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Tendencies in the Tempo of Prehistoric Agricultural Expansions

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Abstract

This paper reviews the data and some models of premodern farming expansions. Comparison of archaeological data and models makes it possible to estimate the relative importance of demic and cultural diffusion, as well as the number of hunter-gatherers that were incorporated in the populations of early farmers per farmer and generation. At continental and large scales, most inland spread rates around the world were about 1 km/year and driven mainly by demic diffusion. However, the 1 km/year general rate is an average, which is useful as a metric that can be contrasted with the regional variation to understand the processes that sped or slowed expansion. At regional scales, estimations of spread rates performed so far refer to the Neolithic in Europe and Anatolia, the areas from which more radiocarbon dates are available. Along the inland European route, early farmers found increasing densities of hunter-gatherers and the wave of advance slowed down. Competition for space explains this slowdown reasonably well. In contrast, along the western Mediterranean, the expansion was extremely fast and can be explained by very long dispersal distances, about 300 km per generation. Other factors such as non-isotropic dispersal, mountains, soils, climate, diseases, etc. could have also affected spread rates.

Keywords Spread rates · Agricultural expansions · Demic diffusion · Cultural diffusion

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Introduction

Current work on geographical expansions of farming and herding in prehistory is totally based on the method of radiocarbon dating, originally developed by W. F. Libby and colleagues (Arnold and Libby 1949). The superiority of the accuracy offered by radiocarbon dating is clear from the fact that it yields dates for the Neolithic in most regions that are 1,000 to 3,000 years older than those estimated by means of previous methods (Clark 1965; Renfrew 1973). In his major work on the spread of the Neolithic, Gordon Childe (1957, p xiii) stressed that in about a decade since its discovery, radiocarbon dating had "indeed vindicated the Orient's priority over Europe in farming." Similarly, Colin Renfrew (1973) remarked that radiocarbon dating led to the surprise that the earliest farmers in the Old World were not those from Egypt but from the Near East. Clark (1965) selected 86 early farming sites from southwest Asia, Europe and Africa (the oldest ones for each region), divided them in three periods, and prepared the first map that clearly displayed a gradual spread of the Neolithic from the Near East across Europe. Ammerman and Cavalli-Sforza (1971, 1984) performed linear regressions of distances and dates of early farming sites and obtained the first statistically sound spread rate for the Neolithic in Europe, about 1 km/year. Besides Europe, agriculture appeared at several areas of the world and its range often expanded throughout huge regions (Bellwood 2005; Larson et al. 2014). In farming expansions, the 'wave of advance' or 'front' is defined as the line that separates (at a given time) the regions where agriculture is present from those where it has not yet arrived. The distance moved by such a wave of advance per unit time is called the spread rate and is measured in km/year.

The study of spread rates (also called front speeds) has several motivations. The first one is a general scientific curiosity to understand physical, ecological, biological, and social phenomena. The speeds of combustion flames, biological invasions, epidemics, cultural expansions, etc., can be described by similar mathematical models. In spite of the huge differences between such systems, in all of them it is appealing to apply quantitative methods in order to understand the observed values of the front speeds. Thus, the aims of this first motivation are to measure front speeds and to explain why they have their observed values and not other ones.

A cultural trait (e.g., agriculture) may expand its geographic range via demic and/or cultural diffusion (Cavalli-Sforza 1971). Under demic diffusion, the trait spreads due to the dispersal and reproduction of individuals with the cultural trait considered. In contrast, under cultural diffusion the range expands due to the transmission of the cultural trait to individuals of another population that was previously present in the region considered. In general, both demic and cultural diffusion can play a role. A second motivation to analyze prehistoric agricultural expansions is that the spread rates are related not only to the dispersal and reproductive behavior of farmers (demic diffusion), but also to the degree of incorporation of hunter-gatherers (cultural diffusion) already inhabiting the regions in which agriculture spreads. In fact, this was the original motivation to analyze the spread rate of the Neolithic in Europe. Indeed, the discovery by Ammerman and Cavalli-Sforza that the spread rate was about 1 km/year (using archaeological data) was an important reason for them to propose that the incorporation of hunter-gatherers had probably been of little importance (in disagreement with the beliefs of most archaeologists at the time). The rationale behind their proposal was that when they used reproduction and mobility parameters of farmers (obtained from ethnographic data) into a mathematical, purely demic model, they obtained a spread rate of about 1 km/year, i.e., similar to the value estimated from archaeological data (Ammerman and Cavalli-Sforza 1973, 1984; Cavalli-Sforza 1971).

A third motivation is that in some cases, measuring the spread rates of farming expansions makes it possible to infer aspects of human behavior that have not been estimated by other means. A very clear example is the following. The measurement of the spread rate of the Neolithic along the western Mediterranean has made it possible to estimate that the mean distances moved per generation by early farmers were about 300 km (Fort 2022b; Isern et al. 2017a). In this context, a generation is the average age difference between a person and one of her/his children, about 32 years according to ethnographic data of preindustrial farmers (Fort et al. 2004a). Another example is that the observed slowdown of the Neolithic along the inland route of Europe can be explained quantitatively by assuming that farmers and hunter-gatherers competed for the available space. A third example is the suggestion by some authors that some fast inland rates can be explained by nonisotropic dispersal (i.e., that pioneering farmers are more likely to migrate in directions closer to that of the front propagation). The present paper reviews those and other examples that make it possible to link the tempo of ancient farming expansions to the behavior of the individuals of the populations involved.

Finally, a fourth motivation is that once the average spread rate of an agricultural expansion is known, measuring faster or slower speeds in different specific regions may be of interest to try to understand processes that speed up or slow down the expansion. Two relevant aspects have been already mentioned above: the incorporation of hunter-gatherers speeds up the front, and the competition for space between farmers and hunter-gatherers slows down the expansion. Other factors that may decrease or increase spread rates are diseases, geographical features (e.g., coasts, mountains, rivers etc.), latitude (mainly via insolation), soils, climate, etc. At present such effects are poorly known for most agricultural expansions but some results are already available, as reviewed below.

For the purely demic case, the spread rate is related to the population behavior (dispersal and reproduction) according to well-known mathematical models. The first such model was proposed by Fisher (1937) and Kolmogorov et al. (1937). Later several improvements were introduced with the aim to obtain more realistic descriptions, e.g., to take into account the cohabitation between parents and their children. Twenty years ago, it was suggested explicitly that the analysis of agricultural spread rates could make it possible to distinguish between demic and cultural diffusion (Cavalli-Sforza 2003). In the last decade this proposal by Cavalli-Sforza has been formalized by means of new mathematical models that include not only demic diffusion but also cultural diffusion (Fort 2011, 2012, 2021a). All of those models are based on cultural transmission theory (Cavalli-Sforza and Feldman 1981). For a recent review on mathematical models, see Fort (2023). The present paper focuses on the archaeological aspects and refrains from explaining the details of the most elaborate mathematical models.

Besides the Neolithic in Europe, since year 2014 the spread rates of other expansions of agriculture and/or stockbreeding have been estimated from archaeological data. This review collects the spread rates estimated by many authors and summarizes the possible tendencies that have been detected in recent years (Fort 2021b, 2022a, 2023). The present paper pays particular attention on how knowledge of spread rates can provide information about aspects of ancient human behavior, such as the mean distance moved per generation, the percentage of early farmers that interbred with hunter-gatherers, the competition for space between farmers and hunter-gatherers, etc. Spread rates for Paleolithic populations are substantially more uncertain due to the paucity of archaeological data available (Fort et al. 2004b) and will not be discussed in the present paper.

This review is organized as follows. The next section deals with average spread rates at continental and large scales. The following section is devoted to regional variations. The Discussion section surveys some of the models that attempt to understand the measured rates and to relate them to key features of human behavior. The Discussion section also deals with estimations of the relative importance of demic and cultural diffusion. The last section contains concluding remarks.

An Average Premodern Expansion Rate of 1 km/year

As explained above, Ammerman and Cavalli-Sforza (1971) were the first to estimate the spread rate of a premodern farming expansion using sound statistical methods. They obtained a rate of about 1 km/year. More recently, their methods and additional ones have been applied to many ancient agricultural expansions. Nowadays there are already enough results to reach some conclusions of general validity. This section proposes that prehistoric farming expansions tend to spread at about 1 km/year at the continental scale (or more generally, at sufficiently large scales within a continent). This proposal is supported by spread rates obtained from archaeological data in the following 12 examples, which come from many different regions of the world and are summarized in Table 1.

Example 1. The Neolithic Transition in Europe

At the start of the Holocene (about 12,000 years ago), in southwest Asia temperature and humidity rose abruptly. In the Fertile Crescent, plant species highly tolerant to the new conditions (such as wheat and barley) begun to be cultivated by hunter-gatherers. Similarly, the beginning of husbandry shows up in the form of the disproportionate kill-off of male caprines (Shennan 2018). After several thousand years, these and other plant and animal species had morphological traits indicative of domestication and formed the so-called Neolithic package that spread into Europe. This package included, among others, the plant species wheat, barley, lentils, peas, and

Table 1 Summary of premodern expansions of farming and/or herding. The spread rates are also plotted in Fig. 2.

Expansion	Location	Maximum distance (km)	Time interval (cal. year BP)	Spread rate (km/year)
CONTINENTAL AND LARGE SCALES				
1. Neolithic	Europe and Near East (Fig. 1)	4,500[a]	13,000[b]–5000	0.9–1.3
2. Neolithic	Iran to Indus Valley	2,800	8000–5000	0.6–1.3
3. Neolithic	India	1,400	5000–3000	1.7–1.9
4. Rice farming	East Asia (Fig. 3)	3,000[c]	7000–1000	0.7–1.3
5. Bantu - East	East Africa (Fig. 4)	1,300	3400–1400	0.5–1.5
6. Bantu - South	East Africa (Fig. 4)	2,800	3400–1400	1.3–2.5
7. Khoekhoe	Southwest Africa	1,600[d]	2200–1100	1.2–3.6
8. Saladoid-Barrancoid	South America	2,500	4600–3000	0.6–1.0
9. Incised-Punctate	South America	1,700	1600–800	1.1–2.7
10. Tupiguarani	South America	3,600	2400–1600	1.5–1.9
11. Una	South America	1,800	2400–1000	0.7–0.9
12. Rice farming	Japan	1,300	2800–900	1.6–2.5
REGIONAL SCALES FOR THE NEOLITHIC				
13. Balkans	Europe	400	8190–7940	1.2–2.1
14. Inland route	Europe (Figs. 1a and 5)	1,200	7750–5000	1.6 → 0.0[e]
15. Alps	Europe (Fig. 1a)	326	6750–5500	0.09–0.14
16. Galicia	Europe (Fig. 6)	242	6900–6200	0.26–0.29
17. Cantabrian region	Europe (Fig. 6)	115	7100–6600	0.11–0.23
18. Anatolia to Greece	Anatolia and Europe	1,100	10,200–7500	0.7–1.4
SEA TRAVEL				
19. Neolithic	West Mediterranean	3,200	7820–7400	7.5–10.6
20. Lapita	West Oceania	4,550	3550–2750	> 8

[a] 4,500 km for great circles and 5,100 km for shortest paths.

[b] From Fig. 1b. This value would be 9000 cal. year BP if we considered only PPNB/C sites in the Near East (see main text, example 1).

[c] 3,000 km for great circles and 4,000 km for shortest paths.

[d] 1,600 km for great circles and 2,500 km for shortest paths.

[e] Gradual slowdown from the southeast (Balkans) to the northwest (northern Sea).

chickpeas (Charles 2007) and the animal species sheep, goats, pigs, and cattle (Dobney et al. 2013). Studies on ancient human genetics have recently pinpointed the origin of Early European Neolithic farmers in northern Mesopotamia, i.e., northern Syria, northwestern Iraq, and southeastern Anatolia (Altınışık et al. 2022; Lazaridis et al. 2022). From there, the Neolithic spread across Anatolia and Europe.

In agreement with the archaeological and genetic results summarized in the previous paragraph, the oldest European Neolithic sites are located in the southeast, from which the Neolithic spread gradually across Europe. Figure 1a is an interpolation map of the dates of Early Neolithic sites (black circles). The map in Fig. 1a was obtained by applying the universal linear kriging method. This method is widely recognized as the best one when there is a spatial trend in the data (in our case, the spread of farming from the southeast). Other methods such as polynomial surface interpolation (trend surfaces), natural neighbor, and ordinary circular kriging yield less detailed maps (Fort et al. 2012; Isern et al. 2012). Figure 1a shows clearly the spread from the southeast (lower right) westwards and northwards. Moreover, this map is useful to detect regional features. For example, slowdowns in the Alpine region and northern Europe appear as regions where the isochrones (i.e., lines separating contiguous colors in Fig. 1a) are closer to each other.

Quantitative estimations of spread rates have been performed since more than 50 years ago. As mentioned in the introduction, the first statistically reliable study was performed by Ammerman and Cavalli-Sforza (1971). They gathered dates for 53 sites and estimated the distance of each site as a great circle (i.e., the shortest distance between two points on the Earth if assumed a sphere) from the site that yielded the highest correlation coefficient r (Jericho). The maximum distances were about 4,300 km. They noted that according to statistical theory (Mather 1946), the regression of times versus distances should be preferred to that of distances versus times if distances did not have any error. However, distances are not exact due to several reasons (e.g., the presence of the Mediterranean Sea). For this reason, Ammerman and Cavalli-Sforza (1971) fitted a principal axis linear regression, which led to a spread rate of 1.0 km/year. The correlation coefficient r, which cannot be larger than 1, was rather high ($r = 0.89$) so a uniform spread rate is a reasonable approximation at the continental scale. However, they noted geographical variations such as a faster speed in the western Mediterranean and a slowing down in Scandinavia.

Decades after the seminal work by Ammerman and Cavalli-Sforza (1971), several studies collected larger databases and applied various statistical methods that led to similar results. Firstly, Gkiasta et al. (2003) performed a principal axis regression on the dates of 510 Early Neolithic sites and obtained a spread rate of about 1.3 km/year ($r = 0.73$) using great-circle distances relative to Jericho (this is not necessarily the origin with highest value of r for this database, because their aim was to compare with the results using the same origin as Ammerman and Cavalli Sforza in 1971). Similarly, Davison et al. (2007) combined the database by Gkiasta et al. (2003) with additional ones and obtained a speed of 1.1–1.3 km/year with 95% confidence level (CL) by regressing great-circle distances from Jericho versus dates ($r = 0.80$).

A database of 735 dates (the oldest one per site) gathered by R. Pinhasi yielded 0.9—1.1 km/year with 95% CL by regressing dates versus great circles (Fig. 1b).

The same database led to the range 1.1–1.3 km/year (also with 95% CL) by regressing dates versus shortest paths, i.e., paths taking into account the presence of the Mediterranean Sea (Pinhasi et al. 2005). The origin with highest value of r for each type of distance was used as presumed origin ($r = 0.82$ using calibrated dates, both for great circles and for shortest paths). The maximum distances were about 4,500 km for great circles and about 5,100 km for shortest paths, and the time interval from this database was 13,000–5000 cal. year BP (Fig. 1b). The corresponding overall range (0.9–1.3 km/year) is included in Fig. 2 (leftmost error bar) and Table 1.

A geostatistical analysis was performed by Bocquet-Appel et al. (2012), who used dates from 940 Early Neolithic sites and considered a grid of 2,220 squares (70 km × 70 km each) covering Europe. They used, for each square, the average of its two oldest Neolithic dates. They did not fit any linear regressions but applied the kriging interpolation technique (Bocquet-Appel et al. 2009) to obtain isochrone maps and local spread rates. The latter had an average spread rate of 1.1 km/year (Bocquet-Appel et al. 2012). This agrees well with the results from the linear regression technique, summarized above.

Spatial simulations of Neolithic spread with realistic parameter values showed that assuming a start for the spread from Jericho at its oldest Neolithic date (11,863 cal. year BP), the Neolithic package would have arrived to Europe about 2,000 years earlier than when it actually arrived (Fort et al. 2012). This inconsistency was solved as follows. The development of the Neolithic in the Near East was a slow process, with different innovations appearing at different places during several thousand years. Eventually, a homogeneous set of vegetal and animal domesticates (called the Neolithic package) was adopted in the prepottery Neolithic B/C (PPNB/C) cultures. It was from these cultures that the spread into Europe proceeded. When simulations were performed by assuming that the Neolithic package spread from the Near East at about 9000 cal. year BP (which is roughly the average date of the PPNB/C sites in the database used), simulations yielded reasonable arrival times in Europe. Using great-circle distances with origin at the oldest PPNB/C site (Hemar) and combining linear regressions of times versus distances and distances versus times using 903 Early Neolithic sites in Europe (gathered by M. vander Linden) and 16 PPNB/C sites, the spread rate was 0.5–1.3 km/year with 95% CL and $r = 0.7$ (Fort et al. 2012).

Baggaley et al. (2012a) introduced an innovative approach based on Bayesian inference and applied it to the dates of 302 Early Neolithic sites in Europe. They defined the ‘background’ spread rate as that unaffected by the enhanced propagation along coasts and rivers (see also Davison et al. 2006) and combined prior estimates of these three speeds with the archaeological dates. Depending on the number of parameters estimated and other model details, they obtained a background spread rate of about 1.2 km/year in Baggaley et al. (2012a), about 1.0 km/year (0.8–1.4 km/year with 95% CL) in Baggaley et al. (2012b), and again about 1.0 km/year (0.9–1.0 km/year with 95% CL) in Henderson et al. (2014). Their results are clearly consistent with those obtained by using more traditional statistical approaches (as summarized in the previous paragraphs).

In summary, the spread rate of the Neolithic in Europe has been estimated by many different authors and statistical approaches, and all them agree with the

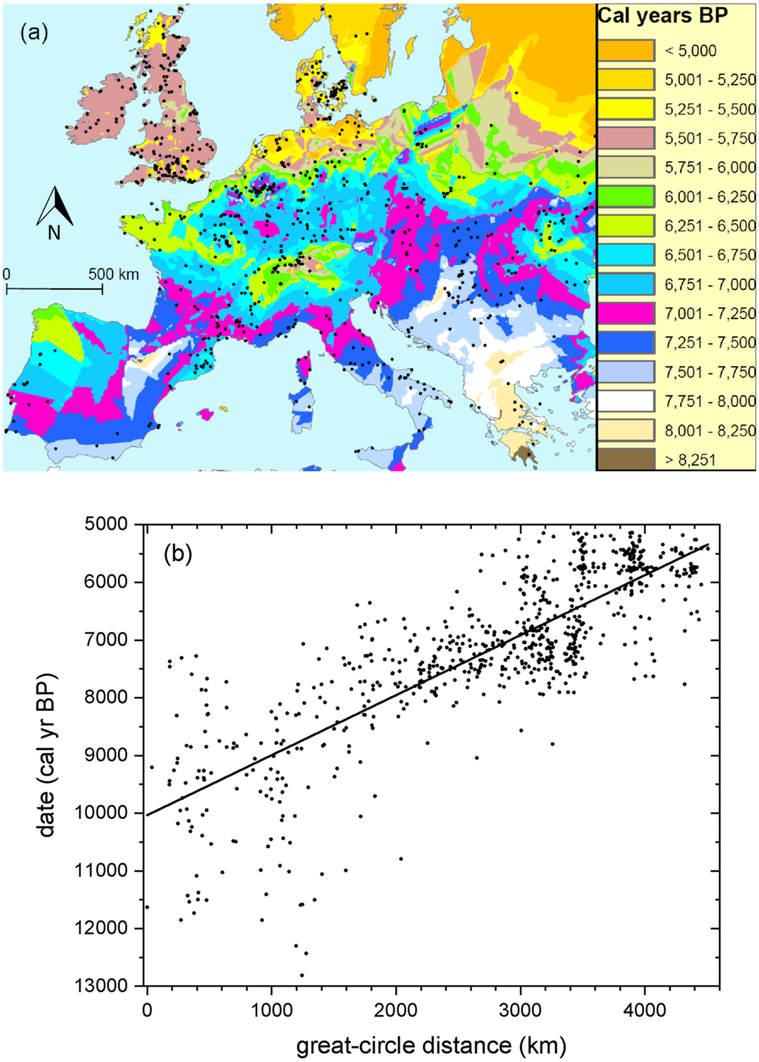

Fig. 1 (a) Interpolation map of the spread of the Neolithic in Europe. We can see the gradual spread from the southeast, as well as the slowdowns in the Alps and northern Europe. The database was collected by vander Linden (Supp. Info. to Fort et al. 2012). Modified from Fort (2015). (b) Linear regression of calibrated dates of sites in the Near East and Europe versus great-circle distances from the site that yields the highest value of the correlation coefficient *R*, namely $R = 0.82$. In fact, many sites in the Near East yield similar values of *R*. The spread rate (inverse of the slope) is 0.9–1.0 km/year. As explained in the main text, combining the ranges of the spread rate using great-circle and shortest-path distances leads to the overall range 0.9–1.3 km/year (shown as the leftmost error bar in Fig. 2). Modified from fig. 2c in Pinhasi et al. (2005).

tendency suggested in the title of this section, namely a spread rate of about 1 km/year. The next subsections consider other premodern expansions of farming and/or herding, in order to find out whether this tendency holds in general or not. The answer is affirmative, and this is important because it suggests that the parameter values used in mathematical models (e.g., Ammerman and Cavalli-Sforza 1973, 1984) are realistic. Moreover, it makes it possible to analyze regional variations and to understand the processes that could have sped or slowed expansion, as well as their implications in terms of human behavior (next section).

Examples 2 and 3. The Neolithic Transition in Southern Asia

The Neolithic spread from the Near East westwards across Europe, as described in the previous subsection, and also eastwards across southern Asia. The eastern wave of advance originated in the region of the Zagros Mountains, a huge mountainous area (about 1,500 km × 500 km) between the Caspian Sea and the Persian Gulf. This region was an independent center of agriculture, as shown by the cultivation of wild plants (barley, wheat, lentil, pea, etc.) during more than 2,000 years and their subsequent domestication in the Zagros. Domesticated emmer (a species of wheat) appeared at about 9800 cal. year BP (Riehl et al. 2013). A similar process unfolded with animals, with the beginning of goat management between 11,700 and 10,200 cal. year BP. The first domesticated sheep appeared in the region after 9000 cal. year BP (Zeder 2025). Recent studies on ancient human genetics have also concluded that

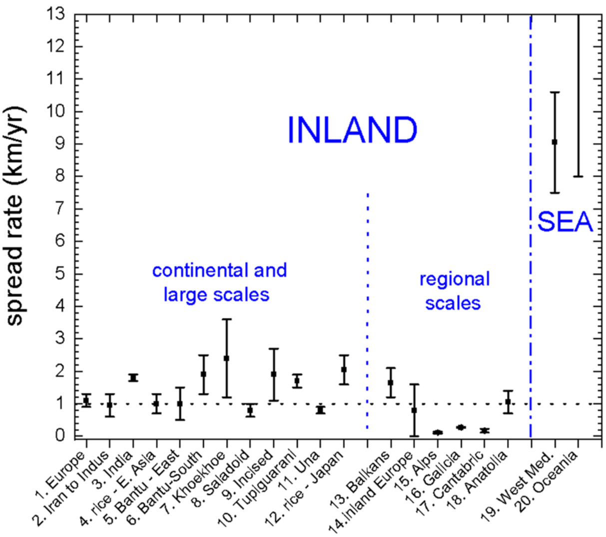

Fig. 2 Spread rates of farming and/or stockbreeding in several parts of the world. The horizontal axis displays a list of examples, and the error bars give their estimated spread rates. The horizontal dotted line corresponds to a spread rate of 1 km/year. The vertical dashed-dotted line separates the inland examples (left) from those involving sea travel (right). The inland examples are further subdivided by the vertical dotted line into the spread rates measured at continental or large scales (left of the dotted line) and the spread rates measured at regional scales (right of the dotted line). All values are also reported in Table 1. Figure created by the author.

the Zagros was the cradle of the eastern Neolithic spread into South Asia (Broushaki et al. 2016; Lazaridis et al. 2016).

The eastern Neolithic front spread mainly across Iran, Afghanistan, Pakistan, and India. An important difference between the western and eastern waves of advance is the following: in Europe there was neither farming nor herding until the Neolithic arrived. In contrast, in some regions of southern Asia (specially the eastern ones) farming and/or pastoralism were already established before the arrival of near eastern domesticates (mainly wheat and barley). For example, in the Deccan Plateau of southern India Early Neolithic sites have only local domesticates (millets and pulses) alongside cattle, sheep and goats. In contrast, later sites also include wheat and barley (de Souza et al. 2022).

Gangal et al. (2014) were the first to analyze the eastern spread quantitatively. They compiled a database with radiocarbon dates from 160 Early Neolithic sites and archaeological age determinations for 229 sites. For any given distance range, the ages of the corresponding sites displayed a lot of variation (up to 6,000 years), so Gangal et al. (2014) grouped data into distance bins and assigned a larger weight to older dates in each bin. This yielded for the propagation of the Neolithic across southern Asia, including the Indus Valley, an average spread rate of 0.6–0.7 km/year (with 95% CL and $r = 0.87$).

More recently de Souza et al. (2022) have gathered a database including only radiocarbon-dated sites of cultures or phases known to have cultivated crops of near eastern origin, such as barley or wheat (143 dates). They have tuned the spread rates in several terrain classes and used spatial simulations to obtain the best possible agreement between the arrival times of the simulated Neolithic wave of advance and the dates in their database. In this way, they have obtained speeds in the range 0.6–1.3 km/year for the spread across Iran, Afghanistan, Pakistan, and the Indus Valley (with an overall distance of approximately 2,800 km and the time interval 8000–5000 cal. year BP). Figure 2 and Table 1 include this speed range estimated by de Souza et al. (2022), namely 0.6–1.3 km/year (error bar 2). Note that it contains the range estimated by Gangal et al. (2014). On the other hand, in India (i.e., east of the Indus Valley) de Souza et al. (2022) have detected a faster spread rate (1.7–1.9 km/year), which is also plotted in Fig. 2 (error bar 3) and is clearly visible in their isochrone map (the distance covered in India is about 1,400 km and the corresponding time interval is 5000–3000 cal. year BP; both of them are included in Table 1). De Souza et al. (2022) have suggested that this enhanced rate could be due to the fact that, as explained above, local domestication was already established in parts of India and this could have led to a more rapid cultural acquisition of the domesticates from the Near East. Possible reasons leading to fast spread rates are discussed in detail in a separate section below. The spread of farming in the Indian subcontinent had been previously simulated by Patterson et al. (2010), who noted the inaccuracy of the data available at the time and developed a model that allows for the survival of foragers in regions where environmental conditions do not favor agriculture.

For the spread of the Neolithic in southern Asia, the issue of the origin of distances deserves a detailed explanation. Gangal et al. (2014) used the site of Gesher (one of the earliest Neolithic sites in the Jordan Valley) as the origin of distances because it led to the highest value of the correlation coefficient. On the other hand, de Souza et al. (2022) used the site of Mureybet (Syria) and, alternatively, that of Dhra (Jordan), as the origin of distances because early cereal cultivation has been reported at both sites. However, as reviewed in the first paragraph above of this subsection, both archaeology and ancient genetics have independently concluded that the eastern Neolithic wave of advance begun at the Zagros. This makes it difficult to justify the start location for the spread (i.e., the origin of distances) in any of these three sites (Gesher, Mureybet, and Dhra), because all of them are located substantially to the west of the Zagros. Indeed, the distances from any of the three sites mentioned above (Gesher, Mureybet, and Dhra) to Ghogha Golan are between 800 km and 1,000 km. These considerations do not invalidate the important work by Gangal et al. (2014) and de Souza et al. (2022) because the origin of distances does not affect the interpolation maps and is unlikely to change the main conclusions from their linear regressions. However, future studies on the spread of the Neolithic in southern Asia will probably yield more accurate spread rates if they use distance origins in the Zagros.

Example 4. The Spread of Domesticated Rice in Eastern Asia

In contrast with Europe, where wheat and barley were the most important Neolithic crops, in the transition from hunting-gathering to farming in eastern, southeastern, and southern Asia, rice was the main staple cereal (Fuller 2011). Millet, another important crop, was domesticated in northern regions rather than rice. Five different regions of northern China have been proposed as possible independent origins of millet cultivation and domestication, and three regions in the Yangtze Basin have been considered as separate homelands of rice domestication (Stevens and Fuller 2017). The identification of domesticated crops is usually based on the analysis of charred archaeobotanical evidence. The evolution of wild rice into domesticated rice is well-documented for the Lower Yangtze, where the proportion of domesticated (nonshattering) rice spikelet bases shows a clear increase over time. In the same region there is a gradual trend of increasing grain size since about 8000 cal. year BP until about 7000 cal. year BP, which also tracks the process of rice domestication (fig. 2 in Stevens and Fuller 2017).

Silva et al. (2015, 2018) gathered a very useful database of ancient rice. They analyzed the combined data for predomesticated and domesticated rice and did not find any linear dependence for the arrival date of rice farming versus distance. The spread rate (in km/year) was estimated by Cobo et al. (2019) on the basis of the following considerations. Rice was fully domesticated after a millennium or more of predomestication cultivation (Fuller et al. 2007b, a). This process in eastern Asia is similar to the development of the Neolithic package in the Near East, in the following sense: As explained in the subsection above devoted to example 1, it took several thousand years for the Neolithic package of domesticates to develop in the Near East before the Neolithic begun to spread into Europe, and this implies that a linear dependence with reasonable arrival times in Europe can be found only by neglecting the older sites (which correspond to the formation of the Neolithic package, before it spread). Similarly, archaeological data suggest little or no spread of rice before domestication (Silva et al. 2015, 2018), hence Cobo et al. (2019) considered only the dates of domesticated rice (not those of predomesticated cultivated rice). This yielded a database of 331 dates (the oldest one per site) from which they obtained the interpolation map shown in Fig. 3. According to this map, the spread of domesticated rice took place between 7000 and 1000 cal. year BP (this is the range reported in Table 1 for the spread of rice farming in eastern Asia). In order to estimate the spread rate, Cobo et al. (2019) excluded India, Pakistan, and Sri Lanka because rice genomic data support an independent domestication of rice in this region and this agrees with the existence of very old dates in it (see Fig. 3). For similar reasons, they also excluded a few anomalously old sites in Laos, Cambodia, and near Hemudu in the Lower Yangtze. Finally, regions separated from the continent by very large sea distances were not included either because, as seen below, when sea travel was involved the spread rates can be substantially different. Using the resulting 185 sites, they performed a linear regression of dates versus distances relative to Chengtoushan, the oldest site (red square in China, upper right of Fig. 3) and found a spread rate of 0.7–0.9 km/year using great circles (95% CL, $r = 0.78$, distances up to about 3,000 km) and 1.0–1.3 km/year using shortest paths (95% CL, $r = 0.82$, distances up to about 4,000 km). Thus Fig. 2 includes the overall range 0.7–1.3 km/year (error bar 4). These shortest paths were estimated by means of the free internet application google maps (https://www.google.com/maps), which finds out the shortest route and distance on foot between two points following present roads. Obviously, present roads have some modifications (bridges, tunnels, highways, etc.) relative to the routes used thousands of years ago. However, distances will be presumably similar because roads are very stable over long times. Moreover, roads take into account topographical and environmental factors that may affect human motion. Thus, distances along existing roads are considered as reasonable measures for shortest and most feasible routes (Glass et al. 1999; Whitley and Dorn, 1993, p. 647). They are probably realistic for large obstacles compared to the mean displacement per generation of farmers. In contrast, small obstacles are unlikely to deflect the individual displacements per generation, and thus the direction of spread of the wave of advance. Thus, it seems reasonable to regard such shortest-path distances as an upper bound and great-circle distances as a lower bound when comparing to mathematical models of waves of advance (Cobo et al. 2019).

Examples 5 and 6. Bantu Expansions

On the basis of archaeological and glottochronological data, it is believed that populations of farmers speaking Bantu languages spread from the Nigeria–Cameroon border area (west Africa) across most of subequatorial Africa, excluding the rainforest and southwestern Africa. These Bantu expansions transformed vast regions of Africa, originally inhabited by hunter-gatherers, into a continent of mainly farmers. They made pottery and cultivated oil palm and yams using stone tools (Vansina 1990) and dispersed eastwards and southwards some 5,000 years ago. Some authors attempted to calculate spread rates by using only two dates (Vansina 1990) or a few ones (Collet 1982). More accurate calculations became possible when Russell et al.

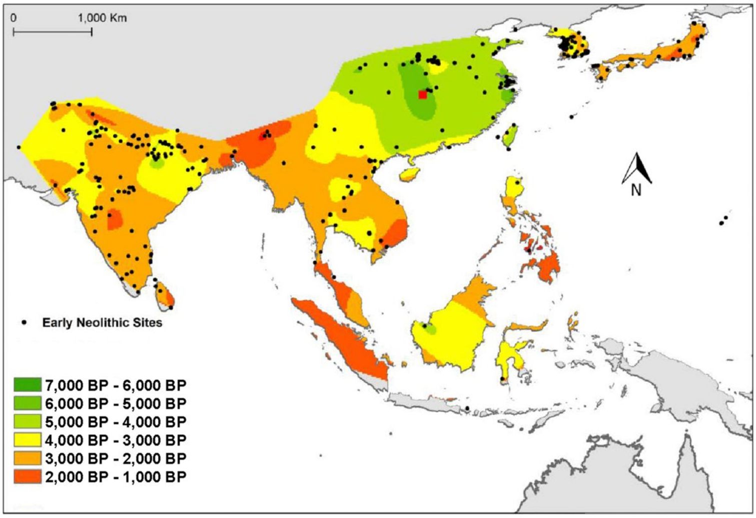

Fig. 3 Interpolation map of arrival times of domesticated rice in southern and southeastern Asia, obtained from the dates of 331 early sites (circles). The red square is the very old site of Chengoushan (Middle Yangtze, China, dated 6200 BP), from which Cobo et al. (2019) computed the distances to the other sites in order to estimate the spread rate. The result is 0.7–1.3 km/year and is shown as error bar 4 in Fig. 2(Color figure online). Modified from Cobo et al. (2019).

(2014) compiled an extensive database. There is no consensus for the paths followed during the western part of the spread, but there is agreement that the Bantu population eventually reached the great lakes area in southeastern Africa, from where they spread eastwards and southwards. In this region, agriculture was based not only on root and tree crops but also on cereals, combined with the raising of stock. It also introduced the first metallurgy, i.e., the Early Iron Age.

Using the database by Russell et al. (2014), Isern and Fort (2019) focused on eastern and southeastern Africa because it contains numerous and reliable enough archaeological dates so that spread rates can be estimated (see Fig. 4). In a first step, from the 70 original dates, six were excluded because they correspond to preBantu cultures and/or unreliable samples (due to possible disturbances, old-wood effects, etc.). The 64 remaining dates are shown in Fig. 4a. Linear regressions were computed by calculating great-circle distances under the assumption that each of the five oldest sites (diamonds in Fig. 4) were the origin of the spread. However, similarly to what happened in example 2 above, the data dispersion was huge (this is clearly seen in Fig. 4a) in the sense that for a given distance the dates varied by 2,000 years, so the correlation coefficient was moderate (e.g., $r = 0.65$ if choosing as origin Mubuga V, the oldest site). Thus, the second step was to exclude dates so late that they could not have corresponded to the earliest Bantu spread (i.e., dates later than 1350 cal. year BP) as well as those which are clearly later than the surrounding sites. This yielded a refined database of 31 'early spread' sites, shown in Fig. 4b, with dates in the range 3400–1400 cal. year BP. This is the range included in Table 1 for the Bantu expansions. It is clear from Fig. 4b that the spread was substantially slower eastwards (example 5) than southwards (example 6). For the eastern expansion ($N = 13$ sites), the maximum distance was about 1,300 km and Isern and Fort (2019) found a spread rate of 0.5–1.5 km/year (we have recomputed their 80% CL ranges with 95% CL) by combining the rates from the two oldest origins (Mubuga V, dated 3371 cal. year BP and Kabacusi, dated 2978 cal. year BP). These two origins yielded the highest correlation coefficients ($r = 0.84$ and $r = 0.79$, respectively). For the southern expansion ($N = 22$ sites), the maximum distance was about 2,800 km and the spread rate was 1.3–2.5 km/year (95% CL) by applying the same procedure ($r = 0.87$ and $r = 0.86$ for Mubuga V and Kabacusi, respectively). These ranges are included in Fig. 2 (error bars 5 and 6) and Table 1. The rate to the east is consistent with about 1 km/year (horizontal dotted line in Fig. 2) and that to the south is about twice faster (this will be discussed after summarizing other examples).

Example 7. The Spread of Khoekhoe Herders

In contrast with the Bantu farmers discussed in the previous subsection, the Khoekhoe were pastoralists that neither grew crops nor had any iron-working technology. They made pottery and reared domestic cattle, sheep, and goats. The Khoekhoe spread nonagricultural herding and their languages southwards across southwestern Africa, which was until then populated by hunter-gatherers. Archaeological evidence for the Khoekhoe expansion is meagre in comparison with that from the Bantu expansions (Sadr 2013). According to Russell (2004), in southern Africa rainfall is high in the east and low in the west and this is why farming expanded in the east (previous subsection) and herding in the west (this subsection).

Early attempts to measure the spread rate of the Khoekhoe expansion were inconclusive due to the scarcity and uncertainty of the data available at the time (Sadr 1998). Russell (2004) was the first to perform linear regressions of calibrated dates versus great-circle distances. She considered a specific domesticate (the African fat-tailed sheep), for which the data available spanned a distance of about 500 km. Later, Jerardino gathered a database that includes additional species, extends over about 1,600 km (using great-circle distances), and leads to faster spread rates (although the dates in the Jerardino and Russell databases are fully consistent). Jerardino et al. (2014) noted that most Khoekhoe sites are located near the coast, so we cannot guarantee that the wave of advance propagated across huge inland areas. Indeed, it has been proposed since long ago that herding spread southward along the western African coast and then eastwards. In fact, this affects only one site in the database used by Jerardino et al. (2014). By calculating its shortest-path distance, i.e., essentially its distance along the coast (about 2,500 km) from the oldest site in the database, Jerardino et al. (2014) obtained, after neglecting clearly late sites and considering only the oldest date per site ($N = 10$ sites), a spread rate in the range 1.2–3.6 km/year with 95% CL and $r = 0.85$ (in fact Jerardino et al. 2014 reported the 80% CL interval, but we have recomputed it with 95% CL). The overall time interval of this expansion is 2200–1100 cal. year BP. It is worth to note that according to Fig. 2, the Khoekhoe spread rate (error bar 7) is possibly the fastest one estimated so far for inland expansions although it is also the most uncertain one (i.e., it has the

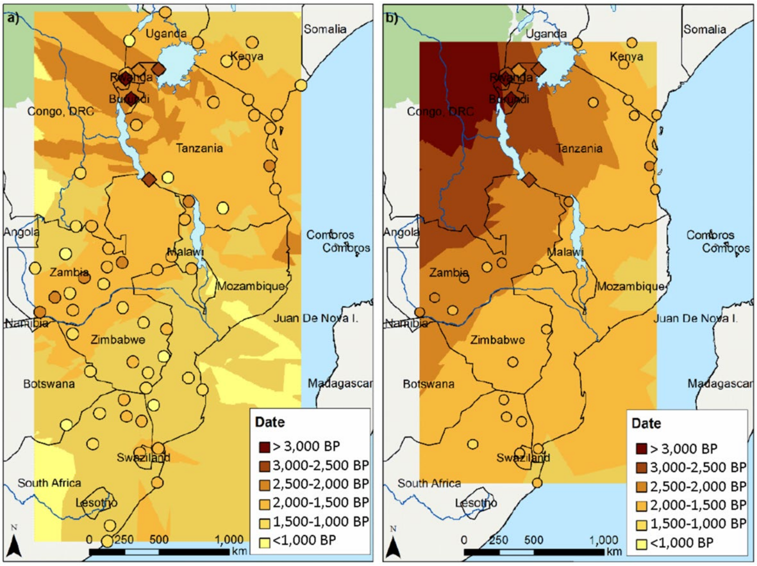

Fig. 4 Interpolation maps of the Bantu expansion in southeastern Africa. Panel (a) contains all 64 sites. Panel (b) contains only the 31 sites classified as 'early spread', which increase the correlation coefficients and make it possible to estimate spread rates. The three great lakes are, from north to south, Victoria, Tanganika, and Nyasa or Malawi. The five sites considered by Isern and Fort (2019) as possible origins of the spread, shown as diamonds, are from northeast to west and then south, Katuruka (Tanzania), Mucucu II (Rwanda), Kabacusi (Rwanda), Mubuga V (Burundi), and Kalambo Falls (Zambia–Tanzania border at the southern edge of lake Tanganika). Rainforest areas are shown on green background (upper left) and almost reach the three northwestern diamonds. The spread rate is 0.5–1.5 km/year for the eastern expansion and 1.3–2.5 km/year for the southern expansion. These ranges are shown as error bars 5 and 6 in Fig. 2, respectively(Color figure online). Modified from Isern and Fort (2019).

widest error bar). More detailed discussions on this result are included below (in the subsections on fast inland spread rates and the mainly demic character of prehistoric farming expansions).

Examples 8 to 11. Expansions of Farming Cultures in South America

America is a continent for which little work on spread rates of agriculture has been carried out so far. Therefore, the following four farming cultures in tropical South America are of utmost interest. The spread rates reported below were estimated by de Souza et al. (2020) using principal axis regressions and great circle distances. They also noted that these populations combined cultivation of domesticates with the management of other species in tropical forests.

The Saladoid-Barrancoid material culture begun its spread from the Orinoco at about 4600 cal. year BP, and it had expanded across most of the Amazon by about 3000 cal. year BP (Table 1). These farmers cultivated maize, manioc, yam, and other species. They expanded mostly over territories populated by hunter-gatherers, not by other farmers. For this culture de Souza et al. (2020) estimated the spread rate

0.6–1.0 km/year (95% CL), as shown in our Fig. 2 (error bar 8), over great-circle distances up to about 2,500 km ($r = 0.92$). They obtained this range, as well as those for the other three cultures discussed in the next paragraphs, by means of the following procedure. Due to the large variation in dates (for similar distances), sites were grouped in great-circle distance classes or bins (as also done by Gangal et al. 2014 in example 2 above). A major (or principal) axis regression was performed using the oldest site per bin with a date generated from its calibrated probability distribution. They performed 999 regressions and reported the 95% CL intervals for each of several likely origins. The bin width (between 100 and 500 km, with a minimum of five bins) and the site used as origin of distances were those leading to the highest value of the correlation coefficient.

The Incised-Punctate culture spread from the Orinoco at about 1600 cal. year BP, arriving at the Lower Amazon at about 800 cal. year BP (Table 1). These populations made a characteristic ceramic decoration and cultivated maize, manioc, and squash. They expanded over territories populated by other farmers. The spread rate was 1.1–2.7 km/year (95% CL) according to de Souza et al. (2020), who performed this estimation using great-circle distances up to about 1,700 km ($r = 0.91$, error bar 9 in our Fig. 2).

The Tupiguarani spread from about 2400 cal. year BP across the Amazon and beyond, reaching parts of Brazil and as far south as the pampas of Buenos Aires by about 1600 cal. year BP (Table 1). In spite of this huge geographical range, its pottery is remarkably homogeneous. They expanded over territories populated by hunter-gatherers outside the Amazon, but for the latest part of the expansion they also intruded into areas occupied by other farmers. They cultivated maize, beans, and other plants. From a linear regression up to distances of about 3,600 km, de Souza et al. (2020) estimated that the spread rate was 1.5–1.9 km/year (95% CL, $r = 0.82$, error bar 10 in our Fig. 2).

Unlike the three former cultures, all of which originated in the Amazon, the Una tradition spread farming and ceramics from a more southerly cradle in the Paraná and Sao Francisco headwaters at about 2400 cal. year BP, across the central Brazilian savanna until about 1000 cal. year BP (Table 1). They expanded mostly over territories populated by hunter-gatherers, not by other farmers. For this culture, de Souza et al. (2020) estimated a spread rate of 0.7–0.9 km with distances up to about 1,800 km (95% CL,$r = 0.93$, error bar 11 in our Fig. 2).

Example 12. The Spread of Rice Farming in Japan

In the Japanese islands, the arrival of rice farming marks the end of the Jomon period and the start of the Yayoi one. The Jomon economic system, which was based on hunting, fishing, and gathering, came to an end with the arrival of a cultural package that has yielded remains of farming tools, paddy fields, new pottery styles, characteristic burials and dwellings, etc. This cultural package came from the Korean peninsula and spread northwards across the Japanese archipelago (Mizoguchi 2013).

Very recently Crema et al. (2022) have focused on the spread of rice farming in Japan by compiling a database of radiocarbon dates on domesticated rice grains from 132 sites with dates in the time interval 2800–900 cal. year BP (Table 1). Note that this range is in agreement with the interpolation map in Fig. 3. Due to the fact that the arrival date of rice farming is the variable of interest to estimate the spread rate, Crema et al. (2022) applied quantile regression by using the 10% earliest dates. They also applied Bayesian techniques, with the aim to minimize the effect of a calibration plateau. According to Crema et al. (2022), this approach yields for the overall spread rate the range 1.6–2.5 km/year (90% CL) assuming that the dispersal begun at the site with the earliest date in their dataset. This range is included in our Fig. 2 (error bar 12) and Table 1. The distances are up to about 1,300 km. It is true that Bayesian techniques require the assumption of prior distributions with parameter values that may in principle have an effect on the results (see eqs. [5]–[7] below fig. S1 in Crema et al. 2022). However, the interesting point here is the fastness of the spread rather than its precise value. In this sense it is important to note that applying the usual, non-Bayesian quantile regression approach these authors obtained a still higher speed (fig. S1 in Crema et al. 2022). This agrees with their finding that the spread of rice farming in Japan was remarkably fast. Crema et al. (2022) also considered a model with nonuniform spread rates and obtained regional results that seem to depend strongly on the assumed values of several parameters (fig. S5 in Crema et al. 2022).

It is of considerable methodological interest to mention that Bayesian techniques are sometimes used to combine several dates (for example, of early farming sites in a given region) into an overall range (e.g., Perrin and Manen 2021). This is very useful to make qualitative comparisons between regions (as done by Perrin and Manen 2021) but not to estimate the arrival dates of farming in several regions and perform a linear regression (or other statistical analyses) to estimate the spread rate. The reason is that, in general, regional dates obtained by means of Bayesian approaches will yield a different spread rate than using the oldest date per region instead (for a specific example, see Sect. S1, point (18) in Fort 2022b).

All 12 examples above agree with our proposal that at continental or large scales, prehistoric farming expansions spread at speeds of about 1 km/year. This is clearly seen in Table 1 or, perhaps more clearly, in Fig. 2 because the error bars of the spread rates for examples 1 to 12 cluster around the value 1 km/year (horizontal dashed line in Fig. 2).

Regional Variations in the Spread Rate

Guilaine has proposed that the Neolithic advanced in Europe with punctual halts or pauses (Guilaine 2001, 2013, 2019), so that phases of rapid expansion took place between phases of rest. This is Guilaine's arrhythmic model, in which the phases of rest lead to profound cultural transformations. The arrhythmic model is not necessarily at odds with the wave of advance model due to Ammerman and Cavalli-Sforza because the latter can be a useful average of the arrhythmic, more detailed model (Fort 2022b). Indeed, Guilaine (2019) has remarked that Ammerman and Cavalli-Sforza (1971) realized from the beginning that the spread rate varied geographically. They introduced their uniform-rate model as a valid approximation at the continental scale, noting that the spread was faster in some regions and slower in others.

Rasse (2008) produced isochrone maps that show the existence of punctual decelerations in the spread rate. Some of them are located in regions where Guilaine (2013) noted periods of rest, namely central Anatolia, western Greece, the Middle Danube Basin, and the Northern European Plain. However, other regions of deceleration according to the isochrones by Rasse (Portugal, eastern Iberia, southern France, and northern Italy) are not among those proposed by Guilaine (2013). The work by Rasse (2008) is an interesting, qualitative approach that highlights the importance of the arrythmia. Similarly, Silva and vander Linden (2017) considered the polygon that contains all Neolithic sites for each 100 year interval and observed that the polygonal area increases during some periods but remains constant during others (pauses).

The reasons for the existence of pauses in the spread of the Neolithic are unknown, but some authors have suggested several working hypotheses. One of them is that perhaps in some regions early farmers encountered resistance from Mesolithic populations (Bánffy 2006; Guilaine 2013). A second possibility is the influence of spatially varying environmental variables, including soils (Guilaine 2013). A third possible cause is that climate change could in some cases have had an influence on the decisions of early farmers to migrate or not (e.g., Leppard 2014). According to other authors, the exceptional fishing resources of some areas could have also paused the spread of farming (Zvelebil and Rowley-Cowny 1984). Cultural processes have been also evoked as possible causes (Guilaine 2013). Still another possible reason is a population decline, e.g., due to disease (Rascovan et al. 2019). However, as far as we know, no conclusive evidence for any of these causes has been reported. In fact, a lot of quantitative work is still needed to determine accurately the locations and durations of pauses, as well as the spread rates between them. The main spreads are (1) the Balkans, (2) central Europe, (3) Britain, (4) Scandinavia up to the latitude of central Sweden, and (5) a further spread northwards (Shennan 2018). This section summarizes regional variations in the spread of the Neolithic in Europe, and then uses them to discuss the arrhythmic model in more detail.

Before analyzing specific regional speeds, it is important to mention two points. First, the main interest of estimating regional spread rates is to understand the factors that sped or slowed the expansion of the Neolithic. Second, performing regional estimations is not an easy task. Many published estimations illustrate this difficulty. An example is the Linearbandkeramik (LBK), the earliest Neolithic culture in central Europe (two of its main features are a distinctive incised band decoration on pottery and the construction of large longhouses). Ammerman and Cavalli-Sforza (1971) estimated by linear regression a speed of 5.6 km/year for the LBK. Similarly, they reported 2.1 km/year for the Neolithic in the western Mediterranean ($r \approx 0.9$) and 0.7 km/year in the Balkans. However, they stressed that the few dates available at the time made such regional estimations probably unreliable. In fact, they obtained low correlations ($r \approx 0.5$) for the LBK and the Balkans. Biagi et al. (2005) estimated a much faster speed for the Balkans (3.7 km/year) by using only two sites, with the aim to obtain an approximate point estimation rather than a precise range. Dolukhanov et al. (2005) pointed out that the LBK speed might have been about 4 km/year or faster but they remarked that this is just a very rough guess based on the width of the probability distribution of all LBK dates combined. Later, the same group (Henderson et al. 2014) estimated the range 1.4–4.2 km/year along the Danube–Rhine corridor (which includes the LBK area), based on a background speed of about 1.0 km/year for overall Europe plus an additional rate of 0.4–3.2 km/year. Note the very large error bar of this estimate. The same problem (very large errors) was found by Bocquet-Appel et al. (2012), who estimated for the LBK a slower speed (0.8 ± 0.6 km/year) that those mentioned above. For some other European Neolithic cultures, Bocquet-Appel et al. (2012) found an error that was even larger than the corresponding average speed. The work by Bocquet-Appel et al. (2012) is similar to more recent studies (Fort 2015; García-Sanjuan et al. 2022) that also use interpolation maps to estimate local spread rates. However, apparently no general method to estimate the errors of the thus obtained spread rates at the regional level has been developed. Perhaps the main conclusion stemming from these previous studies is how difficult it is to obtain accurate results for the spread rate and its error in specific regions. The problems encountered are not only due to methodological issues, but also to the fact that it is probably necessary to use databases with only dates of highest quality, e.g., by excluding charcoal samples (to avoid the old-wood effect), dates on species that are not clearly domesticated, etc. (Brami and Zanotti 2015; Zilhao 2011).

The next subsections survey some regions in Europe and Anatolia for which spread rates have been estimated using sound statistical methods. Unfortunately for other continents there are less data, and for this reason essentially no sound estimations have been performed on their regional rates. We would like to stress, however, that even for Europe and Anatolia the regional results below should be regarded as preliminary because in the future it is likely that their precision will be increased by using more complete and accurate databases.

Example 13. The Balkans

The central Balkans (Serbia and Kosovo) was the entrance of the Neolithic from Greece towards the inland route of Europe. The Starcevo culture, which appears at about 8200 cal. year BP, is the earliest Neolithic one in this region and displays characteristic pottery, pit houses, clay figurines, etc. In this region, Mesolithic populations seem to have lived mainly in isolated areas of the Danube Gorges, where fishing resources were exceptional and strong interactions between early farmers and autochthonous hunter-gatherers have been detected, both on the basis of strontium data (Boric and Price 2013) and ancient genetics (Mathieson et al. 2018).

Porcic et al. (2020) obtained 300 Accelerator Mass Spectroscopy (AMS) dates from the central Balkans and combined them with all other existing radiocarbon dates from the literature in the same region. They applied linear regression to estimate the spread rate, with a maximum distance between sites of only about 400 km. This is a remarkable achievement because before their work most statistically significant regressions had been performed at the continental level, with the purpose to compensate the uncertainty in the dates by considering sites separated huge distances, up to about 4,000 km (e.g., Fig. 1b). The approach by Porcic et al. (2020) has two main steps. Firstly, they excluded all dates with standard error above 100 years. Secondly, they noted that in their study area the earliest Neolithic dates are in the south, and that the oldest Neolithic date in Hungary (which is immediately to the north of their study area) is 7948 cal. BP. This suggests that the Neolithic arrived before this date to their study area, so they excluded all dates later than 7948 cal. BP. This left only 26 dates (14 dated by them and 12 from the literature). Next, Porcic et al. (2020) calculated distances by using as origin an Early Neolithic site in Greek Macedonia, i.e., close to the south of their study area. We report their result using principal axis regression, which seems justified because the origin of distances can have a substantial effect on the distances due to the smallness (explained above) of their study area. They obtained the speed range 1.2–2.1 km/year (95% CL, $r = 0.7$), which is included in our Fig. 2 (error bar 13) and Table 1. The time range of their dates was about 8190–7940 cal. year BP, i.e., only about 250 years. Porcic et al. (2020) also noted the following two points of methodological interest. (i) Regressions of times versus distances lead to larger errors (i.e., wider ranges) in the spread rate than principal axis regressions. (ii) Grouping the 26 dates into 8 distance bins and using the oldest date from each bin lead to higher values of r but inflated the errors in the spread rate. In future work it would be of interest to analyze both points for other examples and try to understand under which conditions they hold.

The estimate 1.2–2.1 km/year by Porcic et al. (2020) for the central Balkans illustrates the nonuniformity in the spread rate (arrythmia), in the sense that its mean value (about 1.7 km/year) is substantially faster than the average at the continental level (about 1.0 km/year, see example 1 above). Possible causes for this enhanced speed are considered in the Discussion section.

Example 14. The Neolithic Slowdown Along the Inland Route in Europe

The interpolation map in Fig. 1a makes it possible to recognize regional trends in the arrival of the Neolithic in Europe. Each color corresponds to a time interval of 250 years. In Fig. 1a we see that there was an inland route of Neolithic spread from Greece in the northwestern direction (i.e., parallel to the eastern Adriatic coast) crossing the Balkans, later Hungary and Austria, next the Czech Republic and Germany, and then Denmark. There are several Early Neolithic cultures along this route: Starcevo (in the Balkans, previous subsection), Köros (mainly in Hungary), the LBK (in Austria, the Czech Republic and Germany), and finally the Funnel Beaker (TRB, in northern Germany and Scandinavia). Although cultural features such as pottery and dwellings were different, all of these cultures shared the same economic basis, namely farming and stockbreeding of domesticated species belonging to the Neolithic package (as detailed in the subsection above devoted to example 1).

Figure 1a suggests that there is a gradual variation in the spread rate along the inland route, for the following reasons. Firstly, in the southeast of Europe the spread was faster than in subsequent regions because the area of each color is larger in the Balkans than in Hungary and Austria. Secondly, in northern Germany the area of each color is still smaller. Thus, there was a slowdown in the northwestern direction.

Several authors have analyzed this slowdown. Using spatial numerical simulations, Davison et al. (2006) hypothesized lower diffusivities (i.e., displacements per generation) in northern latitudes and obtained a mildly slower spread in northern Europe. Similarly, Silva and Steele (2014) assumed a decrease of the spread rate with increasing latitude (and a latitudinal cutoff at 1,100 m, above which the front would not propagate) and this improved the regression correlation with distances measured along least-cost paths (for example, if a slow region such as a mountain causes the front to surround it, the least-cost distance is that measured along this curve).

By preparing interpolation maps of the database of Early Neolithic sites collected by Pinhasi (Supp. Info. to Pinhasi et al. 2005), Isern and Fort (2010, 2011, 2012) estimated the spread rate as a function of position in the northwestern direction, from the southeast (Balkans) to the northwest (North Sea). Methodological details are given in the caption to Fig. 5. In this figure, the vertical axis gives the spread rate and the horizontal axis gives the position along the northwestern direction (y=0 corresponds to the Balkans and y=1,200 km to northern Germany). The overall time interval is 7750–5000 cal. year BP (Isern and Fort 2012, Figs. 1, 2). We see in Fig. 5 (squares) that the spread rate decreases from about 1.6 km/year to 0.0 km/year. This range is included in Fig. 2 (error bar 14) and Table 1. The model leading to the line in Fig. 5 will be discussed in detail below (subsection on slow inland spread rates).

More recently Betti et al. (2020) introduced several arbitrary ‘axes’ or expansion paths and detected the slowdown by measuring the distance along each axis as a function of time (the latter was estimated by interpolation of radiocarbon dates). Those axes were not necessarily parallel to the local front propagation direction, which is not a problem because these authors did not measure any spread rate. From all of these studies, based on different methodologies, we conclude that a Neolithic slowdown is a well-established featured in northern Europe. Possible causes of this slowdown are explained in the Discussion section.

Example 15. The Alpine Region

The Neolithic spread westwards along the Mediterranean coast and arrived to northwestern Italy and southern France at about 7700 cal. year BP. Between 7500 and 6900 cal. year BP it reached the northern French Alps from the west. The main remains are flint lithic assemblages (that are clearly related to Neolithic populations in southern France) and some charred cereal grains (Nicod et al. 2019). On the other hand, in the northern Alps of Switzerland, there are lakeside settlements with charred and waterlogged cereals and pulses. It has been argued that Alpine lakes, especially larger ones, were strongly selected locations by early farmers because they have an ameliorating effect on the climate in their immediate vicinity and this improves crop production in comparison to the rest of Alpine locations, where the growing season is very short (Halstead 1989). It is interesting that Alpine Neolithic populations had long-distance contacts, as shown by the fact that a bladelet found in the French Alps was made with obsidian from the Island of Sardina, some 700 km to the south (Nicod et al. 2019).

It is well-known that the Neolithic spread slowly in the Alpine region. This was discovered by Ammerman and Cavalli-Sforza (1971) and ratified later by isochrone maps (Ammerman and Cavalli-Sforza 1984; Fort 2015; Gkiasta et al. 2003; Henderson et al. 2014). According to Fig. 1a, the Neolithic wave of advance first surrounded the Alps and later climbed up these mountains. Here the isochrones are quite close to each other (compared to most of Europe), so the spread was slower. Note that each isochrone is a closed line inside the previous one. For such cases, a well-known method (in the field of biological invasions) to estimate the spread rate is to measure the area inside each isochrone, calculate the radius of the circumference with the same area and fit a straight line (Ammerman and Cavalli-Sforza 1984, p. 70; Skellman 1951). In this way, it is found that the spread rate is 0.09–0.14 km/year with 95% CL ($r = 0.99$, $n = 6$ areas). This spread rate is included in Fig. 2 (error bar 15) and Table 1. The time interval of the isochrones used from Fig. 6 is 6750–5500 cal. year BP and the maximum characteristic distance is 326 km (estimated as twice the radius of the circumference with the same area as the 6750 cal. year BP isochrone).

Example 16. Galicia

Galicia, the northwestern part of the Iberian Peninsula (upper left corner in Fig. 6), is one of the most distant regions from the spatial origin of the Neolithic in the Near

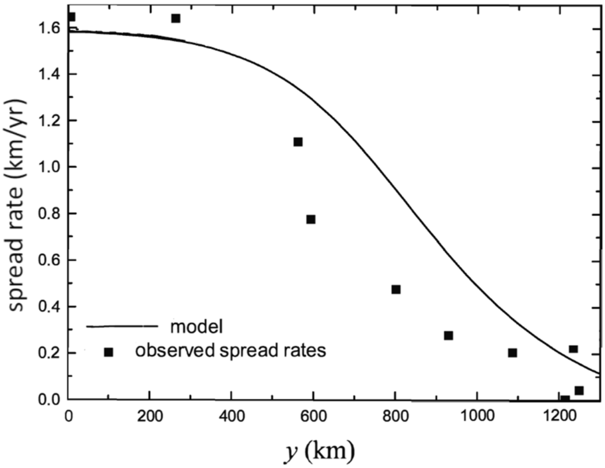

Fig. 5 The slowdown of the Neolithic along the inland route in Europe (Isern and Fort 2010, 2011, 2012), quantified by considering a rectangular corridor (400 km wide) from the southeast to the northwest (y=0 is located in the Balkans and y=1,200 km in northern Germany). Each area in this corridor between two isochrones separated 250 years (see Fig. 1a) has been used to obtain a value for the spread rate (squares). It is seen that the spread rate decreases from 1.6 to 0.0 km/year (and this leads to error bar 14 in Fig. 2). The full line is the prediction of a model that takes into account that the Mesolithic population density increases along this corridor, see Eq. (5). This increase causes the gradual decrease in the spread rate (full line) that agrees with the data (squares) without fitting the value of any parameter. Modified from Isern and Fort (2012).

East. In Galicia, the expansion of the Neolithic came to an end as it reached the Roman "Finis Terrae" (i.e., the place where the earth ends). The evidence available indicates a first phase of forest clearing at about 7000–6500 cal. year BP without cultivation (Fábregas and Suárez 1999), possibly due to herding activities according to some authors (López-Sáez et al. 2010). Later, from about 6500–6000 cal. year BP onwards, cereal cultivation is detected (López-Sáez et al. 2010) together with the presence of animal domesticates, especially sheep. Ceramics display features typical of the Iberian Neolithic (Fábregas and Suárez 1999).

According to Fig. 6, the Neolithic arrived in the Iberian Peninsula along the Mediterranean coast, from which it spread until finally reaching Galicia. This region contains most of the almost circular isochrones in the upper left in Fig. 6. The spread rate can be estimated by means of essentially the same method that we have applied to the Alpine region in the former subsection. For Galicia this yields the spread rate 0.26–0.29 km/year with 95% CL ($r = 0.999$, $n = 8$ areas). This spread rate is included in Fig. 2 (error bar 16) and Table 1. The time interval of the isochrones used from Fig. 6 is 6900–6200 cal. year BP and the maximum characteristic distance is 242 km (estimated as the radius of the portion of circumference with the same area and shape as the 6900 cal. year BP isochrone).

Example 17. The Cantabrian Region

The northern Atlantic coast of the Iberian Peninsula (leaving aside Galicia in the west) is usually referred to as the Cantabrian region (from west to east it comprises three administrative units, namely Asturias, Cantabria, and the Basque Country). Early Neolithic crops in the Cantabrian region have dates in the seventh millennium BP and consist of four cereal species, three of them wheats (emmer, einkorn, and common or bread wheat), and barley. Pulses have not been found but this is possibly due to sample poverty combined with their less likely preservation (Cubas et al. 2016). The most abundant domestic animals are ovicaprines and they also appear in the seventh millennium BP. Pottery assemblages are also attributed to this epoch and in some sites (especially in the western sector) they are present without association to the exploitation of domesticated species (Cubas et al. 2016).

It is well-known that the Neolithic spread slowly northwards in the Cantabric region. This corresponds to the isochrones in the upper center in Fig. 6. In contrast with the regions analyzed in the two previous subsections, in the Cantabric region the isochrones are almost straight lines so we cannot approximate the area inside an isochrone to a circle or a portion of it. Nevertheless, we can estimate the spread rate by measuring the distance between the isochrones corresponding to 7100 cal BP and 6600 cal BP and dividing this distance by 500 years. Measuring this distance at different locations (using in each case a direction that is approximately orthogonal to the isochrones) and averaging leads to the range 0.11–0.23 km/year (with 95% CL) for the spread rate ($n = 5$, maximum distance = 115 km). This range is included in Fig. 2 (error bar 17) and Table 1.

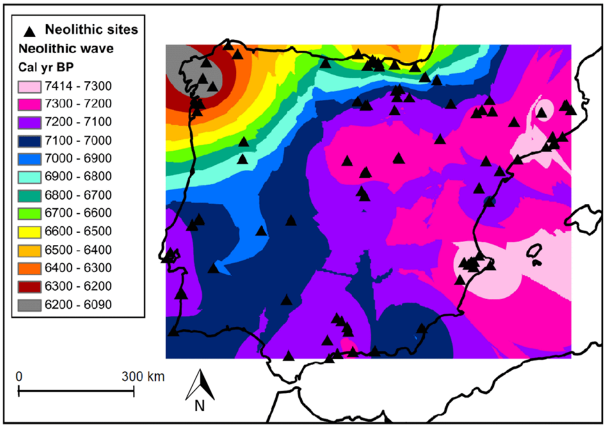

Fig. 6 The spread of the Neolithic in the Iberian Peninsula. The earliest dates are in the east (Mediterranean coast). In the north the spread was slower because the isochrones are closer to each other than in the south. The spread rates in Galicia (upper left) and the Cantabric region (upper center) are 0.26–0.29 km/year and 0.11–0.23 km/year, respectively, and they are shown error bars 16 and 17 in Fig. 2. Modified from Isern et al. (2014).

Example 18. Central Anatolia to Thrace and Greece

Up to the 1960s it seemed that Early Neolithic populations had not used the inland territory of the entire Anatolian Peninsula due to the harsh climatic conditions of the Anatolian Plateau, so only a maritime route of Neolithic dispersal along the Mediterranean coast was considered. Later on, Neolithic sites were discovered in central Anatolia and the present consensus is that there were two Anatolian Neolithic routes: a maritime one and an inland one (Özdogan 2019). More recently, monumental buildings have been found in southeastern Anatolia (sites of Göbeklitepe, Karahantepe, etc.), which testify a substantial social complexity at the earliest stages of Neolithization in this region (Özdogan 2024).

In a remarkably complete study, Brami and Zanotti (2015) gathered a database of Early Neolithic dates from 71 sites in Thrace (southern Bulgaria, northwestern Turkey and northeastern Greece), the rest of Greece, central and western Anatolia. They performed linear regressions and noted that there is more error in the dates that in the distances. Therefore, the regression of times versus distances should be preferred according to statistical theory (Mather 1946) and it yields the range 0.7–1.4 km/year for the spread rate (error bar 18 in Fig. 2). Brami and Zanotti (2015) obtained this result by using the oldest site as origin of distances. The maximum distance was about 1,100 km, and the dates were between about 10,200 until about 7500 cal. year BP (Table 1). The inland and coastal spread rates could not be estimated separately, because most Anatolian sites in that database are in the south. Brami (2015) also constructed summed probability distributions of calibrated radiocarbon dates for several regions, and estimated an interval of between 1,500 and 2,000 years between the arrival of farming to central and western Anatolia, which is substantially long compared to the intervals between western Anatolia and Thrace or Greece. Additionally, Brami and Zanotti (2015) computed two maps of isochrones: a first map using the oldest date for each of the 71 sites, and a second map excluding dates considered of low reliability. The latter were defined as those with standard deviations above 100 years, from bone samples dated before the introduction of AMS, from burnt bone, and dates possibly affected by the old wood effect. The origin of this effect is that only the outer rings of trees are alive, so samples from the inner rings of a large tree will substantially overestimate the age when it was cut down. In this specific database, samples removed to avoid this effect included bulk samples in which carbon of unknown provenience from the sediment was mixed with carbon from the charcoal, unidentified charcoal samples, and long-lived tree charcoal samples from structural timbers such as posts and roof beams. This second database included only 26 sites. The maps based on both databases display a spread westwards but the isochrones in central Anatolia are closer to each other for the most precise dataset, which is consistent with a slower spread or even a halt, as also noted by Guilaine (2013). However, there is only one site per isochrone in that region (fig. 7 in Brami and Zanotti 2015), so it would be of interest to include additional dates when they become available (as well as to extend the database to eastern Anatolia).

The Arrhythmia in Europe

From the six European regional examples above (examples 13–18), it is reasonable to consider that the 1 km/year general rate is only an average, which is useful as a metric that can be contrasted with the regional variation to understand the processes that sped or slowed expansion. More general models of waves of advance with, e.g., biased dispersal (Fort 2020; Porcic et al. 2021) and/or cultural transmission (Fort 2011, 2012, 2021a) could explain fast rates such as that reported for the Balkans (example 13 above). On the other hand, in some regions, e.g., the inland route of Neolithic dispersal, the Alps, Galicia, and the Cantabrian region (examples 14–17 above) the spread can be slower than the average 1 km/year and this may be explained by generalized models of waves of advance based on space competition (see the caption to Fig. 5) and/or other effects such as climate (Betti et al. 2020; Davison et al. 2006), topography (Davison et al. 2006), soils, diseases, etc.

We would like to stress that the arrhythmic model, i.e. a succession of spreads with different speeds separated by pauses (Guilaine 2001, 2013, 2019) could in principle be consistent with generalized wave of advance models, faster or slower than average, as appropriate for each region (this is discussed in more detail in the Conclusions section). The previous paragraph summarizes some examples but it is fair to admit that few regional studies exist. Clearly a lot of work will be needed to estimate regional rates accurately and compare them quantitatively to generalized models of waves of advance (those models are surveyed in the Discussion section).

Some Farming Spreads Involving Sea Travel Are Very Fast (About 10 km/year)

Example 19. The Western Mediterranean

Ammerman and Cavalli-Sforza (1971) as well as Guilaine (2001) noted that the Neolithic spread faster along the western Mediterranean than in inland Europe. Zilhao (2001) was the first to realize that excluding potentially uncertain dates (due to several causes of error) led to statistically indistinguishable dates from central Italy to Portugal, which implies at a very fast speed indeed. A crucial insight by Zilhao (2001) was to note the importance of the old wood effect, i.e., that samples of wood charcoal, wood from oak pillars, and other remains potentially from the inner rings of large trees can lead to dates with very large errors (e.g., 600 years).

When Zilhao (2001) published his landmark study there were not enough dates of high quality to estimate the spread rate quantitatively. Fortunately, this has become possible recently. A regression of times versus distances along the coast for the earliest sites in 6 European coastal regions (Isern et al. 2017a) yields 7.5–12.5 km/year (80% CL, $r = 0.96$, $N = 6$, maximum distance about 2,500 km). Another study with a different database including some additional regions that are separated longer distances leads to a similar result, namely 7.5–10.6 km/year with 80% CL (Fort 2022b). This range is included in our Fig. 2 (error bar 19) and Table 1. It was reached by considering the oldest site in each of nine coastal regions, with a maximum distance along the coast of about 3,200 km and a time interval of about 7820–7400 cal. year BP. The methodology was a resampling procedure that drew nine dates (one per site) by requiring that the probability of drawing a specific date for a given site is equal to the probability of that date in the corresponding calibrated probability distribution. The next step was to perform a linear regression of dates versus distances along the coast for these nine dates. Finally, this resampling and regression procedure was repeated many times.

The following issue can be useful in future work on this and other examples. A single linear regression using the means of the calibrated distributions for the nine earliest regional dates yields 9.1 km/year ($r = 0.84$), i.e. the same mean spread rate as for the range above (7.5–10.6 km/year). However, the widely-used approach based on Student's t distribution to estimate the slope error (Draper and Smith 1981) yields a rather different result (5.9–12.3 km/year, also with 80% CL). Therefore, using Student's t distribution to estimate the error is not accurate in this example. This is a relevant methodological point. It implies the breakdown of the method based on Student's t distribution to estimate the error in the slope of a linear fit. This method is used by many computer programs on statistics and relies on two assumptions (Draper and Smith 1981): that the probability distribution of each date is a Gaussian (which is not true for calibrated dates) and that the means of those distributions are centered along the fitted straight line (which is not true for this example).

The range mentioned above (7.5–10.6 km/year, error bar 19 in Fig. 2) corresponds to an extremely rapid speed indeed, much faster than all 18 inland expansions discussed above (see Fig. 2). According to both analytical equations and numerical simulations, such a fast Neolithic spread implies that early farmers moved between 240 and 427 km per generation along the western Mediterranean coast (Fort 2022b). This example shows clearly that estimating spread rates from archaeological data and comparing to mathematical models can unveil key aspects of human behavior, in this case the average distance moved per generation (see also Isern et al. 2017a).

Example 20. Oceania

Extant Austronesian languages testify the largest linguistic expansion in prehistory in terms of extent: over halfway around the world, from Madagascar to Easter Island. According to Bellwood (1997), this expansion begun at about 6000 year BP from the mainland of southern China into Taiwan, where initial Austronesian languages were spoken before further expansion took place. Later, the spread proceeded southwards to the Philippines and finally it branched in two directions: eastwards via small islands at the north of New Guinea to Easter Island, and westwards via Sumatra to Madagascar (for a map, see fig. 1 in Diamond and Bellwood 2003). This reconstruction is based on observations and methods of comparative linguistics, including the striking fact that words for crop plants and various terms of horticultural practice in Oceania are derived from reconstructed languages in island South Asia rather than from the native Papuan languages spoken in New Guinea (Bellwood 1997; Kirch 2000).

Archaeologically, for the spread eastwards a very clear trail of pioneer farming sites have been dated from islands close to the north of New Guinea to Samoa (Bellwood 1997). These sites correspond to the Lapita culture, characterized by a pottery closely related to ceramics from the Philippines, stone adzes, pigs, fowls, root crops such as taro and yams, coconut, bananas, etc. (Kirch 2000). East of Samoa, the sites no longer belong to the Lapita culture but radiocarbon dates indicate a subsequent eastward expansion of farming. When the dates of this spread are analyzed in detail, three phases can be discerned: (1) an initial expansion eastwards (Lapita culture) from the area of the Mussau Island (near New Guinea) until the region of the Samoa and Tonga Islands; (2) a standstill of about 1,500 years; and (3) a second spread (of nonLapita Austronesian speakers) across much longer stretches of open ocean reaching Easter island to the east, New Zealand to the south, and the Hawaiian islands to the north. The total distance covered was about 4,550 km in the first spread and about 6,550 km in the second one. So far it has not been possible to measure both spread rates, possibly because of their fastness, but a lower bound of 8 km/year for the Lapita spread (3550–2750 cal. year BP) was derived (Fort 2003). We include it in Fig. 2 (error bar 20) and Table 1. Montenegro et al. (2016) have simulated seafaring voyages under realistic wind conditions and argued that the standstill in the Samoa region could be due to the need of technological innovations to enhance the capability of windward voyaging.

Both sea expansions above (examples 19 and 20) are much faster than all 18 inland expansions (Fig. 2). We might be tempted to conclude that premodern farming expansions involving sea travel are necessarily faster than inland ones. However, two examples are very few (compared to the 18 inland examples). Moreover, the spread rate for the eastern Mediterranean has been never quantified using statistically sound methods but could perhaps be much slower. Indeed, according to Ammerman apparently it took about 2,300 years for the Neolithic wave of advance to propagate from Cyprus to southern Italy, although the distance between them is only about 1,500 km (Ammerman 2011). If this estimation (about 0.65 km/yr) is realistic, it is surprisingly slow for sea travel. In future work, it would be important to collect a database of reliable Early Neolithic dates for the eastern Mediterranean and try to estimate the spread rate and the correlation coefficient using additional regions. When enough data become available, the same could be attempted for other farming expansions involving sea travel, e.g., for the Neolithic along the coasts of the Scandinavian Peninsula.

Discussion

All spread rates of farming and/or herding in prehistory reported in this paper are plotted in Fig. 2. They are also included in Table 1, together with their locations, maximum distances and time intervals. As noted above, Fig. 2 displays a clear tendency for inland spread rates to have values of about 1 km/year. In this section, our first aim is to present a possible explanation of this tendency. The second one is to consider deviations (i.e., inland spread rates that are faster or slower than the 1 km/year average) and review the possible explanations of these deviations that have been proposed in the literature.

Why Are Inland Agricultural Spread Rates About 1 km/year?

Figure 2 shows that most inland spread rates are close to 1 km/year. Therefore this result, first discovered by Ammerman and Cavalli-Sforza (1971) for the European Neolithic, seems a tendency of expansions of farming and/or herding all over the world. There are certainly some deviations (see Fig. 2), and they will be discussed after summarizing a mathematical model (the so-called wave-of-advance model) that explains why farming often spreads at about 1 km/year.

If a small number $N_{initial}$ of individuals reaches a region, then the model assumes (in agreement the ethnographic data) that during the first generations the number of individuals (due to the overall effect of births and deaths) increases exponentially, i.e., $N = N_{initial}e^{at}$. Intuitively, this equation means that if after some time interval the number of individuals doubles, it will double again after the same time interval, and so on. Here e could be any number, but Euler's number $e = 2.71828$ is always used because it leads to simpler equations, e.g., Eq. (2) below. Parameter a is called the initial growth rate and it measures how fast the number of individuals N grows. Values of a can be estimated from data on populations that settled in empty space, by plotting the number of individuals N as a function of time t and fitting this function ($N = N_{initial}e^{at}$). So far data for five different preindustrial populations have been reported and they yield similar values of a, see Bancells and Fort (2024), Supp. Info., Sect. S1b. An alternative, simpler (but less accurate) method to estimate a is described below Eq. (2).

Note that the value of a informs on the evolution of the population number in time (indeed, the units of a are year^{-1}) but not in space. In order to obtain an equation for the spatial spread rate of a population front (which has units km/year), we also need to take into account how the population evolves in space. Some ethnographic works contain lists (or histograms) of intergenerational distances d, e.g., distances between the birthplaces of a parent and one of his/her children. Such distances are used to estimate the so-called diffusion coefficient D. In the simple case in which all individuals have the same value of d, D can be estimated from the equation (for a derivation see, e.g., Fort and Méndez 1999)

$$D = \frac{\mathrm{d}^2}{4T}. \tag{1}$$

Here T is the generation time, defined as the mean age difference between a parent and his/her children. The units of D are km^2/year.

Fisher (1937) and independently Kolmogorov et al. (1937) derived an equation that was applied to biological invasions by Skellman (1951) and to Neolithic spread by Cavalli-Sforza (1971) and Ammerman and Cavalli-Sforza (1973). This is the so-called 'wave-of-advance model'. Cavalli-Sforza (1971) phrased it as follows. A population that is originally present in some region, increases in size and has a short-range migration, will expand with a constant spread rate given by

$$s = 2\sqrt{aD}. \tag{2}$$

This is called Fisher's speed, and it is measured in km/year. The mathematical derivation of this equation assumes that dispersal is isotropic, i.e., individuals move equally along all directions (e.g., Fort and Méndez 1999). The first application of Eq. (2) to the Neolithic was elegantly presented by Cavalli-Sforza (1971, pp. 91–92) as follows: "Unfortunately there are not yet any direct measurements of the growth rate or the migration of Neolithic people, but (…) population growth rates observed in the occupation of empty islands (…) are of the order of doubling each generation. As to migration rates, those observed in today's African famers give 20–30 km. It is remarkable that, using these growth and migration rates, the expected radial rate comes very close to the observed rate." The calculation leading to this conclusion is simple and proceeds as follows. Using that $N = N_{initial}e^{at}$ (as explained above), if the population doubles ($N = 2N_{initial}$) each generation ($t = T$) then $2 = e^{aT}$. Assuming a generation time of $T = 25$ years (Ammerman and Cavalli-Sforza 1973), then $a = 0.028$ year^{-1}. Therefore, according to Eq. (1), if $d = 20$ km then $D = \frac{d^2}{4T} = \frac{20^2}{4 \cdot 25} = 4\,\frac{\mathrm{km}^2}{\mathrm{year}}$. Analogously, if $d = 30$ km then $D = \frac{30^2}{4 \cdot 25} = 9\,\frac{\mathrm{km}^2}{\mathrm{year}}$. Using these values into Eq. (2), we obtain a spread rate s between $0.7\,\frac{km}{year}$ and $1.0\,\frac{km}{year}$. This range is consistent with the observed one for the spread of the Neolithic in Europe (between $0.9\,\frac{km}{year}$ and $1.3\,\frac{km}{year}$, see Fig. 1b). Moreover, the range from Eq. (2), i.e., between $0.7\,\frac{km}{year}$ and $1.0\,\frac{km}{year}$, also agrees with the observed fact that ancient farming expansions with continental or large scales usually had spread rates of about 1 km/year (Fig. 2). More refined equations than (2) lead to the same conclusion, namely that mathematical models predict a spread rate of about 1 km/year for farming populations expanding their geographical range (Fort and Méndez 1999; Isern et al. 2008). All of these models are called demic, to distinguish them from those that include cultural transmission.

According to Anthony (1990), the wave-of-advance model by Ammerman and Cavalli-Sforza (1973, 1984) can describe the spread of populations with short-distance isotropic dispersal, but not long-distance displacements neither nonisotropic dispersal. This is correct for the original model (Ammerman and Cavalli-Sforza 1973, 1984) but similar models are nowadays available to describe both long-distance dispersal (Fort 2022b; Isern et al. 2017a) and nonisotropic displacements (Fort 2020; Fort and Pujol 2007). Anthony (1990) also proposed that the wave-of-advance model by Ammerman and Cavalli-Sforza (1973, 1984) may account for population movements averaged over large spans of time but not on short scales. This is also correct, because the wave-of-advance model is valid as an approximation at large scales of space and time. It is thus a macromodel that does not take into account the preferences of early farmers for specific locations, but is perfectly consistent with micromodels. The latter type of models, also called “leapfrogging” (Zvelebil 2000), take into account the non-homogeneous preference of locations by farmers (Hauzeur and Jadin 2013; van Andel and Runnels 1995). Such micromodels are useful to describe local dynamics but not large-scale phenomena, such as the average value of the spread rate over thousands of kilometers.

First Deviation: Fast Inland Spread Rates. Possible Explanations

We observe in Fig. 2 that some spread rates seem to be faster than 1 km/year, because their error bars do not overlap this value but are above the horizontal dotted line. This subsection reviews two possible causes that may lead to such fast inland Neolithic spread rates: cultural transmission and biased dispersal. Both mechanisms and possible examples of each are also summarized in the first two rows of Table 2.

The first possible mechanism behind fast spread rates is cultural transmission. It can be defined as the incorporation of hunter-gatherers into the populations of farmers/herders. As already noted by Childe (1957, p. 287), cultural transmission will increase the spread rate of farming/herding, simply because there will be more farmers so more of them will disperse. Gronenborn (1999, p. 182) also favored a scenario in which there is cultural transmission in addition to demic diffusion. When there is cultural transmission, Fisher’s equation (2) is generalized by [see Eq. (S11) in Fort 2012]

$$s = 2\sqrt{\left(a + \frac{\eta}{T}\right)D}, \tag{3}$$

where η is a parameter called the intensity of cultural transmission. For $\eta = 0$, no hunter-gatherers are incorporated into the populations of farmers, so there is only demic diffusion (no cultural transmission) and Eq. (3) is the same as Eq. (2). For

$\eta > 0$, some hunter-gatherers are incorporated and the front of agriculture propagates faster, i.e., the spread rate s is given by Eq. (3) and higher than that given by Eq. (2). The quantitative meaning of parameter η is simple to understand by considering the following cases. If the incorporation of hunter-gatherers in the populations of farmers is due to interbreeding between hunter-gatherers and farmers, η is the portion of early farmers that interbreed with a hunter-gatherer (Fort 2011). This is the same as the number of hunter-gatherers that interbreed with an early farmer, per farmer and generation. On the other hand, if there is not interbreeding but acculturation (e.g., if complete families of hunter-gatherers become farmers), then η is the number of hunter-gatherers converted per early farmer and generation (Fort 2012). If there is both interbreeding and acculturation, η is the sum of both contributions (Fort et al. 2018).

In a seminal work, Aoki et al. (1996) calculated the spread rate for a model in which the interaction between farmers and hunter-gatherers was proportional to the product of their population densities. In contrast, Eq. (3) follows from an interaction rigorously derived from cultural transmission theory (Cavalli-Sforza and Feldman 1981; Fort 2012). Another kind of interaction, which is called conformism, is widely observed in human populations (Henrich 2001; Wakano 2012) and assumes that the probability of acculturation is higher than the fraction of the population with the cultural trait considered (farmers in our case). Importantly, for the usual conformist models (Boyd and Richerson 1985; Henrich 2001; Kandler and Steele 2009), Eq. (3) is still valid (see Sec. S4 in Fort 2015).

The value of the intensity of cultural transmission η, which appears in Eq. (3), can be estimated by plotting an ancient genetic cline, i.e., the percentage of early farmers with a genetic marker as a function of distance from the Near East and comparing to simulations. So far this has been done only for Early Neolithic Europe, leading to the result $0.01 \leq \eta \leq 0.03$, which indicates that between 1% and 3% of early farmers interbred with a hunter-gatherer (Isern et al. 2017b). It is interesting that if we use this range for η and the same ethnographic values of a, D and T as below Eq. (2), Eq. (3) yields a correction for the spread rate of only about 1% relative to Eq. (2). Thus, the effect of cultural transmission on the Neolithic spread rate in Europe seems to have been very small at the continental scale. However, in some specific regions the value of η may be higher and thus the effect of cultural diffusion more important. Such an analysis from ancient genetic data has not been performed yet but higher values of η seem likely in some areas. For example, anomalously strong interactions between farmers and hunter-gatherers have been detected (both archaeologically and genetically) in some Danubian sites with exceptional fishing resources such as Malak Preslavets in Bulgaria or Vlasac and Lepenski Vir in the Serbian Iron Gates (Brami et al. 2022; Mathieson et al. 2018). In the future, when there are enough ancient genetic data from such areas, it will probably be possible to estimate higher, regional values of both η and the effect of cultural transmission (as compared to the continental-scale estimations reported above). It is also possible to estimate a range for η from purely archaeological (not genetic) data, as explained below (in the subsection on the mainly demic character of prehistoric farming expansions).

It is unfortunate that apparently there are not yet enough ancient genetic data to estimate the value of η for any other prehistoric farming expansion besides the

Neolithic in Europe. However, several authors have suggested that cultural transmission could be relevant in some expansions with special features. Firstly, de Souza et al. (2022) have suggested that the reason why the Near Eastern Neolithic spread rapidly in India (see our Fig. 2, error bar 3) could have been cultural transmission, favored by the fact that local domestication was already established in parts of India. A second example of fast spread is the southern Bantu expansion in eastern Africa (Fig. 2, error bar 6), for which herding loanwords (Ehret 1998) as well as genetic data (Sikora et al. 2011) have led to the suggestion that these Bantu populations could have incorporated individuals from local populations. Thirdly, Khoekhoe herders expanded rapidly across southwestern Africa (Fig. 2, error bar 7) and this could be related to the fact that, according to some authors, substantial numbers of hunter-gatherers became herders in this specific expansion (Diamond 2002; Sadr 2013), perhaps because herding could be simpler to learn than farming (Sorensen 2016). Fourthly, Crema et al. (2022) have suggested that cultural transmission could have influenced the spread of rice in Japan (error bar 12 in our Fig. 2) by means of intermarriages between farmers and hunter-gatherers conditioned by preexisting social networks.

A second possible mechanism behind fast spread rates is nonisotropic dispersal. Here the idea is that if farmers have a preference to disperse in directions close to that of the wave of advance than in other directions, the wave of advance will spread faster. The simplest model with such a preference leads to the following equation for the spread rate (see, e.g., Fort and Pujol 2007)

$$s = 2\sqrt{aD} + U, \tag{4}$$

where U measures the anisotropy in the dispersal. If dispersal is isotropic (i.e., if farmers have the same probability to disperse in all directions), then $U = 0$ and we recover Fisher's equation (2). If it is more likely for farmers to disperse in directions close to that along which the wave of advance propagates, then $U > 0$ and the speed given by Eq. (4) is faster than that for isotropic dispersal, Eq. (2).

It is known that such a mechanism (biased dispersal) can lead to fast spread rates, even in the absence of cultural diffusion (Fort 2020), and that this effect can be large enough to explain the fast spread rates of the southern Bantu and Khoekhoe expansions (error bars 6 and 7 in Fig. 2). Dispersal probabilities in prehistoric farming expansions have not been measured, so at present it is not possible to prove the importance of biased dispersal in specific expansions. However, this limitation could change because some ancient parent-child pairs buried in different places have been identified. If many such pairs were found, it could be possible to estimate the probability of dispersal as a function of the angle relative to the front spread direction, and to check whether this effect can explain some fast expansions or not. For example, Porcic et al. (2021) have suggested that biased dispersal may explain the fast spread rate estimated by them in the Balkans (error bar 13 in our Fig. 2).

For the sake of completeness, it is of interest to add that concerning the theoretical calculations of spread rates, a mathematical effect that can lead to faster calculated values is to take into account the detailed shape of the probability distribution of distances moved by farmers per generation (Isern et al. 2008) rather than only the diffusion coefficient D given by Eq. (1). This leads to more precise but complicated equations than (2)–(4). As remarked by Shennan (2018), these distributions are not bell shaped (although they are sometimes assumed to be so) and, moreover, small long-distance probabilities can substantially increase the spread rate. It has been also suggested that the preference of early farmers to settle in specific areas (van Andel and Runnels 1995) might lead to trajectories (in which each straight line or move corresponds to one generation) with groups of short-length moves interspersed with longer ones (such trajectories are produced by e.g., the so-called Lévy distributions). However, only a few distributions of the intergenerational distances moved by preindustrial farmers have been obtained from ethnographic records (Bancells and Fort 2024), and so far, no studies have attempted to proof that they are Lévy-shaped. If they were, this would certainly provide a very interesting analogue to well-known ecological results but it would not affect the spread rates, in the sense that they would be calculated more precisely from the observed set of intergenerational distances than using a distribution curve fitted to them.

Second Deviation: Slow Inland Spread Rates. Possible Explanations

We note that in Fig. 2 some spread rates are below 1 km/year (dotted horizontal line). This subsection reviews possible effects that have been suggested to cause this deviation. These mechanisms and possible examples of each are also summarized in rows 3 to 8 of Table 2.

Firstly, the last model in the previous subsection can explain not only fast but also slow expansions (Fort and Pujol 2007). Indeed, if it is more likely for farmers to disperse in directions close to the opposite one to that of the front propagation, then $U < 0$ and the speed given by Eq. (4) is slower than Eq. (2). The latter corresponds to the case in which farmers disperse with the same probability in all directions ($U = 0$).

A second possible reason behind slow spread rates is that famers may find higher hunter-gatherer densities in some areas, and this can cause a stronger competition for space between both populations. Consider a region in which the population density of hunter-gatherers M increases with the distance y (the latter is measured along the propagation direction of the wave of advance). If M_{max} is the value of M at the end of this region, we can define the dimensionless variable $m(y) = \frac{M(y)}{M_{max}}$. Then the simplest model that takes into account competition for space between farmers and hunter-gatherers leads to the following equation for the spread rate (Isern and Fort 2010)

$$s = 2\sqrt{aD(1 - m(y))}. \tag{5}$$

If there are no hunter-gatherers then $M(y) = 0$, so $m(y) = 0$ and Eq. (5) is the same as Eq. (2). On the other hand, if there are hunter-gatherers then $M(y) > 0$, and the spread rate (5) is slower than that given by Eq. (2). Moreover, if the relative population density of hunter-gatherers $m(y)$ increases with y then the spread rate given by Eq. (5) decreases with y. Figure 5 shows that such a model (full line) explains reasonably well the slowdown of the Neolithic along the inland route in Europe (Isern and Fort 2012). In this example the spread rate diminishes from 1.6 to 0 km/year (Fig. 5, squares and Fig. 2, error bar 14). A very attractive feature of this kind of competition models is that they do not use any free or adjustable parameters. Indeed, the only difference between Eqs. (2) and (5) is that the hunter-gatherer population density $M(y)$ appears in Eq. (5) in dimensionless form, $m(y) = \frac{M(y)}{M_{max}}$, and this function does not need to be fitted because $M(y)$ as well as its maximum value, M_{max}, can be estimated by means of archaeological data (see fig. 1 in Isern and Fort 2011).

A third possible mechanism behind slow spread rates may be high altitudes above sea level. A very clear example of the latter effect is the slowness of the Neolithic spread in the Alps (see Fig. 1a and example 15 above). At present, the precise mechanism leading to this slowness is apparently unknown. One possibility is, of course, non-isotropic dispersal (Eq. (4) with $U<0$), as already described in the second paragraph of this subsection.

A fourth possible cause of slow spread rates is some climatic effect. For example, Betti et al. (2020) and Davison et al. (2006) have suggested that the harsh climate in the north might be one reason for the slower spread of the Neolithic in northern Europe. This might be due, e.g., to the need of agricultural adaptations in northern latitudes because fewer hours of insolation per day, lower temperatures, etc. can make the cultivation of certain crops substantially less productive than in southern latitudes. However, according to Colledge et al. (2005), when early farmers established new settlements, they cultivated the most productive crops and simply dropped the others, so a delay in the spread due to the need to time for crop adaptation seems unlikely. Moreover, as far as we know there is not any mathematical model that explains the slowdown from climatic variables, less still without fitting any parameter value (in contrast, competition models such as Eq. (5) achieve this for northern Europe, as explained above and seen in Fig. 5). On the other hand, a recent remarkable study (Cortell-Nicolau et al. 2025) has shown that a mathematical model without any climate effects reproduces fairly well the population increases of farmers and the decreases of hunter-gatherers (as estimated from archaeological data) during the transition to farming in three different regions: Denmark, eastern Iberia, and the Island of Kyushu (Japan).

A fifth effect that could lead to slow spread rates is slower net reproduction. In some examples this might be due to effects related to latitude (Fort et al. 2018), and in other examples to other reasons. One of them could be disease. It is well-known that humans and animals living in close contact with each other generated favorable conditions for the emergence of infectious diseases in prehistoric farming populations (Rascovan et al. 2019). In case such an effect had been particularly strong in specific regions, the net reproduction (due to births minus deaths, and quantified by the initial growth rate a) of farming populations would have decreased, thereby leading to lower values of the spread rate s according to Eq. (2).

Finally, a sixth possible mechanism is that mainly cultural spread may be slower than demic-cultural models if hunter-gatherers converted into farmers disperse shorter distances (Fort 2015).

Most Spreads of Agriculture in Prehistory were Mainly Demic

Let us define $s_{\eta=0}$ as the value of the spread rate s without cultural diffusion ($\eta = 0$), i.e., for purely demic diffusion. If the spread rate s is given by Eq. (3) then $s_{\eta=0}$ is given by Eq. (2) simply because Eq. (3) for $\eta = 0$ yields Eq. (2). The difference between both spread rates (i.e., $s - s_{\eta=0}$) is zero in the absence of cultural diffusion ($\eta = 0$) and increases with increasing values of η. Thus this difference ($s - s_{\eta=0}$) is a measure of the importance of cultural diffusion in the spread rate of the expansion under consideration. For this reason, the relative cultural effect is defined as this difference divided by the total spread rate s, i.e. (Fort 2012)

$$CE = \text{cultural effect} = \frac{s - s_{\eta=0}}{s} \cdot 100. \tag{6}$$

Similarly, the demic effect is the purely demic spread rate $s_{\eta=0}$ relative to the total s, i.e.

$$DE = \text{demic effect} = \frac{s_{\eta=0}}{s} \cdot 100, \tag{7}$$

so that $CE + DE = 100\%$.

The cultural and demic effects can be obtained by comparing the spread rate s from the mathematical model to that implied by the archaeological data. We outline, as a worked example, this procedure for the spread of the Neolithic in Europe (Fort 2012). Figure 7a shows the spread rate s as a function of the intensity of cultural diffusion η, obtained by using an equation of the type of Eq. (3) above (see the caption to Fig. 7). The upper (full) curve in Fig. 7a has been plotted by using the ethnographic values of the initial growth rate a and generation time T that lead to the maximum value for the spread rate for each value of η ($a = 0.033\, year^{-1}$ and $T = 29\, year$). Similarly, the lower (dotted) curve in Fig. 7a uses the ethnographic values that lead to the minimum possible spread rates ($a = 0.023\, year^{-1}$ and $T = 35\, years$). The full curve in Fig. 7b is the cultural effect CE obtained directly from the solid curve in Fig. 7a by noting that, according to the full line in Fig. 7a, for $\eta = 0$ (left-hand side) the spread rate is $s_{\eta=0} = 0.917$ km/year. So, the full line in Fig. 7b has been obtained simply by using Eq. (6) and the value of s for each value of η according to the full line in Fig. 7a and $s_{\eta=0} = 0.917$ km/year. Similarly, according to the dashed line in Fig. 7a $s_{\eta=0} = 0.676$ km/year, so the dashed line in Fig. 7b has been obtained by using Eq. (6) with s for each value of η obtained from the dashed line in Fig. 7a and $s_{\eta=0} = 0.676$ km/year. Finally, the horizontal hatched rectangle in Fig. 7a is the spread rate of the Neolithic in Europe (0.9–1.3 km/year, see the caption to Fig. 1b). We see in Fig. 7a that consistency between the model (area between the curves) and the archaeological range (dashed rectangle) implies that $\eta < 2.5$, i.e., that each

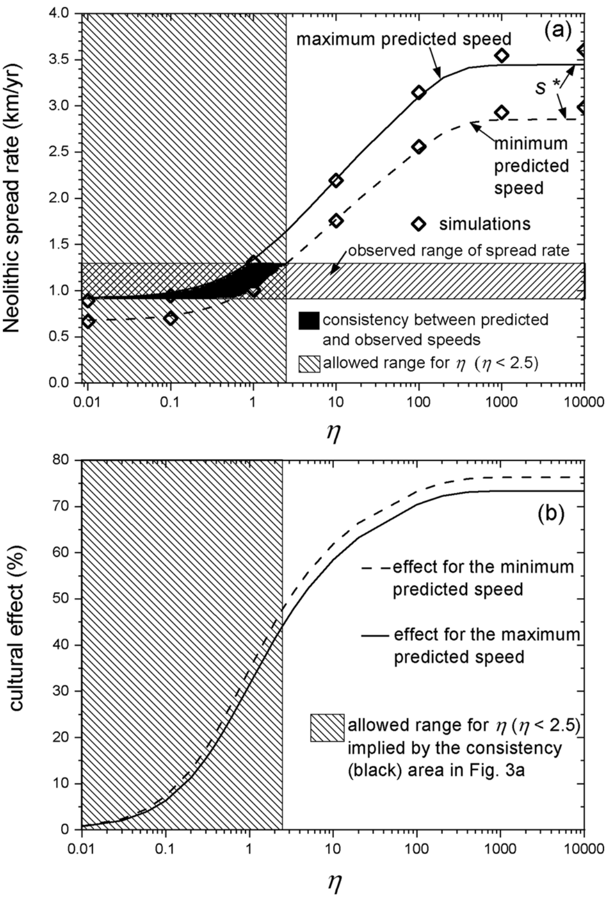

Fig. 7 (a) The full curve is the maximum spread rate, obtained for $a = 0.033\,\text{year}^{-1}$ and $T = 29\,\text{year}$. The dashed curve in Fig. 2a is the minimum spread rate, obtained for $a = 0.023\,\text{year}^{-1}$ and $T = 35\,\text{year}$. The model applied (Fort 2012) is more complicated and precise than Eqs. (2)-(3) because it uses the complete set of probabilities and dispersal distances per generation rather than only the diffusion coefficient given by Eq. (1). Here we have used the dispersal probabilities and distances of the Issongos (a population of preindustrial farmers), namely $\{p_j\}$ ={0.42; 0.23; 0.16; 0.08; 0.07; 0.02; 0.01; 0.01} and $\{d_j\}$ ={2.3; 7.3; 15; 25; 35; 45; 55; 100} km. Other populations yield similar results. The horizontal hatched rectangle is the spread rate of the Neolithic in Europe, i.e. 0.9-1.3 km/year (see the caption to Fig. 1b). It is seen that η cannot be larger than 2.5, i.e., that each early farmer acculturated at most 2.5 hunter-gatherers on average. (b) The full curve in this panel has been obtained by using Eq. (6) and the full curve in (a). The dashed curve has been obtained by using Eq. (6) and the dashed curve in (a). It is seen that the maximum cultural effect is 48%. Modified from Fort (2012, 2022a).

early farmer acculturated at most 2.5 hunter-gatherers on average (see the text below Eq. (3)). Moreover, according to Fig. 7b the cultural effect *CE* cannot be larger than 48% (Fort 2012). Thus, the demic effect *DE* is 52% or higher. This is above 50%, so purely archaeological data (i.e., without using genetics) are enough to conclude that the spread of the Neolithic in Europe was mainly demic. This conclusion is consistent with the large differences in genetic markers and genomic ancestries that have

Table 2 Mechanisms that affect spread rates. The last column reports proposals by several authors rather than well-established examples. An exception is the Neolithic in Europe, which is a strong case of demic-cultural spread according to analyses of genetic clines (Fort and Pérez Losada 2024; LaPolice et al. 2025). Genetic effects reported as 'unknown' have not been analyzed, to the best of the author's knowledge.

Mechanism	Archaeological effect	Genetic effect	Possible examples
Cultural transmission	Faster spread rate (Fig. 7a)	Genetic clines	Neolithic in Europe (Figs. 1 and 7a) and India, southern Bantu (Fig. 4) and Khoekhoe expansions, rice spread in Japan
More likely dispersal in directions close to that of the front	Faster spread rate	Unknown	Neolithic in the Balkans, Southern Bantu expansion (Fig. 4), Khoekhoe expansion
Less likely dispersal in directions close to that of the front	Slower spread rate	Unknown	Neolithic in the Alps (Fig. 1a), Galicia (Fig. 6), and the Cantabrian region (Fig. 6)
Competition with hunter-gatherers	Gradual slowdown of the spread rate (Fig. 5)	Unknown	Inland Neolithic route in Europe, from the Balkans to northern Germany (Fig. 5)
High altitudes	Slower spread rate	Unknown	Neolithic in the Alps (Fig. 1a)
Crop adaptation to cold climate	Slower spread rate	Unknown	Neolithic in northern Europe and Scandinavia
Slow net reproduction (due to latitude, disease, etc.)	Slower spread rate	Unknown	Neolithic in Scandinavia
Mainly cultural spread with short-range dispersal of acculturated hunter-gatherers	Slower spread rate	Unknown	Neolithic in northern Europe, the Alps and west of the Black Sea

been detected by comparing Mesolithic to Early Neolithic populations in Europe (Bramanti et al. 2009; Mathieson et al. 2015; Nikitin et al. 2019). A mainly demic spread of the Neolithic in Europe also agrees with the conclusions from the analysis of Neolithic genetic clines, as explained in paragraph 3 below Eq. (3).

The same procedure has led to estimations of the cultural effect CE for the following expansions (Fort 2012, 2021b, 2022a, 2022b): the spread of the Neolithic in Europe ($0\% \leq CE \leq 48\%$), the spread of domesticated rice in eastern Asia ($0\% \leq CE \leq 42\%$), the southern Bantu expansion ($8\% \leq CE \leq 47\%$), the eastern Bantu expansion ($0\% \leq CE \leq 37\%$), the spread of Khoekhoe herders ($3\% \leq CE \leq 68\%$), the spread of the Neolithic in Scandinavia ($0\% \leq CE \leq 42\%$) and along the western Mediterranean coast ($0\% \leq CE \leq 21\%$, from Fort 2022b). In only one of these seven expansions (the Khoekhoe) the cultural effect CE could perhaps have been larger than 50%. This is the only expansion of herding for which we know the spread rate, and a high cultural effect might be related to the fact that herding seems easier to learn than farming (see the subsection above on fast inland spread rates). Interestingly, for a different spread of herding analyses of human DNA dated about 7000 cal. year BP from the Sahara also indicate that cultural diffusion was important (Salem et al. 2025). In any case, the data available at present strongly suggest that most prehistoric farming expansions were mainly demic (because $CE \leq 50\%$ is consistent with all of the results above).

We stress that the percentages of CE in the previous paragraph are average ranges obtained by considering continental or large scales but in specific regions the cultural effect could have deviated considerably from the continental average, as suggested by the existence of substantial regional variations in spread rates (see fig. 2 in the present paper and Bocquet-Appel et al. 2012; Fort 2015; García-Sanjuan et al. 2022; Henderson et al. 2014). Hopefully, in the future new databases including only highly-reliable radiocarbon dates will be compiled following adequate guidelines (Bánffy et al. 2018; Brami, and Zanotti 2015; Oross et al. 2020; Zilhao 2011) and they will lead to more accurate estimations of regional cultural and demic effects. For this purpose, it would also be very useful to perform estimations of the initial growth rate a in different regions from archaeological data (because the value of a is used to calculate CE, see the text below Eq. (7) and Fig. 7). Some authors have attempted this by analyzing summed probability distributions over time intervals of only about 100 years (Blagojevic et al. 2024).

Bocquet-Appel (2002) estimated the proportion of juvenile individuals in Late Mesolithic and Early Neolithic European cemeteries and detected higher values in Early Neolithic ones. This demographic transition has been also observed in other regions, and, remarkably, it has been used to infer values of the population growth rate a that are consistent with the ethnographic range used above, i.e. $0.023 year^{-1} \leq a \leq 0.033 year^{-1}$ (Guerrero et al. 2008).

It is of interest to compare the percentages of CE above, which have been estimated from archaeology, to those estimated from ancient genetics. As explained three paragraphs below Eq. (3), at present there are enough ancient genetic data only for the Neolithic in Europe, and they lead to the estimation $0.01 \leq \eta \leq 0.03$ for the intensity of cultural transmission. Resorting to Fig. 7 we see that this implies a cultural effect of $0.7\% \leq CE \leq 2.3\%$ (Fort 2022a). Remarkably, this is consistent and much more precise than the range $0\% \leq CE \leq 48\%$ obtained above from archaeology (also for the spread of the Neolithic in Europe). This suggests that ancient genetics is substantially more accurate than archaeology to estimate the percentages of cultural and demic diffusion. However, future work should take three points into account. First, the estimation above from ancient genetics ($0.01 \leq \eta \leq 0.03$) is not based on a detailed set of dispersal distances and probabilities but on a simple simulation in which 38% of farmers do not move and all of the rest move 50 km per generation (Isern et al. 2017b). Future, more complex genetic simulations should be based on realistic dispersal distances and probabilities from ethnography (such as those in the caption to Fig. 7). Combining such genetic results for several ethnographic populations will surely lead to a wider genetic range for CE. Second, in several areas such the Iron Gates or Britain genetic admixture was more significant (Fig. 3 in Koptekin et al. 2025), hence analyzing the corresponding genetic data may lead to higher values of η and therefore a wider overall range for CE. Third, the estimation from archaeology may become more precise if the error in the spread rate is diminished by gathering a database composed only of highly-reliable radiocarbon dates.

Cultural Spreads in Prehistory

It is worth to stress that not all spreads of cultural traits in prehistory were mainly demic. Indeed, whereas most spreads of farming and stockbreeding appear to have taken place mainly by demic diffusion, the range expansions of some traits were essentially cultural. A well-known example is the spread of pottery, which has been examined both in farmer and hunter-gatherer populations. Concerning farmers, in the Near East agriculture was initially aceramic (prepottery Neolithic cultures). When pottery appeared, it spread very rapidly to regions where the mainly demic wave of advance of farming had already arrived. The spread rate has not been measured and it is surely difficult to do so, due to its fastness and the relatively small distances involved. However, this example indicates clearly that cultural diffusion can have a much faster tempo than demic diffusion (Cavalli-Sforza 2003).

Concerning hunter-gatherers, very recently Dolbunova et al. (2022) have estimated the range 6–10 km/year for the inland westwards spread of pottery in eastern Europe by performing linear fits to the seven most reliable sites and combining the ranges from eight different likely origins (correlation coefficients up to $r = 0.92$, $N = 7$). Similar to previous work on the spread of pottery (Jordan et al. 2016), they measured distances along least-cost paths, i.e., curved lines that take into account non-homogeneities (e.g., geographical variations in altitude). According to our Fig. 2, such a rapid range expansion (6–10 km/year) has been never observed for inland demic diffusion in prehistory. This strongly suggests that, also among hunter-gatherers, the spread of ceramics was dominated by cultural diffusion.

A crucial feature of farming is that it enabled population densities to grow up to about 100 times higher than those supported by hunting and gathering (Ammerman and Cavalli-Sforza 1984). It is reasonable to believe that such an overwhelming superiority was a key factor in the spread of farmers in regions originally inhabited by hunter-gatherers. Another difference between farming and other innovations (such as pottery) is the following. As pointed out by Cavalli-Sforza (2002), demic diffusion is the leading mechanism in the spread of innovations such that they require the learning of new techniques that are not easily acquired and require important changes of customs and way of life (an example of such an innovation is agriculture). In contrast, cultural diffusion dominates when innovations are easier to learn (e.g., pottery, see Dolbunova et al. 2022). The reasoning behind this distinction is that when an innovation or cultural trait requires years of learning and a radical change in lifeways, adult individuals will rarely perform such a drastic transition (i.e., they will be reluctant to copy the cultural trait from other individuals). However, children born in families that already have the cultural trait will naturally acquire it from their parents and the innovation will spread slowly across the landscape because children have to grow up over many years before they can separate from their parents and carry the cultural trait with them. In contrast, if an innovation (e.g., pottery) requires little learning, it can be easily transmitted from neighboring individuals of the same generation in a much shorter time scale, so it will tend to spread substantially faster.

Conclusions

The present paper probably constitutes the largest empirical cross-cultural exploration of agricultural expansion rates so far. This review reports the spread rates of 20 premodern expansions of farming and/or herding, including 3 new estimations (the Alps, Galicia, and the Cantabric), and discusses them in relation to major quantitative theories with the potential to generate and test hypotheses. As shown by Fig. 2, at continental and large scales most inland spread rates were about 1 km/year. Well-established demic mathematical models, e.g., Eq. (2), agree with rates around 1 km/year. However, this agreement holds only at large spatial scales. If we look at the regional level, there is considerable variation in the spread rate. Europe and Anatolia are the areas for which there are more data, and they show that a spread rate of about 1 km/year is not realistic in some regions. For example, the spread rate was faster in the central Balkans, 1.2–2.1 km/year (Porcic et al. 2020) and slower along the inland route of Neolithic spread in Europe, where it decreased from 1.6 to 0.0 km/year (Fig. 5). At first sight, we could be tempted to conclude that for such regions the reproduction growth rate a, generation time T and/or diffusion coefficient D had values outside the ranges suggested by ethnographical observations. However, this is not the only potential explanation. An alternative possibility is that the values from ethnography are also realistic in prehistory but the classical mathematical wave-of-advance model, Eq. (2), needs to be refined in some regions. For example, some speeds below 1 km/year are a natural consequence of competition for space between early farmers and hunter-gatherers. This effect is captured by Eq. (5), which leads to slower spread rates than Eq. (2) for the same values of a, T and D and explains quantitatively the gradual slowdown of the Neolithic along the inland route in Europe (Fig. 5). Another interesting model is nonisotropic dispersal, Eq. (4), which can lead either to slower or faster spread rates than Eq. (2) for given values of a, T and D.

A third example is the presence of cultural in addition to demic diffusion, Eq. (3), which leads naturally to faster speeds than purely demic diffusion, Eq. (2), for the same values of a, T and D. As reviewed in the present paper, other possible factors that may decrease or increase the spread rate but have not yet been formalized by means of mathematical models. Some examples include climatic effects (Betti et al. 2020; Davison et al. 2006), altitude (Ammerman and Cavalli-Sforza 1971, 1984; de Souza et al. 2022) and disease (Rascovan et al. 2019).

Overall, we see that the 1 km/year value is useful as a reference that is approximately valid at continental and large scales, but there is substantial regional variation (Fig. 2). Regional differences in the spread rate can be useful to understand specific features of human behavior at work in different regions. This can be done quantitatively by comparing the spread rate from archaeological data to that according to mathematical models, e.g., Eqs. (2)–(5). One example is the fast spread rate along the western Mediterranean coast (about 9 km/year), which combined with mathematical models and simulations strongly suggests displacements of about 300 km per generation (Fort 2022b; Isern et al. 2017a). In sharp contrast, many inland expansions have spread rates of only about 1 km/year (Fig. 2), which suggests that the dispersal distance is only about 50 km (Fort et al. 2007). Thus, comparing sea and inland spread rates makes it possible to uncover a major difference in the dispersal behavior of pioneering farmers. The reason why the spread rates and dispersal distances were much larger for some sea expansions than for inland ones is unknown, but the following explanation has been proposed. Since humans can walk at a speed of about 5 km/h, the characteristic distance for inland expansions (about 50 km) can be covered by foot in a single day (with a 10-hour walk). In contrast, travelling the much longer characteristic distance for fast sea expansions (about 300 km) would require 6 walking days and this would make it difficult for pioneering farmers to visit their parents often. However, reconstructions of the boats presumably used by ancient Polynesian farmers can attain speeds of about 19 km/hour (Finney 1977), so 15 hours would be enough to travel about 300 km. This suggests that boats made it possible to cover such long distances in only one or two days, so that early farmers could easily keep in contact with their families. This is one possible explanation of the fact that some sea expansions are much faster (Fort 2022b).

Another illustration of the potential of combining archaeological data and mathematical models is the estimation of the number of hunter-gatherers that were incorporated in the populations of early farmers, per farmer and generation (see the text below Eq. (3) and Fig. 7). The results summarized in this paragraph and the previous one show that comparison between archaeological data on one hand and mathematical models (or simulations based on them) on the other is a powerful approach to unveil some key aspects of prehistoric human behavior, which in some cases cannot be inferred by other means.

At continental and large scales, most expansions of farming and/or herding seem to have been driven mainly by demic diffusion, with cultural transmission playing only a secondary role. However, some prehistoric expansions of cultural traits other than farming and herding can be dominated by cultural diffusion. Moreover, the spread rates of mainly cultural expansions can be much faster than those of mainly demic expansions (because the cultural trait involved can be transmitted some distance away without need to wait for children to grow up and disperse away from their parents). The spread of pottery is an example of a fast, mainly cultural spread, both for farmers and hunter-gatherers.

There is an acute need of archaeological data to improve the estimations and increase the number of expansions analyzed. Future work, especially dealing with regional studies and/or very fast expansions, will surely require high-quality radiocarbon dates. Similarly, more genetic data from ancient individuals in world regions where agriculture spread are needed. It is very encouraging that for the spread of the Neolithic in Europe, ancient genetic data combined with spatial simulations of genetic clines have shown that only between about 1% and 3% of Early Neolithic farmers interbred with hunter-gatherers.

This vein of research is likely to keep in progress in the following decades and deliver further and more precise measurements of spread rates and genetic clines, leading to quantitative estimations of key features on human behavior (such as dispersal distances per generation, interbreeding percentages, competition dynamics, etc.) for many ancient expansions of farming and herding around the world.

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