Spatial dimensions increase the effect of cultural drift

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ABSTRACT

The transition from hunter-gathering to agriculture (Neolithic) spread gradually across Europe from the Southeast. A reduction in cultural diversity of crop farming practices has been previously observed by comparing pre-LBK Neolithic sites in Greece and the Balkans (dated about 8500 yr BP) to LBK Neolithic sites in Central Europe (dated about 7000 yr BP). The decrease in crop diversity is statistically significant even when considering only the species less likely to have been subject to smaller productivity due to climatic factors (reductions in growing season, temperature, daylight, etc.). This reduction in cultural diversity has not been explained previously. In this paper we show that spatial drift, which occurred on the front of the advancing wave of pioneer settlements, can explain the observed loss of diversity during the LBK range expansion. Our results suggest that spatial dimensions can have a relevant effect also in other case studies in which cultural drift is important.

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1. Introduction

Cultural drift is the change in the relative frequency of a cultural trait in a population due to random sampling and chance (for some seminal examples, see Neiman, 1995; Hahn and Bentley, 2003). Clearly, this effect is expected to be important for small population sizes. It has been suggested that drift has an observable effect on cultural evolution (Diamond, 1978), but quantitative tests are very difficult to assess (Shennan and Wilkinson, 2001; Bentley and Shennan, 2003; Mesoudi and Lycett, 2009). In contrast to previous work, our purpose here is to explore the effect of spatial dimensions. The role of population fronts on cultural drift has not been analyzed previously. We report simulation results to study drift effects on the leading edge (pioneering settlements) of a human invasion front. Our specific case study draws on a non-spatial drift study by Conolly et al. (2008). We show that spatial drift can explain the evolution of cultural diversity in the LBK culture in Neolithic Europe. In contrast, non-spatial models could not explain the cultural dynamics observed in this case study (Conolly et al., 2008). Therefore, when spatial effects are taken into account, drift has a more significant effect than previously recognized. This also suggests that the loss in LBK crop diversity may be a product of spatial drift. Our results can be useful in a broader context, because they show the importance of taking into account spatial dimensions in cultural evolution. Indeed, cultural drift is

important in many topics besides our specific case study (LBK cultural dynamics), e.g. in explaining losses of skills and technologies (Diamond, 1978; Henrich, 2004), the frequency distributions of cultural traits such as first names (Hahn and Bentley, 2003), dog breeds (Herzog et al., 2004), pottery decorations (Neiman, 1995; Shennan and Wilkinson, 2001), scientific paper citations (Simkin and Roychowdhury, 2003), patent citations (Bentley et al., 2004), etc.

The Neolithic transition is the change from hunter-gathering to farming economics. In the Near East, this crucial historical process took place by 11,000 calibrated years Before Present (cal yr BP). From there, the Neolithic transition spread gradually across Europe, reaching Greece and the Balkans by 8500 cal yr BP (pre-Linearbandkeramic (LBK) Neolithic), Central Europe by 7000 cal yr BP (LBK Neolithic), and eventually the British Islands by 6000 cal yr BP (Conolly et al., 2008; Pinhasi et al., 2005).

In order to understand the progression of the Neolithic transition in Europe, mathematical models based on reaction-diffusion equations have been developed (Ammerman and Cavalli-Sforza, 1984; Fort and Méndez, 1999; Ackland et al., 2007; Fort et al., 2007). Such models assume that the Neolithic front was driven mainly by the reproduction and movement of farming populations (demic diffusion) and not by imitation (cultural diffusion). However, most such models predict only the speed of the demic front but do not deal with cultural dynamics. One possible reason is that no systematic trends on the cultural evolution of the early Neolithic populations had been well-established by archaeologists until very recently. However, Conolly et al. (2008) recently succeeded in identifying a systematic Neolithic cultural trend. Indeed,

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they quantified a significant reduction in cultural diversity. They did so by comparing the presence of domestic crops in pre-LBK settlements in Southeast Europe to LBK settlements in Central Europe (Fig. 1). Because they selected the crops less likely to have been affected by climatic factors, they reasonably assumed that this reduction in cultural diversity is a cultural rather than ecological process (Conolly et al., 2008). They also showed that, according to *non-spatial* simulations, drift cannot explain the observed LBK diversity loss. Here we report *spatial* simulations of LBK cultural dynamics, based on integrating cultural transmission (Conolly et al., 2008) and front propagation (Fort et al., 2007) models.

The initial wave of advance of agriculture from the Near East is widely regarded as demic, but is has been argued that later on there was significant cultural diffusion and indigenous adoption, specially in Northern Europe (Zvelebil and Lillie, 2000). Therefore, there is no consensus on the relative importance of demic and cultural diffusion in some regions of Europe. However, in the case of the LBK expansion across Central Europe most scholars agree that the Neolithic wave was mainly demic (Shennan and Edinborough, 2007).

It is known that some LBK patterns of crop use cannot be satisfactorily explained in terms of adaptation to new ecological and climatic conditions (Colledge et al., 2005; Bakels, 2007; Coward et al., 2008). In order to avoid any ecologic or climatic effects, Conolly et al. (2008) considered only the 8 crop species less likely to have been subject to reduced productivity in Central Europe (Table 1). They used the statistic t_F (Neiman, 1995) as a measure of the diversity in cultural traits (crop use in our case),

$$t_F = \frac{1}{\sum_{i=1}^{8} p_i^2} - 1, \tag{1}$$

where p_i is the relative frequency of crop i ($i = 1,2,...,8$), obtained by dividing the number of sites of occurrence of crop i by the sum of

Table 1
Number of sites, crop frequencies p_i and crop diversity t_F based on presence of eight principal species less likely to have been subject to reduced productivity in Central Europe.

Common Name	Taxa	pre-LBK	p_i pre-LBK	LBK	p_i LBK
Oats	*Avena* sp.	13	0.094	6	0.025
Hulled barley	*Hordeum vulgare*	25	0.18	18	0.075
Naked barley	*Hordeum vulgare* var. *nudum*	10	0.072	14	0.058
Pea	*Pisum sativum*	18	0.13	41	0.17
Millet	*Panicum miliaceum*	3[a]	0.022	10	0.042
Free threshing wheat	*Triticum aestivum/ durum*	16	0.11	11	0.046
Emmer	*Triticum dicoccum*	27	0.19	76	0.31
Einkorn	*Triticum monococcum*	26	0.19	65	0.27
Total occurrences		138		241	
Diversity (t_F)		5.6[a]		3.7[a]	

[a] Corrected from Conolly et al. (2008) with approval by James Conolly.

these numbers over all crops (see Table 1). As shown in Table 1, the evolution of the Neolithic front is characterized by a substantial reduction if the value of the diversity t_F in LBK settlements as compared to pre-LBK settlements (Fig. 1). Let us stress that Conolly et al. (2008) showed that *non-spatial* cultural transmission models cannot explain this observed decrease in cultural diversity. Motivated by the fact that a similar problem arises in population genetics (Edmonds et al., 2004), in this paper we take into account the role of spatial dimensions in order to see if the observed reduction in cultural diversity can be explained.

It has been recently shown, both analytically (Vlad et al., 2004) and with numerical simulations (Edmonds et al., 2004), that the effect of spatial dimensions on the fate of genetic mutations appearing during a population range expansion is very important, as follows. If the mutation appears in a place located on the leading
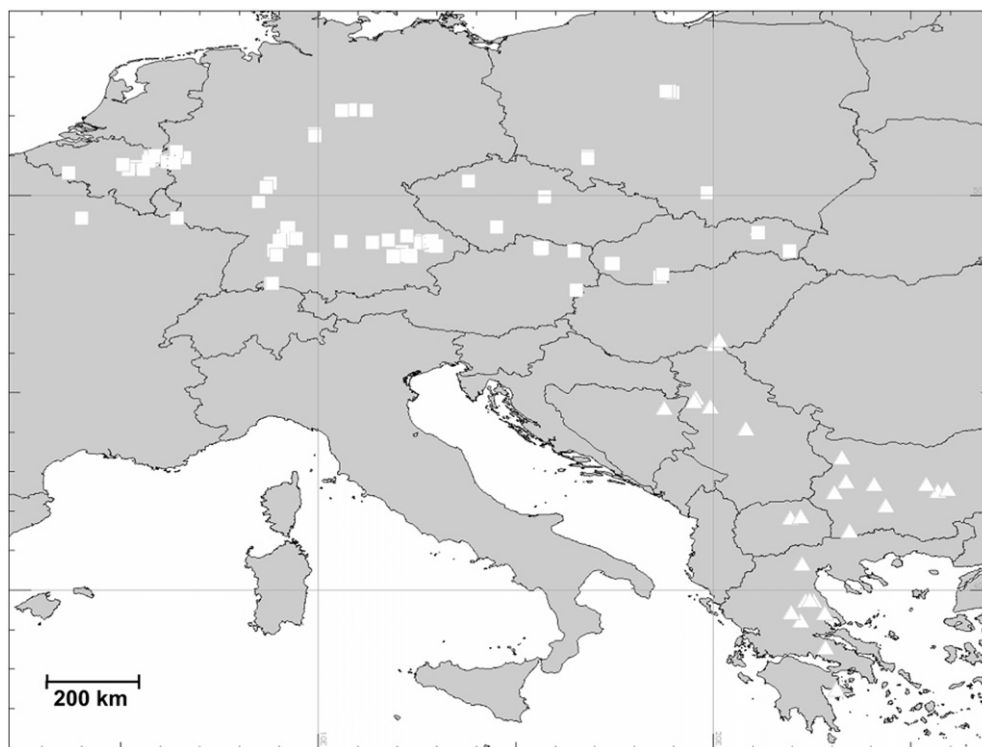

Fig. 1. Map of locations of pre-LBK (triangles) and LBK (squares) sites used in this analysis (see Table 1). Adapted from Conolly et al. (2008).

edge of the front (i.e., where there are only a few individuals), then the mutant frequency will be initially very high, and the mutation will probably spread. On the other hand, if the mutation appears behind the front (i.e., where the population density is close to saturation), then its initial frequency will be very low, and it will have poor chances to spread. Is there an analogous process for cultural transmission, such that it may explain the LBK diversity loss in Table 1? Intuitively, it is clear that spatial front propagation models, in contrast to non-spatial models used previously (Conolly et al., 2008), take into account that in the front leading edge there are only a few pioneering settlements, and this can increase the chances for cultural traits to decrease or even disappear.

Despite good reasons to believe that our results are underestimates, below we find that the observed reduction in cultural diversity can be naturally explained simply by taking into account the spatial dimensions.

2. Methods

Our model takes into account only vertical transmission (i.e., from parents to children) and not horizontal transmission (i.e., from non-parents), for the following reasons: (i) the parameters of horizontal transmission are very difficult to estimate form the scanty observations available (Cavalli-Sforza and Feldman, 1981); (ii) ethnographic work indicates that farming practices are usually both relatively conservative and transmitted vertically (Coward et al., 2008), so the effect of horizontal transmission should be small; and (iii) adding horizontal transmission would only reinforce our conclusions, because it would lead to an increased loss in cultural diversity (this is due to the fact that copying in small populations increases the chances of some traits being lost, and has been also shown by simulations by Conolly et al., 2008). Therefore, our results are admittedly underestimates, but we will show that they are sufficient to explain the observed decrease in cultural diversity, and we expect that substantially more complicated models would yield similar results. The same comments can be made about possible effects of transmission error rates (Conolly et al., 2008).

Each settlement is represented by a string of eight binary digits (0 or 1), indicating the absence or presence of each crop in Table 1 at the settlement considered. Let $N(i,j,t)$ stand for the number of settlements at node (i,j) and generation t. The maximum number of settlements per node is N_s, corresponding to the saturation density of farmers (see Sections 3 and 5).

We simulate the evolution of the population numbers and culture (crop use) under net reproduction, dispersal and vertical cultural transmission. In the simulations, two-dimensional space is represented by a square grid of cells 50 km 50 km each, because 50 km is the characteristic dispersal distance for pre-industrial farmers (Fort et al., 2007). The grid has 1000×1000 nodes, and initially the grid is empty of Neolithic settlements except at the central node, representing the starting area of the pre-LBK culture (which is located in Greece according to Fig. 1). An initial population of N_s settlements is located at the central node of the grid. The diversity in this initial population must be close enough (but not necessarily identical) to the calculated pre-LBK diversity in Table 1. To achieve this, the model starts with an initial set of N_s settlements randomly generated by drawing from a larger population (e.g. 100 settlements) with the observed diversity value $t_F = 5.6$ (from Table 1).

3. Calculation

Each iteration corresponds to one generation or 32 years (Fort et al., 2004). Each simulation run corresponds to 60 generations (i.e., about 1900 years, which is a time period similar to that elapsed

between the oldest pre-LBK and the latest LBK sites, see Conolly et al., 2008). We perform the following steps for each generation.

(i) Dispersion. For each occupied node, a randomly-selected fraction p_e of the settlements remains at the same place (we use the mean value $p_e = 0.38$ for the persistency, as measured for pre-industrial agricultural populations, see Fort et al., 2007). A randomly-selected fraction of settlements $(1 - p_e)/4$ disperses into each of the 4 neighboring nodes. All settlement numbers are rounded to the nearest integer, such that the total number of settlements is preserved.

(ii) Reproduction. Following Conolly et al. (2008), we use a birth rate $b = 5\%$ per year (and a death rate $d = 4\%$ per year in step (iv) below). The birth rate $b = 0.05$ yr^{-1} is implemented as follows. The effect of the birth rate is such that $dP/dt = bP(t)$, where t is the time measured in generations. Integrating this equation we obtain $P(t + 1) = P(t)e^{bT}$. On the other hand, we define the fecundity R_0 such that $P(t + 1) = R_0 P(t)$. Comparing both equations yields $R_0 = e^{bT} \approx 5$ (where $T = 1$ generation $= 32$ yr), so for each settlement we generate 4 new, additional settlements in the way explained in step (iii). If this yields a number of settlements above N_s, then the final number is limited to N_s.

(iii) Vertical transmission is applied before mortality (so that parents can transmit the cultural traits to their children before the parents die). The value (0 or 1) indicating the absence or presence of each cultural trait (crop) from a randomly-selected *old* settlement is passed to a randomly-selected *new* settlement in the same node, so that each new agent is a clone of its parent (as in Conolly et al., 2008).

(iv) Mortality. The net growth is $a = 1\% = 0.01$ yr^{-1} as in Conolly et al. (2008), so the death rate is $d = b - a = 0.04$ yr^{-1}. Therefore, the net fecundity is $R_{0\ net} = e^{-aT} = 1.4$. For this reason, we apply mortality by removing at random the necessary number of settlements such that the final settlement number at the node considered is the nearest integer to 1.4 times the initial number (before steps (ii)–(iii)).

At the end of step (iv), the relative frequency p_i of each cultural trait (crop) at each node is computed by dividing the number of settlements of occurrence of crop i by the sum of these numbers over all crops ($i = 1,2,…,8$). The values of p_i thus obtained are used to compute the cultural diversity t_F at each node using Eq. (1).

The combined output of 20 runs is used to produce boxplots of cultural diversity (see Section 4) that can be compared with archaeologically-observed values (Table 1).

According to Zimmerman et al. (2009), the characteristic population density of the LBK was about 0.6 people/km². This yields around 1500 people per node in our grid (each node corresponds to a cell of $50 \cdot 50 = 2500$ km²). Also according to Zimmerman et al. (2009), a reasonable estimate of the number of inhabitants of LBK settlements is about 300 people. This yields 5 settlements/node. Therefore, we have used $N_s = 5$ as a characteristic value to analyze the evolution of cultural diversity. We have also checked that the role of drift remains important for other values of N_s (see Section 5 and electronic supplementary material).

4. Results

Fig. 2 shows the number of settlements plotted as a function of distance, for several time intervals up to 60 generations, which is a time period similar to that elapsed between the oldest pre-LBK and the latest LBK sites (see Section 3). The invading population front of farmers in Fig. 2 moves at a constant speed, and we have checked that its value is in agreement with the corresponding
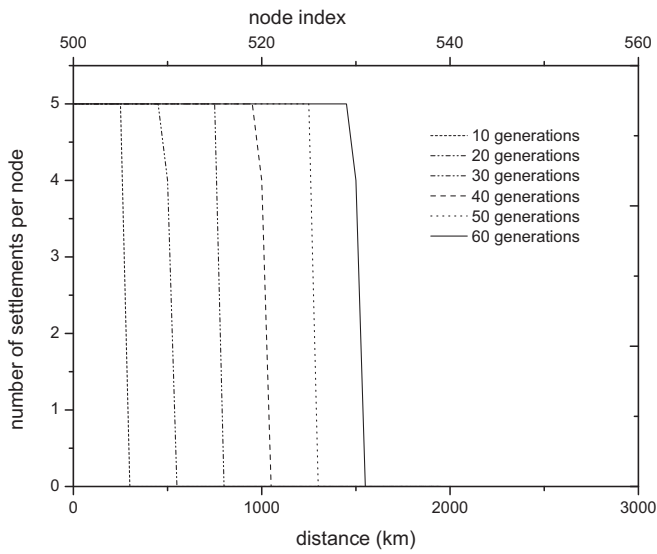
Fig. 2. Demic wave of advance of Neolithic settlements, obtained from our simulations. The distance between two neighboring nodes is 50 km, and the other parameter values used are $p_e = 0.38$, $R_0 = 5$ and $R_{0\ net} = 1.4$ (see Section 3). The distance traveled by the front is about 1500 km, in agreement with the distance between the furthest pre-LBK and LBK sites in Fig. 1.
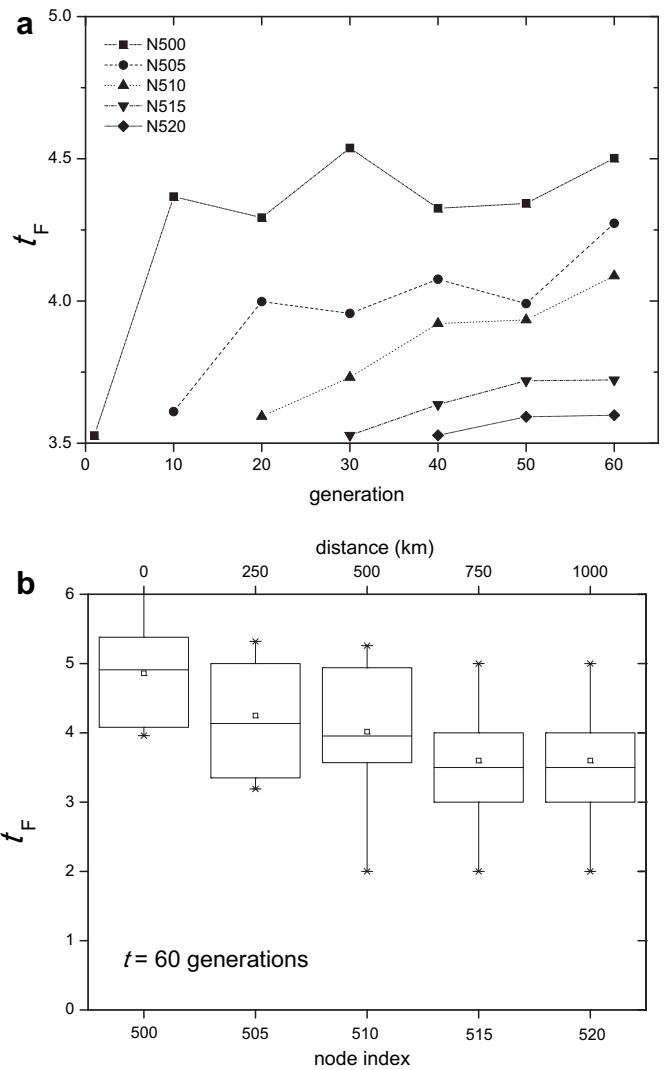

Fig. 3. (a), Cultural diversity as a function of time at several nodes of the spatial grid, for a single simulation run. The node with index 500 corresponds to the initial point of the demic wave of advance considered (distance = 0 km, located in Greece in Fig. 1). The node with index 520 (distance ≈ 1000 km) corresponds to the center of gravity of the LBK sites (squares in Fig. 1). (b), Cultural diversity as a function of distance from the Greece/Balkans region, 60 generations after the beginning of the LBK range expansion. The lower and upper bounds of each box give the 25% and the 75% of simulations results, respectively. The line dividing each box is the median (50%), the small square is the mean, and the crosses correspond to 1% and 99% of simulation results. The whiskers give the most distant non-outliers (i.e., below 1.5 times the interquartile range from the corresponding end of the box). The horizontal thin lines are the minimum and maximum values (in this case, they coincide with the whiskers).

analytical result (see Eq. (17) in Fort et al., 2007). We see from Fig. 2 that the distance traveled by the Neolithic demic front is about 1500 km, which agrees with the distance between the furthest pre-LBK and LBK sites in Fig. 1. Thus, the origin in Fig. 2 corresponds to the central node in our grid (node 500, distance = 0 km) and is located in Greece in Fig. 1, whereas the final nodes in Fig. 2 (around node 530, or distance ≈ 1500 km) are located in the Belgium/Germany region in Fig. 1. It is important to stress that dispersion, reproduction, death and cultural transmission take place at all nodes, i.e. not only on the leading edge of the invasion front but also behind it (see the Section 3 for details).

Fig. 3a shows the evolution of the cultural diversity of crops, t_F, at the initial node of the population expansion (node 500, distance = 0 km) and several other nodes, for a single simulation run. Note that for all nodes (except the initial one, with distance = 0 km) no values of t_F appear in Fig. 3a until some time is elapsed. This is due simply to the fact that the population front has not yet arrived (e.g., for node 520, located at a distance = 1000 km from the expansion origin, the front takes 40 generations to arrive, in agreement with Fig. 2). At the initial point of the population expansion (node 500, distance = 0 km), it is seen in Fig. 3a that the value of the cultural diversity t_F drops abruptly at the first generation (from an initial value of about $t_F = 5.6$, see Section 2). This is due to the fact that, after part of the population disperses *away* from the initial point, some species can be lost and the diversity therefore diminishes. In contrast, at the second and later generations population dispersal *into* the initial node is possible from neighboring nodes (which are no longer empty) and, therefore, some cultural traits can be imported. This is why the drop in cultural diversity is not so abrupt after the first generation at the central node (node 500, distance = 0 km) in Fig. 3a. Note also that in Fig. 3a the value of the cultural diversity t_F tends to be smaller at larger distances from the origin, as expected due to repeated drift effects at the propagating leading edge of the front. The lowest value of t_F is therefore reached at the center of gravity of the LBK sites (node index ≈ 520, distance ≈ 1000 km). We stress that these results have been obtained for a singe simulation run. Therefore, in Fig. 3b we present averages over many runs.

Fig. 3b shows the cultural diversity of crops, t_F, obtained from the simulations at the end of the LBK expansion (generation 60). t_F is plotted as a function of distance from the origin (node 500, distance = 0 km) up to the center of gravity of the LBK sites (node index ≈ 520, distance ≈ 1000 km). Each box-plot in Fig. 3b is made up of 20 simulation runs, each one starting with an initial population randomly created from a distribution that matches the measured frequencies as shown in Table 1 (see Section 2). Note that towards the end of the population expansion (time ≈ 60 generations) the value of the cultural diversity at the *initial* point (node 500 or distance = 0 km) attains the range $4 \leq t_F \leq 5$, in agreement with Fig. 3a. In contrast, the effect of spatial drift is much more important at nodes located *far away* from the initial point, as expected, where the values of the cultural diversity are much lower ($3 \leq t_F \leq 4$ at node index ≈ 520 or distance ≈ 1000 km).

5. Discussion

Fig. 3b shows a consistent drop in cultural diversity at the final time, from settlements in the node index 500 (corresponding to the pre-LBK region in Fig. 1) down to a mean value of $t_F = 3.6 \pm 0.6$ (at node 520, corresponding approximately to the center of the LBK region in Fig. 1). It is very important that this final value ($t_F = 3.6 \pm 0.6$) from the space-time simulations is in agreement with the LBK value according to the archaeological observations in Table 1 ($t_F = 3.7$). The box-plot heights in Fig. 3b reflect the variability of the simulation results, because the mechanisms of dispersion, growth, mortality and cultural transmission take place stochastically, using randomly-selected settlements (see Section 3).

In contrast to non-spatial models (Conolly et al., 2008), our space-time simulations predict a substantial decrease in cultural diversity (Fig. 3b). The reason is simply that the population numbers at the leading edge of the invasion front are necessarily very low (Fig. 2), corresponding to pioneering settlements of Neolithic farmers, and such low population numbers increase the role of drift. In our case study, the role of drift corresponds to the chances of cultural traits being lost. In population Genetics, the role of drift corresponds to the chances of mutations to spread (Edmonds et al., 2004; Vlad et al., 2004).

Changing the values of the model parameters within anthropologically realistic ranges leads to much the same results, as we show in turn.

The value of the persistency varies between 0.19 and 0.54 (Fort et al., 2007), but we have checked that using such values in the simulations does not change the results appreciably.

The characteristic dispersal distance (distance between two neighboring nodes) varies in the range 33–69 km (Pinhasi et al., 2005), but the only implication of this range is that the 30 nodes traveled by the population front in Fig. 2 would correspond to the range 990–2070 km (instead of about 1500 km as in Fig. 2). However, this range is consistent with the distance implied by the location of the sites in Fig. 1, so the same simulations are appropriate and, therefore, the same decrease of cultural diversity as in Fig. 3 is obtained.

In Figs. 2 and 3 we have used a birth rate of $b = 0.05 \text{ yr}^{-1}$, a death rate of $d = 0.04 \text{ yr}^{-1}$ as in Conolly et al. (2008) and a generation time of $T = 32$ yr (Fort et al., 2004). We have checked that the results are much the same using other values within realistic ranges, namely $0.04 \le b \le 0.06 \text{ yr}^{-1}$, $0.01 \le a \le 0.03 \text{ yr}^{-1}$, $d = b - a$ (Conolly et al., 2008) and $27 \le T \le 36$ yr. Concerning this range of T, note that when modeling population fronts, the generation time T is not the mean age of parents at birth of the first child, but averaged over all children (Fort et al., 2004).

To check the consistency of the results, simulations and Fig. 3b were repeated with $N_s = 10$, 20 and 40 settlements. Again, a gradual reduction of diversity was obtained, similar to Fig. 3b (the final values are higher, as expected, but the change is very slight: $t_F = 3.8$, 4.0 and 4.1, respectively, see Figs. S1–S3 in electronic supplementary material). All of these values are close to the observed value for the LBK crop diversity ($t_F = 3.7$, from Table 1). It is very important that all of these values are also substantially lower than the final value obtained when the space dimensions are not included in the simulations ($t_F = 5.1$, from Fig. 4 in Conolly et al., 2008).

6. Conclusions

In this paper we have shown that spatial drift drastically changes the evolution of cultural diversity, and that this effect can explain the reduction in crop diversity that is observed from the archaeological data of the LBK Neolithic expansion. Admittedly, our models could be further complicated, but we expect that the results would not change appreciably. We have considered only vertical transmission (i.e., copying of cultural traits from the parents, see Section 3) but horizontal transmission (copying from non-parents) has a much smaller effect for farming practices (Coward et al., 2008) and would lead to an additional loss of diversity (see Section 2). Therefore, it would only strengthen our conclusions. Moreover, we think that it is not clear whether it is more realistic to apply horizontal transmission once per generation or once per year (Conolly et al., 2008). In any case, if horizontal transmission often takes place once per generation, its effect would probably be very small indeed. Similarly, including learning/transmission errors would lead to an additional loss of diversity, but again this effect is very small (Conolly et al., 2008).

Finally, it is interesting to note that here we have considered crop diversity, but our approach could be also applied to analyze the effect of spatial drift on the evolution of other sets of cultural traits, e.g. ceramic traditions (Neiman, 1995; Shennan and Wilkinson, 2001). For the specific set of traits considered, it should be carefully analyzed whether horizontal transmission and innovation can be neglected (as done here for crop farming practices) or not. In the latter case, it may be very difficult to estimate the parameter values necessary to include horizontal transmission and/or innovation in the spatial simulations, and those values will certainly depend on the specific set of cultural traits considered. In spite of this, we can ask the question of whether we expect to see a similar reduction in diversity (to that reported here for crop farming practices) due to spatial drift or not. If horizontal transmission has a non-negligible effect, it will only increase the diversity loss due to the role of the spatial dimensions (see Section 2). Therefore, a reduction in cultural diversity will still be observed. On the other hand, if innovation has a non-negligible effect, it will obviously tend to increase cultural diversity. Whether this increase will cancel out the decrease in diversity (due to the spatial dimensions and/or horizontal transmission) or not will depend on whether the innovation rate is fast enough or not (for the specific set of cultural traits and culture considered). More importantly, innovation can lead to a different and very interesting effect, namely the spreading of rare cultural variants appearing on the leading edge of the wave of advance (i.e., in regions where the population density is low). To the best of our knowledge, this cultural effect has not been yet observed. It would be strictly analogous to the surfing effect of mutations on the wave of advance of an expanding population (Edmonds et al., 2004; Vlad et al., 2004; Hallatschek et al., 2007).

The main conclusion of this paper is that spatial drift can explain the decrease of cultural diversity in the LBK culture in Neolithic Europe. In contrast, non-spatial models seem unable to explain this decrease (Conolly et al., 2008). This suggests that the loss in LBK crop diversity may be a product of spatial drift. Our results also lead to a conclusion of broader interest, namely that when spatial effects are taken into account, drift has a drastically more significant effect than previously recognized.

Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jas.2011.01.004.

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