ARTICLES

MODELLING THE NEOLITHIC TRANSITION IN THE NEAR EAST AND EUROPE

Joaquim Fort, Toni Pujol, and Marc Vander Linden

For the Neolithic transition in the Near East and Europe, this paper compares the isochrones predicted by computational models to those obtained by interpolating the archaeological data. This comparison reveals that there is a major inconsistency between the predictions of the models and the archaeological data: according to the models, the Neolithic front would have arrived to Greece in less than half the time interval implied by the data. Our main new results are as follows. (a) This inconsistency can be solved by including only Pre Pottery Neolithic B/C (PPNB/C) sites in the Near East; (b) the model that yields the lowest mean error per site in the arrival time of the Neolithic across the Near East and Europe is obtained by allowing for sea travels up to distances of 150 km; and (c) Mountain barriers have a negligible effect on the spread rate of the Neolithic front at the continental scale.

Para la transición del Neolítico en el Oriente próximo y Europa, este artículo compara las isocronas predichas por modelos computacionales a las obtenidas interpolando los datos arqueológicos. Dicha comparación revela una incoherencia notable entre las predicciones de los modelos y los datos arqueológicos: según los modelos, el Neolítico habría llegado a Grecia en menos de la mitad del tiempo que tardó según los datos. Nuestros principales resultados nuevos son: (i) Esta incoherencia puede resolverse incluyendo sólo yacimientos PPNB/C en el Oriente próximo; (ii) El modelo que arroja el mínimo error medio por yacimiento en el tiempo de llegada del Neolítico en Oriente próximo y Europa se obtiene permitiendo viajes por mar con distancias de hasta 150 km; (iii) Las barreras montañosas tienen un efecto despreciable sobre el ritmo de expansión del Neolítico a escala continental.

The earliest Neolithic sites in the Near East appeared about 13,000 calibrated years before present (cal yr B.P.) (Ozdogan and Basgelen 1999; Pinhasi et al. 2005; Willcox et al. 2009). The Neolithic transition then spread gradually across Europe until it reached the British Islands and southern Scandinavia by 6,000 cal yr B.P. (Pinhasi et al. 2005). There are two main competing models of the Neolithic transition in Europe. The demic diffusion model considers that the driving force of this transition was the dispersion of farming populations. In contrast, the cultural diffusion model assumes that the main mechanism was the imitation of the behavior of farmers by hunter-gatherers. Whereas the demic diffusion model does not deny the possibility of cultural diffusion or local adoption in some specific areas, it assumes that agriculture was spread at the continental scale by dispersing farming populations (Ammerman and Cavalli-Sforza 1971, 1973, 1984; Renfrew 1987). On the other hand, the cultural diffusion model accepts that population dispersal played a role in some special places, but argues that the movement of ideas rather than people is essential to understanding the Neolithic transition over most of Europe (Dennell 1983; Edmonson 1961; Whittle 1996; Zvelebil 1986). The demic model predicts genetic clines across Europe with extreme gene frequencies in the Near East (Ammerman and Cavalli-Sforza 1971). This prediction of demic diffusion agrees with synthetic maps of classical genetic markers in present Europeans (Menozzi et al. 1978). It is true that genetic clines can also arise by other mechanisms different from Neolithic demic diffusion (e.g., from the arrival of modern humans

Joaquim Fort and **Toni Pujol** ■ Complex Systems Lab, Escola Politècnica Superior, University of Girona, 17071 Girona, Catalonia, Spain (joaquim.fort@udg.edu, toni.pujol@udg.edu)
Marc Vander Linden ■ School of Archaeology and Ancient History, University of Leicester, University Road, LE1 7RH Leicester, United Kingdom (mmagvl1@le.ac.uk)

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30–40,000 years ago). However, the possibility of a substantial contribution of Near Eastern farmers to the European gene pool has received support by nuclear (Chikhi et al. 1998) and Y-chromosome DNA data (Balaresque et al. 2010). Further potential support for the demic model can be found in the observed correlation between genetic and archaeological distances (Sokal et al. 1991). Moreover, very recent mitochondrial DNA (mtDNA) (Bramanti et al. 2009) and craniometric (Pinhasi et al. 2009) data from ancient humans indicate a limited initial admixture between farmers and hunter-gatherers. This is contrary to the predictions of models based on cultural diffusion, i.e., on the assumption that hunter-gatherers converted into farmers (because if this had been the case, the genetic composition of both populations should be similar). Therefore, demic diffusion models seem necessary for a proper description of the Neolithic spread in the Near East and Europe. It is thus of interest to compare in detail the predictions of demic models with archaeological data. In fact, forty years ago it was already noted that the rate of spread of the Neolithic transition varies substantially in space (Ammerman and Cavalli-Sforza 1971:table 2). This point has been also stressed in recent years (Ammerman 2003:21; Price 2003:280). However, detailed quantitative comparisons of the regional trends observed to those predicted under different demic models are still scarce (see however, Davison et al. 2006, 2007 for very interesting comparisons dealing with the role of waterways and with the boreal Neolithic, respectively).

Ammerman and Cavalli-Sforza (1973, 1984) were the first to apply a mathematical model to the spread of farming from the Near East and across Europe. Their model is based on Fisher's equation,

$$s = 2\sqrt{aD}, \qquad (1)$$

where s is the speed of the population front of farmers. In this equation, a is called the growth rate of farmers and is a measure of their reproductive success (a is an increasing function of the number of surviving children per generation, see Fort, Pujol, and Cavalli-Sforza 2004). On the other hand, D is the diffusion coefficient of farmers, and is a measure of how far away they move per generation. Therefore, the speed s of the population front increases with the net reproduction (parameter a) as well as with the dispersion in space (parameter D) of the population. This was to be expected intuitively, but equation (1) goes beyond intuition by giving a quantitative prediction for these dependencies. Indeed, reasonable values for the parameters a and D can be estimated from ethnographic data (Ammerman and Cavalli-Sforza 1984:155; Fort and Méndez 1999). Using such values, equation (1) yields a speed s of about 1 km/yr, which is consistent with the speed obtained by analyzing the archaeological data (Ammerman and Cavalli-Sforza 1971, 1984; Pinhasi et al. 2005). More refined models yield similar results (see Steele 2009 and Fort 2009 for two recent reviews).

Can a simple equation such as (1) describe all of the relevant details of the spatial propagation of such a complex social process as the transition to farming, which took place over such a huge and non-homogeneous landscape as the Near East and Europe? We should expect not. Front speed equations such as (1) are useful as a first approximation. They can only yield a homogeneous, average description of the Neolithic front propagation. Thus, such models are just a first step, albeit a very appealing one (because of its mathematical simplicity). They cannot describe any local effects (e.g., sea travel). For this reason, non-homogeneous models (i.e., taking into account sea travel, mountain barriers, etc.) have been recently developed (Davison et al. 2006). In the present paper we develop this line of research further by comparing the isochrones predicted by mathematical models to those obtained by interpolating the archaeological data. We shall see that this procedure reveals a major inconsistency between the archaeological data and the models. This problem had not been noted previously, and it arises not only for homogeneous models (e.g., equation [1]) but also for non-homogeneous models (e.g., taking into account sea travel and/or mountain barriers). Based on archaeological arguments, we shall propose a reasonable solution. In our opinion, identifying and solving this problem is not only an interesting point in itself, but also necessary to develop future models of the spread of the Neolithic transition across the Near East and Europe. We shall also find that allowing for sea travels up to 150 km leads to the best match between the model predictions and the data, and that mountain barrier effects can be neglected (as they have a very small effect on the global scale).

We would like to stress that the direct quantitative comparison of isochrone maps obtained by interpolating archaeological data to those predicted by computational models seems a potentially fruitful approach. Although here we focus on the Neolithic transition in the Near East and Europe (because for this phenomenon there are many data available), our methods could be potentially applied in the future to many other spatial spread phenomena with archaeological interest, for example, the Clovis colonization of North America (Hamilton and Buchanan 2007), its possible implications on megafaunal mass extinctions (Alroy 2001), and on the terminal Pleistocene in South America (Anderson and Gillam 2000; Goebel et al. 2008; Steele et al. 1998); the lateglacial recolonization of Northern Europe (Fort, Pujol, and Cavalli-Sforza 2004); the Austronesian Neolithic range expansion (Fort 2003); preceramic dispersals of maize and root crops into Panama (Dickau et al. 2007); the diffusion of maize to the southwestern United States (Merrill et al. 2009); and so on.

Materials and Methods

Archaeological Data

The first step of our work was the realization of a database of 14C dates for the early Neolithic in Europe and the Near East. The starting point of our data collection for Europe was the database collated at the University College of London (Shennan and Steele 2000), supplemented with the RADON online database for Central Europe (Furholt et al. 2002), the IPCTE database for Eastern Europe (http://arheologie.ulbsibiu.ro/radiocarbon/download.htm), the online inventory for Portugal provided by the Instituto Português de Arqueologia (http://www.ipa.min-cultura.pt/), date lists by radiocarbon laboratories (http://c14.arch.ox.ac.uk/database/db.php; Zaitseva and Dergachev 2009), and various published data surveys (Forenbaher and Miracle 2005; Jadin 2003; Lanting and van der Plicht 2000; Manen and Sabatier 2003; Schulting and Richards 2002; Sheridan 2007; Whittle et al. 2002). For the Near East, we used the CONTEXT database (http://context-database.uni-koeln.de/). We screened all the data, excluded those irrelevant or incorrect, kept the oldest date for every site such that it had a standard deviation less than about 150 yr (otherwise we used the most reliable date available), and calibrated them using the Calib 5.0.1 software (Stuiver et al. 2009). This yielded a total of 903 European sites and 87 CONTEXT Near-Eastern sites.

Supplementary material for this paper is available at http://copernic.udg.edu/QuimFort/fort.htm. The excel file Supporting Data 1 contains the 919 sites and dates used in our final analysis (903 European sites and 16 CONTEXT Near Eastern PPNB/C sites, see the Results section below). The excel file Supporting Data 2 contains the complete list of 87 CONTEXT sites and dates for the Near East.

Simulation Programs

In order to convert longitude and latitude into Cartesian *(x,y)* coordinates and vice versa, we used a rectangular grid on an Albers conic equal-area projection. The rectangular grid is made up of squares with side 50 km, which is the value corresponding to the characteristic mobility per generation obtained from measured data for pre-industrial populations (Ammerman and Cavalli-Sforza 1984; Fort et al. 2007). We index each grid node as *(i,j),* with $1 \le i \le 180$ and $1 \le j \le 102$.

In the homogeneous models, we apply the following reactive random-walk computation scheme, which has been justified previously (Fort et al. 2007),

Step 1 (reproduction): At every node *(i,j)* of the grid and time t (measured in generations), we compute the new number of Neolithic farmers $P'_N(i,j,t)$ after reproduction from that before reproduction $P'_N(i,j,t)$ at the same node as (Fort et al. 2007)

$$\begin{aligned} P'_N(i,j,t) &= R_{0N} P_N(i,j,t) && \text{if} \quad P_N(i,j,t) < P_N^{\max} / R_{0N}, \\ P'_N(i,j,t) &= P_N^{\max} && \text{if} \quad P_N(i,j,t) \ge P_N^{\max} / R_{0N}, \end{aligned} \qquad (2)$$

where R_{0N} is the net reproductive rate (or fecundity) per generation. The second line in Eq. (2) is necessary for the population density not to increase above the saturation density of farmers, $p_N^{\max}$ and $P_N^{\max} = l^2 p_N^{\max}$ is the maximum number of farmers per node. In our simulations we use for $p_N^{\max}$ the same value as that applied by Currat and Excoffier in their genetic simulations of the Neolithic transition, namely p_N^{max} = 1.28 farmers/km^2, which is in agreement with anthropological data (Currat and Excoffier 2005). However, the value of p_N^{max} is not important as it has no effect on the front speed (thus we expect that our results would not change in case we allowed for p_N^{max} to depend on the spatial position). Also, using a logistic function instead of Eq. (2) would not change the front speed but would yield negative values of the population density (this is a well-known feature of discrete-time equations which makes no biological sense, see Fort et al. 2007).

Step 2 (dispersal): The new population density after dispersal is computed as a contribution due to the population that stays at the node *(i,j)* considered plus another one due to the population arriving from the four nearest-neighbor nodes,

$$P_N(i,j,t+1) = p_e P'_N(i,j,t) + \frac{(1-p_e)}{4}\begin{pmatrix} P'_N(i-1,j,t) + P'_N(i+1,j,t) \\ +P'_N(i,j-1,t) + P'_N(i,j+1,t) \end{pmatrix}, \quad (3)$$

where p_e is the persistence (i.e., the fraction of the population that does not disperse). It has been shown that substantially more complicated models using a probability distribution for the dispersal distance yield similar front speeds (Isern et al. 2008, especially Table 2). Each cycle (steps 1 and 2) corresponds to a time interval of 1 generation or T years.

The parameter ranges have been estimated from observations of pre-industrial farmer populations as $.19 \le p_e \le .54$ (Fort et al. 2007), $29 \le T \le 35$ yr/gen (Supp. Text S3 in Pinhasi et al. 2005), and $2.1 \le R_{0N} \le 2.3$ (from the growth rate range $.73 < a < .85$ gen^{-1} in Fort and Méndez [1999] and the relationship $a = (\ln R_0)/T$ [see note 26 in Fort et al. 2007]). Such high values of the growth rate ($.021 < a < .029$ yr^{-1} or $2.1 < a < 2.9$ percent) have been estimated from data on contemporary populations which settled in empty space (Birdsell 1957) and are also consistent with estimations based on cemetery data at the onset of the Neolithic transition (e.g., Guerrero et al. 2008, p. 67–69 obtain a = 2.4 percent). Let us also stress that the generation time T does not correspond to the age of parents at birth of the oldest child, but to that averaged over all children, as appropriate to model population range expansions (Fort, Jana, and Humet 2004). In all simulation maps (see below) we have used the mean values R_{0N} = 2.2, T = 32 yr and p_e= .38 (the latter is the mean of the observed values of p_e given in Fort et al. 2007). However, using other values within the ranges above would not change our main results and conclusions.[1] We also checked that the front speed from the simulations agreed with the analytic prediction available for the homogeneous model based on Eqs. (2)–(3) (this is in turn a refinement of Fisher's equation (1), see Fort et al. 2007, especially Eq. [17]).

In the non-homogeneous models, we apply the same two-step procedure as above, but taking into account sea travels and mountain barriers (see Appendix A). In order to prevent some sites from being isolated in the simulation grid, we considered mountains as barriers at altitudes higher than 1750 m above sea level. Nevertheless, our conclusions would be the same for any other value of this threshold, and even neglecting the effect of mountain barriers altogether (see Appendix B).

The arrival time of the Neolithic at each site was estimated as that for which the model considered predicts a population density equal to 90 percent of the saturation density (however, changing the value of this percentage has a negligible effect on the results).

The simulation programs and all data files necessary to run them are available at http://copernic.udg.edu/QuimFort/fort.htm.

We used the Natural Neighbor option in the Spatial Analyst extension of the GIS software to obtain the interpolation maps, both for the archaeological dates and for the arrival dates of the Neolithic front as predicted by models at the same sites.

Results

Archaeological Data

We first computed the great-circle distance relative to Jericho for each of the 903 European and 87 Near-Eastern sites. Performing linear regressions of these distances versus the calibrated dates and vice versa, we obtained for the spread rate s = .5–.9 km/yr (95 percent confidence-level interval) and for the correlation coefficient r = .8. Such values are consistent with previous results

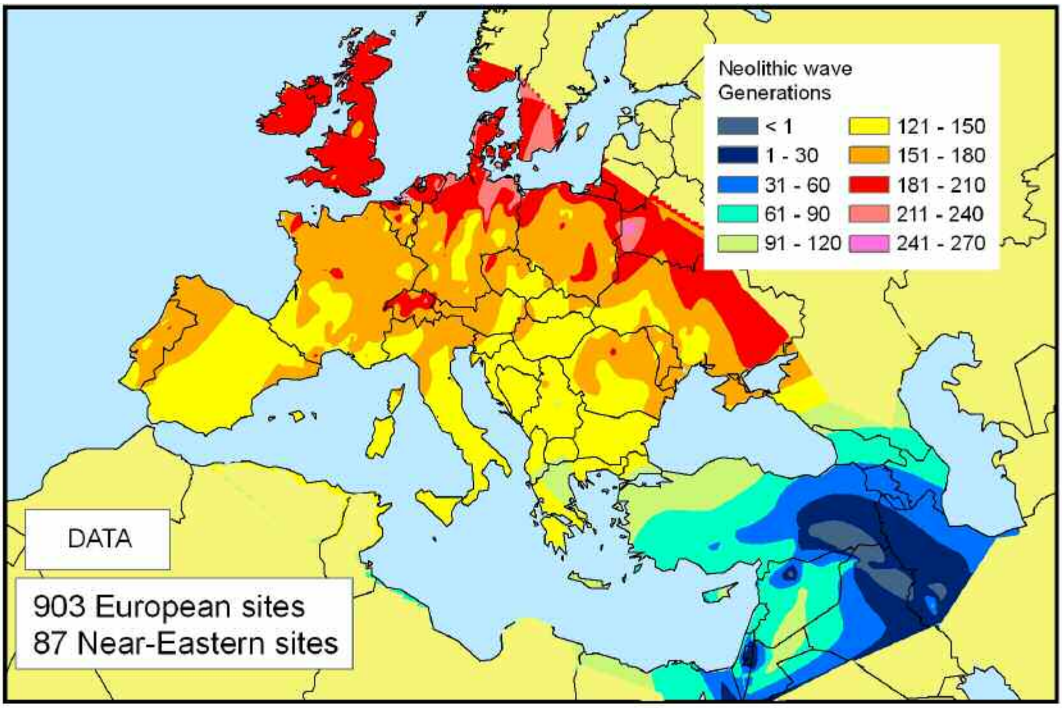

Figure 1. Propagation of the Neolithic front, obtained by interpolation of the archeological data (903 European and 87 Near-Eastern sites). The time origin corresponds to the date of Jericho (11863 cal yr B.P.). Note that it takes the front about 120 generations to reach Greece. Compare to the models in Figures 2 and 3, where the front reaches Greece in less than 60 generations. One generation corresponds to 32 years (Fort, Jana, and Humet 2004), but this conclusion does not change for other reasonable values of the generation time.

(Pinhasi et al. 2005), and this high value of r indicates that a constant spread rate is a good description of the process at the continental scale (we used Jericho as origin because other sites in the Near East gave similar or lower values of r).

The result of interpolating the same 990 dates is shown in Figure 1, where the time origin corresponds to the date of Jericho (however, using other Near Eastern sites as origin yielded similar maps). The following two points are observed in Figure 1.

1. The spread is faster Westwards than Northwards, a feature that cannot be accounted for by homogeneous models such as Fisher's (Eq. [1]) but that can be described by non-homogeneous models allowing for sea travel (see below).

2. More importantly, according to Figure 1 the time elapsed from the oldest Near-Eastern sites to the arrival of the Neolithic front to Greece would have been about 120 generations. Is this in agreement with computational models? In the next subsection we present some modeling results to tackle this question.

Simulation Programs

Figure 2 shows that according to our homogeneous model (Eqs. [2]–[3]), the front reaches Greece in less than 60 generations, i.e. in less than half the time it seemed in fact to require (Figure 1). Figure 3 shows that this conclusion does not change for non-homogeneous models, i.e., when sea travels and mountain barriers are included (because the effect of sea travels is just to increase the front speed in the Mediterranean region and the effect of mountains on the front speed is very small, see Appendix B). Therefore, there is a major inconsistency between archaeological data (Figure 1) and the computational models (Figures 2–3). Below we propose a solution to this problem.

The discrepancy between the arrival time of the Neolithic to Greece according to the archaeological data (Figure 1) and the models (Figures 2–3) can be interpreted archaeologically as follows. The beginning of the Neolithic in the Near East does not really correspond to the propagation of a

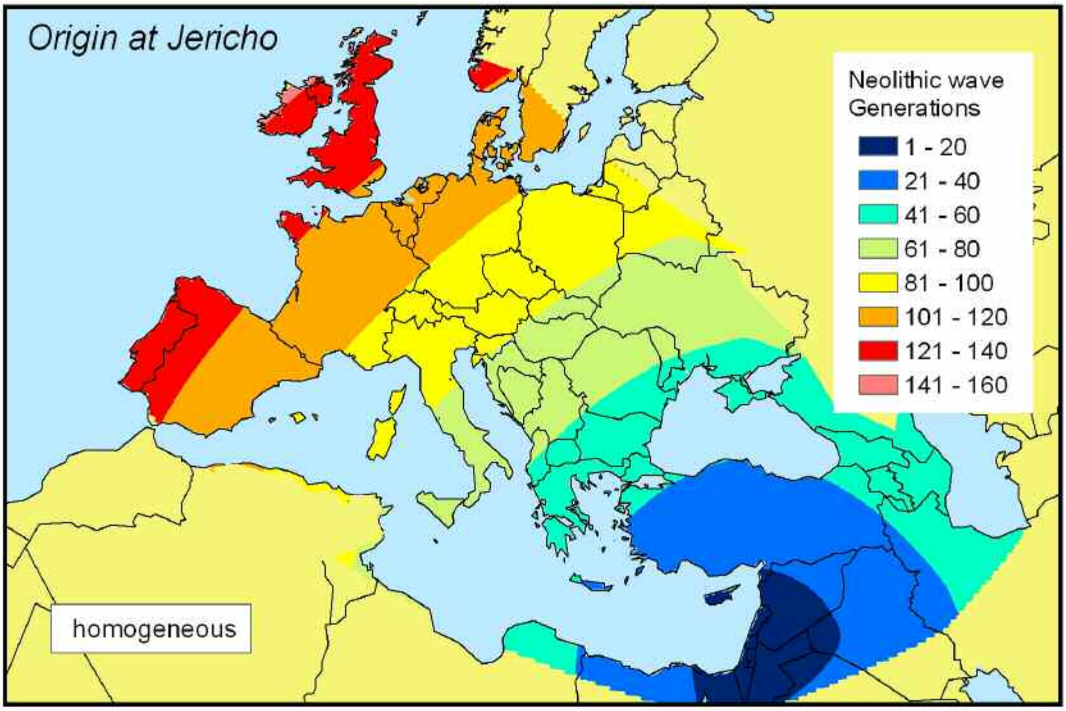

Figure 2. Homogeneous model (i.e., seas and mountains are ignored). Propagation of the Neolithic front form a single origin located at Jericho. Note that the front reaches Greece in less than 60 generations, i.e., less than half the time according to the archaeological data (Figure 1). Jericho has been used here as origin because, according to the archaeological data, it yields the highest value for the correlation coefficient in the regression of distances versus dates (*r* = .8). However, the same conclusion holds using any of the other Near Eastern sites as origin. An interpolation has been performed over the arrival times at 990 sites (in order to use the same approach as in Figure 1).

front, because some innovations appeared at a very early date, others later on, often at different places, and it took some time for a more homogeneous package to develop (Zeder 2008). In fact, such a development seems quite general (Barker 2006) and can be for instance observed in the U.S. Southwest (Kohler et al. 2008). In any case, this is a very different situation than what we see in Europe, where there is a well-established set of farming practices which spread. In the Near East, the PPNB/C cultures correspond to the final, more homogeneous set of farming practices, from which the spread to Europe proceeded (Kuijt and Going-Morris 2002). It thus seems reasonable to identify them with the initial conditions from which the spread into Europe took place. Therefore, in the rest of this paper, for the Near East we will use only data associated with the PPNB/C cultures.

Using only the 16 PPNB/C sites for the Near East (out of the original 87 sites), two simulation approaches are possible. The first one is to assume a single origin, e.g., at the oldest site (Hemar). The second one is to set the region corresponding to the PPNB/C culture (i.e., a region containing the 16 sites) with a single date that is characteristic of these sites. Both approaches seem reasonable from an archaeological point of view. We followed the latter one because it yields lower errors (Table 1, last row). Therefore, in the rest of our simulations in this paper we set the regions in Figure 4 full of farmers at 9,000 cal yr B.P., which is roughly the average date computed over the 16 PPNB/C sites.

The reason why the models with a single origin of farmers at Jericho give such large errors (Table 1, second row) can be clearly seen in Figure 5: such models (blue dots) assume an initial time too old for the propagation of the Neolithic front (namely the date of Jericho, which is 11,863 cal yr B.P.). To a lesser extent, the same problem happens for models with a single origin at Hemar (the oldest PPNB/C site), which is dated 10,418 cal yr B.P. (Table 1, third row—not shown in Figure 5). The models that set the

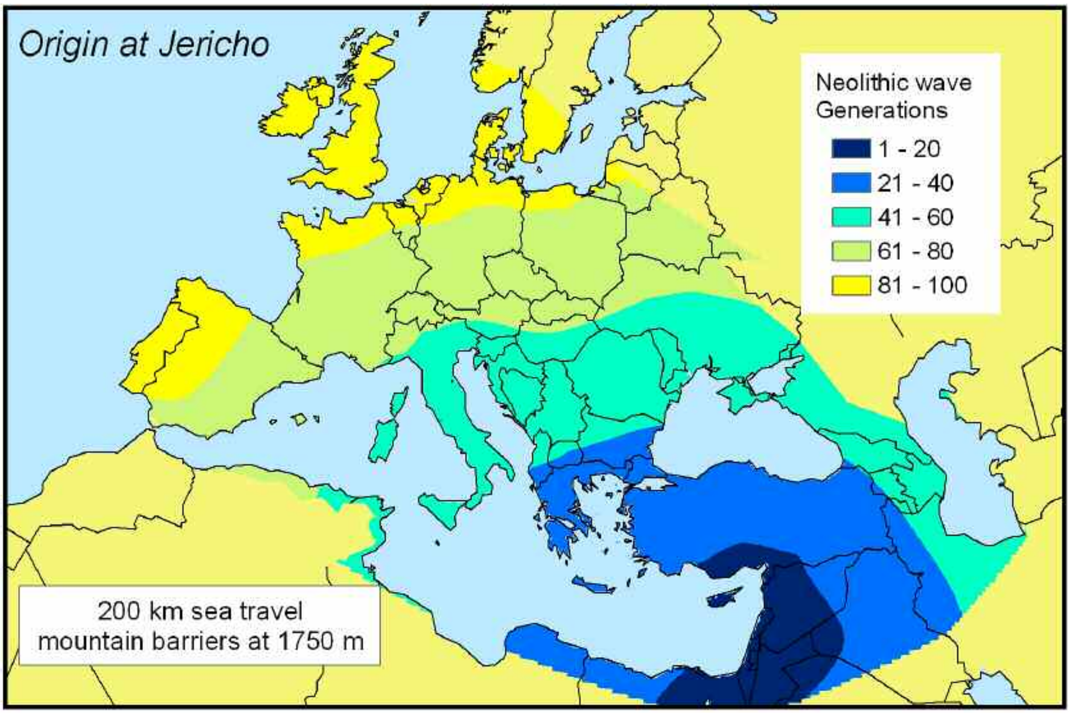

Figure 3. Non-homogeneous model (i.e., sea travels and mountain barriers are taken into account). Note that the front reaches Greece sooner than in Figure 2. This is due to the fact that sea travels lead to a faster front in Mediterranean region. In this example, sea travels up to 200 km and mountain barriers above 1750 m have been applied, but the same conclusion is reached for any other reasonable values of these two parameters.

PPNB/C area full of farmers at 9,000 cal yr B.P. (last row in table 1 and red dots in Figure 5) agree much better with the archaeological data (black dots in Figure 5).

The linear regressions of the of the 903 European and 16 PPNB/C Near-Eastern sites (black circles in Figure 5) yield s = .5–1.3 km/yr for the speed of the Neolithic front (95 percent confidence-level interval), and r = .7 for the correlation coefficient. It is not surprising that s is somewhat faster and r lower than for all 990 Sites, because substantially older dates (up to about 14,000 cal yr B.P.) were included for 990 sites.[2]

Discussion

In the previous section we explained that using only PPNB/C sites in the Near East is archaeologically reasonable. But does this make the arrival time to Greece implied by the data consistent with that predicted by models? The answer is affirmative, as it can be seen by comparing Figure 6 (interpolation of the 919 dates) to Figure 7 (homogeneous model). This removes the inconsistency explained in the previous section. For this reason, we think future wave-of-advance models of the Neolithic transition in Eurasia should include only sites for the Near East associated to PPNB/C cultures. Having solved the inconsistency, finally we will discuss other relevant features of the Neolithic spread and compare them to several simulation models.

The homogeneous model (Figure 7) yields a realistic overall spread rate (1.0 km/yr), but the simulated population wave of advance arrives too late to the Adriatic and Iberian peninsulas as compared to the observed front (Figure 6). Therefore, let us consider non-homogenous models.

For the reason explained at the end of the Materials and Methods section, we consider mountains with heights above 1750 m as barriers. However, this value has a negligible effect on the propagation of the Neolithic front on the continental scale (see Appendix B). On the other hand, seas cannot be considered as barriers to population movement because the Neolithic arrived to is-

Table 1. Mean Error Per Site in the Arrival Time of the Neolithic Front.

Dataset (in addition to the 903 European sites)	Initial Conditions used in the Simulations	Mean Error, Homogeneous Model (no Seas, no Mountains)	Mean Error, Model with Sea Travels < 100 km and Mountains > 1750 m	Mean Error, Model with Sea Travels < 150 km and Mountains > 1750 m	Mean Error, Model with Sea Travels < 200 km and Mountains > 1750 m
87 Near-Eastern sites	Single origin at Jericho	2088 yr (Figure 2)	2024 yr	2508 yr	2899 yr (Figure 3)
16 PPNB/C sites	Single origin at Hemar	815 yr	759 yr	1152 yr	1553 yr
16 PPNB/C sites	PPNB/C areas full of farmers at 9,000 cal yr BP (Figure 4)	685 yr	680 yr (Figure 8a)	**542 yr** (Figure 8b)	646 yr (Figure 8c)

Note: Mean errors in the arrival time of the Neolithic, according to several models and under different initial conditions. The error is defined as the mean magnitude of the difference between the oldest Neolithic date measured at a site minus the arrival time of the Neolithic front at that site (as predicted under the model and initial conditions stated). When including all of the 87 Near-Eastern sites (first row), the conclusions would be much the same if another site instead of Jericho were used as origin (see caption to Figure 2). The same happens when using only the 16 PPNB/C sites (second and third rows) and another site instead of Hemar as origin (Hemar is the oldest of the 16 PPNB/C sites, which do not include Jericho). Changing the height of mountain barriers leads to much the same results (see Appendix B).

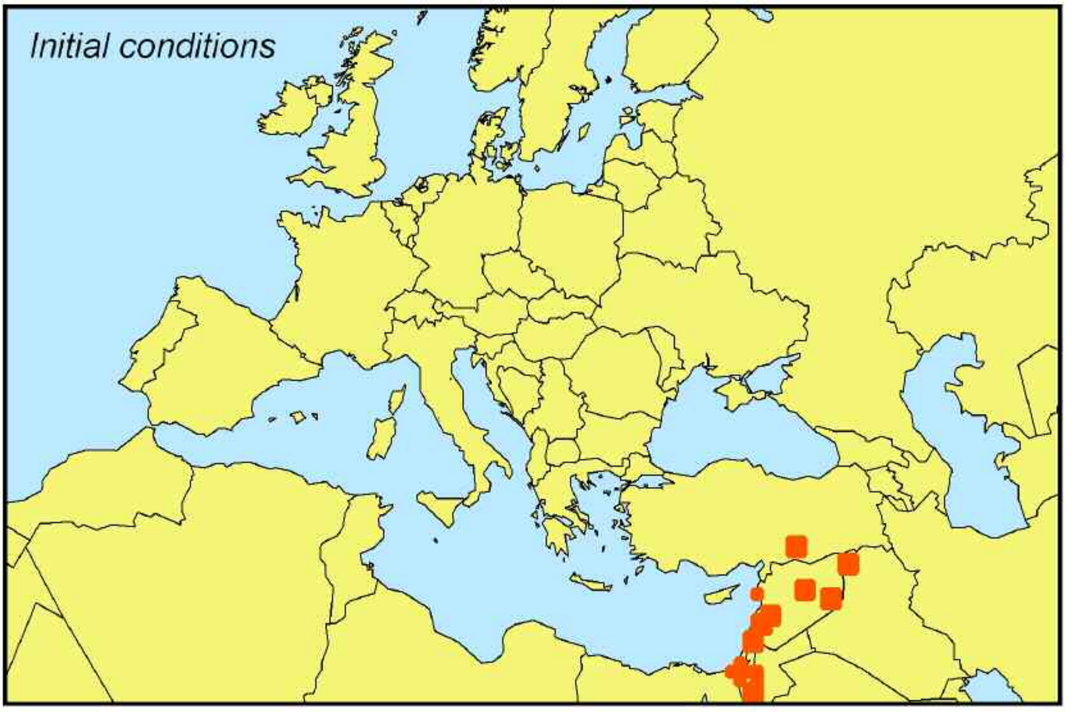

Figure 4. Initial conditions used in the simulations reported in the last row in Table 1 and Figures 7-8. The population density of farmers is set to saturation density at 9,000 cal yr B.P. in the red areas, which contain all of the 16 PPNB/C sites.

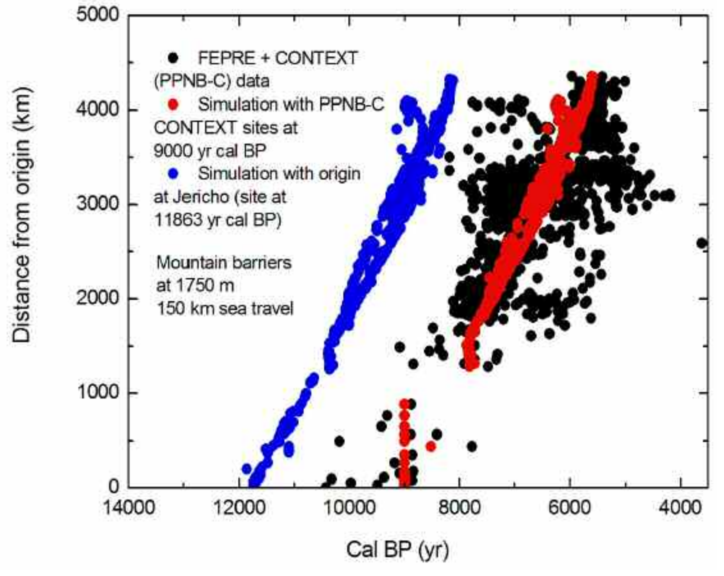

Figure 5. Each point corresponds to either a site in the Near East (lower part of the plot) or to a European site. Assuming a single origin of farming populations at Jericho yields unrealistically early arrival dates to all sites (blue circles, with distances computed from Jericho) compared to the radiocarbon data (black circles). Setting all PPNB/C sites full of farmers at 9,000 yr B.P. (red circles, with distances from Hemar) yields much better agreement with the data (black circles, also with distances from Hemar). Results are shown for a single model (sea travel allowed up to 150 km and mountain barriers set above 1750 m), but these conclusions remain the same for all other models.

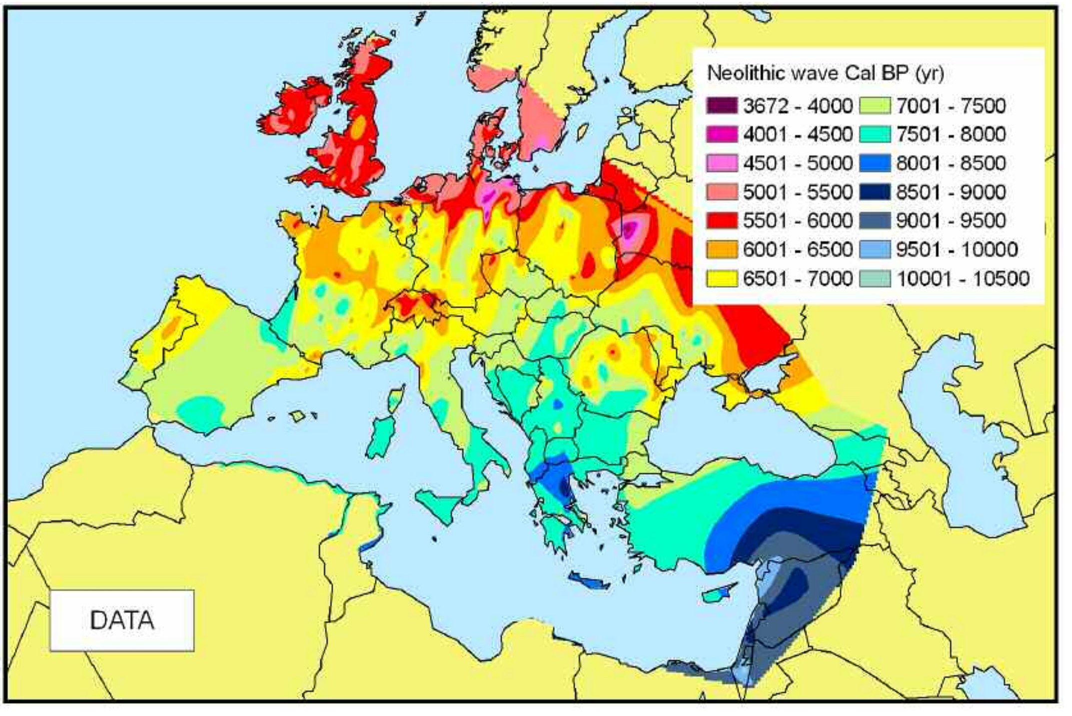

Figure 6. Interpolation of the earliest Neolithic dates at the 903 European and 16 PPNB/C sites. In this figure as well as in Figures 7-8, each color corresponds to a 500-yr interval.

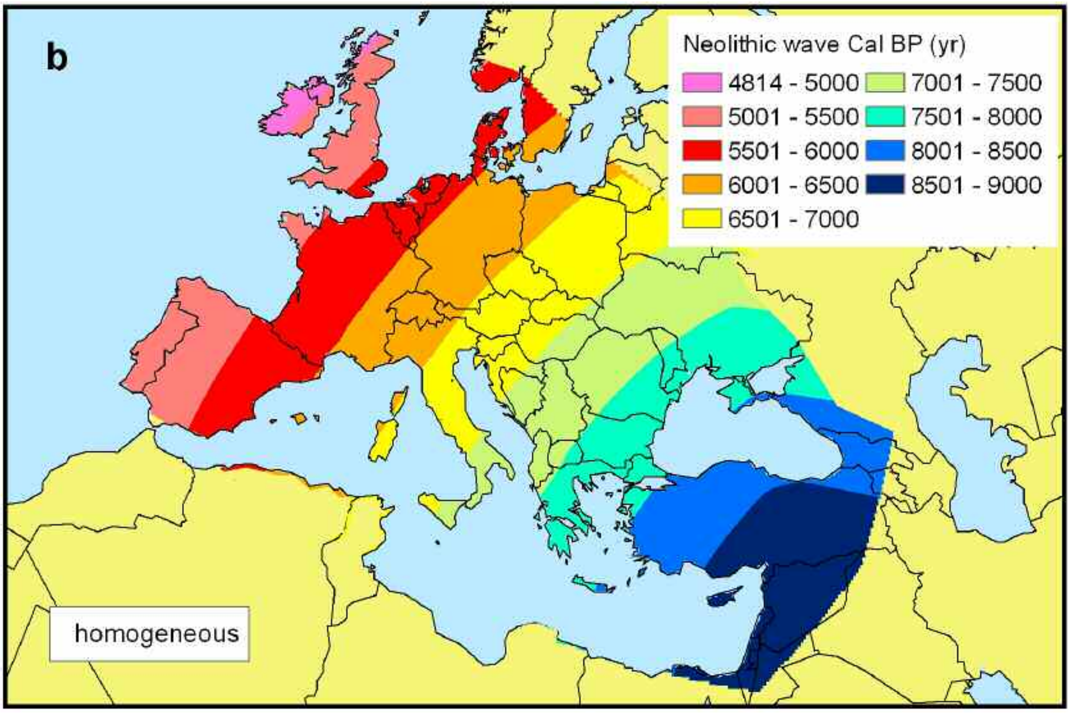

Figure 7. Front spread as predicted by a homogeneous model. Sea and mountain effects are neglected. Here the contours are not exactly circular because the initial population of farmers is not located at a single point, but at the region corresponding to the PPNB/C sites (see the Results section and Figure 4), and to a lesser extent because an interpolation has been performed over the arrival times at the 919 sites (in order to use the same approach as in Figure 6).

lands such as Cyprus (by about 10,300 cal yr B.P., see Ammerman 2010a, 2010b). This implies the existence of sea travels up to, at least, 100 km. Similar and longer distances have been also reported by several ethnographic studies of pre-industrial farmers in other regions of the world (Fort 2003). Therefore, it is reasonable to develop models that include sea travels (see Appendix A). A model with sea travels up to 100 km predicts that the front would enter Italy from the North (Figure 8a), but this is inconsistent with the data (Figure 6). We also computed the mean error per site in the arrival time of the Neolithic front for several values of the maximum sea travel distance (see Table 1). The minimum error was obtained for sea travels up to 150 km (Figure 8b), which lead of course to a faster Neolithic spread along the Mediterranean than sea travels up to 100 km (Figure 8a). Finally, for sea travels up to 200 km (Figure 8c) the front is too fast, leading to less error for the arrival time to the Iberian peninsula but much more error at the British Islands and Greece (compare Figures 8c and 8b to Figure 6). Admittedly, mathematical models cannot capture the full complexity of the patterns observed in the data (Figure 6). However, in spite of its conceptual simplicity, the model in Figure 8b does perform substantially better than the homogeneous model in Figure 7: (a) the improvement in the Adriatic peninsula and the British Islands is obvious from the figures; (b) the front arrives to the Iberian peninsula almost 2000 yr too late in Figure 7, but this value decreases by 50 percent in Figure 8b; (c) the improvement is statistically clear from the results for the mean error per site over all of Europe (see the caption to Figure 8).

As mentioned above, the earliest Neolithic sites in Cyprus are dated about 10,300 cal yr B.P. This is substantially earlier than the date we have assumed for the beginning of the spread of the Neolithic from the Near East into Europe, namely 9,000 cal yr B.P. In principle, one could think that this problem could be solved by changing the initial date of the spread from 9,000 cal yr B.P.

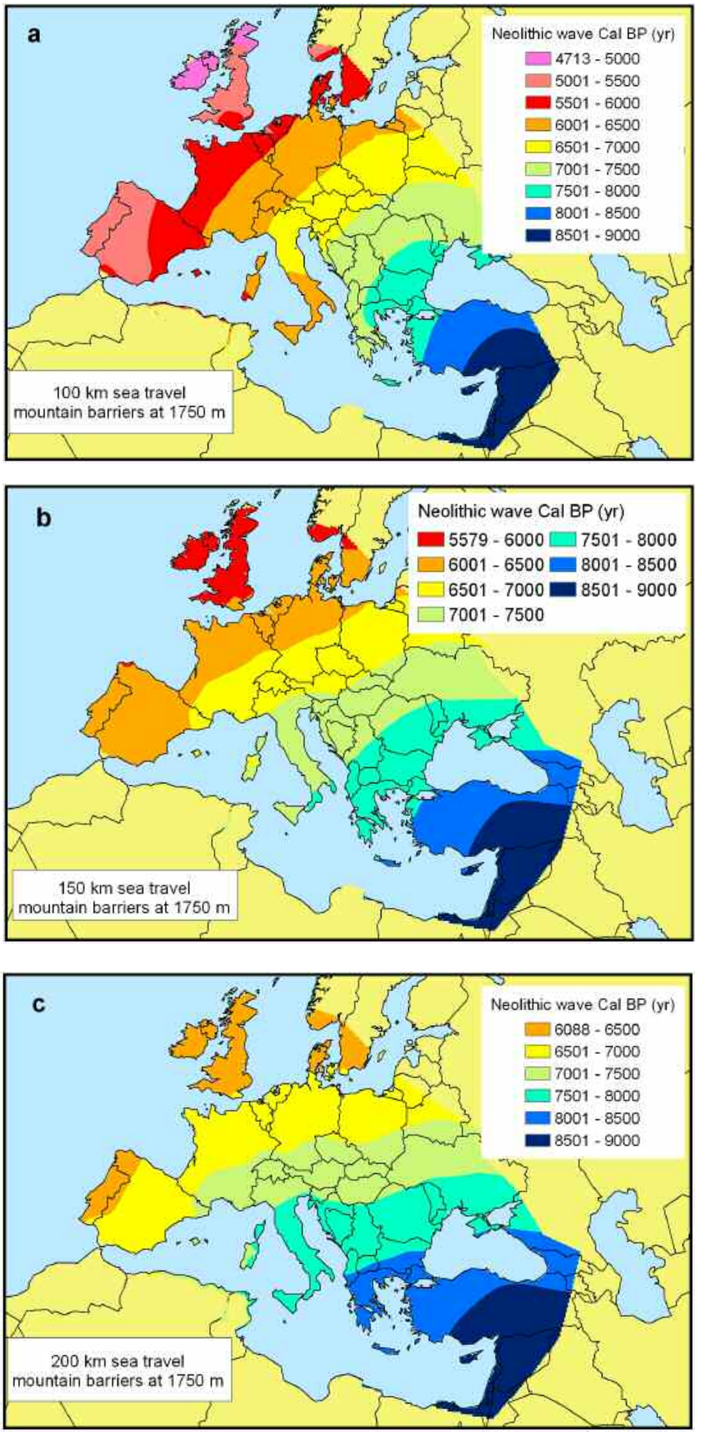

Figure 8. Results of models including sea travel. (a) Sea travel up to 100km. This front is very similar to the homogeneous one in Figure 7 (the mean error per site in the prediction of the arrival time of the Neolithic transition front is 680 yr here versus 685 yr in Figure 7). (b) Sea travel up to 150 km (this model yields the lowest mean error, namely 542 yr). (c) Sea travel up to 200 km (the mean error is again larger than in case b, namely 646 yr, because comparing to Figure 6 it is seen to predict too early arrival times to Britain and Greece in spite of performing better in the Iberian peninsula).

into 10,300 cal yr B.P. However, this does not work because then all red dots in Figure 5 would move 1,000 yr to the left, so the mean error per site would be very large (almost the same as for the blue dots, i.e. for the classical approach in which the spread begins at Jericho at 11,863 cal yr B.P.). In other words, the spread into Europe would be too early. A simple way to solve this problem, i.e., to attain consistency between our model and the old dates in Cyprus (about 10,300 cal yr B.P.) is just to consider Cyprus as part of the Middle Eastern culture which later spread into Europe. Indeed, note that the date 9,000 cal yr B.P. we have used corresponds to the start of the spread into Europe, not to the arrival time into Cyprus. In other words, the presence of the Neolithic in Cyprus by 9,000 cal yr B.P. (in our model) is consistent with its arrival there by 10,300 cal yr B.P. (as implied by the data), just as the presence of the Neolithic in the Near East by 9,000 cal yr B.P. is consistent with the existence of Near-Eastern Neolithic sites dated 10,000–12,000 cal yr B.P. Admittedly, then, there was a delay since the arrival to Cyprus (10,300 cal yr B.P.) and the beginning of the spread into Europe (9,000 cal yr B.P.). Such a delay suggests that the early farmers in Cyprus did not move long distances by boat. This statement fits very well with the paradox, first noted by Ammerman (2010a, 2010b), of the slowness of the spread from Cyprus into Italy as compared to its fastness earlier (from the Near East to Cyprus) and later (from Italy to Portugal). Indeed, very recently Ammerman (2010a, 2010b) has suggested that the marine foragers made seasonal visits to Cyprus and it was them (and not the early farmers) who had the boats and long-distance sailing capability in that region of the Mediterranean. This could explain the fact that the first farmers in that region were not active seafarers, as suggested both by Ammerman (on the basis of the slow spread rate of the Neolithic from Cyprus to Italy) and by the results of the present paper (on the basis of the delay of about 1,300 yr between the arrival of the Neolithic into Cyprus and its spread into Europe).

Conclusions

We have compared the isochrones obtained by interpolating the archaeological dates for the earliest Neolithic (Figure 1) to those predicted by mathematical models (Figures 2–3). In this way, we have found a major inconsistency between the predictions of the models and the archaeological data: according to the models, the Neolithic front would have arrived to Greece in less than half the time interval implied by the data. This inconsistency can be solved by including only PPNB/C sites in the Near East, which correspond to the generalization of farming practices that later on spread across Europe. We have also found that the model that yields the lowest mean error per site in the arrival time of the Neolithic across the Near East and Europe is obtained by allowing for sea travels up to distances of 150 km. Moreover, according to the simulation models, mountain barriers have a negligible effect on the spread rate of the Neolithic front on the global, continental scale. However, some local features do arise in the simulations due to mountain effects, e.g. to the Alps (compare Figure B2 to Figure B1). Future work, focusing on local-scale features of the Neolithic spread, could try to compare such mountain effects to more detailed archaeological data. Similarly, it would be of interest to analyze quantitatively other local effects pointed out in the literature, e.g., the slowness of the spread between Cyprus and Greece (see Perlès 2001, Pinhasi et al. 2005, and especially Ammerman 2010a, 2010b), which seems surprising in a society with seafaring capability.

The quantitative comparison of isochrone maps predicted by models to those obtained by interpolating the archaeological data has been based here on the computation of the mean error per site. In future work, it would be interesting to perform further analyses based, e.g., on the juxtaposition of both kinds of maps in order to get a clear display of areas of agreement and disagreement between models and observations.

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Appendix A. Models with Sea Travel and Mountain Barriers

For homogeneous models, a fraction p_e of the population stays at the original node and a fraction $(1 - p_e)/4$ migrates to each of the 4 nearest neighbors (see Eq. [3]). This is depicted in Figure A1. In contrast, for non-homogeneous models we have to distinguish between nodes on land (black circles in Figure A2), mountains (white circles) and seas (blue circles). Mountains are considered as barriers to population settlement and travel. Sea nodes are also unavailable for settlement, but not for travel. All paths across the sea but with destination on land are considered, as long as the straight-line distance from the origin (red circle) is less than the maximum sea-travel distance prescribed by the model (200 km in Figure A2). Similarly to the homogeneous model (Figure A1), in Figure A2 a fraction p_e of the population stays at the original node, a fraction $(1 - p_e)/3$ jumps to the right, a fraction $(1 - p_e)/3$ to the left, and a fraction $(1 - p_e)/3$ is equally distributed to the destination nodes of all possible sea-travel paths.

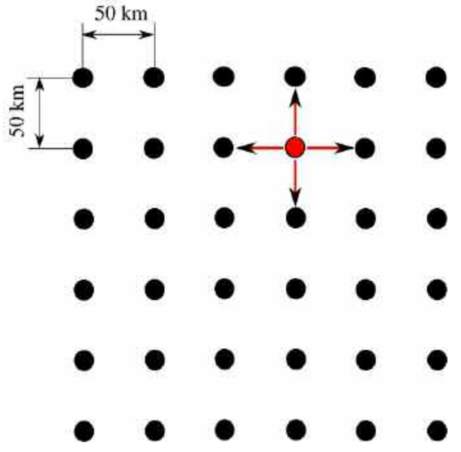

Figure A1. Homogeneous model. The population may jump from any node (red circle) in the vertical/horizontal directions and reach its 4 nearest neighbors. Compare to Figure A2.

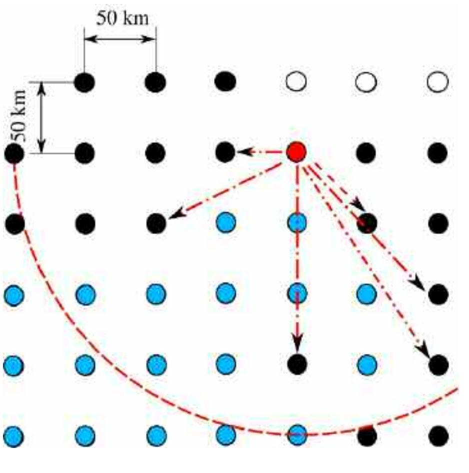

Figure A2. Non-homogeneous model. Black circles stand for land, blue circles for sea and white circles for mountains. In our simulations the population is redistributed by taking into account, besides jumps in the horizontal and vertical directions (as in Figure A1) also jumps across the sea (with a maximum distance of 200 km in this example).

Of course, the details of our sea-crossing algorithm could be changed in several ways, e.g., by allowing for longer sea travels along coastlines than into islands (this would reflect a more limited navigational capability or confidence). However, travels into islands up to 100 km at least should be allowed (in order for the Neolithic front to reach Cyprus, as implied by the archeological data). This distance is similar to that in our best model, which allows for sea travels up to 150 km both along coastlines and into islands (see table 1). Thus, we do not expect that such more complicated models would change our results appreciably.

Appendix B. Effect of Mountain Barriers on the Neolithic Wave of Advance

We used elevation data from the SRTM30 near-global digital elevation model (ftp://e0srp01u.ecs.nasa.gov/). This model comprises data from the Shuttle Radar Topography Mission with 30 m x 30 m spatial sampling and the U.S. Geological Survey's GTOPO30 dataset. Information from the SRTM30 datasets has been extracted using GRASS (Geographic Resources Analysis Support System). GRASS is an open-source, freely-distributed GIS (Geographical Information System) software (http://grass.itc.it/).

We evaluated the elevation of sites by means of the SRTM30 database and this yielded altitudes above 1000 m for 26 sites. In addition, 12 of those 26 sites are located within four surrounding nodes with altitudes above 1000 m in the grid, so the population cannot reach them if the mountain barriers are set at altitudes above 1000 m in the simulations. Therefore, we have considered mountain barriers only at altitudes above 1750 m in the simulations presented in our paper. We will

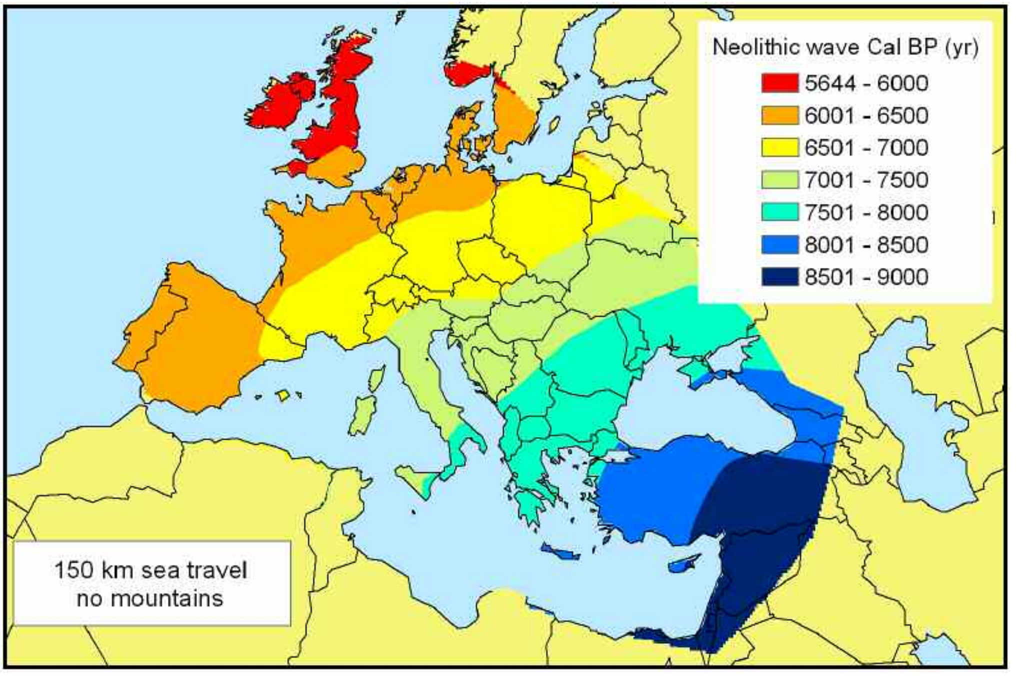

Figure B1. Propagation of the Neolithic front, according to a model that allows sea travel but does not take mountains into account. The mean error per site (defined as in Table 1) is 558 yr. It is thus very close to that for mountain barriers above 1750 m, namely 542 yr (Figure 8b), so the effect of mountain barriers is negligible.

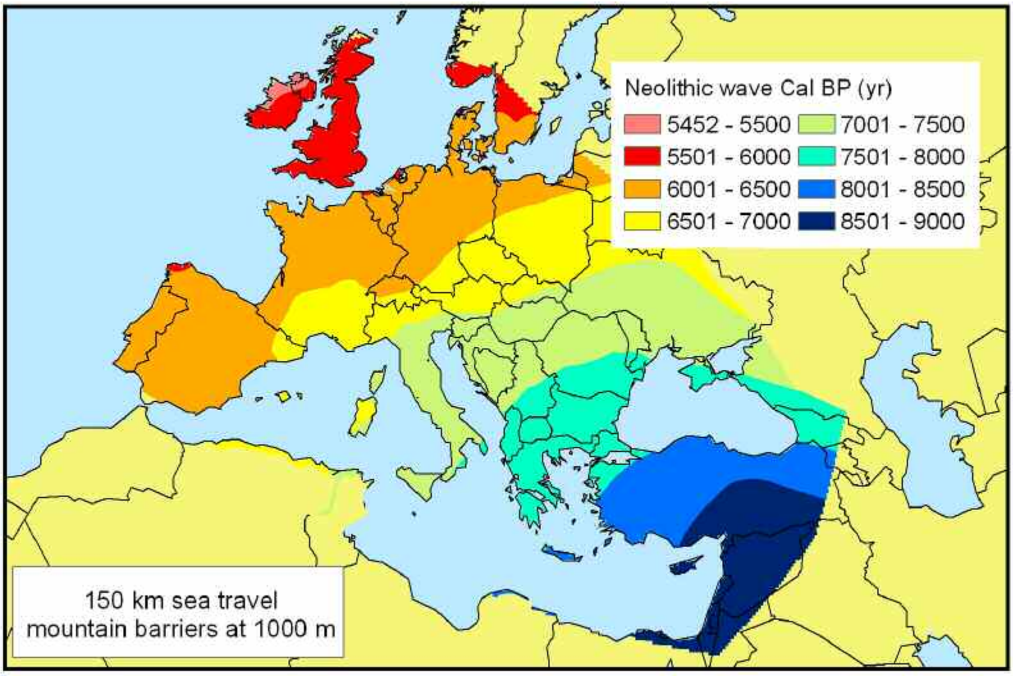

Figure B2. Propagation of the Neolithic front, according to a model that considers mountains with heights above 1000 m as dispersal barriers and unsuitable for farming. Comparing to Figures B1 (no barriers) and 8b (barriers above 1750 m), it is seen that the effect is again negligible (mean error per site 529 yr).

now see, however, that the conclusions would not change because the simulation maps are very similar by using any other value, or even neglecting mountain effects altogether.

Figure B1 is a simulation including sea travels but neglecting mountain barriers. It is seen that it is very similar to Figure 8b, which includes mountain barriers for altitudes above 1750 m. On the other hand, in Figure B2 mountain barriers were set at altitudes above 1000 m. Clearly, mountain barriers have a negligible effect on the overall propagation of the front (except in some local regions in Figure B2, e.g. due to the Alps and to the effect of mountains in Anatolia on the region between the Black and Caspian seas). Therefore, the conclusions of our paper would be the same if other values instead of 1750 m were used as the threshold for the minimum altitude of mountain barriers (Figure B2), or if the effect of mountains were neglected altogether (Figure B1). In Figures B1 and B2 we have assumed that sea travel is possible up to 150 km (as in Figure 8b), but the same conclusion is reached for any other values of this parameter.

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Notes

1. Because of the wide persistence range, we performed some additional simulations with $R_{0N} = 2.2$ and $T = 32$ yr but changing the value of the persistence. First we used 990 sites and found that, for a single origin at Jericho and an homogeneous geography, the front still reaches Greece in less than 60 generations (as in Figure 2) using either p_e=.54 or p_e=.19 instead of p_e=.38. Second, we used 919 sites and found that, for all 16 PPNB/C sites full of farmers at 9000 cal yr B.P., the best model corresponds to sea travel up to 200 km for p_e=.54 and up to 100 km for p_e=.19, close to the value of 150 km found for p_e=.38 (last row in Table 1). Moreover, in both cases the minimum mean error per site is very close to the mean error per site for sea travel up to 150 km (555 yr versus 564 yr for p_e=.54; and 596 yr versus 601 yr for p_e=.19 respectively). Therefore, the main conclusions of this paper do not change.

2. The following simple, hypothetical example can be very useful to understand this decrease in the correlation. For the dataset (0,1), (1,1), (3,2), (4,2), (5,3), (6,3) the correlation is r = .9, but it decreases to r = .7 if the first two pairs of values are omitted. This is similar to omitting substantially older archaeological dates when performing a distance-versus-time regression. Similarly, the slope (which corresponds to the speed) somewhat increases (from .37 to .40) also in this hypothetical example.

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