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Climate shaped how Neolithic farmers and European hunter-gatherers interacted after a major slowdown from 6,100 BCE to 4,500 BCE

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The Neolithic transition in Europe was driven by the rapid dispersal of Near Eastern farmers who, over a period of 3,500 years, brought food production to the furthest corners of the continent. However, this wave of expansion was far from homogeneous, and climatic factors may have driven a marked slowdown observed at higher latitudes. Here, we test this hypothesis by assembling a large database of archaeological dates of first arrival of farming to quantify the expansion dynamics. We identify four axes of expansion and observe a slowdown along three axes when crossing the same climatic threshold. This threshold reflects the quality of the growing season, suggesting that Near Eastern crops might have struggled under more challenging climatic conditions. This same threshold also predicts the mixing of farmers and hunter-gatherers as estimated from ancient DNA, suggesting that unreliable yields in these regions might have favoured the contact between the two groups.

The beginning of the Holocene saw a major shift in human subsistence strategies in the Near East, from foraging to an increased reliance on domesticated animals and crops (the Neolithic economy[1]). This change in food procurement, with the development of agriculture and animal husbandry, was accompanied by other major economic and societal changes, including sedentism, higher population density and villages with permanent habitation and storage structures. From around 7,000 BCE (ref. [2]), farming appeared in Southeast Europe and spread quickly throughout the continent. The rapid diffusion of the Neolithic lifestyle in Europe, following an approximate south-east to north-west direction, suggested a wave of population dispersal from the Levant (demic diffusion), instead of a slower conversion of European hunter-gatherer populations to farming by cultural diffusion. Craniometric analyses of European early Neolithic farmers and Mesolithic hunter-gatherers provide some support for the demic diffusion model[3], although the interpretation of skeletal morphology is somewhat equivocal[4]. Recent ancient DNA studies of early Neolithic farmers throughout Europe, from the Mediterranean regions to Ireland and Scandinavia, found marked genetic differences compared with local hunter-gatherers and a close similarity with early Near Eastern farmers, especially from the Anatolian region[5–10]. Based on these different lines of evidence (that is, archaeological, phenotypic and genetic), it is now widely accepted that the arrival of agriculture in Europe was accompanied by an influx of people, not just ideas, from the Near East.

While the overall picture has become increasingly clear, the wealth of new archaeological data has also revealed substantial regional differences in the expansion speed of farming[11–14]. In particular, radiocarbon dates from early Neolithic sites suggest a marked slowdown of the Neolithic diffusion approaching the North and Baltic Seas[15–17]. Different explanations have been put forward to explain the reduction in diffusion speed at higher latitudes. A possible explanation is that the Near Eastern package of crops might not have performed well in the colder and wetter climate of Northern Europe, making it difficult for Neolithic farmers to establish new permanent colonies and to thrive[18–21]. Colledge et al.[22] described a marked change of the Neolithic crop package across Europe, in terms of significantly lower species diversity of cereals and pulses in Central and Northwest Europe compared with sites in Southwest Asia, Southeast Europe and the Mediterranean. While the authors attribute some changes in the use of crops in Northwest Europe to cultural factors, climatic conditions are also deemed responsible for the lower diversity in the crop package.

An alternative explanation for the slowdown is that early farmers might have encountered a higher density of hunter-gatherers in northern regions compared with Central or Southern Europe, possibly because a favourable coastal environment ensured that hunting, fishing and gathering were particularly reliable and productive[23–26]. The presence of large, successful foraging communities could have posed a stronger resistance to the establishment of new settlements by incoming farmers[13,16,24]. Another explanation is that the mode of diffusion of agriculture changed after the first wave into Southern and Central Europe, with acculturation of local foraging populations playing an increasingly important role at the northern edge of the continent[15,24].

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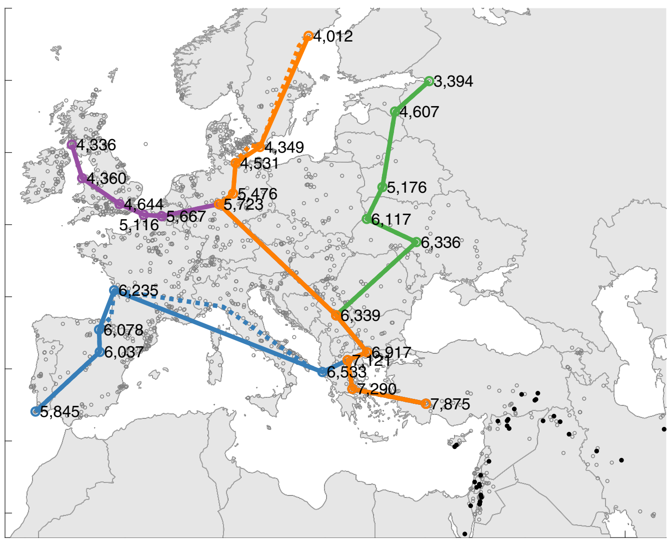

Fig. 1 | Four major axes of expansion of the Neolithic transition. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian and Northeast European axes, respectively. Key dates are highlighted. The Neolithic sites in the Levant before the expansion into Europe (dates up until 7,500 BCE) are shown in black. Country borders were plotted using ref. [74].

In this study, we formally test the role of climate in driving the tempo of the spread of farming in Europe by assembling a large database of first arrival dates of domesticates throughout the continent, and analysing changes in speed in relation to palaeoclimatic reconstructions. We also synthesize and reanalyse ancient DNA data to quantify the interaction between early farmers and local hunter-gatherers in the context of the observed climate-driven patterns.

Results

Our analysis of a database of 1,448 securely dated early Neolithic sites throughout Europe showed that the expansion was not homogeneous, but rather progressed along several main axes. We characterized these axes by identifying locations that lead to an expansion of the minimum convex polygon including all sites up to a certain date (Extended Data Fig. 1). These points fell along four main axes of expansion (Fig. 1 and Supplementary Video 1): (1) along the Mediterranean (later referred to as the Mediterranean axis); (2) across Central Europe and into the United Kingdom (the Central European axis); (3) northwards through Central Europe and into Scandinavia (the Scandinavian axis); and (4) into Northeast Europe (the Northeast European axis). The expansion along each axis tended to have a rapidly expanding front, as well as progressive, slower infilling of neighbouring areas (see Supplementary Video 1). For our analysis, we focused on the expansion fronts: along each axis, we assigned dates of passage for all points constituting the axis using a linear interpolation, from which we estimated the expansion time and cumulative distance covered since the beginning of the expansion (Fig. 2a).

Following an initial rapid expansion, we observe a marked slowdown along the Central European (approximately 6,200 BCE), Scandinavian (approximately 5,400 BCE) and Northeast European axes (approximately 5,700 BCE), as shown by the flattening of the expansion curves in Fig. 2a, highlighted by the black sections. During each axis-specific slowdown period, mean expansion speeds dropped to the lowest values observed in the entire dataset (Extended Data Fig. 2). We note that the slowdown on the Central European axis occurred before it reached the Atlantic coast, and was thus not a mere consequence of having to cross the English Channel. The decrease in speed is absent on the Mediterranean axis, which probably involved sea voyaging[27] and terminates when reaching the Atlantic coast of the Iberian Peninsula. To investigate the role of climate in driving the tempo of the Neolithic expansion, we superimposed the area of slowdown with a number of variables from palaeoclimatic reconstructions. We tested whether the three episodes of slowdown are characterized by a given climatic condition by simulating 10,000 expansions using a correlated random walk (CRW) with the same distribution of step sizes and turning angles, as well as the same splitting topology, as the observed routes, to capture their spatial autocorrelation (using an approach analogous to that used for testing movement patterns in animals[28]). A climatic variable was deemed to be significantly associated with the slowdowns if the range of its values for the three locations of the observed slowdown was smaller than the expected range from the simulated CRWs that mimic the characteristics of the expansions (see Methods for details). There was a clear correspondence with the number of growing degree days above 5 °C (GDD5; a measure of heat accumulation during the growing season), with the slowdowns occurring below 2,000 GDD5 ($P = 0.0324$; Fig. 2a,b). To a lesser extent, there was also a correspondence with mean monthly average summer temperature (with the slowdown occurring when temperatures dropped below 16 °C; Extended Data Fig. 3; $P = 0.097$). The GDD5 measure is commonly used by agricultural scientists and practitioners to evaluate the viability of plants or cultivars in different regions, and to model their pace of growth[29,30]. In contrast, there was no link with the mean winter temperature ($P = 0.5988$; Extended Data Fig. 4), precipitation in the driest month ($P = 6.043$; Extended Data Fig. 5) nor other variables that captured the average climate over the whole year (annual mean temperature ($P = 0.1687$) and net primary productivity ($P = 0.6812$); Extended Data Figs. 6 and 7). The link between the speed of the expansion and variables that characterize the growing season of crops supports the hypothesis that the slowdown was linked to reaching regions with climatic conditions that were inappropriate for species originally domesticated in the Near East. Supporting this conclusion, we note that the Mediterranean axis (that is, the only axis to show no signs of slowdown) moved along a path characterized by a favourable growing season (both in terms of GDD5 and summer temperature) until it reached a natural barrier.

We investigated whether the relationship between incoming farmers and hunter-gatherers from Western Europe (WHG) changed once the expansions started slowing down, with increased admixture between the two groups. We collated published genome-wide data from 295 Neolithic individuals (Fig. 3a), then quantified the relative contribution of hunter-gatherer ancestry using the f_4 statistics in the form f_4(Mbuti, WHG; Anatolian Neolithic, European Neolithic), which has been shown to be a good predictor of population-level estimates of hunter-gatherer ancestry[31]. To account for the lack of independence of samples from the same or close-by locations, we used a generalized least-squares framework that takes into account the covariance of estimates of f_4, as estimated by jack-knifing. Even after accounting for the progressive increase in hunter-gatherer ancestry that occurred later in the Neolithic (modelled as an increase in hunter-gatherer ancestry with time since the arrival of the Neolithic at a given location), there was a significant increase in the genetic contribution of hunter-gatherers into Neolithic individuals with decreasing GDD5 (Fig. 3b; $\chi^2_1 = 3.84$; $P = 0.0499$), with a marked increase below 1,700 GDD5. Thus, it appears that areas of slow expansion were also characterized by higher genetic admixture between the incoming farmers and the local hunter-gatherers.

Finally, we investigated whether the slowdown and associated increased admixture could be due to higher densities of hunter-gatherers. We used three datasets of locations of Holocene hunter-gatherer archaeological sites[32–34], which have been used in

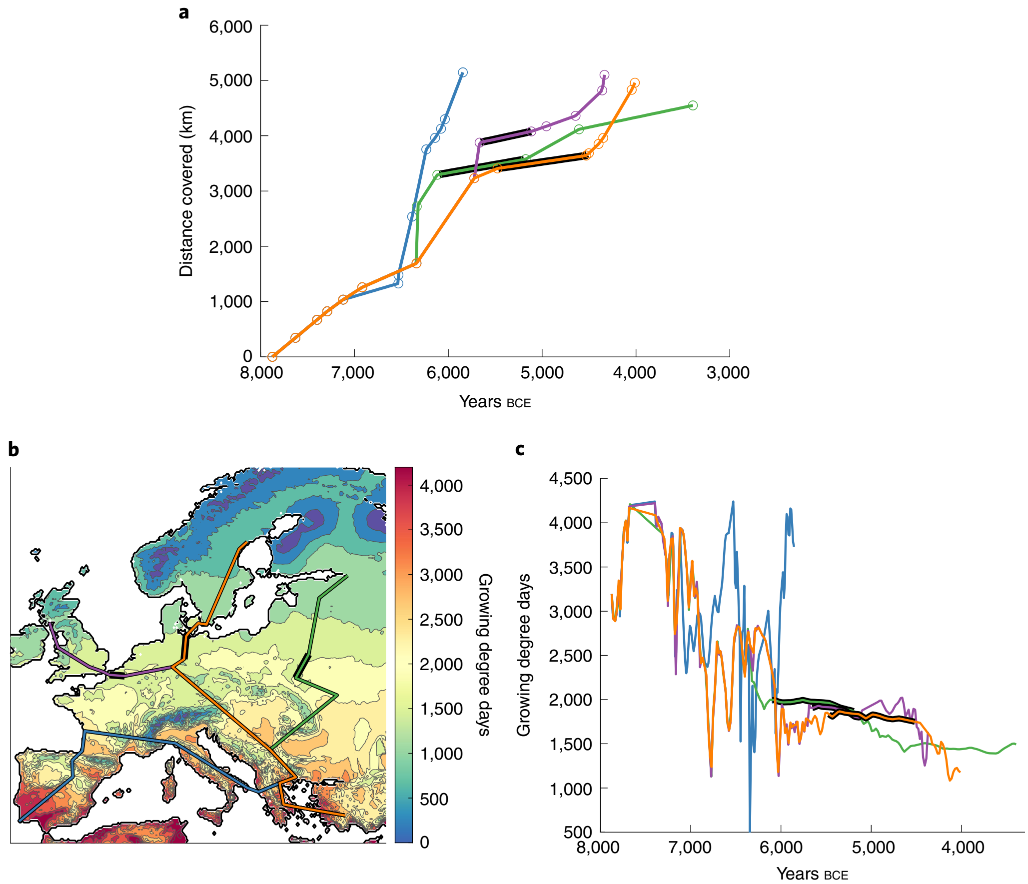

Fig. 2 | Axis-specific expansion speeds and climatic conditions. a, Cumulative distance covered along each expansion axis. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian and Northeast European axes, respectively. The slowdown is highlighted by black lines. **b**, The expansion axes, with their respective slowdowns, superimposed on a map of growing degree days at 5,500 BCE. **c**, Growing degree days experienced along each expansion axis.

the past as a proxy for population densities. We failed to find any clear association between the density of archaeological sites and the areas of interest (Extended Data Fig. 8), but we note that in all datasets densities of sites seem to mostly reflect modern country boundaries, suggesting that these datasets are too biased in terms of sampling effort to be informative.

Discussion

The pace of expansion of farming in Europe, as reconstructed by our large database of dates, encountered a marked slowdown in Northern Europe, as previously suggested by other authors[15–17,19,26], adding further weight to the argument that the Neolithic expansion was not a continuous process of diffusion, but a series of episodes of varying speeds. The expansion dynamics recovered from our algorithm is qualitatively similar to the one described by Silva and Steele[17], who used a path-tracing approach to model radiocarbon dates of Neolithic arrivals. In their analysis, an expansion model with an altitudinal cut-off and a latitudinal gradient in the rate of spread provided the best fit to the relationship among pottery types. It is more difficult to relate our dates to the analysis by Silva and Vander Linden[35], who looked at the expansion as a diffusive process rather than focusing on specific axes of expansion; however, qualitatively, our analysis seems to capture the key period of slowdown at high latitudes that was also highlighted by their approach. Our analysis provides a clear mechanism for this latitudinal slowdown, linking it to a decline in GDD5 (and, to a lesser extent, summer temperatures)—that is, to the suitability of summer for the growth of early Neolithic crops. It seems probable that the conditions in Northern Europe were too different from the original Levantine conditions where the crops evolved, limiting the success of some of them. Indeed, it has been noted that the number and variety of crops used by early farmers decreased during the expansion into Central and Northern Europe[22,26,36]. Conolly et al.[37] found that cultural drift alone cannot explain the pattern of decrease in crop diversity, and that other variables (in particular, regional climate and cultural preferences) must have played a role. The fact that a similar decline in crop diversity—or indeed a slowdown in expansion speed—is not observed along the Mediterranean axis[36] also supports the interpretation that the lower crop diversity and the decrease in speed in Northern Europe are probably related to climate.

The establishment of cereal cultivation in the British Islands and Scandinavia, around 4,600-4,000 BCE (refs. [38–40]), is followed by a sharp decrease and even disappearance of cereals from the archaeological record for several centuries[40,41], suggesting that their yield might not have been enough, or might have been too unpredictable, to support the local populations. Where cereal cultivation continued, such as in some Scottish islands and part of Scandinavia, there was a marked shift towards the use of barley, which is more resilient to cold temperatures and general stress[41,42]. The original Neolithic package included cereals that are planted in autumn and harvested in summer[43]. Instead, spring varieties of barley are cultivated today in northern latitudes, planted in spring and harvested in autumn, with no need to survive the harsh winters of Northern Europe. It is possible that the original winter varieties were not well suited to the

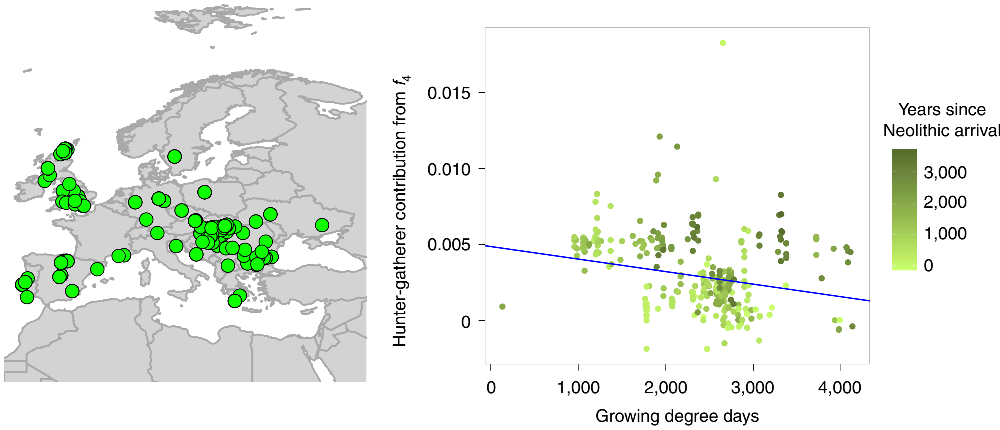

Fig. 3 | Hunter-gather ancestry and climatic conditions. a, Map of Neolithic samples for which estimates of hunter-gatherer genetic ancestry are available. Country borders were plotted using ref. [74]. **b**, Contribution of hunter-gatherer ancestry against growing degree days (GDD5). The line of best fit was estimated using a generalized least-squares framework.

colder and wetter climate of Northern Europe, and that agriculture started thriving in the British Isles in the Early Bronze Age because of the introduction of spring varieties[41].

Admixture between incoming farmers and local hunter-gatherers increased as the former ventured into areas with a less favourable growing season, in good agreement with the slowdown revealed by archaeological arrival dates. This provides a mechanistic explanation for a previously noted increased hunter-gatherer admixture at higher latitudes[31]. A possible link between the speed of expansion and admixture with hunter-gatherers had also been suggested by Silva and Vander Linden[35]. Their conclusion was based on anecdotal evidence based on a few genetic estimates of admixture; the large number of genomes that have been sequenced since allowed us to formally make the link between climate and admixture. It seems likely that as food production became less reliable incoming Neolithic farmers had to increasingly rely on hunting and gathering, bringing them into contact with the indigenous communities of hunter-gatherers, and perhaps favouring exchanges of goods and local knowledge. Our analyses of densities of Mesolithic archaeological sites fails to reveal any clear pattern that could support an interpretation that this increased admixture was due to relatively larger hunter-gatherer communities in more extreme climates, but we note that this proxy is ill suited to infer actual population densities. Two recent studies[44,45] that used climate niche models to predict climatic suitability from sites (an approach that corrects, to some extent, for sampling bias in different regions) also did not predict higher densities of hunter-gatherers in the areas of high admixture highlighted by our study, supporting the view that increased contact was mostly a consequence of climatic factors.

A key aspect that remains to be explored is the dynamics of the later expansion following the slowdown. This expansion was fast, as already noted by Silva and Vander Linden[35], suggesting an improvement in farming techniques; yet, admixture with local hunter-gatherers continued at a high rate in these newly settled regions. A possible explanation is that, even with the improved food production techniques that allowed them to move into harsher climates, the livelihood of these newly expanding farmers was more reliant on hunting and gathering compared with what happened in more benign climates, bringing them into contact with indigenous hunter-gatherers irrespective of their speed of expansion. This question will only be answered by a more detailed investigation that is beyond the scope of this paper.

In addition to the particularly pronounced slowdown of the Neolithic expansion identified in our dataset and earlier attempts[15–17], which we have shown to be strongly linked to climatic conditions, we note that previous studies have suggested the existence of other periods of lesser local slowdowns[14,35]. Not captured by our approach, these pulse–pause episodes may have possibly been caused by factors other than climate, such as demographic or sociocultural conditions[46].

By synthesizing information on archaeological sites, palaeoclimate reconstructions and ancient DNA, we were able to obtain a consistent picture across Europe of how climatic factors affected the initial expansion of Neolithic farmers and their interaction with local hunter-gatherers. An important test of the universality of these relationships will be a detailed analysis of the Neolithic expansion into regions further east, for which there are very few radiocarbon dates at present. While the expansion of agriculture in East Asia is not well characterized compared with the European record[47], recent work based on ancient DNA[48] has revealed an analogous pattern of increasing hunter-gatherer ancestry at higher latitudes, suggesting a similar dynamics to the one inferred for Europe. In terms of future studies, of particular interest will be areas that might have been colonized by farmers from the mountainous eastern part of the Near East, as the crops domesticated in those challenging climates might have been hardier than those from Anatolia, leading to the prediction of the slowdown occurring under more extreme climatic conditions.

Methods

Archaeological dates of first arrival of the Neolithic. We expanded and updated Pinhasi and colleagues'[49] dataset of dates from Early Neolithic sites, from 735 to 1,448 sites throughout Europe, the Middle East, Western Asia, and the Arabian Peninsula (Fig. 1 and Supplementary Data 1). Only one date per site was recorded, the earliest radiocarbon date reliably associated with Early Neolithic cultures with evidence of domestication (thus, Neolithic sites defined solely on the presence of pottery or other material culture that could not be directly linked with domestication were excluded). We discarded all dates with a standard deviation of over 200 years, as well as dates associated with dubious stratigraphy, outlier dates from long-living material such as trees, and dates likely to be affected by a reservoir effect of unknown magnitude. A list of discarded dates and a brief explanation for the decision is available as Supplementary Data 1. The dates were collected from published papers, books, or online databases up to the summer of 2015. Only sites with evidence of domesticates (either plant or animal) were included, rather than simply pottery. All dates were calibrated using OxCal version 4.2.3[50], based on the IntCal13 atmospheric curve[51]. Our dataset is available to the public and the wider scientific community as an important resource for future studies (Supplementary Data 1).

The earliest occurrence of Early Neolithic cultures with evidence of domesticates and the wave of expansion of farming outside the Levant was visualised by creating a series of maps at 100-year intervals based on calibrated dates BCE, for the period between 7,500 and 3,000 BCE (Supplementary Movie 1).

Although the calibrated dates often have a margin of error higher than 100 years, and therefore exact arrival times should be taken with a degree of caution, the high temporal definition allows a better understanding of the expansion axes.

The chronology and geographic location of the Neolithic sites was used to determine the main directions of Neolithic expansion into Europe. We used an approach based on minimum convex polygons to capture the axes of expansion: in the presence of axes out of an origin (and under the assumption that they are sufficiently separate in space), any expansion along one of them should also increase the minimum convex polygon that underlie all locations (Extended Data Fig. 1). Only sites in the Levant and Europe were included in the analyses; the expansion south into the Arabian Peninsula and East into Tajikistan had a limited number of sites with irregular spatial distribution, making it difficult to define likely expansion axes. Sites older than 8,000 calibrated years BCE were used to define a core area for the development of farming. The temporal and geographic expansion of domesticates outside the core area was analysed at 100-year intervals; at each step, a minimum convex polygon was fitted to the sites' geographic distribution and used to identify the new vertices of Neolithic expansion (R package grDevices, function *chull*). To reduce noise and identify the main axes of expansion, we only selected new vertices that were at least 50 Km away from the previous nearest vertex. The new vertices were connected to previously identified vertices in order to define the expansion routes. To identify to which previous vertex the new vertex should be connected, we selected up to four geographically close existing vertices, including the closest one and up to three others within 150% of the distance between the new vertex and the closest existing vertex. To choose among these possible connecting vertices, we looked at the number of filling-in sites that appeared near the connecting segment (within 50 Km from the segment) in the following 300 years; we selected the segment with the highest density of filling-in sites (number of sites divided by segment length). A visual explanation of this process is provided in Extended Data Fig. 1. The process of vertex selection was first carried out in continental Europe (excluding Scandinavia), and repeated separately for Great Britain and Scandinavia. Once the process was completed, we reviewed the resulting routes of expansion and identified the most important axes; for this purpose, we ended all expansion routes when they reached a substantial geographic barrier, such as an ocean or a sea with no evidence of crossing, and we removed offshoots shorter than 1000 Km. We note that this approach does not presume any particular mechanism. Thus, in the case of the coastal expansion along the Mediterranean, it is bound to produce a coarse reconstructions; however, any refinement would require arbitrary decisions about the mode of expansion, leading to circularity in later analyses.

Based on the sequence of dated sites defining the main axes of expansion into Europe (Fig. 1), we assigned dates of passage for all points constituting the axes a using linear interpolation. This provides the speed of the expansion at any time, or, equivalently, the cumulative distance covered since the beginning of the expansion (Fig. 2a).

Palaeoclimate reconstructions. Next, we assigned values of environmental variables to each point on the expansion axes. Climatic variables were based on 1,000 year interval climate reconstructions of monthly temperature, precipitation and cloud cover generated by the Hadley Centre global climate model HadCM3 model[52] with specifications reported elsewhere[53]. We downscaled these data from their original 2.5°×3.5° resolution to a 1/6° grid by means of the delta method[54] and high-resolution present-day observed climate data[55]. The delta method also bias-corrects the simulated data, by applying the difference (bias) between present-day simulated and empirical climate to past simulated climate. This ensures that the obtained reconstructions are close to present-day observed climatic conditions at times when the difference of simulated climate to present-day simulated climate is small. Based on monthly values, we estimated daily average temperature values T_{avg} for each year using a piecewise cubic Hermite interpolation. These were used to calculate annual Growing Degree Days (GGD5) as $\sum_{i=1}^{365} \max(T_{avg}\text{-}T_{base},0)$, where $T_{base}=5\,°\text{C}$. Based on the downscaled climate variables, we used Biome4[56] to compute annual net primary productivity (NPP).

We tested whether the slowdown in the three routes occurred under unusual climatic conditions. To do so, we needed to generate simulated expansions that had similar characteristics to the real one, matchings its topology. We generated 10,000 expansions using CRWs—an approach commonly used to model animal movement to generate the null distribution of a given property of spatial tracks. We note that we do not necessarily see a CRW as a mechanistic description of the expansion dynamics, but rather a statistical null model to generate expansions with the appropriate spatial structure. Specifically, we used functions in the adehabitatLT package[57]. First, we estimated the appropriate variance in turning angles and step size variable *h* by pooling all unique steps in the three expansions up to the points where the slowdown occurred (avoiding double counting steps in common among multiple routes). We then generated 10,000 CRWs with a branching pattern equivalent to the one observed in the real data, based on the number of steps in common among the routes. Finally, for each environmental variable, we estimated the range (maximum versus minimum value) across the terminal points of the three routes, and compared the observed range with the ranges obtained from the CRWs. Using the standard deviation of values at the terminal points instead of the range gave qualitatively similar results. The proportion of simulations with a range narrower than the observed one gave the probability of observing the slowdowns occurring within a given climatic isocline by chance.

Admixture with hunter-gatherers. We collated available ancient genome-wide data for European Neolithic samples. In total, genotypes that overlapped with the Human Origins and Illumina genotyping platforms[7] from 292 individuals were pooled together from datasets published in refs. [31,58–60]. These genotype calls were merged with data from: five Mbuti individuals from the Simons Genome Diversity Panel[61]; hunter-gatherers from western Europe (KO1 (ref. [62]), Villabruna[63], La Braña[64] and Loschbour[65]); and Anatolian Neolithic samples[9]. The qpDstat program in the ADMIXTOOLS package[66] was used to calculate the statistic f_4(Mbuti, WHG; Anatolia_Neolithic, test) where the test population was each of the European Neolithic samples in turn. This *f*4 configuration was used in ref. [67], and was shown to correlate well with the proportion of Mesolithic admixture into Neolithic populations. To account for the correlated demographic history of our samples, we took the approach used in ref. [63]. In brief, the covariance matrix of the errors was estimated by a weighted block jackknife (with five centimorgan blocks), and the relationship between f_4 and the predictors (GDD5 and time since the arrival of the Neolithic at a given location) was quantified using a generalized least-squares framework (see ref. [63] for details of the relevant calculations).

Density of hunter-gatherer archaeological sites. We obtained data on the distribution of late Palaeolithic and Mesolithic sites during the Holocene from three published sources: the Palaeolithic Radiocarbon Europe Database version 21 (ref. [34]) (we extracted sites younger than 9,500 BCE); Steele and Shennan[33]; and Pinhasi et al.[32]. We note that even though densities of sites have been used as a proxy for population density in the past, this interpretation can be problematic because the number of sites occupied by the same number of individuals is dependent on settlement systems and mobility strategies[68–70], as well as seasonal aggregations of groups and fission–fusion behaviour, as is well documented in ethnographic studies of hunter-gatherers[71–73].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data collected for this study are available from the Open Science Framework repository (https://osf.io/2hcqr/?view_only=c06b3949770549379ff7e5e4eceaf876).

Code availability

The code used in this study is available from the Open Science Framework repository (https://osf.io/2hcqr/?view_only=c06b3949770549379ff7e5e4eceaf876).

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Author contributions

A.M. devised the project. L.B. and R.P. collected the archaeological data. L.B. calculated the expansion routes together with A.M. R.B. curated the palaeoclimatic reconstructions and conducted the analyses of climate and expansion speed together with A.M. and A.E. L.K.B. conducted the CRW analysis together with A.M. E.R.J., M.L. and P.M.D. collected the ancient DNA data and ran the relevant analyses together with A.M. F.T. collated the information on Mesolithic sites. A.M. wrote the first draft of the paper together with L.B., R.B. and E.R.J. L.B., R.B., E.R.J., A.E., F.T., V.S., M.L., P.M.D., L.K.B., P.R.N., J.S., R.P. and A.M. interpreted the results and revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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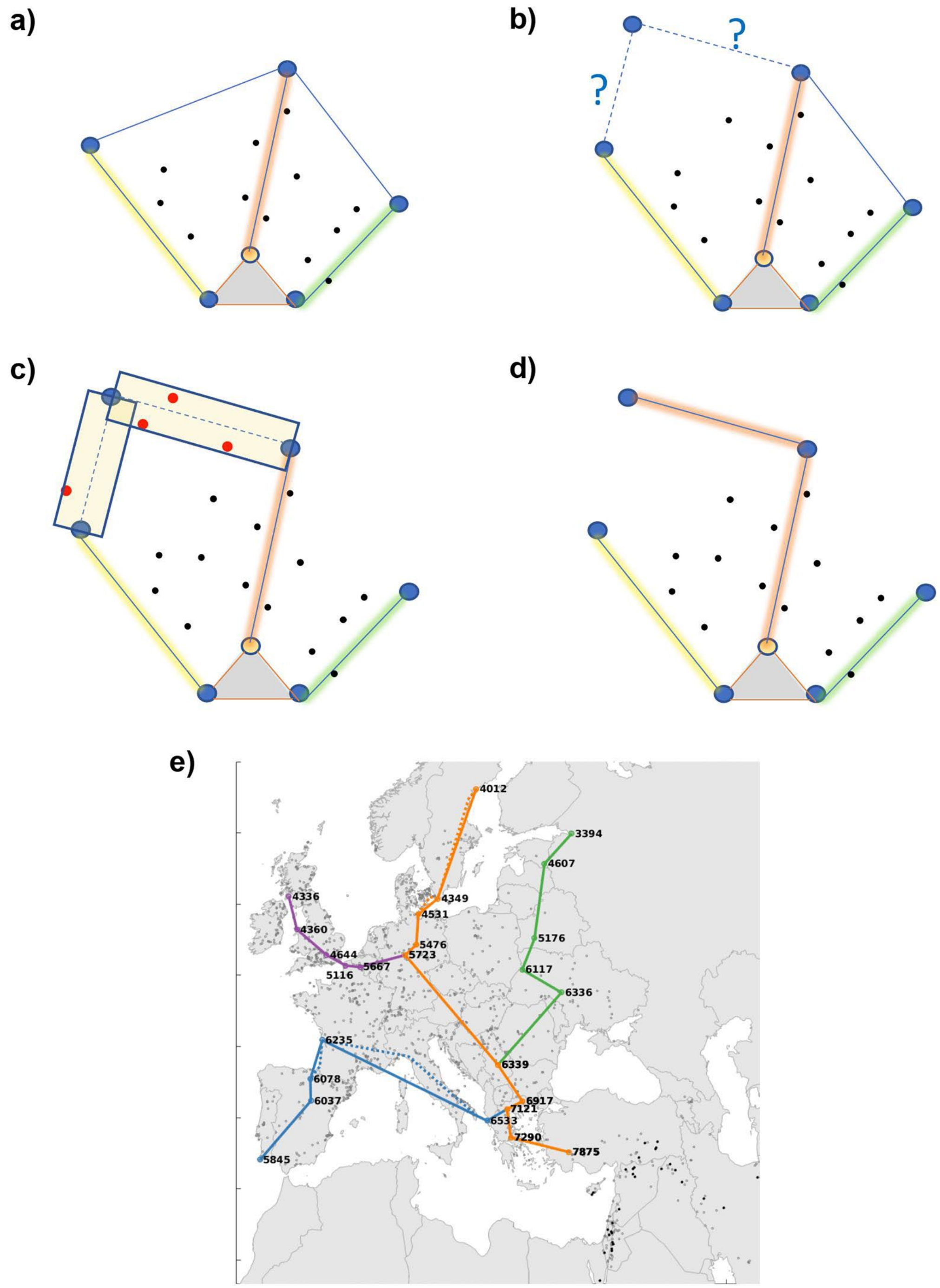

Extended Data Fig. 1 | Process of selecting the connecting segments of the Neolithic expansion routes. a, Main vertices (blue circles) and routes of expansion (in yellow, red and green) from the core area (grey polygon) at time *X* before common era (BCE); Neolithic sites present before time *X* indicated as small black circle and blue circles, blue lines showing the minimum convex polygon around the sites' distribution. **b**, At time *X* - 100 years, a new main vertex of expansion is identified by redrawing a minimum convex polygon over the updated set of Neolithic sites. Two possible connecting segments are identified (dashed lines), including the shortest segment connecting with previous vertices, and an additional segment whose length was less than 150% of the former. **c**, To identify the most likely expansion route, we counted the number of Neolithic sites that occurred in the following 300 years (up to time *X* - 400 years; small red circles) within a buffer zone of 50 Km either side of the connecting segments (orange shaded rectangles) and divided it by the segment length. **d**, The segment with the highest density of filling-in sites in the following 300 years was selected. **e**, Solid lines show the obtained expansion routes. Where these cross oceans in unrealistic ways, we added a minimal set of additional waypoints to force routes to run along coasts instead (dashed lines). Country borders were plotted using ref. [75].

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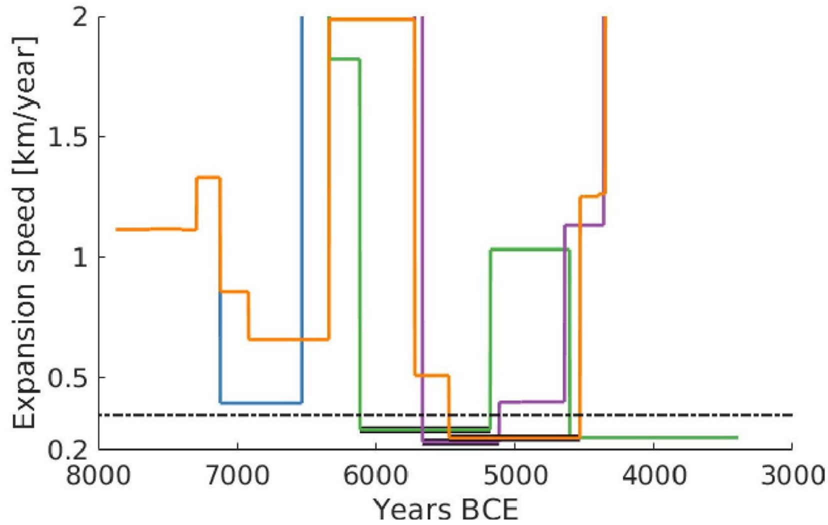
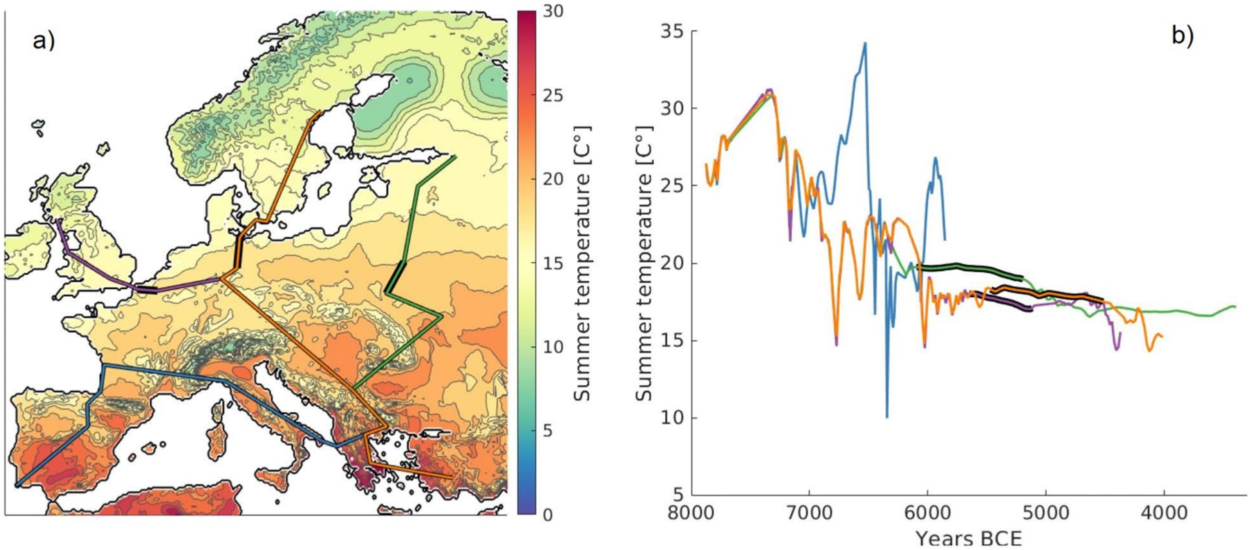
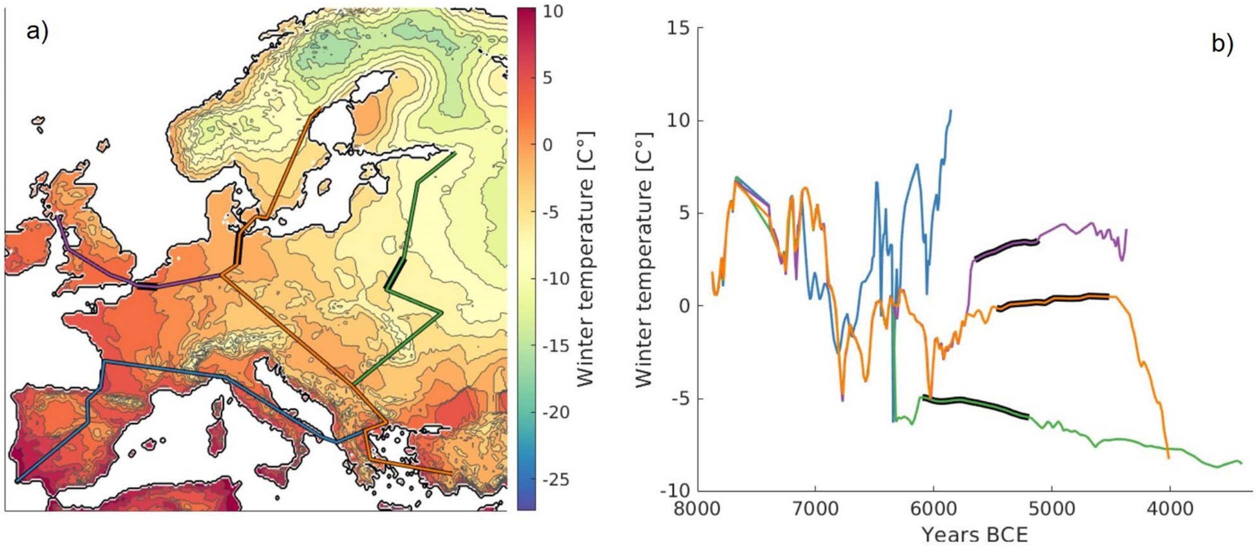


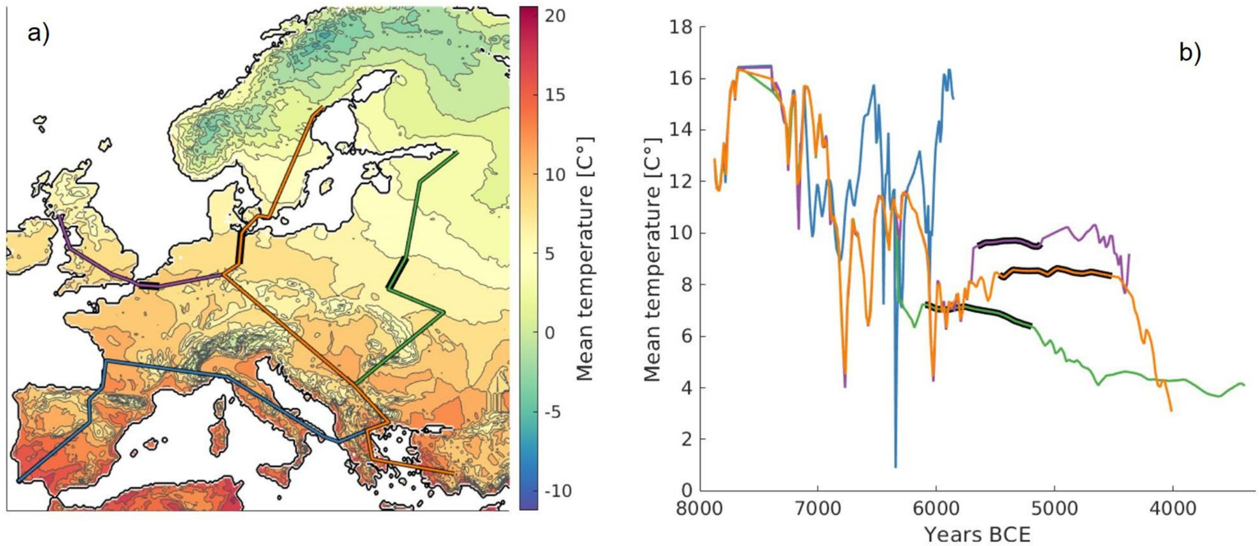
Extended Data Fig. 2 | Mean expansion speeds of each expansion axis. Lisnes were obtained by taking the derivative of the cumulative distances in Fig. 1. Colours correspond to the same routes as in Fig. 1. Slowdowns are highlighted by a black line. The dashed black line represents a threshold below which expansions were considered to be subject to a slowdown.



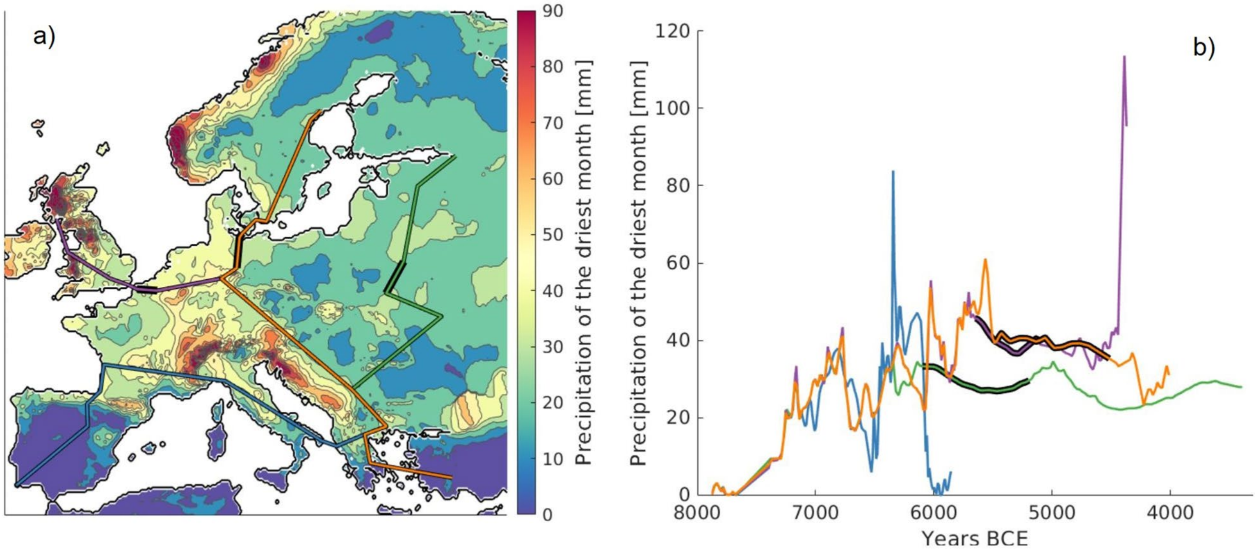
Extended Data Fig. 3 | Expansion axes and mean summer temperature. a, The expansion axes superimposed on a map of mean summer temperature days at 5,500 BCE. **b**, Mean summer temperature experienced along each expansion axis. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian, and Northeast European axis, respectively. The slowdown is highlighted by a black line.



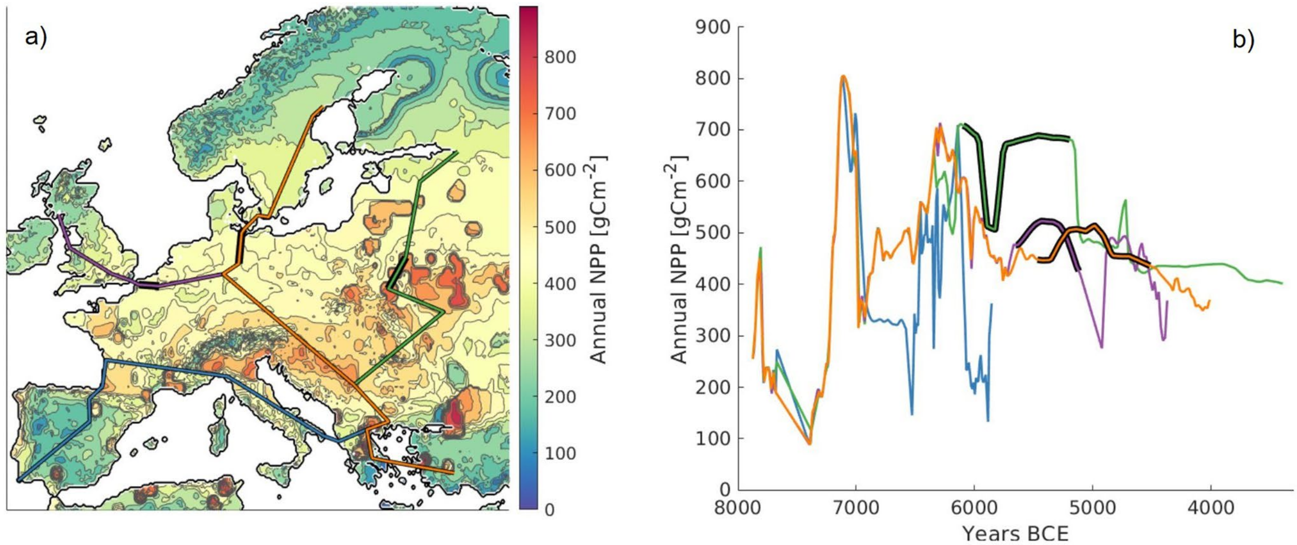
Extended Data Fig. 4 | Expansion axes and mean winter temperature. a, The expansion axes superimposed on a map of mean winter temperature days at 5,500 BCE. **b**, Mean winter temperature experienced along each expansion axis. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian.



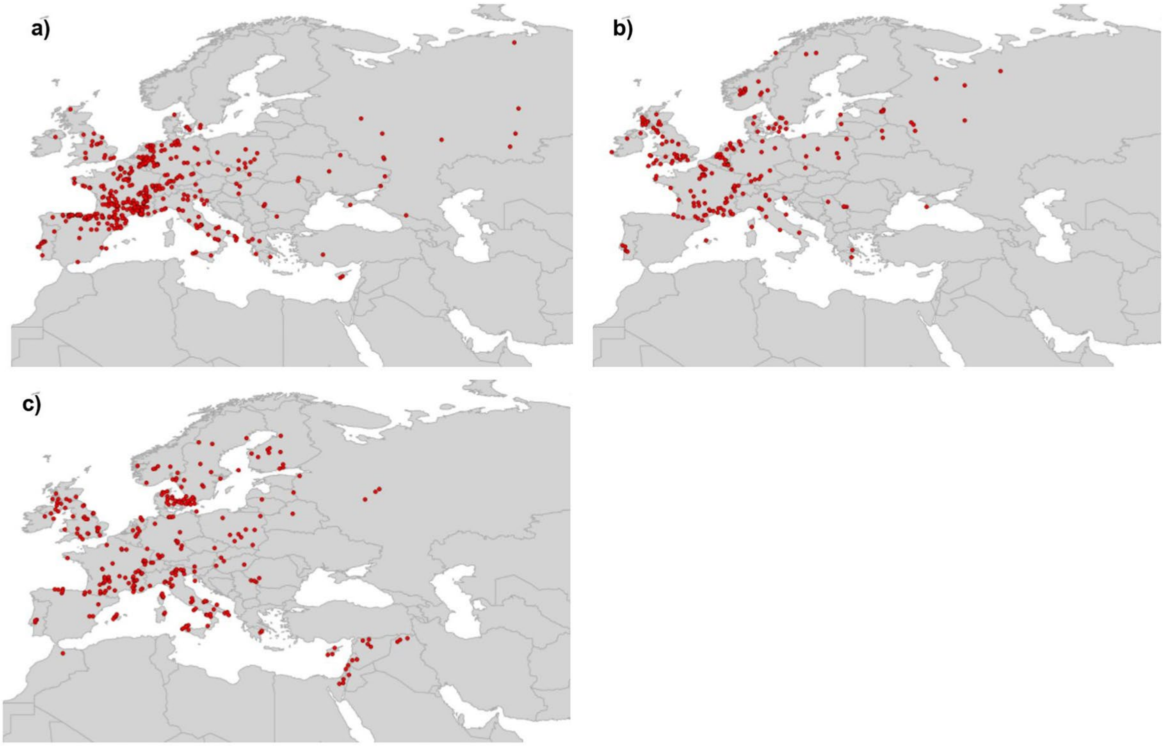
Extended Data Fig. 5 | Expansion axes and mean annual temperature. a, The expansion axes superimposed on a map of mean annual temperature days at 5,500 BCE. **b**, Mean annual temperature experienced along each expansion axis. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian, and Northeast European axis, respectively. The slowdown is highlighted by a black line.



Extended Data Fig. 6 | Expansion axes and precipitation of the driest month. a, The expansion axes superimposed on a map of precipitation of the driest month days at 5,500 BCE. **b**, Precipitation of the driest month experienced along each expansion axis. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian, and Northeast European axis, respectively. The slowdown is highlighted by a black line.



Extended Data Fig. 7 | Expansion axes and net primary productivity. a, The expansion axes superimposed on a map of net primary productivity days at 5,500 BCE. **b**, Net primary productivity experienced along each expansion axis. Blue, purple, orange and green lines represent the Mediterranean, Central European, Scandinavian.



Extended Data Fig. 8 | Distribution of Late Palaeolithic and Mesolithic sites during the Holocene. Maps are based on data from **a**, the Palaeolithic Radiocarbon Europe Database v21[34] (younger than 9,500 BCE); **b**, Steele and Shennan[33]; and **c**, Pinhasi, Foley and Lahr[32]. Country borders were plotted using ref. [74].

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