Ancient DNA and the spread of the Neolithic in Europe

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Introduction

The Neolithic transition meant not only the beginning of agriculture, but also a global socioeconomic transformation for human populations. In Europe, agriculture spread from the Near East and across the continent from about 8,000 y BC to 3,000 y BC. Identifying the driving mechanisms of this spread has been a key issue. The study of archaeological remains suggests that the main driver was the spread of farmers (demic diffusion) [1], although the importance of cultural diffusion (adoption of farming by hunter-gatherers) varied from region to region [2].

Demic and cultural diffusion would yield different genetic patterns in the Early Neolithic populations, and recent ancient DNA studies also point toward a mostly demic expansion [3].

Here we compare genetic clines from Neolithic mtDNA data with the results of a demic-cultural wave-of-advance model, to obtain a first direct estimate of the relative importance of demic diffusion over cultural diffusion.

Clines of ancient mtDNA

Neolithic DNA database

We have gathered a database of 514 Neolithic individuals whose mtDNA has been determined, and we grouped them into "regional cultures" according to their geographical and cultural closeness [4].

We want to asses the relative importance of the demic and cultural diffusion processes in the Neolithic spread. So we shall compare with our computational model only Early Neolithic regional cultures (selecting those with at least eight individuals associated to them, for better statistical significance; squares in Fig. 1).
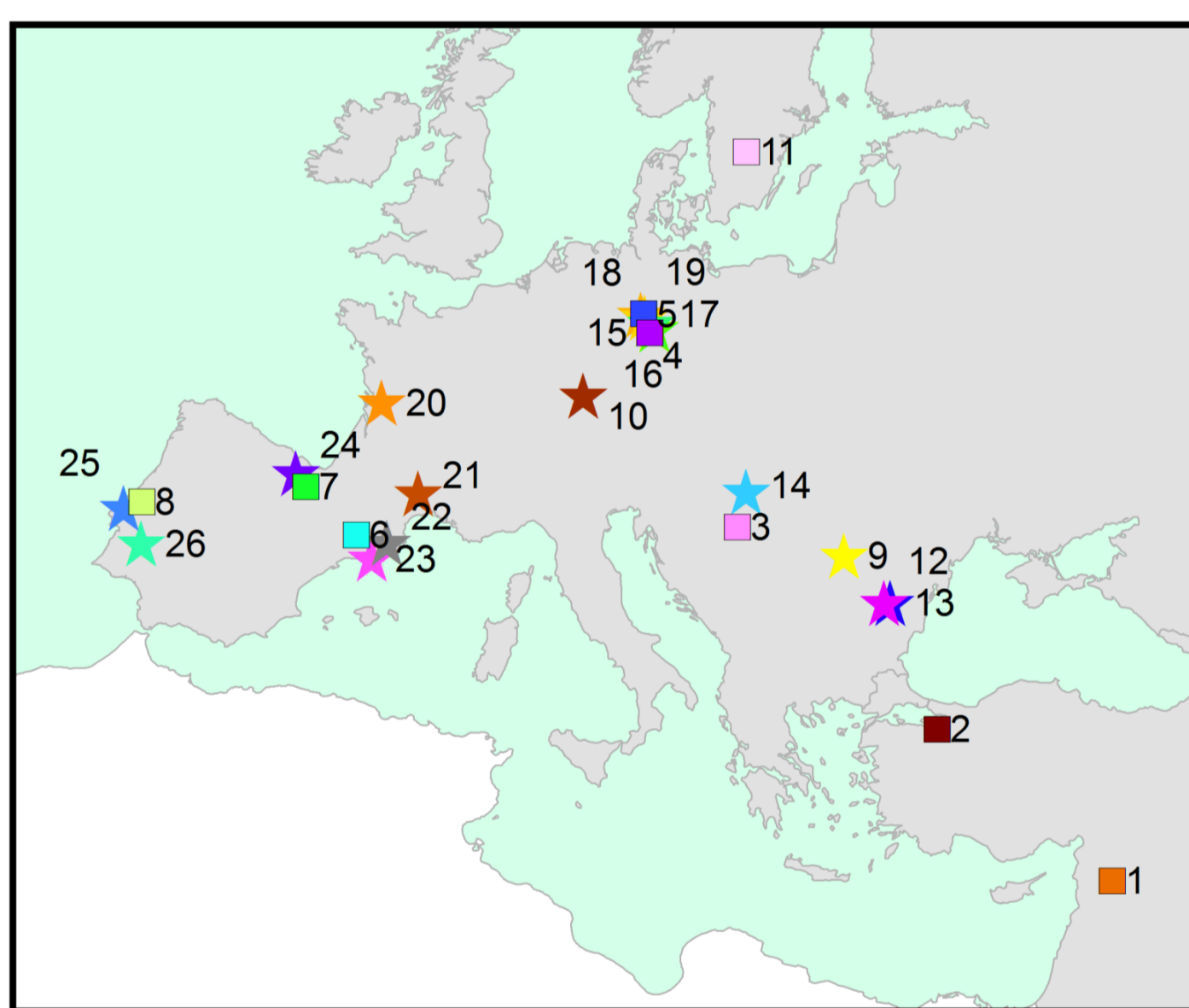

Fig. 1 Geographic distribution of the 26 regional cultures with more than two individuals associated to them (corresponding to a total of 509 individuals). Squares indicate the nine Early Neolithic regional cultures that we compare with the simulation results.

Early Neolithic genetic cline

Several mitochondrial haplogroups have been proposed as Neolithic markers (haplogroups N1a, T2, K, J, HV, V, W, and X) [5, 6]. We have selected for our analysis a marker presenting high enough frequencies for statistical significance, with a wide geographic distribution and virtually absent in pre-Neolithic populations.

Figure 2 shows how the presence of the marker in Early Neolithic populations diminishes with the distance to the Near East (see also Fig. 3). This is the cline that we want to reproduce with our computational model.
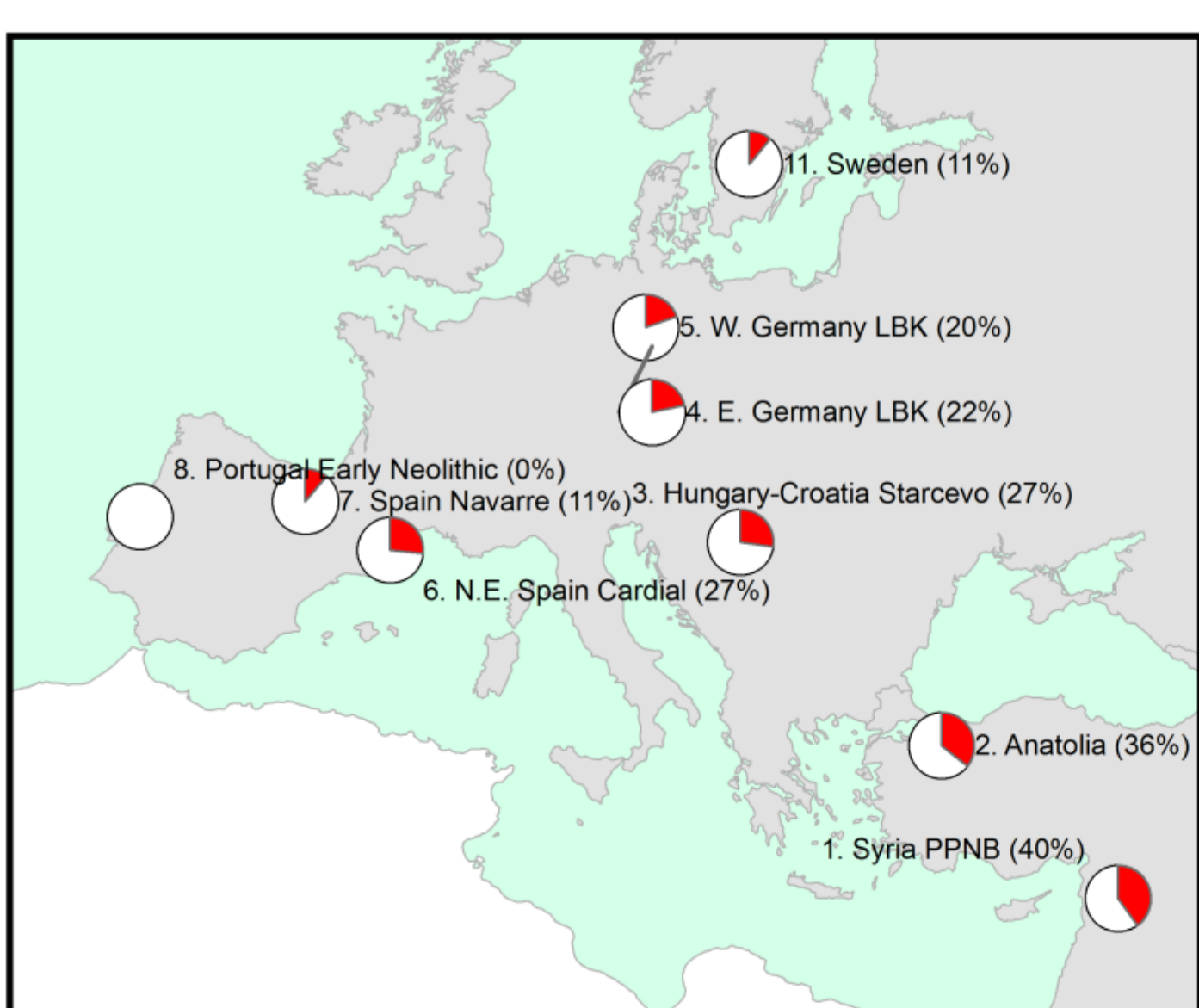

Fig. 2 Percentage of Neolithic population with the Neolithic marker (red sectors) for the nine Early Neolithic regional cultures in the database. The presence of the marker diminishes with increasing distance from the Near East.

Computational model

We developed a computational model for the Neolithic spread to predict the relative presence of a Neolithic marker among the early farming populations.

The simulations run on a Cartesian grid of cells of 50kmx50km. In each cell we can have population from three population groups:

- HG: hunter-gatherers (without Neolithic marker)
- N: farmers with Neolithic marker
- X: farmers without Neolithic marker

Initial conditions

The simulations start at the cell containing the oldest **archaeological** date for a PPNB site (Ras Shamra), at 8,233 cal BC [7]. Initially this is the only cell with farmer population (3,200 individuals), and all the other cells have initially hunter-gatherer population (160 individuals per cell).

The **genetic** initial conditions (populations N and X) at the origin cell are set so that, at 7,258 cal BC, we have 40% of population with the marker (N) at the location of the regional culture "Syria PPNB", in agreement with the data (Fig. 2).

Dispersion

Cells are classified into: sea, coast, land, mountain. Population can settle only in land or coast cells.

At each iteration, and for every cell, the farmer populations (N and X) disperse as follows:

- 38% of the population stays (**persistence**).
- 62% of the population moves to the 4 nearest neighbors in equal number (**land travel**).
- The population that would move to a mountain cell is distributed among the other destinations.
- The population that would relocate to a sea cell is equally distributed among the coast cells within a radius of 150km, reachable by straight lines (**sea travel**).

We assume the HG population stationary.

Interaction

When hunter-gatherers and farmers coexist in a cell, they may interact and form **mixed cultural couples**. Applying cultural transmission theory we have [8]

$$couples\ HGN = \eta \frac{P_{HG} \cdot P_N}{P_{HG} + P_N + P_X}, \qquad (1)$$

$$couples\ HGX = \eta \frac{P_{HG} \cdot P_X}{P_{HG} + P_N + P_X}, \qquad (2)$$

where $\eta \in [0,1]$ is the intensity of interbreeding. The value $\eta = 1$ would correspond to a situation with equal probability to mate into one's or the other group. Lower values correspond to a preference to mating into one's group.

After this step, we have P'_{HG}, P'_N and P'_X unmated individuals. We do not expect a preference among farmers for mating within their own genetic group, so we can compute the **cross-mating between genetic groups** as follows ($\eta = 1$)

$$couples\ NX = \frac{P'_N \cdot P'_X}{P'_N + P'_X}. \qquad (3)$$

Now we have P''_N and P''_X unmated farmers. Finally we compute the **couples between members of the same group** as follows

$$couples\ HH = P'_{HG}/2, \qquad (4)$$
$$couples\ NN = P''_N/2, \qquad (5)$$
$$coulpes\ XX = P''_X/2. \qquad (6)$$

Reproduction

In this step we apply the following assumptions:

- Children from mixed cultural couples will be farmers [9].
- Farmer or mixed couples have $2R_{0F}$ children, and HG couples $2R_{0HG}$ children ($R_{0F} = 2.45$, $R_{0HG} = 1$).
- 50% of the children from mixed genetic couples inherit the Neolithic marker (a more complex model with gender differentiation yields equivalent results).

Thus the final population after an iteration is

$$P_{0H}(t+1) = 2R_{0HG}\ couples HH \qquad (7)$$

$$P_N(t+1) = 2R_{0F} \begin{bmatrix} couples NN + 0.5couples NX \\ + 0.5couples HN \end{bmatrix} \qquad (8)$$

$$P_X(t+1) = 2R_{0F} \begin{bmatrix} couples XX + couples HX \\ + 0.5couples NX + 0.5couples HN \end{bmatrix} \qquad (9)$$

Results

We run our simulations for different values of the interbreeding parameter η. In Fig. 3 we represent the predicted percentage of the Neolithic marker (mtDNA haplogroup) present at the locations and dates of the nine regional cultures in Fig. 2 (lines in Fig. 3).

- For $\eta = 0$ (no cultural diffusion), no cline is observed.
- For a given $\eta > 0$, the % of the marker diminishes with increasing distance (similarly to the data), because more distance from the origin means more time for the farming population to interbreed with hunter-gatherer populations (who lack the Neolithic haplogroup).
- A higher value of η yields a faster decrease in the % of the marker, since more intense interbreeding means that the farmer population incorporates more individuals lacking the Neolithic haplogroup.
- $\eta \approx 0.02$ yields the best fit between model and data (as this it the only curve that falls within all error bars in Fig. 3). Therefore, we can explain the cline requiring only about 2% of the farmers to interact with hunter-gatherers.
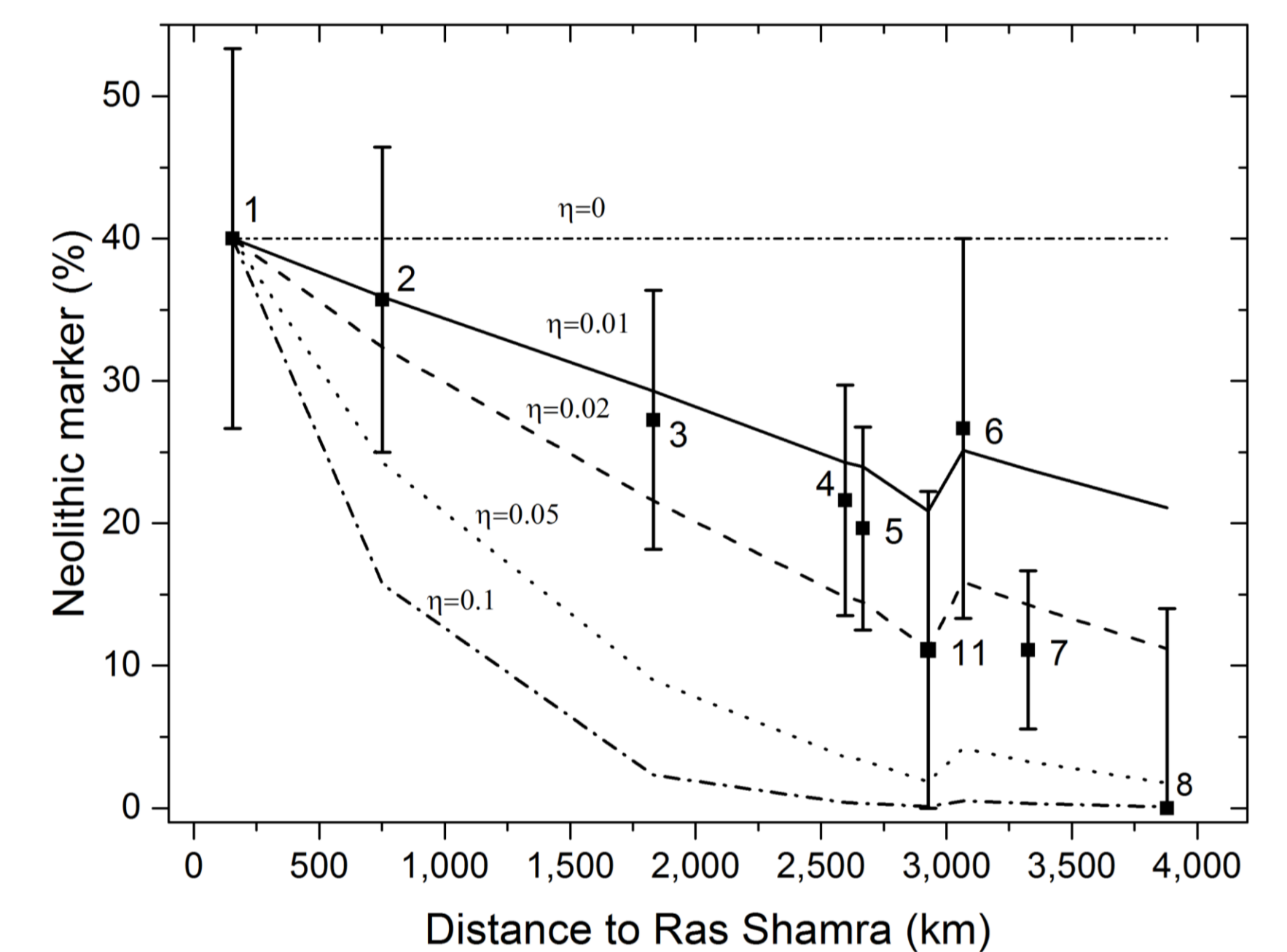

Fig. 3 Observed and simulated percentage of the Neolithic marker (mtDNA haplogroup) in Early Neolithic populations as a function of the great-circle distance from Ras Shamra (simulation origin). Symbols correspond to the regional cultures in Fig. 2. Lines represent the simulated results measured at the same locations and dates as the aDNA data for different intensities of cultural diffusion (η). (Adapted from Ref. [4].)

Conclusions

The analysis of ancient DNA data shows a geographic cline in the presence of a Neolithic marker (mtDNA haplogroup) in Early Neolithic populations.

We have developed a computational model that combines demic dispersal and population growth with cultural transmission theory. This model can predict a cline similar to the observations.

The best fit between model and data is obtained for $\eta = 0.02$. Because the approach applied here to cultural diffusion (interbreeding or vertical cultural transmission; Eqs. 1-2) and acculturation (or horizontal/oblique cultural transmission) are mathematically similar in their effects [1], we can conclude that only about 2% of the farmer population was involved in cultural diffusion [4].

Therefore, although the cline cannot be explained without cultural diffusion, the most relevant process was demic diffusion.

Funding

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