

## 16 The Neolithic transition: Diffusion of People or Diffusion of Culture?

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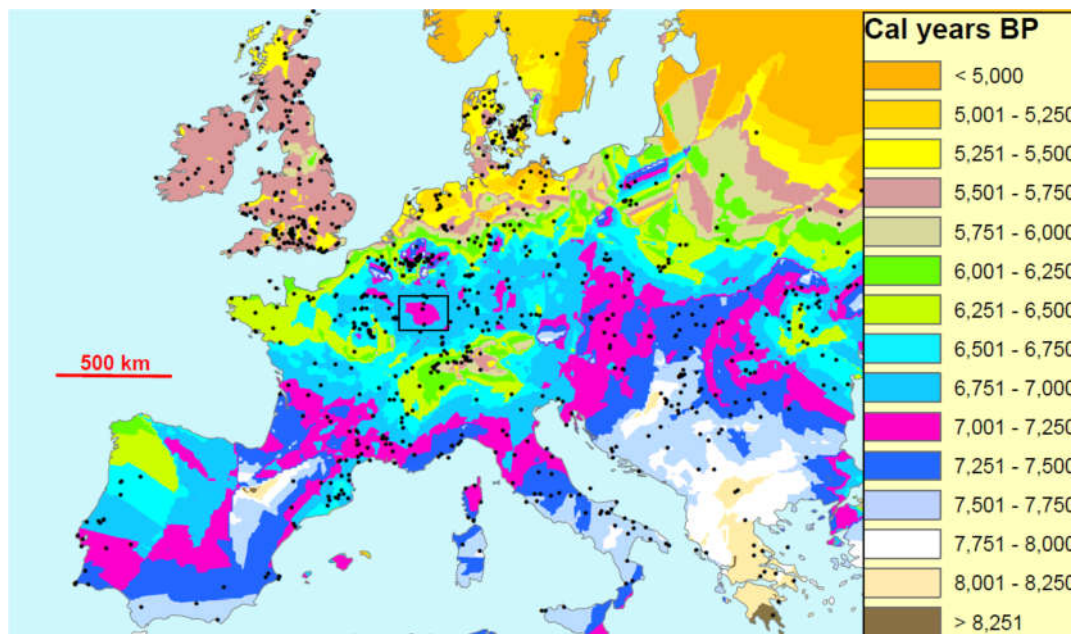
### 16.1 Introduction

The Neolithic transition is defined as the shift from hunting-gathering (Mesolithic) into farming and stockbreeding (Neolithic). The Neolithic arrived at about 8000 years Before Present (yr BP) from the Near East into Southeastern Europe. From there, it spread gradually westwards and northwards across Europe, until about 5000 yr BP. We know this from the radiocarbon dates of remains related to farming and stockbreeding that have been found in archeological sites. Europe is the continent for which more Neolithic sites per unit area have been dated so far than anywhere else in the world, and this is the reason why most models of the Neolithic transition have been applied to Europe. This spread of farming can be seen in Fig. 16.1, which is a recent interpolation of 918 early Neolithic sites [1].

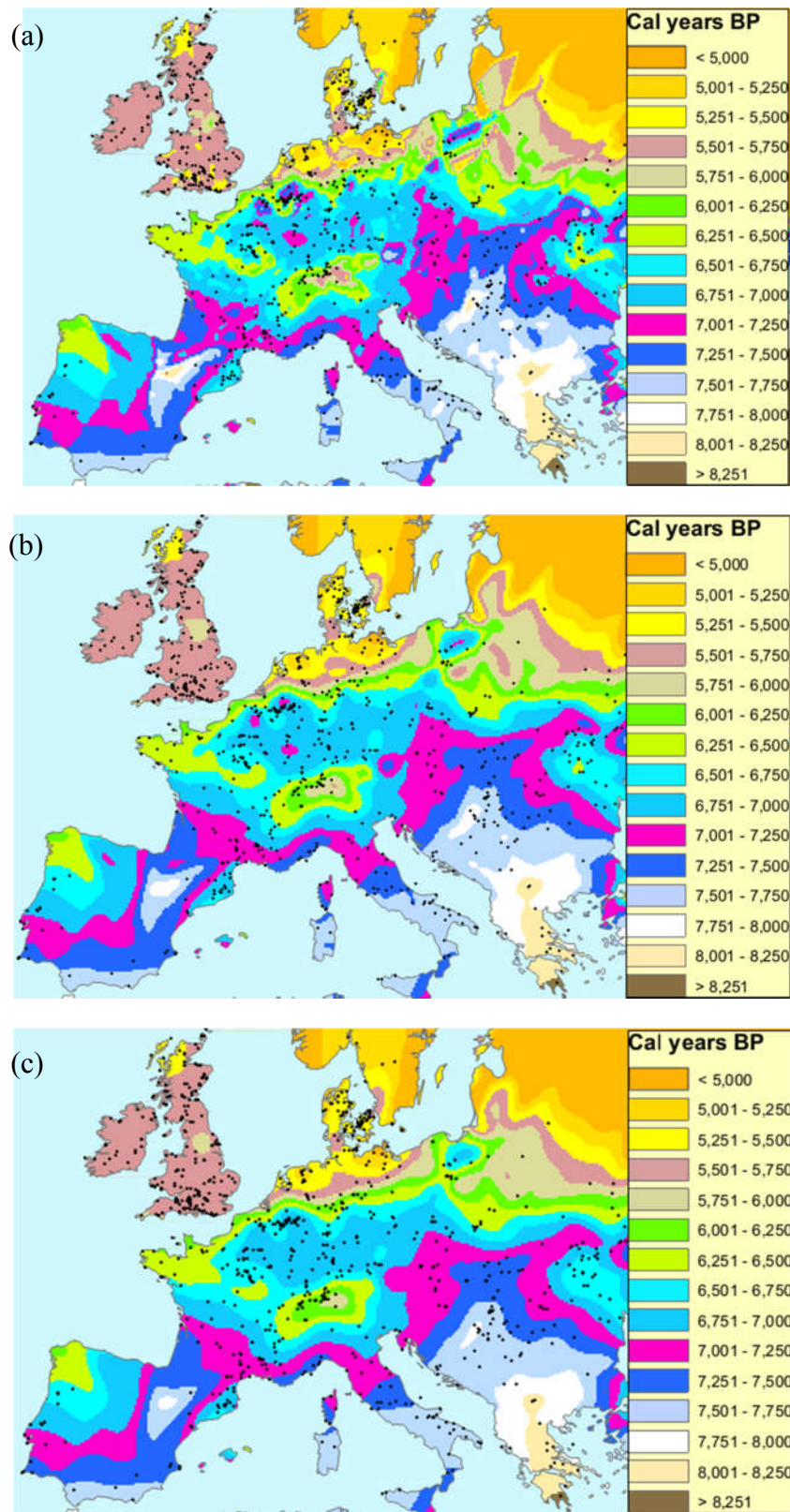
Figure 16.1 shows at once that we are dealing with a gradual spread. Of course, there are some anomalously old regions (e.g., the patch inside the black rectangle in Fig. 16.1). Lemmen and Gronenborn (chapter 17, this volume) rightly point out that some of such anomalous regions may be due to radiocarbon dating errors and/or other problems with the databases supplied by archeologists. This is certainly possible. However, in spite of the fact that such anomalously old regions are rather small and contain only a few sites, Lemmen and Gronenborn (chapter 17, this volume) regard their presence as a 'pitfall' of the quantitative map in Fig. 16.1. They offer, instead, the qualitative map in their Fig. 17.1, which has no anomalous regions simply because it is just a drawing, not the result of any statistical interpolation. But it is important to note that, in order to totally avoid the presence of such anomalous regions in interpolation maps, several strong conditions would have to hold. A crucial one is that local geography should not have any effect, in the sense that all land should be equally attractive to farmers. Otherwise, it is reasonable to expect that farmers will sometimes move to more distant land even if there is nearer, less attractive land (which will not be settled by farmers until later on). The presence of rivers, mountains, different types of soils, etc., probably makes some areas more attractive for farmers than others. For this reason, the presence of anomalously old or young regions (such as the patch inside the black rectangle in Fig. 16.1) is probably unavoidable (even if we had a database totally free of errors and with all dates corresponding exactly to the earliest farming activity at each site). Anyway, the presence of such anomalous regions should not be a problem after all. Smoothing techniques are well-established in geographic analysis. They yield, with increasing coarse graining, maps with decreasing subtleness, where the anomalous regions gradually disappear (Fig. 16.2). This seems one reasonable solution to estimate speed vectors and magnitudes (see below), in spite of the presence of anomalously old/young regions (before smoothing) [1].

Qualitative maps (such as that in Fig. 17.1) are certainly useful and interesting. However, for some analyses we need quantitative maps, which are usually based on interpolation techniques (see, e.g., Fig. 16.1). Quantitative maps are statistically justified. Moreover, they make quantitative comparison to mathematical models possible, e.g., by estimating local spread rates by means of geographical statistical techniques [1]. In this chapter we shall show what spread rates are obtained in this way, and what are their implications for the mechanisms driving the spread of the Neolithic.

The spread of the Neolithic in Europe was clearly gradual, because as we move westwards and northwards, we find more and more recent dates (Figs. 16.1 and 17.1). This suggests that it may make sense to apply diffusive models to the spread of the Neolithic. A quantitative justification is the following. We know from chapter 2 that diffusion equations provide large-scale descriptions of systems where there are, at the small scale, molecules or individuals following random walks (see Fig. 2.5). Does this point apply to the spread of the Neolithic? For the moment, assume a very simple model in which agriculture would have spread only due to the dispersal of farmers. Then each random walk is the trajectory obtained by joining, e.g., the birthplaces of an individual's parent, the individual in question, one of his/her children, and so on. Looking at Fig. 16.1, we can easily estimate that agriculture spread from Greece to the Balkans and Central Europe at a speed of roughly 1 km/yr. Thus, assuming a generation time of about 32 yr [2], farming spread about 32 km per generation. This is much less than the scale of Fig. 16.1 (3000 km or more). This comparison provides a quantitative justification for the use of diffusion equations in models of the Neolithic spread.



**Fig. 16.1.** Interpolation of 918 early Neolithic sites (circles). Each color corresponds to a 250-yr interval. We see that the oldest sites are located in the southeast. Note also that farming propagated faster westwards than northwards. Moreover, slowdowns in the Alps and Northern continental Europe are clearly displayed. The patch inside the black rectangle is an example of an anomalously old region, as compared to its surroundings. Due to the paucity of sites, the contours are less detailed in some regions (e.g., upper right and lower left). Adapted from Ref. [1].



**Fig. 16.2.** Isochrones obtained by smoothing (“coarse graining”) the map in Fig. 16.1 a single time (a), 10 times (b) and 20 times (c) (i.e. with 1, 10 and 20 iteration steps, where each step consists in replacing the date of each individual point of the map by the average of that date and those of the surrounding points). Note that anomalous regions (such as that inside the black rectangle in Fig. 16.1) gradually disappear. This is useful to perform quantitative estimates of local speed vectors and magnitudes (see Fig. 16.4.b for the latter). Adapted from Ref. [1], Supp. Info. Appendix, Sec. S1.

Ammerman and Cavalli-Sforza [3] were the first to apply a diffusive model to the spread of the Neolithic. They used Fisher's wave-of-advance model. In this model, the speed of the Neolithic front is given by Eq. (2.17),

$$v_{Fisher} = 2\sqrt{D\alpha}, \quad (16.1)$$

where  $D$  is the diffusion coefficient and  $\alpha$  the initial growth rate (i.e., the net reproduction rate at low population densities). This relation has already been introduced as Eq. (2.17) in chapter 2. Following Ref. [4] we sketch, for the interested reader, the line of reasoning leading, eventually, to this relation.

Let  $N(x, y, t)$  stand for the population density of Neolithic individuals (i.e., farmers), where  $x$  and  $y$  are Cartesian coordinates and  $t$  is the time. We assume that a well-defined time scale  $T$  between two successive migrations occurs. This model (to be improved in Sec. 16.3) is based on the assumption (see Ref. [5], Sec. 11.2) that, between the values  $t$  and  $t + T$ , we can add up the changes in the number of individuals in an area differential  $ds = dx dy$  due to migrations (sub index  $m$ ) and to population growth (sub index  $g$ ),

$$\begin{aligned} [N(x, y, t + T) - N(x, y, t)]ds &= [N(x, y, t + T) - N(x, y, t)]_m ds + \\ &[N(x, y, t + T) - N(x, y, t)]_g ds. \end{aligned} \quad (16.2)$$

Let  $\Delta_x$  and  $\Delta_y$  stand for the coordinate variations of a given individual during  $T$ . We introduce the dispersal kernel  $\phi_N(\Delta_x, \Delta_y)$ , defined such that  $\phi_N(\Delta_x, \Delta_y)$  is the probability per unit area to move from  $(x + \Delta_x, y + \Delta_y)$  at time  $t$  to  $(x, y)$  at time  $t + T$ . We can rewrite the parentheses in the first term on the right by means of Einstein's approach to diffusion [6], namely

$$\begin{aligned} [N(x, y, t + T) - N(x, y, t)]_m &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} N_{\Delta} \phi_N d\Delta_x d\Delta_y - N(x, y, t) \\ &\approx \frac{\langle \Delta^2 \rangle}{4} \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right), \end{aligned} \quad (16.3)$$

where  $N_{\Delta}$  stands for  $N(x + \Delta_x, y + \Delta_y, t)$ , and  $\phi_N$  for  $\phi_N(\Delta_x, \Delta_y)$ . In the last line in Eq. (16.3) we have performed a second-order Taylor expansion in  $\Delta_x$  and  $\Delta_y$ , and taken into account that  $\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_N d\Delta_x d\Delta_y = 1$ . We have also assumed that the kernel is isotropic, i.e.,

$$\phi_N(\Delta_x, \Delta_y) = \phi_N(-\Delta_x, \Delta_y) = \phi_N(\Delta_x, -\Delta_y), \quad (16.4)$$

and introduced the mean-squared displacement as

$$\langle \Delta^2 \rangle = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \Delta^2 \phi_N(\Delta_x, \Delta_y) d\Delta_x d\Delta_y, \quad (16.5)$$

where  $\Delta^2 = \Delta_x^2 + \Delta_y^2$ . Note that Eq. (16.4) implies that  $\langle \Delta_x \rangle = 0$ ,  $\langle \Delta_y \rangle = 0$ ,  $\langle \Delta_x \Delta_y \rangle = 0$  and  $\langle \Delta_x^2 \rangle = \langle \Delta_y^2 \rangle$ , which has been applied in the last step in Eq. (16.3).

Finally we rewrite the parentheses in the last term in Eq. (16.2) as a Taylor expansion,

$$[N(x, y, t + T) - N(x, y, t)]_g = \left( T F(x, y, t) + \frac{T^2}{2} \frac{\partial F}{\partial t} + \dots \right) \quad (16.6)$$

where  $F(x, y, t)$  is the change in population density per unit time, due to births and deaths.

Expanding the left-hand side of Eq. (16.2) up to first order and collecting terms, we arrive at Fisher's reaction-diffusion equation,

$$\frac{\partial N}{\partial t} = D \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) + F(x, y, t), \quad (16.7)$$

where we have introduced the diffusion coefficient,

$$D = \frac{\langle \Delta^2 \rangle}{4T}. \quad (16.8)$$

which is the two-dimensional analogue of the one-dimensional Eq. (2.3). Concerning the net reproduction function  $F(x, y, t)$ , in chapter 2 an example is presented such that

$$F(x, y, t) = \alpha N(x, y, t) \quad (16.9)$$

(see the last term in Eq. (2.15)). This reproduction function corresponds to exponential growth, because without diffusion ( $D = 0$ ) Eq. (16.7) yields  $N = N_0 \exp[\alpha t]$ , with  $N_0 = N(t = 0)$ . Thus Eq. (16.9) is an example of interest, but the population density would never stop growing. A biologically more realistic case is the so-called logistic growth function,

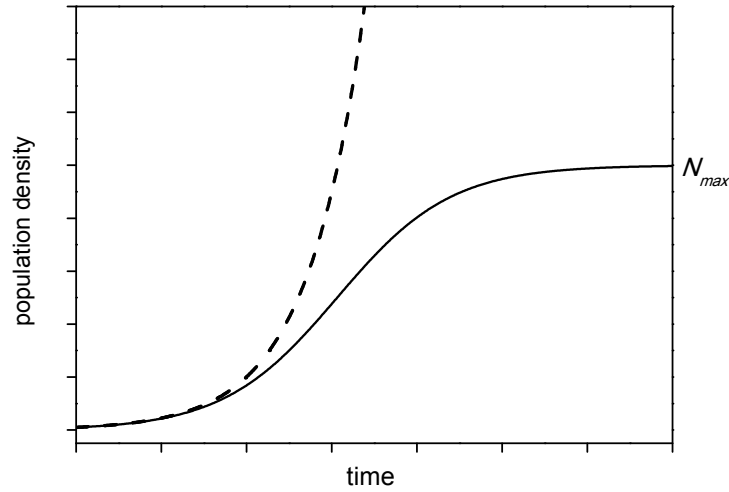
$$F(x, y, t) = \alpha N(x, y, t) \left[ 1 - \frac{N(x, y, t)}{N_{max}} \right], \quad (16.10)$$

where  $N_{max}$  is the saturation density, i.e. the population density at which net reproduction vanishes (note that  $F(x, y, t) = 0$  if  $N(x, y, t) = N_{max}$ ). The functions of exponential and logistic growth are compared in Fig. 16.3. A more detailed introduction into the formalism of logistic growth is provided by section 3.4.1 of chapter 3, with an example of the benefit of this reasoning on predicting the spreading of technological innovations given in section 14.2.2 of chapter 14.

Equation (16.7) with the logistic growth function (16.10) is called Fisher's equation. For our purposes here, we can consider the simple case in which all parameters ( $D$ ,  $\alpha$  and  $N_{max}$ ) are independent of  $x$ ,  $y$  and  $t$ . Travelling wave solutions (also called fronts or waves of advance) are defined as constant-shape solutions, i.e. those depending not on  $x$ ,  $y$  and  $t$  separately but only on  $z = r - vt$ , where  $v$  is the front speed and  $r = \sqrt{x^2 + y^2}$  the radial coordinate.

Kolmogorov *et al.* [7] showed that in Fisher's model, a front is formed and its speed is given by Eq. (16.1), assuming that initially the population density  $N(x, y, t)$  has compact support. In practice, this assumption means that  $N(x, y, t = 0) = 0$  everywhere except in a finite region. This is biologically realistic, in contrast to solutions such that  $N(x, y, t = 0) \neq 0$  for all values of  $x, y$  ( $-\infty < x < \infty$ ,  $-\infty < y < \infty$ ). The latter solutions are not biologically realistic, because in practical applications we always want to analyze the spread of organisms that are initially present in a finite region of space.

Using variational methods, Aronson and Weinberger [8] also showed that the speed of front solutions to Fisher's equation is given by Eq. (16.1) (see Sec. IV.A in Ref. [9] for a simple derivation based on variational principles).



**Fig. 16.3.** Plots of population density  $N$  versus time  $t$ . The dashed line corresponds to exponential growth,  $N = N_0 e^{\alpha t}$  (see the text below Eq. (16.9)), and the full line to logistic growth,  $N = N_0 N_{max} e^{\alpha t} / (N_{max} + N_0 (e^{\alpha t} - 1))$  (see Eq. (16.12)).

Importantly, Fisher's wave-of-advance speed (16.1) does not depend on  $N_{max}$ . Moreover, this speed is the same as for exponential growth (Eq. (16.9)), see Eq. (2.17). Thus the wave-of-advance speed is the same in both the logistic and the exponential models. However, their shape is different, because for exponential growth the population density keeps growing in time, whereas for logistic growth it stops growing at  $N = N_{max}$  (see Fig. 16.3). Thus the waves of advance under logistic growth have the profile shown in Fig. 2.6, where we can see that the population density stops growing once  $N = N_{max}$ . In contrast, for exponential growth the population density keeps growing forever everywhere (see Ref. [10], Figs. 3.3 and Fig. 3.6).

Returning to the spread of the farming, Ammerman and Cavalli-Sforza [3] noted from archaeological dates that the speed of the Neolithic wave of advance was about 1 km/yr. They next asked the following interesting question: what speed does Fisher's model [Eq. (16.1)] predict? In order to answer this, empirical values for  $\langle \Delta^2 \rangle$  and  $T$  are needed to estimate  $D$  using Eq. (16.8). Additionally, an empirical value for  $\alpha$  is needed to estimate the speed from Eq. (16.1). Ethnographic observations of preindustrial populations have measured the displacement of individuals and found the average for the mean-squared displacement per generation  $\langle \Delta^2 \rangle = 1288 \text{ km}^2$  [1,11] and the mean generation time (defined as the age difference between a parent and his/her children)  $T = 32 \text{ yr}$  [2]. Thus we obtain from Eq. (16.8)  $D = 10 \text{ km}^2/\text{yr}$ . On the other hand, for populations which settle in empty space,  $N \ll N_{max}$  and Eq. (16.10) reduces to (16.9), so that we can fit exponential curves (graphically, we can understand this because both curves in Fig. 3 overlap in the left-hand side). Ethnographic data yield the average exponent  $\alpha = 0.028 \text{ yr}^{-1}$  [11]. Using these values into Eq. (16.1) we estimate a front speed of about 1 km/yr, which is similar to the speed obtained from the archeological observations. Indeed, as mentioned above, looking at Fig. 16.1 we can easily estimate that agriculture spread from Greece to the Balkans and Central Europe at a

speed of roughly 1 km/yr (more precise estimations with recent data, based on regression analysis [12] and geostatistical techniques [1], agree with this average). This agreement was first noted by Ammerman and Cavalli-Sforza [3,13]. In this way, Ammerman and Cavalli-Sforza noted that diffusive models are useful not only because they make it possible to describe mathematically a major event in prehistory (the spread of agriculture), but also because they indicate a possible mechanism for it, namely the spread of people (i.e., of populations of farmers). They called this demic diffusion (from the Greek word *demos*, which means people). In contrast, most authors at the time advocated for the learning of farming by hunter-gatherers (i.e., for the spread of agriculture without substantial spread of people) [14]. The latter mechanism is called cultural diffusion.

## 16.2 First improvement: beyond the second-order approximation

In the derivation of Eq. (16.7) we have performed Taylor expansions up to first order in time and second order in space. Without those approximations we obtain, instead of Eq. (16.7),

$$N(x, y, t + T) - N(x, y, t) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} N_{\Delta} \phi_N d\Delta_x d\Delta_y - N(x, y, t) + R_T[N(x, y, t)], \quad (16.11)$$

where the joint effects of reproduction and survival are, again, well-described by the solution to a logistic growth function, namely [5]

$$R_T[N(x, y, t)] = \frac{e^{\alpha T} N_{max} N(x, y, t)}{N_{max} + (e^{\alpha T} - 1) N(x, y, t)}. \quad (16.12)$$

When observed dispersal data are used, the kernel *per unit length*  $\varphi_N(\Delta)$  is defined as the probability to disperse into a ring of radius  $\Delta$  and width  $d\Delta$ , divided by  $d\Delta$ . If individuals of the population  $N$  have probabilities  $p_j$  to disperse at distances  $r_j$  ( $j=1,2,\dots,M$ ), we can write

$$\varphi_N(\Delta) = \sum_{j=1}^M p_j \delta^{(1)}(r_j), \quad (16.13)$$

where  $\delta^{(1)}(r_j)$  is the 1D Dirac delta centered at  $r_j$  (i.e., a function that vanishes everywhere except at  $\Delta = r_j$ ). Since the total probability must be one,

$$1 = \int_0^{\infty} \varphi_N(\Delta) d\Delta, \quad (16.14)$$

and  $\varphi_N(\Delta)$  is clearly a probability *per unit length*. In contrast, the kernel  $\phi_N(\Delta_x, \Delta_y)$  in equation (16.11) is a probability *per unit area* (because it is multiplied by  $d\Delta_x d\Delta_y$ , which has units of area). The normalization condition for  $\phi_N(\Delta_x, \Delta_y)$  is therefore

$$1 = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_N(\Delta_x, \Delta_y) d\Delta_x d\Delta_y = 2\pi \int_0^{\infty} \varphi_N(\Delta) \Delta d\Delta, \quad (16.15)$$

where we have used polar coordinates  $\Delta = \sqrt{\Delta_x^2 + \Delta_y^2}$ ,  $\theta = \tan^{-1} \frac{\Delta_y}{\Delta_x}$  and assumed the kernel is isotropic,  $\phi_N(\Delta_x, \Delta_y) = \phi_N(\Delta)$ . Comparing equations (16.14) and (16.15), we see that the dispersal

probability per unit length (i.e., into a ring of area  $2\pi\Delta d\Delta$ )  $\varphi_N(\Delta)$  is related to that per unit area  $\phi_N(\Delta)$  as [15]

$$\varphi_N(\Delta) = 2\pi\Delta \phi_N(\Delta) \quad (16.16)$$

and equation (16.13) yields

$$\phi_N(\Delta) = \sum_{j=1}^M p_j \frac{\delta^{(1)}(r_j)}{2\pi\Delta}. \quad (16.17)$$

For homogeneous parameter values, the speed will not depend on direction and can thus be more easily computed along the  $x$ -axis ( $y = 0$ ). Consider a coordinate frame  $z = x - vt$  moving with the wave of advance ( $v$  is the front speed). The population density of farmers will be equal to its saturation density in regions where the Neolithic transition is over, and it will decay to zero in regions where few farmers have arrived. Thus we assume as usual the *ansatz* [15]  $N(x, y, t) \approx N_0 \exp[-\lambda z] \rightarrow 0$  for  $z \rightarrow \infty$  (with  $\lambda > 0$ ). Then, assuming that the minimum speed is that of the front (which has been verified by numerical simulations), we obtain for the speed  $v$  of front solutions to Eq. (16.11)

$$v_{NCohab} = \min_{\lambda > 0} \frac{\ln[(e^{\alpha T} - 1) \sum_{j=1}^M p_j I_0(\lambda r_j)]}{T\lambda}, \quad (16.18)$$

where the sub index *NCohab* indicates that this is *not* a cohabitation model (see the next section), and  $I_0(\lambda r_j)$  is the modified Bessel function of the first kind and order zero. In this model, the speed can be found by plotting the fraction in Eq. (16.18) as a function of  $\lambda$  and finding its minimum.

In Ref. [11] it has been shown that the differences in the front speed obtained from Eq. (16.13) and Fisher's approximation, Eq. (16.1), are up to 49% for human populations. So the effect of higher-order terms is not negligible.

### 16.3 Second improvement: cohabitation equations

For human populations, newborn children cannot survive on their own. However, when they come on age they can move away from their parents. This point has led some authors to use an equation of the so-called cohabitation type, namely

$$N(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} R_T[N_\Delta] \phi_N d\Delta_x d\Delta_y, \quad (16.19)$$

where  $R_T[N]$  is again given by Eq. (16.12). Then the speed of front solutions is [17,11]

$$v_{Cohab} = \min_{\lambda > 0} \frac{\alpha T + \ln[\sum_{j=1}^M p_j I_0(\lambda r_j)]}{T\lambda}. \quad (16.20)$$



The reason why Eq. (16.19) is more reasonable than Eq. (16.11) is that, clearly, Eq. (16.11) assumes that individuals born at  $(x, y)$  at time  $t$  (last-but-one term) will not move at all, i.e. they will all still be at  $(x, y)$  on coming of age (time  $t + T$ , left-hand side). Thus, for example, in the simple case in which all parents move, they will leave all of their children alone. Such an anthropologically unrealistic feature makes it clear that Eq. (16.11) is less accurate than Eq. (16.19). For additional derivations and figures showing that Eq. (16.11) is less realistic than the cohabitation Eq. (16.19), see especially Fig. 1 in Ref. [11], Fig. 17 in Ref. [15], and Ref. [17].

A more direct way to see the limitations of Fisher's speed (16.1) is to note that it yields  $v_{Fisher} \rightarrow \infty$  for  $\alpha \rightarrow \infty$ . In contrast, numerical simulations have shown that the cohabitation speed (16.20) yields for  $\alpha \rightarrow \infty$  the value  $v_{Cohab} = r_{max}/T$ , i.e. the maximum dispersal distance divided by the generation time [18,11], which is physically reasonable. Moreover, the error of Fisher's speed (16.1) relative to Eq. (16.20) reaches 30% for realistic human kernels and parameter values [11]. This error is still larger when cultural diffusion is included [1] (next section).

#### 16.4 Demic-cultural model

Up to now we have only considered equations with a single mechanism for the spread of the Neolithic, namely the dispersal of farmers (demic diffusion). But agriculture can be also learnt by hunter-gatherers (cultural diffusion). When this conversion of hunter-gatherers into farmers (cultural transmission) is taken into account, we might be tempted to generalize Eq. (16.19) into

$$N(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} R_T[N_{\Delta}] \phi_N d\Delta_x d\Delta_y + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} c[N_{\Delta}, P_{\Delta}] \phi_N^{converts} d\Delta_x d\Delta_y, \quad (16.21)$$

where  $P_{\Delta} = P(x + \Delta_x, y + \Delta_y)$ . The cultural transmission function  $c[\dots]$  in Eq. (16.21) is due to the conversion of hunter-gatherers into farmers. Thus a similar equation for the population density of hunter-gatherers  $P(x, y, t + T)$  could be proposed, with a minus sign in the last term. A recent derivation has found for the cultural transmission function  $c[\dots]$  (see Ref. [19], Eq. (1))

$$c[N(x, y, t), P(x, y, t)] = f \frac{N(x, y, t) P(x, y, t)}{N(x, y, t) + \gamma P(x, y, t)}, \quad (16.22)$$

where  $f$  and  $\gamma$  are cultural transmission parameters. The kernel  $\phi_N^{converts}(\Delta_x, \Delta_y)$  in Eq. (16.22) is the dispersal kernel of hunter-gatherers that have been converted into farmers. Since they now behave as farmers, let us assume that this kernel is the same as  $\phi_N(\Delta_x, \Delta_y)$ . Then Eq. (16.22) becomes

$$N(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} R_T[N_{\Delta}] \phi_N d\Delta_x d\Delta_y + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} f \frac{N_{\Delta} P_{\Delta}}{N_{\Delta} + \gamma P_{\Delta}} \phi_N d\Delta_x d\Delta_y. \quad (16.23)$$

A model of this kind was applied recently (see Eq. 5 in Ref. [19]). It is an approximation that may be valid in some regions (with mainly demic diffusion) but it cannot lead to a purely cultural model of Neolithic spread (because according to Eq. (16.23) there is no front propagation in the absence of demic diffusion, i.e. for  $\phi_N(\Delta_x, \Delta_y) \neq 0$  only at vanishing distance, i.e. for  $\Delta = (\Delta_x^2 + \Delta_y^2)^{1/2} = 0$ ). Thus we will here consider a more realistic model in two ways. Firstly we take into account that, according to ethnographic observations, hunter-gatherers can learn agriculture from farmers located some distance away [1]. Then Eq. (16.23) is generalized into

$$N(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} R_T[N_\Delta] \phi_N d\Delta_x d\Delta_y + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_N d\Delta_x d\Delta_y \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi'_P d\Delta'_x d\Delta'_y f \frac{N_{\Delta+\Delta'} P_\Delta}{N_{\Delta+\Delta'} + \gamma P_\Delta}, \quad (16.24)$$

where  $N_{\Delta+\Delta'}$  stands for  $N(x+\Delta_x + \Delta'_x, y + \Delta_y + \Delta'_y, t)$ .

In practice, the cultural kernel  $\phi'_P(\Delta'_x, \Delta'_y)$  (which is abbreviated as  $\phi'_P$  in Eq. (16.24)) is a set of probabilities  $P_k$  for hunter-gatherers to learn agriculture from farmers living at distances  $R_k = (\Delta'^2_x + \Delta'^2_y)^{1/2}$ , during a generation time  $T$ . This is similar to the fact, mentioned above Eq. (16.13), that in practice the demic kernel  $\phi_N(\Delta_x, \Delta_y)$  is a set of probabilities  $p_j$  for farmers to disperse at distances  $r_j = (\Delta^2_x + \Delta^2_y)^{1/2}$ , also during a generation time  $T$ .

Secondly we note that after a generation time  $T$ , reproduction will have led to new individuals not only in the population of farmers (first line in Eq. (16.24)) but also in the population of hunter-gatherers converted into farmers (second line in Eq. (16.24)). Thus we finally generalize Eq. (16.24) into

$$N(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} R_T[N_\Delta] \phi_N d\Delta_x d\Delta_y + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_N d\Delta_x d\Delta_y \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi'_P d\Delta'_x d\Delta'_y R_T \left[ f \frac{N_{\Delta+\Delta'} P_\Delta}{N_{\Delta+\Delta'} + \gamma P_\Delta} \right]. \quad (16.25)$$

The speed of front solutions to Eq. (16.25) is [1]

$$v = \min_{\lambda > 0} \frac{\alpha T + \ln \left[ \left( \sum_{j=1}^M p_j I_0(\lambda r_j) \right) \left( 1 + C \left[ \sum_{k=1}^Q P_k I_0(\lambda R_k) \right] \right) \right]}{T\lambda}, \quad (16.26)$$

with  $C = f/\gamma$ . This reduced parameter  $C$  was called the intensity of cultural transmission [19] because, according to Eq. (16.22),  $C = f/\gamma$  is the number of hunter-gatherers converted per farmer at the front leading edge (i.e. in regions such that  $N \ll P$ ). Without cultural transmission ( $C = 0$ ), the demic-cultural front speed, given by Eq. (16.26), reduces to the purely-demic speed, Eq. (16.20), as it should. With frequency-dependent cultural transmission, Eq. (16.22) is more complicated and the equations are longer, but the final results are exactly the same [1].

It is important to note that cultural transmission (the factor in brackets  $[f \dots]$  at the end of the second line in Eq. (16.25)) is applied in a term that also contains the effects of net reproduction ( $R_T$ ) and dispersal (the kernel of farmers  $\phi_N(\Delta_x, \Delta_y)$ ). Thus some hunter-gatherers will learn agriculture from farmers located a distance  $(\Delta'_x, \Delta'_y)$ , and the children of those converted hunter-gatherers will possibly move a distance  $(\Delta_x, \Delta_y)$  (similarly to the children of farmers, first line). Therefore, some hunter-gatherers can learn agriculture from farmers and the next generation (i.e., the children) of those hunter-gatherers will be farmers. Such a conversion during a generation time is reported by ethnographic data [20] and implies that the individual acculturation process is not instantaneous but takes place within one generation time, which seems reasonable for a complex cultural trait as farming.

Finally, a purely cultural model means no demic diffusion. In this model, the front speed can be obtained from Eq. (16.26) without demic diffusion ( $r_1 = 0$  and  $p_1 = 1$ ), namely

$$v_C = \min_{\lambda > 0} \frac{\alpha T + \ln \left[ 1 + C \left( \sum_{k=1}^Q P_k I_0(\lambda R_k) \right) \right]}{T\lambda}, \quad (16.27)$$

where the sub index  $C$  stands for purely cultural diffusion. This is the purely cultural analogue to the purely demic speed given by Eq. (16.20). Both of them are, of course, cohabitation models.

## 16.5 Demic versus cultural diffusion in the spread of the Neolithic in Europe

What do the models above imply for the relative importance of demic and cultural diffusion in the spread of the Neolithic in different regions of Europe? Let us summarize a recent proposal [1], which is based on using the following realistic ranges for the parameters appearing in our equations.

The ranges for  $a_N$  and  $T$  that have been measured for preindustrial farming populations are  $0.023 \text{ yr}^{-1} \leq a_N \leq 0.033 \text{ yr}^{-1}$  and  $29 \text{ yr} \leq T \leq 35 \text{ yr}$  (see the *SI Appendix* to Ref. [19] for details).

The following 5 dispersal kernels  $\phi_N(\Delta_x, \Delta_y)$  have been measured for preindustrial farming populations [11]. For each kernel we also give its purely demic speed range, as predicted by the cohabitation model, Eq. (16.20), with  $a_N = 0.023 \text{ yr}^{-1}$  and  $T = 35 \text{ yr}$  (slowest speed) or  $a_N = 0.033 \text{ yr}^{-1}$  and  $T = 29 \text{ yr}$  (fastest speed).

Population A (Gilishi 15)): purely demic speed range 0.87-1.15 km/yr.

Population B (Gilishi 25): purely demic speed range 0.92-1.21 km/yr.

Population C (Shiri 15) in Ref. (11): purely demic speed range 1.14-1.48 km/yr.

Population D (Yanomamö) in Ref. (11): purely demic speed range 1.12-1.48 km/yr.

Population E (Issongos) in Ref. (11): purely demic speed range 0.68-0.92 km/yr.

We see that demic diffusion predicts Neolithic front speeds of at least 0.68 km/yr. Demic-cultural diffusion will be still faster. Thus it has been suggested that cultural diffusion is responsible for the Neolithic spread in regions with speeds below 0.68 km/yr [1]. For simplicity, let us consider purely cultural diffusion, Eq. (16.27), although a short-range demic kernel can be also included (Sec. S6 in Ref. [1]). In order to estimate the speeds predicted by purely cultural diffusion, we need the following cultural parameters.

The cultural transmission intensity  $C$  from hunter-gathering to farming has been estimated from several case studies in Ref. [19] and the overall range is  $1.0 \leq C \leq 10.9$ .

The following 5 cultural kernels have been estimated from distances from hunter-gatherers camp locations to the villages of farmers, where the hunter-gatherers practice agriculture [1]. For each kernel, we also report the purely-cultural speed range obtained from Eq. (16.27) with  $a_N = 0.023 \text{ yr}^{-1}$ ,  $T = 35 \text{ yr}$  and  $C = 1$  (slowest speed) or  $a_N = 0.033 \text{ yr}^{-1}$ ,  $T = 29 \text{ yr}$  and  $C = 10.9$  (fastest speed).

Population 1 (Mbuti, band I): speed range 0.17-0.36 km/y.

Population 2 (Mbuti, band II): speed range 0.30-0.57 km/y.

Population 3 (Mbuti, band III): speed range 0.32-0.66 km/y.

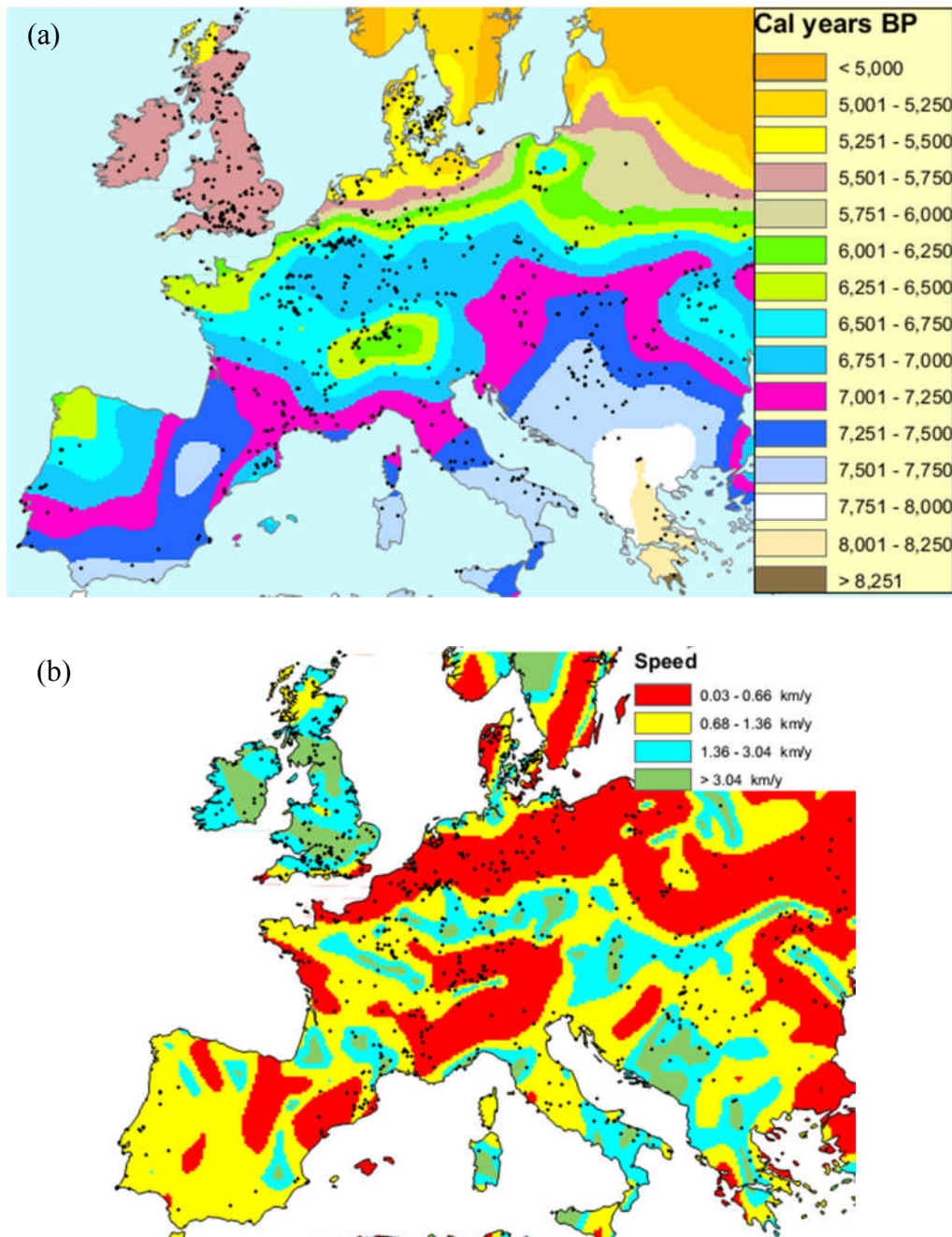
Population 4 (Aka): speed range 0.09-0.19 km/y.

Population 5 (Baka): speed range 0.03-0.07 km/y.

Thus the purely cultural model yields 0.03-0.66 km/y. Note that this is slower than the purely demic speed range found above (0.68-0.92 km/yr):

Finally, for the demic-cultural model, Eq. (16.26), the slowest speed is obviously 0.68 km/y (see the purely demic model above). The relevant result of the demic-cultural model is its fastest speed. This obviously corresponds to the strongest value observed for the intensity of cultural transmission

( $C = 10.9$ ), the fastest cultural kernel (population 3), the fastest demic kernel (population C or D), the highest observed value of  $a_N$  ( $0.033 \text{ y}^{-1}$ ) and the lowest observed value of  $T$  ( $29 \text{ y}$ ). Using these data in Eq. (16.25) we find that the fastest speed is obtained for the demic kernel of population D yielding  $3.04 \text{ km/y}$ .



**Fig. 16.4.** Isochrones obtained by smoothing 40 times the map in Fig. 16.1 (a). Note that most anomalously old/recent areas have been disappeared. Smoothing 60 times yields almost the same map. (b) displays the speed ranges obtained from (a). Closer isochrones correspond to slower speeds. Adapted from Ref. [1], Supp. Info. Appendix, Fig. S4.

In Fig. 16.4.b, the color scale has been chosen so that the red color corresponds to the regions of purely cultural diffusion ( $0.03\text{-}0.66 \text{ km/y}$ , from the purely cultural model above). The demic and

demic-cultural models predict speeds above 0.68 km/y, and are thus too fast to be consistent with the archeological data in the red regions in Fig. 16.4.b. This suggests that cultural diffusion explains the Neolithic transition in Northern Europe, as well as in the Alps and west of the Black Sea. The analysis of the areas where demic diffusion played a role is less straightforward, but it is possible to determine the regions where the speed was *mainly* demic (i.e. where the cultural effect was < 50%) [1]. They correspond to the yellow regions in Fig. 16.4.b. The regions where either demic or cultural diffusion could have dominated are the blue regions in Fig. 16.4 b. The blue regions appear because we have used parameter ranges and several kernels (they would not appear if we had used a single value for each parameter, a single demic kernel, and a single cultural kernel). Finally, in the green regions in Fig. 16.4 the speed is too fast to agree with any of the three models in the present paper, but in continental Europe those regions contain very few sites and will probably disappear using more complete databases (i.e., with more archeological sites).

## 16.6 Conclusions

The models reviewed in this chapter suggest that the spread of the Neolithic in Europe was: (i) fast and mainly demic in the Balkans and Central Europe; (ii) slow and mainly cultural in Northern Europe, the Alpine region and west of the Black Sea (Fig. 16.4.b) [1].

As seen in Fig. 16.4.b, the process was fast (speeds above 0.68 km/y) in Greece, Italy, the Balkans, Hungary, Slovakia, Czechia and central Germany. This wide region includes a substantial part of the Linearbandkeramic (LBK) culture in Central Europe. This is in agreement with the fact that the LBK is widely regarded as demic by archeologists. Also in agreement with our results, some archeologists have argued for the importance of demic diffusion in the Neolithic spread from the Aegean northwards and across the Balkans. On the other hand, our models suggest that farming populations did not spread much into Northern Europe, the Alps and West of the Black Sea (red color in Fig. 16.4.b). In such regions, the transition was slow (speeds below 0.66 km/y) and, according to our models, not driven by demic or demic-cultural diffusion. Some archeologists have previously suggested that cultural diffusion had a strong role in the spread of the Neolithic in Northern Europe, the Alps and West of the Black sea. Note that these are precisely the mainly cultural diffusion regions according to our models (red color in Fig. 16.4.b). For detailed archeological references on the importance of demic and cultural diffusion in different regions of Europe see, e.g., Sec. 3 in Ref. [1]. Ancient genetics also indicates that cultural diffusion was more important in Northern Europe [22], in agreement with our conclusions.

The slowness of cultural diffusion (as compared to demic diffusion) is due to the fact that, according to ethnographic observations, the distances appearing in the cultural kernel  $\phi'_P(\Delta'_x, \Delta'_y)$  are substantially shorter than those appearing in the demic kernel  $\phi_N(\Delta_x, \Delta_y)$  [1]. The intuitive reason may be that that agriculture is a difficult cultural trait to learn, and this leads to short cultural than demic diffusion distances. Note that the cultural distances are defined as those separating hunter-gatherers from the farmers who teach them how to farm. Indeed, according to ethnographic data, in the spread of farming cultural diffusion distances were short as compared to demic diffusion distances [1]. The latter are those along which the children of farmers disperse away from their parents. Such demic distances can obviously be larger than cultural distances, because the children of farmers have already learnt agriculture before leaving their parents.

Models similar to those summarized here have been applied to Paleolithic waves of advance [23], the extremely fast spread of the Neolithic in the Western Mediterranean [24], language substitution fronts [25], etc.

All models considered in this chapter operate with a minimum of parameters. Parameters in the demic model are, for instance, only the initial growth rate  $\alpha$ , the generation  $T$  and the dispersal kernel which, in addition, have been estimated from ethnographic or archeological data. With such constraints one is able to largely avoid any unjustified bias in modeling which may easily occur by the use of too many parameters which, finally, degenerate to simple fitting parameters. For example, in some models of virus infection fronts, it was possible to reproduce the experimental front speeds if choosing several parameter values [26-27]. However, this was not possible for realistic parameter values [27-28]. Later, more refined models reproduced the data without choosing any parameter values [29]. We have to be aware, however, that one may quite reasonably introduce much larger parameter sets as demonstrated in Chapter 17. However, their values (see the caption to table 17.2) become questionable with the lack of possibilities for their determination from reliable, independent sources. Optimum strategies will notably change with changes in data accessibility and in the course of exchange between the scientists in the various disciplines involved in the problem.

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