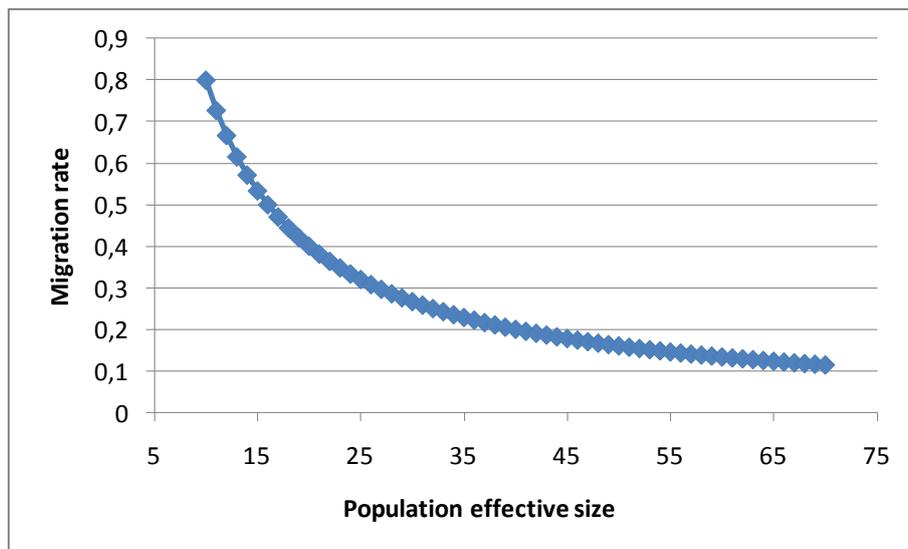


Figure 8. Combinations of the effective and the migration rate which gives  $M^*=8$

These simulations were based on the estimate of population size made by Marlowe of 37 individuals per deme. However how these results have shown either the migration rate was really high or there was combination of high migration rates and big sizes for the population. The latter implies that a census size of 37 could be a subestimation of the real average size of the prehistoric populations. How it is difficult to know which was the case in the Pleistocene, it is very useful to introduce  $M^*$  because this value includes the combined effect of migration rate and effective population size on the  $F_{ST}$  without discriminate which of the two variables has a major role. In this sense taking into account that  $M^*=8$  it is possible to define the value of migration rate using the effective population size (Figure 8). In the case of a effective size of 10 the migration rate should be 0.8 which is a really high value. Besides, note that in the x axis is the effective size of the population and not the census size which is approximately three times higher (Cavalli-Sforza and Bodmer 1970).

## Conclusions

The main conclusion of this work is that our ancestors probably were much more cosmopolitan than the way that we may imagine they were. Given some of the conditions which the prehistoric populations of humans living in, it was found that in order to have  $F_{ST}$  values around 0.076 it is necessary  $M^*=8$ . Then, we are suggesting that if we assumed that the census size of the prehistoric populations of humans was 37, of the 10 individuals in reproductive age in a deme in one generation approximately 8 are migrants. On the other hand it was possible to conclude that the effect of all the deviations put it together over the  $F_{ST}$  values is subadditive. This could be explained because the effect of one deviation could mask the effects of other deviations.

## Future work

These simulations perform well, but they are just a first approach to the dynamics of genetic differentiation in prehistoric populations. They can be improved by adding robustness and introducing more deviations in order to have more realistic conditions. There are several important directions for future research. The first one is to do simulations with more than one group to introduce the dynamics associated to ethnolinguistic units. For example, process like migration, recolonization and fissioning would be different if it is taking into account that there are significant cultural differences between groups. The second one is to find a statistical way to calculate the probability of producing the empirical  $F_{ST}$  value (0.076) using small and isolated demes in a simulation of one of the deviations introduced. This would be complemented by increasing the number of loci of the individuals, which would diminish the variance in the  $F_{ST}$  values. Third, it is desirable to introduce other deviations into the simulations like variation in the deme size, variation in the number of demes –which would allow differentiating between group conflict and population splitting by size– and variation in the number of females and males in each deme. Indeed, there is available ethnographic data to model the shape of the distribution of size for the demes. Finally, it is necessary to improve the deviations already implemented by using more flexible parameters. It is clear that a crash not always kill the same amount of people and that not always the same fraction of the population goes away after splitting. Besides, it would be better to work with age structured populations.

Finally, we suggest that it is necessary to begin rethinking in the evolution of human behaviors under the idea of cosmopolitan ancestors with questions like Were kin selection and direct reciprocity the means for the evolution of cooperation in societies where people were constantly moving?

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