Title: Holocene fluctuations in human population demonstrate repeated links to food production and climate

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Abstract

We consider the long-term relationship between human demography, food production and Holocene climate via an archaeological radiocarbon date series of unprecedented sampling density and detail. There is striking consistency in the inferred human population dynamics across different regions of Britain and Ireland during the middle and later Holocene. Major cross-regional population downturns in population coincide with episodes of more abrupt change in north Atlantic climate and witness societal responses in food procurement as visible in directly dated plants and animals, often with moves towards hardier cereals, increased pastoralism and/or gathered resources. For the Neolithic, this evidence questions existing models of wholly endogenous demographic boom-bust. For the wider Holocene, it demonstrates that climate-related disruptions have been quasi-periodic drivers of societal and subsistence change.

Significance Statement

The relationship between human population, food production and climate change is a pressing concern in need of high-resolution, long-term perspectives. Archaeological radiocarbon dates have increasingly been used to reconstruct past population dynamics, and Britain and Ireland provide both radiocarbon sampling densities and species-level sample identifications that are globally unrivalled. We use this evidence to demonstrate multiple instances of human population downturn over the Holocene that coincide with periodic episodes of reduced solar activity and climate reorganisation as well as societal responses in terms of altered food procurement strategies.

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Introduction

The relationship between human population dynamics, crises in food production and rapid climate change is a pressing modern concern in considerable need of higher resolution, chronologically-longitudinal perspectives. We have collected a large series of radiocarbon dates from archaeological sites in Britain and Ireland, which is a globally unique region for (a) its high density of archaeological radiocarbon sampling, (b) its unusually high proportion of well-identified botanical and faunal material and (c) its balance of dates from both research projects and rescue archaeology. For the first time, this high-resolution evidence can be considered over four different geographic regions and a broad Holocene timespan as a proxy for human demographic variability and subsistence response. We identify several episodes of regionally-consistent population decline – the later 4th millennium BCE, the early 1st millennium BCE and the 13th-15th century CE respectively – that also appear associated with episodes of rapid Holocene climate change towards more unstable, cooler-wetter conditions. We also demonstrate the existence of structured responses to these changes in the form of altered human food production strategies. The most obvious such episodes during the middle and later Holocene are likely consistent with altered north Atlantic storm regimes, reduced solar insolation and climate-related cultural and demographic impacts across north-western Europe.

Archaeological radiocarbon dates typically come from samples of bone, charred or waterlogged wood and seeds that are taken in order to date specific stratigraphic events in the surviving archaeological record. When considered in large-scale aggregate however, they also provide an anthropogenic signal of changing overall levels of past human activity and ultimately population. Some commentators highlight taphonomic and investigative biases in this record, but there is increasing agreement that, if these biases are controlled for and if the number of available dates is sufficiently high, an important demographic signal remains (see Materials and Methods). While in many areas of the world, the anthropogenic radiocarbon record is insufficient to support such aggregate treatment, in Britain and Ireland there is a long well-resourced tradition of sampling, both from active-mode academic research and responsive-mode, development-led archaeology. Furthermore, parts of Britain and Ireland lie towards the perceived margins of effective European-type agriculture and thereby can offer many of the same insights on middle and later Holocene population stability, climate change and food production as other north Atlantic Islands (Greenland, Iceland), but for a much longer and larger history of human settlement. We have therefore gathered over 30,000 existing archaeological dates from British and Irish databases, publications and grey literature reports, while also recording information about sample provenance, context and material/species (**figure 1**). The changing intensity of this anthropogenic radiocarbon record through time can be modelled via summation of the post-calibration probability distributions of individual dates (see Materials and Methods).

Results and Discussion

Looking at the overall summed distribution (**figure 1C**), there is a dramatic upswing in radiocarbon dates ca.4000-3850 BCE that coincides closely with the first arrival of Early Neolithic cereal agriculture in Britain and Ireland. Although caution is required in inferring actual population growth rates directly from rates-of-change in summed radiocarbon, the latter values exceed 1% during this earliest phase, are unlikely to be explained by increased fertility amongst farming groups alone and must in part therefore be due to migrant farmers from the European mainland, a conclusion that is consistent with current archaeological and genetic evidence (1,2). After this Early Neolithic peak, there follows decline ca.3500-3000 BCE and continued moderate downturn thereafter. This is followed by slow Late Neolithic and Early Bronze Age recovery up to a new peak ~2000 BCE, again for which there is a strong isotopic and genetic argument in favour of significant population replacement by groups from continental Europe (2,3,4). After ~1000 BCE (the last part of the Bronze Age), there is then another striking decline and, while a higher uncertainty in the calibration curve at this point inhibits precise characterisation of timing and duration, substantial recovery is only visible again by ~400 BCE. The Roman period exhibits a trough in the aggregate radiocarbon time series that is unlikely to represent a valid picture in England and Wales due to a far weaker tradition of dating Roman sites via radiocarbon (where pottery and coinage is typically used for dating instead, over the period ~50-400 CE), but may well be valid in Scotland and Ireland (see below and Supplementary Information 2). After the Roman period, there is evidence for sustained early Medieval growth, followed by an abrupt decline approximately consistent with the demographic collapse surrounding the historically well-documented episodes of the Great Famine and Black Death (~1270-1450 CE).

This radiocarbon record can be further disaggregated into sub-regions (following commonly proposed divisions, 5) to consider local consistency with, or departure from, the pan-regional pattern (**figure 2**). Restricting comparison to the post-Mesolithic period where dynamics are more abrupt, north-west England/Wales versus Scotland exhibits the highest pairwise correlation (with the range among all regional pairs being r=0.69-0.86), while Ireland exhibits more volatile dynamics than the others (CV=0.52, with the range of the other three being 0.39-0.42). In addition, the specific local radiocarbon trends exhibited by a given region in excess or deficit of the cross-regional pattern typically match very well with that region's known archaeological record, such as the very reduced archaeological evidence from Ireland in the Roman period ~1-400 CE and then sharper than average upward Irish growth ~400-800 CE in a period of both peak, archaeologically-observed settlement activity and historically-documented Irish monastic influence abroad (Supplementary Information 2). However, it is striking that all four chosen sub-regions show the same sharp Early Neolithic demographic peak ~4000-3500 BCE then decline, the same peak at the beginning of the Bronze Age ~2000 BCE, Late Bronze Age decline ~1000-800 BCE, a subsequent peak in the Late Iron Age ~250 BCE and then decline in the later Medieval period ~1250 CE at the end of the sequence. The particular cross-regional consistency at these points in the overall time series suggests an exogenous factor of some kind.

Evidence for an Early Neolithic boom-and-bust in the British Isles has already been noted by previous research, alongside explanations stressing a collapse due either to ecological over-reach by incoming farmers or the abandonment of cereal agriculture in response to declining climate conditions (6-8). **Figure 3** compares the radiocarbon record with well-known climate archives and suggests that an exogenous cause is likely for all three observed episodes of cross-regional population stagnation during (a) the end of the Early Neolithic, (b) the final Bronze Age and earliest Iron Age, and (c) the late Medieval, associated with relatively rapid changes towards more unstable conditions in Britain and Ireland, as well as colder winters and wetter summers. In particular, pan-regional demographic decline in these three episodes is consistent with reduced insolation at Hallstatt-type grand solar minima (every 2100-2500 years, 9-16). They are likewise consistent with periodic episodes of increased terrestrial salt input to the Greenland ice sheet, which in historical periods has been shown to be an excellent glaciochemical indicator of stormier, winter-like conditions and the increased dominance of Atlantic westerlies (17-19). Broadly coincident, later Holocene changes are also observable in North Atlantic oceanic regimes as separately exhibited by increased ice-rafted surface debris and reduced deep-water contributions (20-22). This evidence collectively suggests quasi-periodic solar-forcing of atmospheric and oceanic circulation with wider climatic consequences, associated with accentuated Siberian Highs and Icelandic Lows. We argue that these reorganisations have repeatedly exerted downward pressure on human population in certain parts of north-western Europe as evident for three decline phases in the high-resolution British and Irish archaeological radiocarbon record. It is very probable that similarly-timed impacts were felt by human populations in less well-documented parts of Eurasia (as already partially evident for earlier episodes, 23-24), albeit with different expression in local weather patterns, varying local human response and ultimately different positive or negative consequences for local human society. An important proximate downward forcing mechanism on human population in Britain and Ireland is likely to be exacerbated food production from reduced growing degree days for cereal agriculture and increased risk of crop loss and food insecurity due to storms. However, accompanying social dislocation and intensified epidemic outbreaks are possible accompanying phenomena. By contrast, intervening episodes of climatic amelioration may have provided good conditions for population expansion in certain areas, with the broadly simultaneous Early Neolithic colonisation of southern Scandinavia, Ireland and Britain being one probable example (25).

Radiocarbon-dated plant and animal food sources further provide an unusually well-resolved time series of potential changes in British and Irish food production (**figure 4**), as long as we are careful to consider the possible confounding effects of changing human depositional practices with regard to food remains (26). Overall, the summed probability distribution of dates from starchy food plants (cereals and hazelnuts) broadly matches the demographic signal observed in the entire radiocarbon dataset, but in contrast the relative proportion of each plant type varies significantly. Hazelnuts (*Corylus avellana*), a key comestible for Mesolithic communities prior to the arrival of agriculture, dominate the starchy plant data up to ~4000 BCE, decline in relative popularity with the earliest Neolithic, but then rebound for half a millennium or more during the Middle-Late Neolithic (~3500-2500 BCE), before declining again (for permutation tests, see Supplementary Information 3). In contrast, wheat (*Triticum* sp.) is a high value cereal that first appears and increases sharply at the very start of the British and Irish Neolithic, and then declines equally sharply by the end of the Early Neolithic. Much later during the Bronze Age, its relative presence in the radiocarbon record grows slowly again to a peak ~1000 BCE, before collapsing once more. Barley (*Hordeum* sp.) is a hardier cereal species which also arrives as part of the earliest farming activity and is present throughout later periods. It is less popular than wheat early on, but far more visible during the Middle-Late Neolithic period of inferred population downturn (taking the British Isles as a whole). Oats (*Avena* sp.) only appear in consequential amounts in Britain and Ireland from the Roman period but become increasingly popular in the later Medieval period, partly replacing or complementing barley as a hardier, lower-risk, lower status food for both humans and foddered animals. The use of oats or oat/barley mixes as spring-sown, back-up crops, especially after initial harvest failures is also well-known from Great Famine/Black Death era, English manorial accounts (27). Radiocarbon samples for individual food animal species are fewer and encompass a wider range of meat, hide, wool and dairying strategies not to mention different kinds of deposition. However, comparison between the proportion of animal and plant food data suggests the greater importance of animals (as wild food) prior to the Neolithic and then also their high visibility (as domesticated herds) again in the Late Neolithic and Early Bronze Age (with a focus on *Bos* and *Sus* sp.) whilst more complicated and regionally differentiated stock-keeping strategies emerge from the Middle Bronze Age onwards (Supplementary Information 3).

Although subject to changing cultural depositional practice and representing only a fraction of the wider archaeobotanical and zooarchaeologoical record, the above-described highs and lows of directly-dated food species offer a temporally high-resolution proxy for shifting food production strategies under both advantageous and deleterious climate conditions. For example, wheat has always been a higher value, potentially higher yield cereal, and often a cash crop in later periods (particularly *Triticum aestivum*). It is therefore unsurprising that the proportion of dated wheat samples grows during peak demographic episodes but declines sharply in at least two of the inferred episodes of demographic stagnation and climate downturn: Middle/Late Neolithic and Late Bronze Age/Early Iron Age. In the former episode (after ~3500 BCE), barley takes over as a hardy alternative cereal resource during the initial phase of demographic decline/stagnation, but then gathered hazelnuts and cattle herding become dominant strategies during the later stages and as population slowly rebounds. These indicators are consistent with what we know from larger, indirectly dated bone and crop samples from environmental archaeology (Supplementary Information 3). For the latter episode (after ~1000 BCE), changes occur over what appears to be a shorter period, but again there are proportional increases in barley, animal products and possibly hazelnuts, and overall decline in wheat. Underlying the aggregate wheat pattern however is also regional variation, with sharper wheat declines in Ireland and north/west England, for example, but actually increased wheat proportions in south-eastern England. Such gradual regional differentiation is also a clear feature of land cover and land use from the Middle Bronze Age onwards as inferred from British and Irish pollen archives (Supplementary Information 4). Contrasting patterns of wheat investment are also potentially consistent with two alternative responses to harvest failure attested in historical periods: (a) resource switching to back-up crops in some areas (or by certain social groups) but also (b) continued speculation by others on high value wheat production as wider demand for it spikes. South-eastern England would also be the area that retained the most amenable weather conditions under climate downturn. For the Late Medieval period, crop and animal sample sizes from radiocarbon dates are much lower and the radiocarbon evidence therefore more equivocal, but contemporary documentary sources point clearly to heavily adjusted plant and animal husbandry in the period 1270-1450 CE (28). They also offer an important empirical basis for causal linkages between decreased weather stability and lower temperatures, declining food supply per capita, and further lagged human consequences such as multi-year famines, human and animal epidemics, widespread cereal market speculation, labour shortages and agricultural dis-intensification, increased violent conflict and overall population decline (29). Given these linkages, it is striking that the while a naïve assumption might be that food production and resource switching strategies should have become more successful as they became more technologically sophisticated through time, the population consequences of climate downturns appear no less severe, suggesting no major enhanced resilience in later periods and indeed potentially additional demographic and subsistence risks for economically-integrated, socially-stratified and increasingly nucleated late prehistoric to Medieval societies.

Conclusions

Through a data-intensive approach to the British and Irish radiocarbon evidence we are therefore able to provide a detailed, long-term demographic proxy for the first time, which amongst other things, demonstrates at least three regionally-consistent episodes of population downturn. While other Holocene climate changes may also have had human impacts in this region, and other European regions need not have responded in the same way, these shared episodes of demographic change match quasi-period shifts to more unstable weather regimes in the north Atlantic and well-known solar grand minima. Furthermore, each downturn across Britain and Ireland was of varying longer-term consequence, with subsistence responses such as resource-switching and food diversification that varied through time. Exogenous climatic factors appear more likely to account for these consistencies than endogenous population over-reach on its own, although both these processes may well have operated in tandem. In any case, both archaeological and historical evidence suggest that human action has always played a role in either mitigating or exacerbating climate-driven effects.

Materials and Methods

A radiocarbon date is a measurement of residual radioactivity in a sample containing carbon, with the most widely cited measurement being a ‘conventional radiocarbon age’ that has been corrected for carbon isotopic fractionation (30). This age has a measurement error that is typically assumed to be a Gaussian distribution. Calibrating this radiocarbon age against observed variability in atmospheric radiocarbon through time (as documented by known standards which are mostly tree-ring sequences for the Holocene [31]) produces a post-calibration probability distribution which is irregular due to the non-linear shape of the calibration curve (32). For a regional dataset of many such calibrated probability distributions, it has become commonplace to sum them, under the assumption that a large mass of probability in certain parts of this aggregate time series offers a proxy for greater overall anthropogenic activity and higher human population in that timespan (6). Concerns that certain archaeological sites or site phases have garnered disproportionate and misleading numbers of dates (e.g. because they were better resourced scientific projects) can been addressed by pooling adjacent dates from the same site and rescaling these sub-site clusters before summing distributions between different sites. In this paper, we cluster temporally uncalibrated dates from the same site that are within 100 years of each other (via a complete-linkage, agglomerative hierarchical method [33]). Date distributions falling in the same cluster are pooled and divided by the number of contributing dates in the cluster, before these pooled distributions are aggregated overall. Some software for radiocarbon date calibration normalise the post-calibration distribution of each date to ensure it sums to 1 under the curve before summing multiple dates or performing any other modelling procedure. However, this rescaling leads to not all calendar dates having equal probability of occurrence and creates abrupt spikes in the summed probability distributions at points where the calibration curve is steep (34). We have therefore chosen not to rescale the calibrated date distributions before summation, but address the methodological implications in greater detail in SI, and consider the alternative result where dates are normalised, concluding that the paper's main conclusions remain consistent in either case.

To explore the degree to which an observed summed probability distribution is well-described by a theoretical null model of demographic change, we first fit such a model (e.g. exponential, logistic, uniform) to the observed data on the calendar scale. In this case, a logistic model was preferred given the observed distributional shape and an assumption that there might be post-Neolithic, pre-Roman upper bound to population growth. The model of expected population intensity is then back-calibrated, and a set of conventional radiocarbon ages (equal to the number of observed dates) is simulated proportional to the modelled per-C14 year amplitude. These simulated dates are then calibrated and summed. Repeating this process many times (e.g. 1000) provides a global goodness-of-fit test and 95% critical envelope with which to assess local departures from the theoretical model (6,35). A second kind of test used here holds constant the date of a given sample but shuffles its label (e.g. the geographic region it comes from or the material type/species of the sample). This permutation test creates conditional random sets (e.g. 1000) and a 95% critical envelope with which to assess region-specific or species-specific departures from the global trend (33). Such a technique also addresses the challenge of reduced sample sizes (e.g. for particular plants), as the resulting envelopes are correspondingly larger in such cases.

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Figures

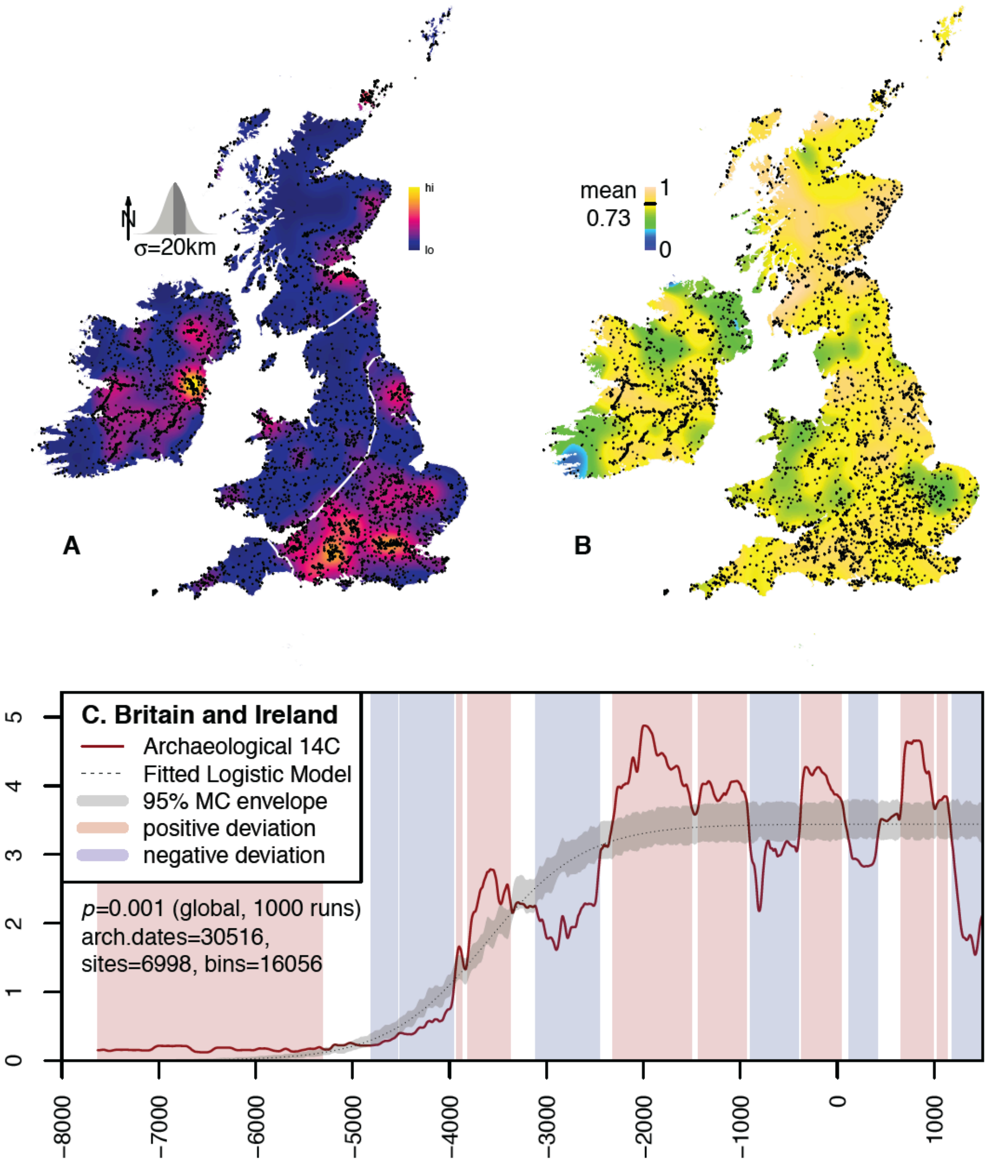


Figure 1. (A) The kernel-smoothed intensity of archaeological radiocarbon dates from Britain and Ireland showing uneven spatial sampling (the sub-regions used in figure 2 are marked with white borders), (B) the proportion of dated samples with genus or species level identifications, (C) a summed probability distribution of all dates compared with a 95% Monte-Carlo envelope of equivalent random samples drawn from a fitted logistic model of population growth and plateau.

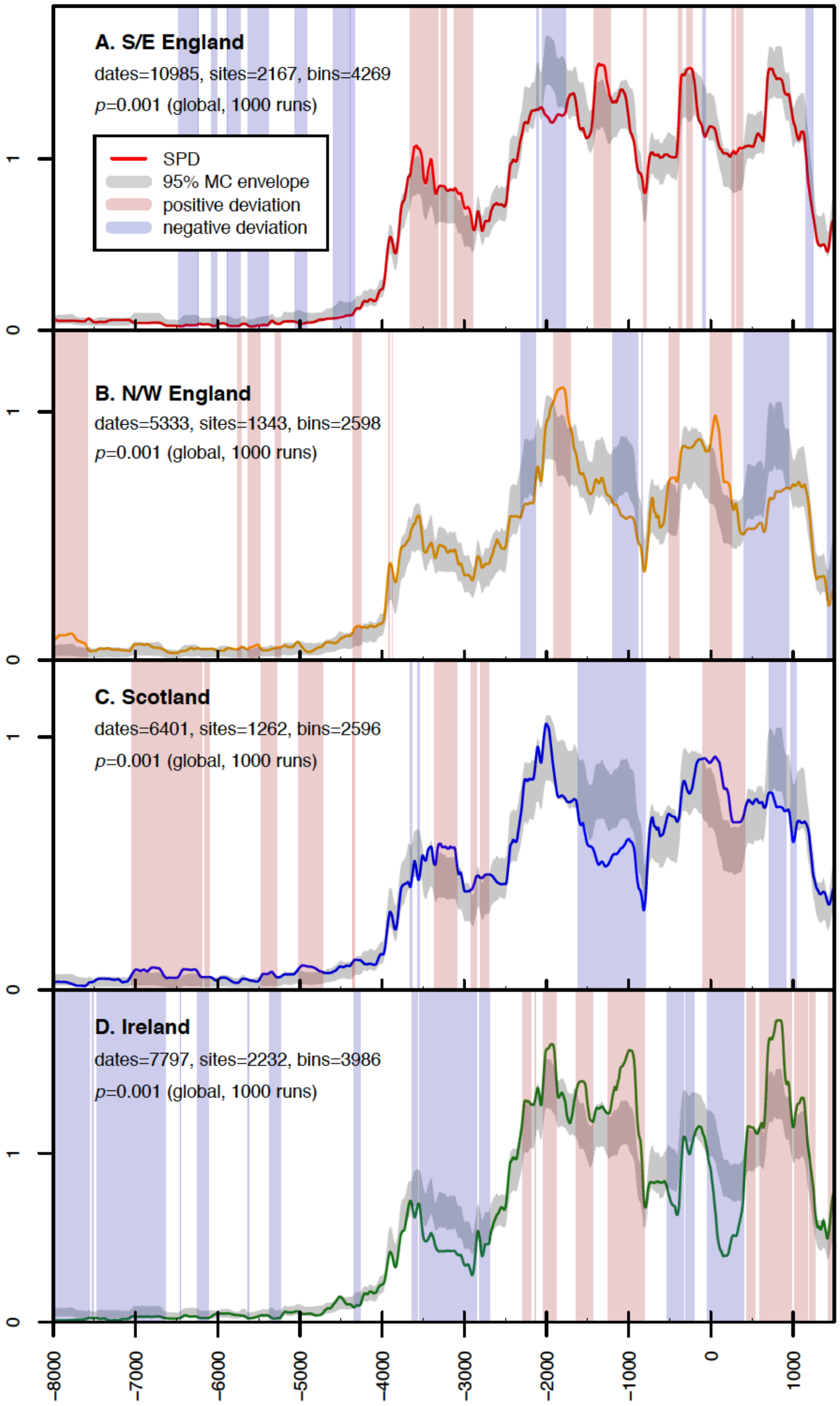


Figure 2. Regional summed probability distributions – for (A) south-east England, (B) northern/western England and Wales, (C) Scotland and (D) Ireland – compared with a 95% Monte Carlo envelope produced by permutation of each date's regional membership.

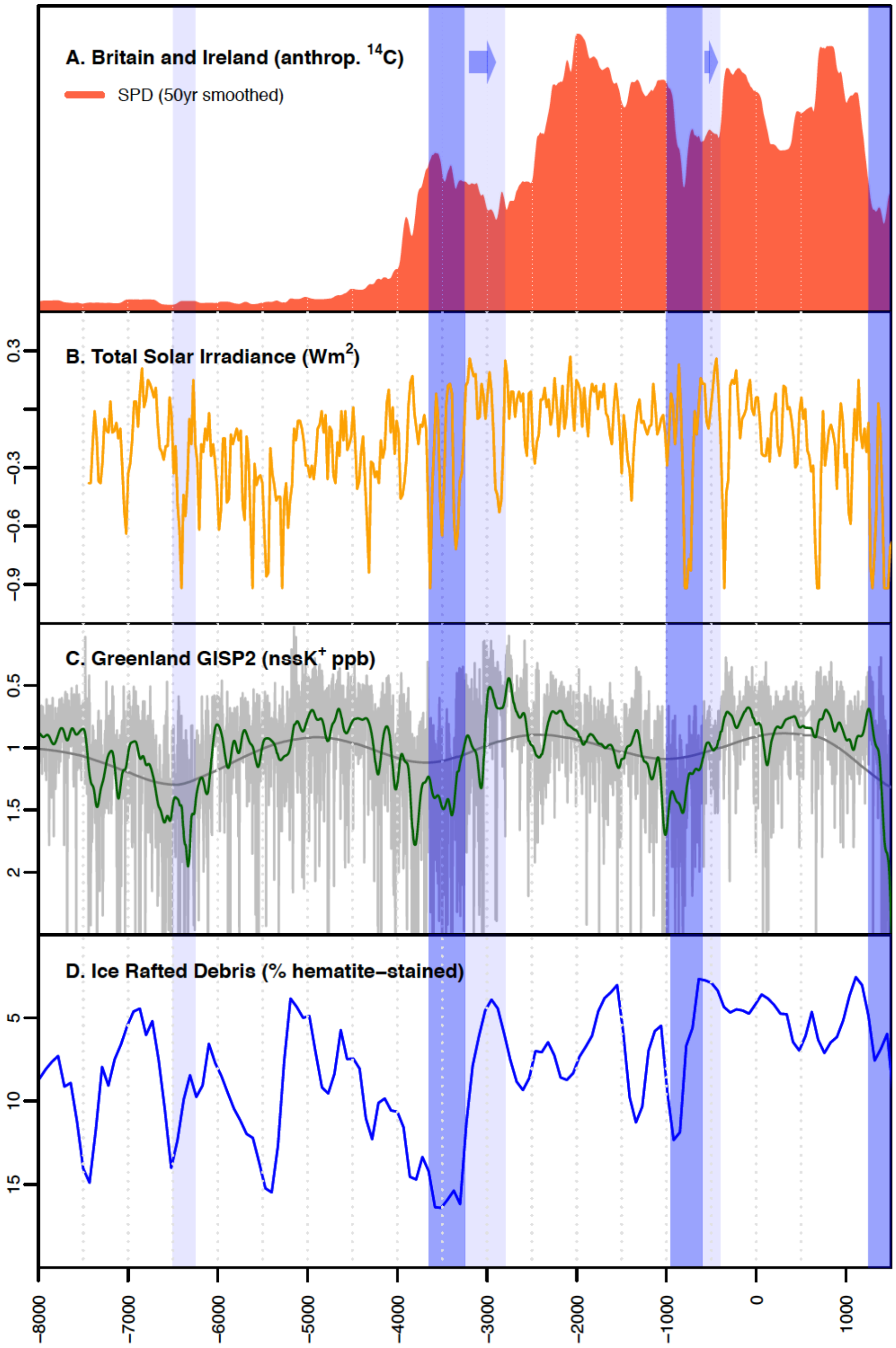


Figure 3. Radiocarbon-inferred population and North Atlantic climate proxies: (A) aggregate anthropogenic radiocarbon dates from Britain and Ireland (as figure 1C, y-axis is linear), (B) total solar irradiance (12), (C) GISP2 potassium ion density (note descending axis, [17]), and (D) North Atlantic ice rafted debris (note descending axis, 19). Shaded blue zones indicate suggested onset and further duration of cold-wet episodes with the first one, the well-known "8.2kyr" event prior to the Neolithic and not addressed directly here.

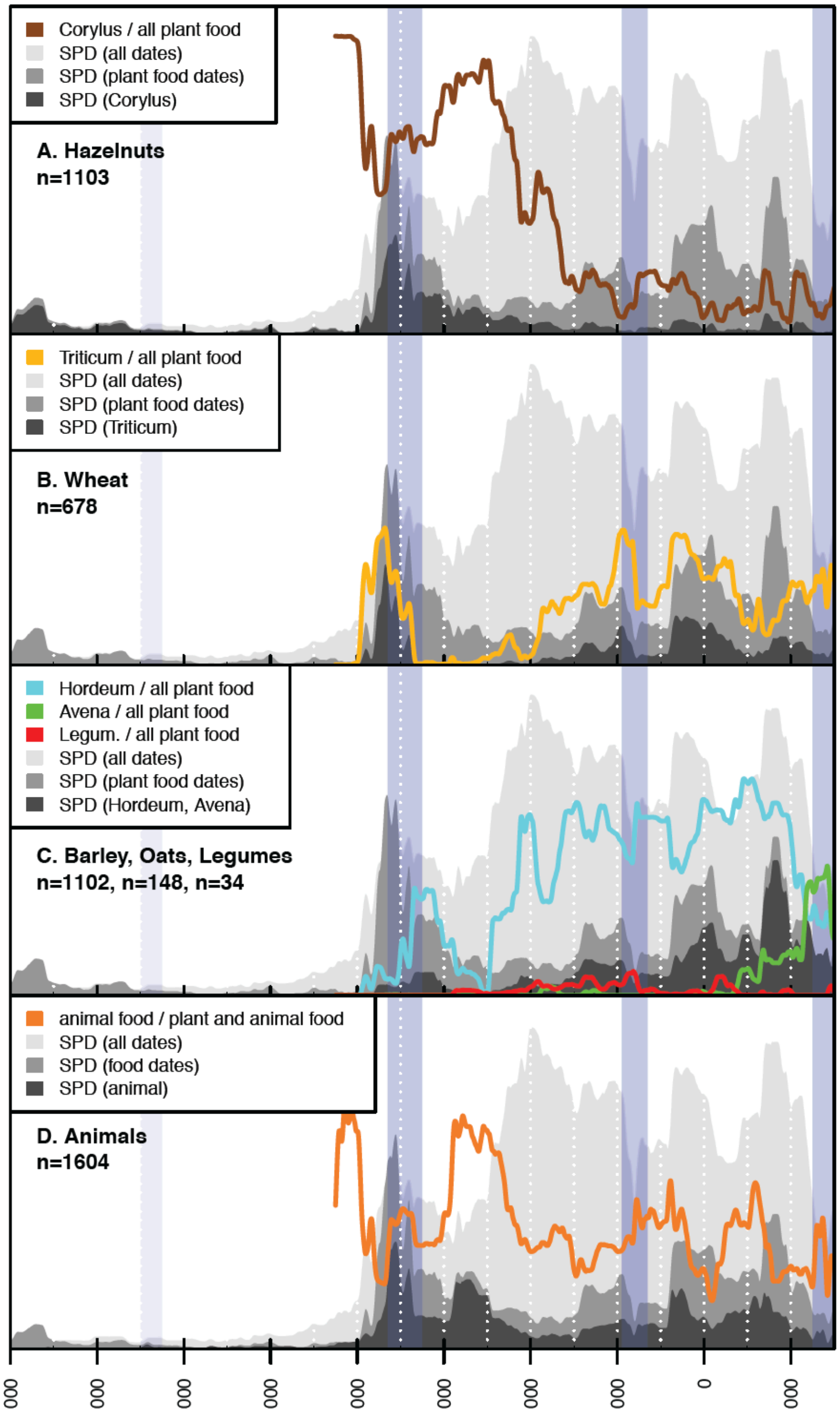


Figure 4. The changing relative importance of major food sources across Britain and Ireland as visible in food samples directly dated for radiocarbon: (A) hazelnuts, (B) wheat (undifferentiated by species), (C) barley, oats and legumes, and (D) animals (those regularly used food sources). The coloured lines are calculated as the proportions (only calculated from ~4250 BCE onwards due to small sample sizes prior to this). Ordinary summed probability distributions are shown in the grey (y-axes are all rescaled 0-1 for easier comparison) and an accompanying permutation tests are provided in figures SI6-SI7.

Supplementary Information

The following supplementary information addresses four topics: 1) the coverage and reliability of aggregate radiocarbon data for Britain and Ireland, along with further methodological justification, 2) the linkage between inferred British and Irish population and broader culture-historical developments, 3) the wider botanical and faunal evidence for changes in British and Irish food production, and 4) a broader view of north-west European palaeoecological trends, especially British and Irish land cover dynamics. These sections also provide further analytical results in support of the main text.

1. Radiocarbon Data and Method Audit

We estimate, on the basis of exhaustive search in certain English counties, that the overall sample of radiocarbon dates collected for this study is likely to represent ~75% of the total dates actually taken on British and Irish archaeological materials since the beginning of radiocarbon dating up to 2016, with the remaining dates either unpublished or to be found in hard-copy publications that are more difficult to search systematically. We have excluded peat, sediment and shell samples from the archaeological dataset used here, as well as all those plant and animal bone dates without a clear anthropogenic relationship or with definite 'old wood' effects. The resulting sampling intensity is between 0.13 and 0.26 dates per 100 years per 100 sq.km across the four different geographical regions, albeit with considerable local variation and the highest numbers in south-eastern England. The overall dataset provides an average of 555 post-Mesolithic archaeological dates per 100 years which is at least an order of magnitude higher than most studies involving summed radiocarbon so far. Even so, there are clear biases arising from differential modern-day archaeological recovery, for example an unusual abundance of dates from development projects around Dublin or in the clear linear patterns of dates taken along Irish road-building schemes of the 1990s and 2000s (main text, figure 1). Similarly, in southern England, a disproportionate contribution is made by dates from gravel extraction and transport infrastructure projects from the 1980s onwards. Additional biases arise from regionally varying investment in housing construction, especially in commuter belt areas. Furthermore, despite the unusually good mix of dates from both developer-led archaeology and traditional academic research projects, certain well-resourced archaeological sites have garnered unusual concentrations of dates (e.g. the Neolithic flint-mining site at Grimes Graves with 307 dates). As already noted in the *Materials and Methods* section, the contributions of chronologically-adjacent dates from the same site have therefore been pooled to mitigate this bias in research intensity.

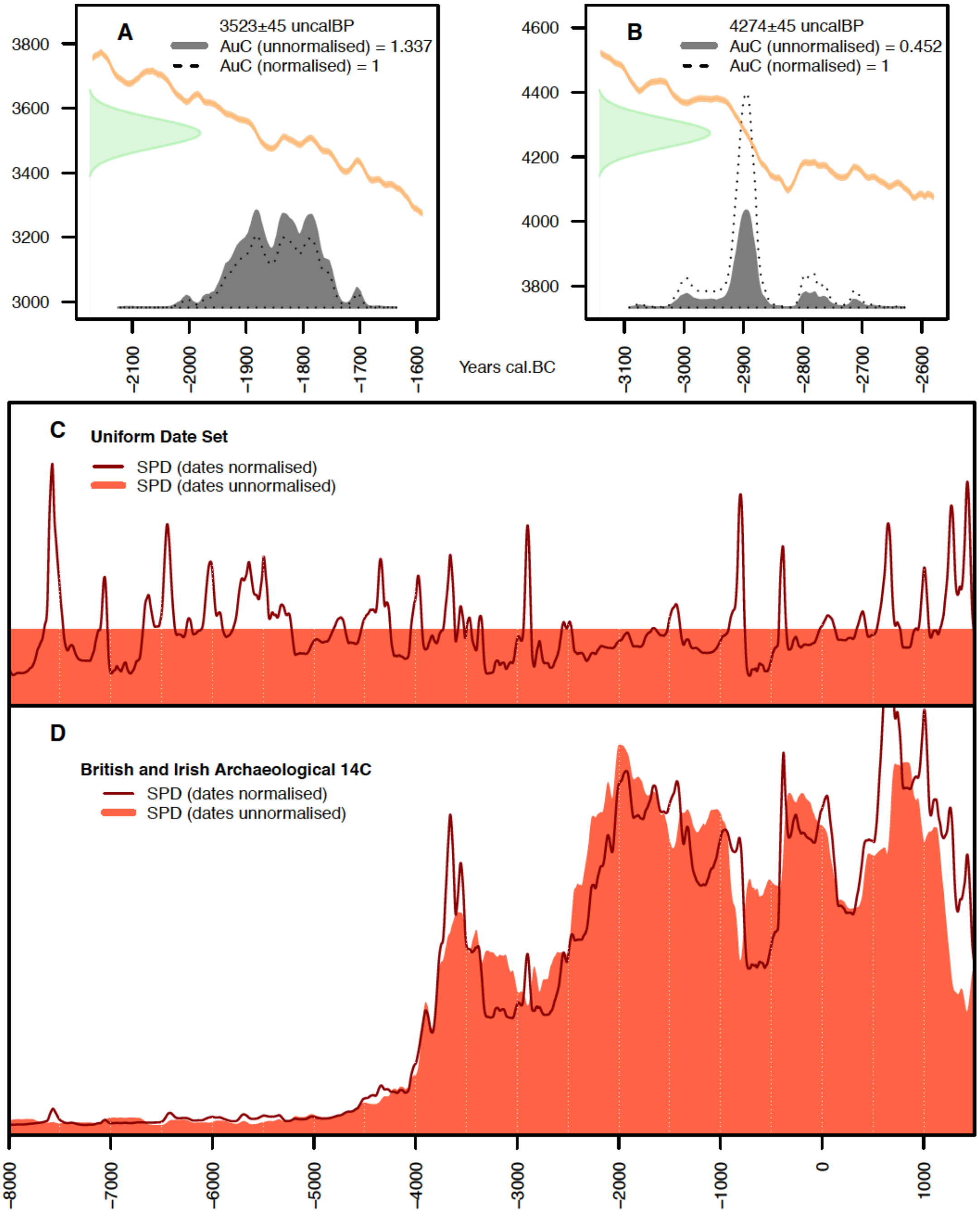


Figure S1. Date normalisation and its consequences: (A-B) two examples of dates at flat and steep portions of the calibration curve respectively and the differences in raw area-under-the-curve after calibration by numerical integration. (C) the summed distributions of uniform set of one date per uncalibrated year (and consistent error) with and without date normalisation (with BCE/CE range same as the next). (D) the summed distribution of all British and Irish archaeological dates, with and without data normalisation.

We have also chosen not to normalise the post-calibration densities of individual dates prior to summing them. Figure S1A-B presents the problem associated with date normalisation in simple form via two uncalibrated dates falling at flat and steep portions of the calibration curve respectively (IntCal13 is used throughout [31]). When a conventional radiocarbon age and its associated Gaussian measurement error are calibrated via a standard arithmetic method (which is very similar in most software), the resulting area that falls under its post-calibration histogram is smaller if the date falls at a steeper portion of the calibration curve and larger at a flatter portion (Figure S1A-B). For many radiocarbon modelling situations, this histogram is then rescaled to 1 under the curve to ensure it can be treated as a standard probability. However, when normalised in this way, the resulting summed densities produce pronounced spikes coincident with steep portions of the calibration curve where a wider set of uncalibrated ages (with their accompanying measurement errors) converts to a narrower set of calendar years (34,36). A clear example is offered by a hypothetical dataset with one dated sample per uncalibrated year and a consistent measurement error. Without normalisation, this uniform distribution on the uncalibrated scale converts to a uniform distribution on the calibrated calendrical scale (with internal mixing of these densities given both the date errors and reticulated nature of the calibration curve), while in contrast it converts to a spikey distribution when dates are normalised (Figure S1C). Although there are methodological strengths and weaknesses in either case, we here have followed Weninger et al. (34) in leaving probability densities unnormalised to avoid such spikes. Figure S1D demonstrates that the choice of one or the other approach does lead to certain differences in the British and Irish time series, with the normalised version exhibiting a more extreme Early Neolithic increase/decrease, a more sustained Late Bronze Age/Early Iron Age decrease and a slight lateral offset in the declines in later periods. However, overall, the summed distributions remain similar, as also do this study's core conclusions, whether one chooses to normalise or not. Furthermore, the ratio-based comparisons and permutation tests we use to consider variability across different food samples and different geographic regions are relatively robust to this choice of whether to normalise or not, because they do not alter the set of sample dates, only shuffle the distribution of labels.

2. Archaeological and Demographic Overview

After a gap during the Last Glacial Maximum, Britain was reoccupied by hunter-gatherer groups soon after ~12700 BCE, early in the late glacial warming period, at a time when there was still a land bridge with continental Europe. These groups were responsible for Cresswellian-type lithic industries, and are part of the wider late Magdalenian re-occupation of northern Europe following the retreat of the ice sheets (37). Thereafter, it remains unclear whether occupation was continuous in Britain through the renewed cold phase of the Younger Dryas (~10900-9700 BCE) after which temperatures rose very rapidly at the beginning of the Holocene. However, rising sea levels had already cut the land bridge that had joined Britain and Ireland by ~14000 BCE (38) and human occupation of the latter did not begin until ~8000 BCE as part of a maritime colonization (39). While observable links between Ireland and Britain appear limited in this early phase, hunter-gatherer groups in Britain remained connected with continental Europe via the plains of Doggerland which were finally inundated by ~6200 BCE if not several centuries earlier (40-41). For the subsequent two millennia Britain continued to be characterised by a hunter-gatherer economy, but with very little sign of substantial contact with mainland Europe.

Neolithic economies and societies appear in Britain ~4200/4100 BCE and by 3800 BCE there is evidence of farming throughout the British Isles, as far as Ireland and northern Scotland (42). This very rapid spread is contemporary with the equally rapid spread of farming into southern

Scandinavia (43), in both cases after a delay of ca.1000 years from the initial arrival of farming in adjacent areas of France and Germany respectively. It has long been disputed whether this arrival in Britain was a result of the adoption of farming practices by local hunter-gatherers or due to the immigration of continental farmers; however, recent genetic evidence strongly supports the latter. In particular, analysis of the genome of a woman from a megalithic tomb at Ballynahatty in Ireland, dated 3343-3020 BCE (2), found that it had very close affinities with other individuals of a similar date in continental Europe, with an ancestry that was predominantly Near Eastern but with evidence for some admixture occurring over the period since the first arrival of farming in central and western Europe ~5500 BCE. The genomic evidence also indicated that the population of which this individual was a member was large, implying immigration on a substantial scale (see also 4) In all four regions of Britain and Ireland considered in this paper, the arrival of farming led to a rapid population boom that had peaked by 3500 BCE and was followed by a sharp fall in Ireland and southern/eastern England. In Scotland and in northern and western England, inferred population levels are more or less maintained for longer but here too they drop markedly from c.3000 BCE and all areas stay low until c.2500 BCE (main text, figure 2).

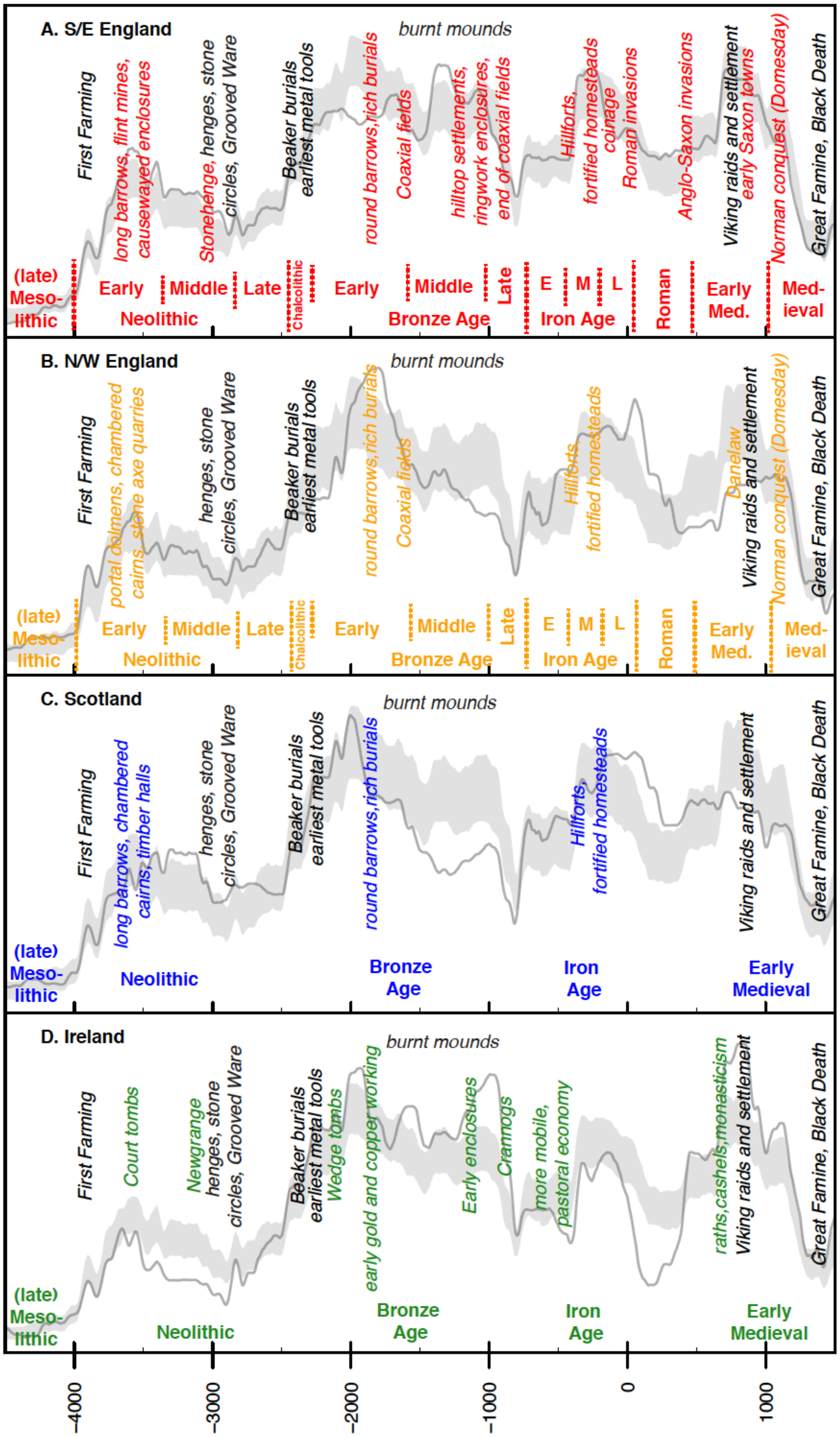


Figure S2. Post-Mesolithic cultural trends in different regions of Britain and Ireland, overlaid on regional population trends inferred from radiocarbon.

After the Early Neolithic boom, there is little evidence of contact between the British Isles and Europe but substantial interaction apparent within Britain, from the Orkney Islands to southern England, and between Britain and Ireland, for example in the widespread occurrence of Grooved Ware pottery, stone circles and henge monuments, as well as passage tombs and megalithic art (44-45). It is noteworthy that the construction of these major monuments, and others such as the Irish passage graves, occurs in the period when inferred population was lower and subsistence was significantly more pastoral and cattle-based, between the Early Neolithic and Early Bronze Age peaks (see main text).

The isolation changes ~2500-2400 BCE with the appearance of continental European Bell Beaker material culture styles in both Britain and Ireland and the earliest evidence of local copper production (e.g. Bell Beaker context at Ross Island in south-west Ireland from ~2400 BCE, [46]). As with the arrival of farming, there has been much discussion of whether the arrival of Bell Beakers was the result of cultural diffusion or human immigration and again the genetics results indicate at least some role for the latter. Cassidy et al.'s analysis (2) of the genomes of three Early Bronze Age men from northwest Ireland buried in a stone cist and associated with Food Vessel pottery found that they were very different from the Ballynahatty individual and closely similar to Late Neolithic, Bell Beaker and Early Bronze Age genomes from Central Europe in having a strong component of steppe ancestry from the Yamnaya or Pit Grave Culture. This makes it very likely that the appearance of Bell Beakers too was associated with a further episode of significant immigration (3) and recent genomic evidence suggests wholesale (>90%) replacement of the preceding Neolithic population over just a few centuries (4). It certainly marks the beginning of a new phase of population growth that led to radiocarbon-inferred population levels at least double those seen during the Early Neolithic boom, suggesting a more productive form of agriculture and/or more favorable conditions. In southern and eastern England, the rich Early Bronze Age 'Wessex' burials (47) occur during this peak.

Over the course of the 2nd millennium BCE, there is divergence in the inferred population trajectories of the four different regions, with a steady decline from the peak in Scotland and in Wales and northern and western England to a low point early in the 1st millennium, while in Ireland and southern and eastern England a high level is largely maintained until c.1000 BCE, after which a precipitous drop follows. In the southern and eastern zone, there is evidence for the laying out of extensive (so-called 'co-axial') field systems from ~1600 BCE, which are then replaced in many areas by larger scale subdivisions after ~1100 BCE (so-called 'ranch boundaries' [48]). Away from this zone there is much more continuity with what went before. From ~1500 BCE it seems that there is a decline in local copper production and an increase in continental imports, reflected in a shift in the control and deposition of the greatest quantities of metal wealth to southern and eastern England, increasingly in the form of ritual deposits in wet places.

From ~1100 BCE the evidence points to increased instability in many areas of both Britain and Ireland. The first hillforts and enclosures appear and there is a proliferation of 'ringworks', circular enclosures, some with ramparts, containing round houses that may have been high-status residences; they also have evidence for weapon production and deposition. In Ireland, the artificial islands known as crannogs, whose main activities seem to have been feasting and metalwork production appear from ~900 BCE, a counterpart to the enormous middens of probable feasting and assembly debris that occur in southern England around the same date (48). The declining importance of bronze and the exchange networks that enabled access to it over the period 800-600 BCE must have had a significant impact on local social patterns and evidence of continental connections decreases. In southern and western England, there are further hillforts in the period 600-400 BCE but these defensive sites have less evidence of houses and more of storage pits and structures so their role is not entirely clear. Dense distributions of small fortified enclosures characterize Wales and the west in the second half of the 1st millennium BCE and there is a similar pattern in northern and western Scotland, where over the period c.600-200 BCE structures developed into the fortified stone elite residences known as brochs (44).

All these developments now have to be seen in the context of the population patterns presented in this paper. The demographic trough beginning ~900-800 BCE (with uncertainty about the shape and duration of the downturn thereafter, due to the flat shape of the calibration curve here) sees inferred populations drop to as much as half of their previous peak in southern and eastern England, after which there is only evidence for clear recovery by ~400 BCE to a level matching the Early-Middle Bronze Age. In Scotland and Wales and northern and western England, the period of decline was longer and the proportional decline much greater, though there is then something of a ‘bounce back’ followed by a more gradual rise to a peak at the same time as in the south and east. In Ireland, the drop is extremely rapid, to as much as half of the peak value, and the inferred population stays at roughly this level until another rapid rise to a peak at the same time as in Britain, though still well down on the Bronze Age. This pattern is paralleled by other evidence pointing to major changes at the end of the Bronze Age, not least a shift to a more mobile and pastoral economy reflected in a long-term shift in settlement patterns and the abandonment of pottery (49). Subsequently, the renewed boom in all regions in the last centuries BCE is reflected in evidence for more intensive use of certain landscapes and environments that had previously seen little exploitation. There was also renewed continental contact with the expanding Roman world and, from the late 2nd century BCE, novel forms of central place appear, especially but not exclusively in the south-east, with similarities to the ‘oppida’ of continental Europe.

In the 1st century AD, Britain was incorporated in the Roman Empire, though its main impact was largely in the English south and east, with Scotland (especially north of the Forth-Clyde line) much less affected. Ireland, on the other hand, was not occupied at all, though there is evidence for extensive contact. In all the regions examined in this paper the Roman period corresponds to a trough of greater or lesser depth in the radiocarbon population proxy. However, it is extremely unlikely that this represents a valid picture in the highly Romanised areas of southern and eastern England, because radiocarbon has been much less important for dating sites in these areas than the use of new fineware pottery traditions and Roman coins (~50-400 CE). In fact, careful Roman population reconstructions from the German Rhineland support claims for massive increase in population from the Iron Age to Roman periods (from 1.2-2.3 to 10.8-17.9 persons/sq.km [50]), while recent detailed synthesis of excavated evidence in south-eastern Britain, suggests a smaller but still substantial doubling of settlement numbers up to a peak by ~200 CE and overall English population that may have reached levels similar to those of the high Middle Ages (51). However, it is unclear how far such inferred growth applies outside of south-eastern Britain, and in Ireland, on the other hand, where dating options are more limited, the radiocarbon indications for a major population downturn between ~1-400 CE may be broadly accurate (49,52).

In much of southern Britain, the end of the Roman period probably brought population decline. As a comparison, detailed evidence from the Rhineland supports a sharp population decrease from the Roman to the Merovingian period (5th to 8th centuries CE; from 10.8-17.9 to 0.9-1.3 persons/sq.km, [50]). However, many parts of southern and eastern England also clearly experienced immigration from continental Europe in this phase so we should not necessarily view the severity of the Rhineland change as directly analogous (51). Analysis of whole genomes from the Early Saxon late 5th-early 6th century cemetery at Oakington in eastern England (53) found that two individuals were most probably recent immigrants, with affinities to modern Dutch populations, one was of local origin, genetically close to British samples of Iron Age date, and one showed a mixed pattern of the kind that would result from interbreeding between the two populations. Three individuals from the Middle Saxon cemetery of Hinxton, in the same region, were of entirely immigrant ancestry and suggest continued immigration up to the 8th century. A similar contrast was found between the genomes of Iron Age and Roman individuals and an individual from a Christian Anglo-Saxon cemetery, all from north-east England (54). Up to 40% of the ancestry of modern populations in southern and eastern England is of Anglo-Saxon origin (55).

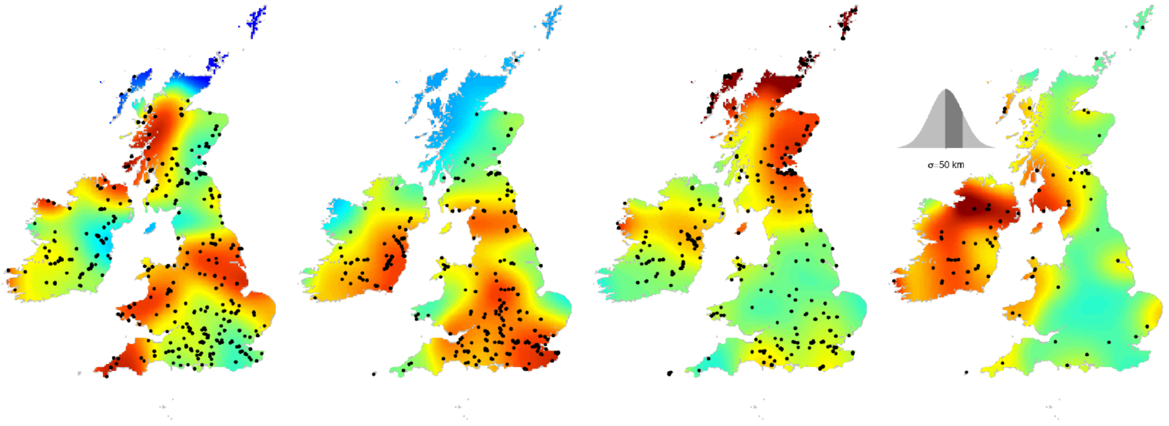
While the lack of a valid picture for the Roman period makes it hard to evaluate the patterns that followed, the Scottish pattern from 500 CE remains flat until after 1000 CE. Wales, together with western and northern England, shows a similar pattern, with possible indications of an upturn in the later part of the period. The south and east, on the other hand, show a clear pattern of population growth from the 8th to the 10th century CE, associated with the growth of towns and trade in the Late Saxon period and the consolidation of the regional Anglo-Saxon kingdoms into a single state. The demographic weight of the south and east compared with the north and west is clearly seen in the distribution of population inferred from the taxable values in the Domesday book of 1086 CE, though the north-east was affected by the massive destruction associated with William I's 'harrying of the North' to crush Saxon rebellions (56).

In many respects, the most interesting demographic pattern in the final part of the chronological sequence discussed here is that for Ireland, where the radiocarbon evidence suggests that the population more than tripled between the end the Late Iron Age, ~400 CE, and 900 CE. In settlement terms this period was characterized by monastic centres, following the Christianisation of Ireland in the 5th century CE, and ringforts (raths or cashels), circular ramparts of earth or stone for the protection of cattle-enclosing buildings, believed to be family farmsteads, of which an estimated 50,000 are thought to have once existed (57). However, recent fieldwork has revealed that other kinds of enclosure complexes also existed that may have represented the centres of large agricultural estates (58). At the start of the period subsistence continued to be based on the cattle pastoralism that had characterised the Iron Age but from the late 7th/8th centuries CE it seems that cereals became more important than before, while cattle, which had been the basis of wealth and status, declined in importance, a development that

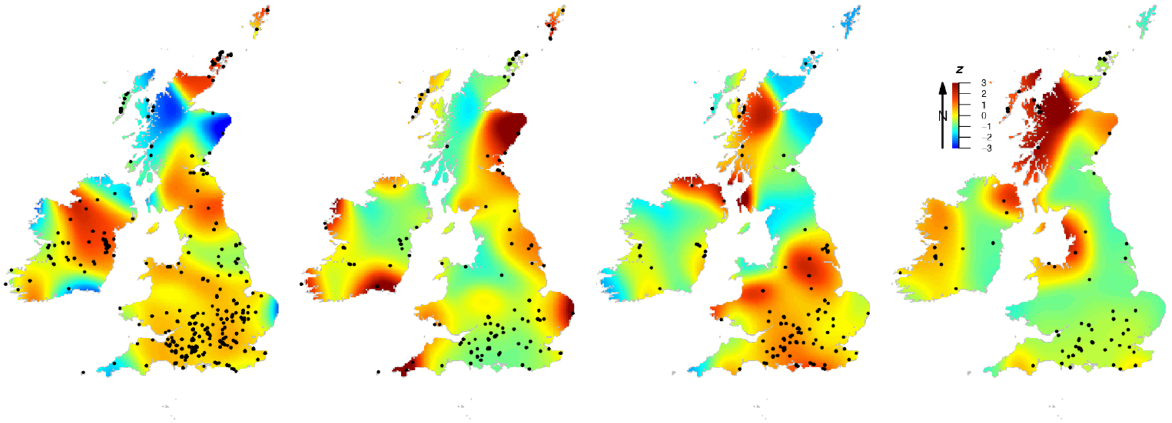
McCormick (58) attributes to an increasing role for silver in exchange transactions. A change is seen in the pattern of grain-drying kilns, from large numbers of small ones to small numbers of large ones and a major expansion in the building of watermills. McCormick (58) sees these developments, which are also accompanied by the replacement of ringforts by open settlements, as an indicator of a decline in small scale subsistence farming and the increasing appropriation of an agricultural surplus by a social elite.

3. Food Production

Direct radiocarbon dates on food-producing plants and animals can be integrated with a much larger body of zooarchaeological and archaeobotanical evidence dated indirectly via archaeological stratigraphy, associated artefacts and/or absolute dates on other materials. Here, we present this wider evidence alongside further analytical treatment of the direct dates by species. Figure S3 plots the spatial distribution of sites with direct radiocarbon dates on different food plant and animal samples across Britain and Ireland, and accompanying relative risk surfaces provide a view of persistent latitudinal and regional trends in food production. For example, the proportion of direct plant food dates that are on oats (*Avena* sp.) is higher in central Ireland and western Britain than it is elsewhere or overall, while the proportion of barley dates is locally higher in Scotland, and wheat is highest in south-eastern Ireland and southern England. Animal dates are in general more widely spread (and prone to effects from smaller sample sizes), but those on cattle bones, for example, are unusually common in northern and eastern Ireland. Figures 4 and S4 complement this spatial perspective by providing a chronologically-sensitive view of changing species proportions from directly dated samples (along with permutation tests in figures S5-7). In addition, Table S1 provides information on the main cereal crops and chronological periods in which they are recorded across Britain and Ireland, along with an indication of their relative tolerance to ecological factors. All of these insights are incorporated into the overview of long-term trends in British and Irish food production food production which follows.



A. Hazelnut (n=1095) B. Wheat (n=691) C. Barley (n=1113) D. Oats (n=149)



E. Cattle (n=1002) F. Sheep/Goat (n=266) G. Pig/Boar (n=203) H. Deer/Rabbit (n=151)

Figure S3. Regional variability in the relative proportions of dates on different plants and animals. The colour scheme indicates standardised scores of positive or negative deviation from the mean proportion of a type versus its parent distribution of either starchy plant foods (A-D) or meat/dairy producing animals (E-H). Black dots show all those archaeological sites with radiocarbon dates of the stated species (NB. relative risk surfaces can be deceptive in areas of low overall sample size)

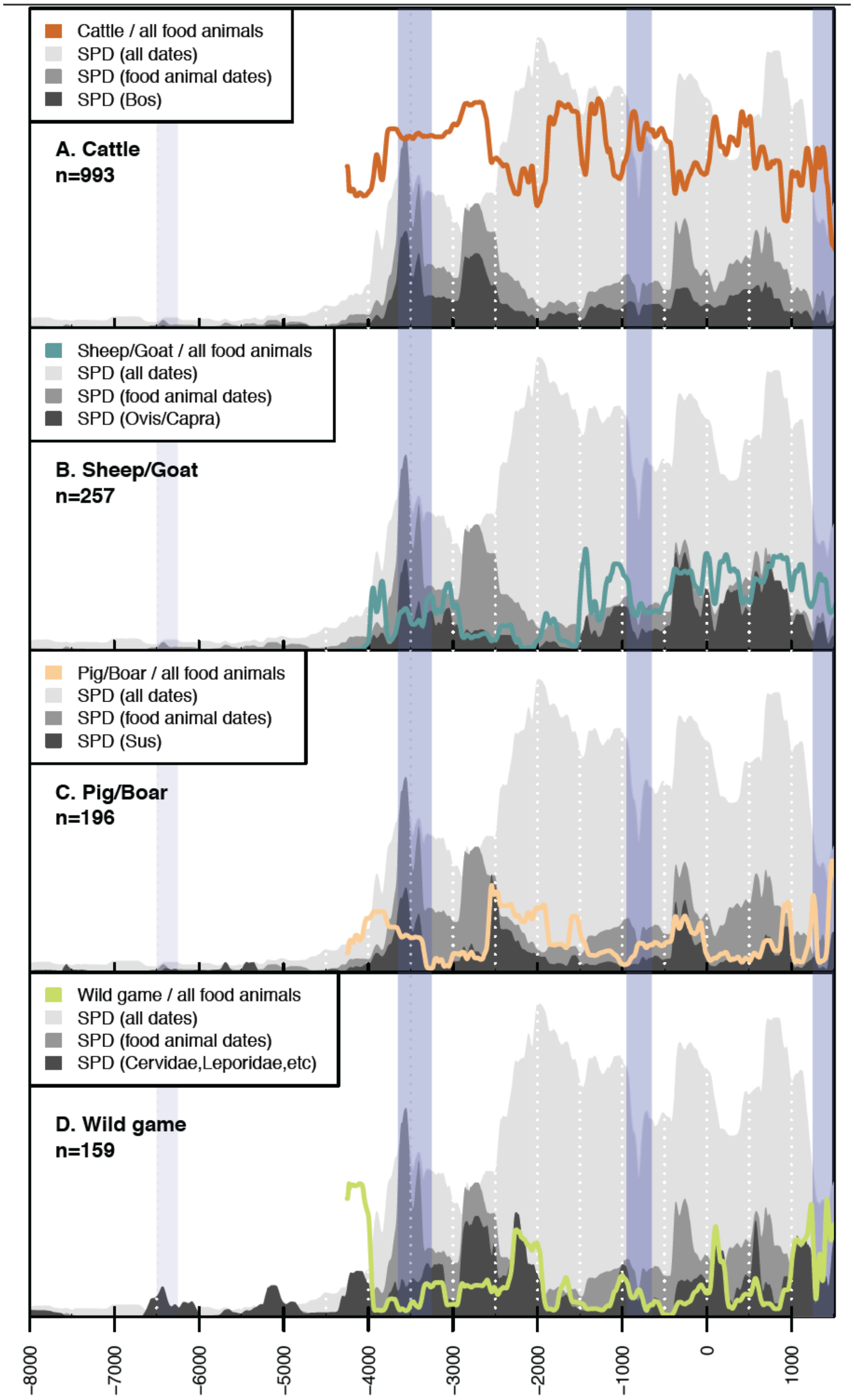


Figure S4. The changing relative importance of major food animal sources across Britain and Ireland as visible in food animal samples directly dated for radiocarbon. The coloured line is a proportional value, while ordinary summed probability distributions are shown in the grey. The blue zones indicate the approximate onset of climate downturns.

Mesolithic communities in Britain and Ireland exploited a changing mix of gathered, hunted and managed resources, with red deer (*Cervus elaphus*) and hazelnuts (*Corylus avellana*) especially prominent (figures 4A, S4D), but evidence also for the use of marine resources and a much wider array of plants and animals (59-63). The shift in food production regimes with the earliest Neolithic is abrupt: early cereals from Ireland, eastern Scotland and England are all of broadly similar date (figure 4B-C, especially 3800-3700 BCE), suggesting multiple points of contemporary arrival (42) and a rapid spread of crops across the whole area in as little as 4-8 human generations. From the beginning, hulled and naked barley (*Hordeum vulgare*), emmer wheat (*Triticum dicoccum*) and probably free-threshing tetraploid wheats are present, while the case of einkorn (*Triticum monococcum*), another early wheat species associated with the spread of farming out of the Near East, is less clear (26,65-67). Analyses of preserved food remains from Dutch Neolithic sites indicates that coarsely ground cereals were cooked with wild plants, including nuts and tubers, and meat as something more like stews rather than a bread (68). Food remains from Neolithic Yarnton, Oxfordshire were also non-bread products based on coarsely ground barley (69). In assessing the evidence of querns in Neolithic Britain, Peacock (70) concludes that flour and breads were not more than a minor component of diet. Flax (*Linum usitatissimum*) is also present in Early Neolithic contexts, but current evidence suggests its use for linen rather than as fodder or oil (64). Isotopic, zooarchaeological and residue evidence suggest relatively low inputs from marine resources to Early Neolithic diet and no pulse remains have yet been conclusively identified (66-67,71-72).

New domestic animals appear at least as early as, if not before, cereals on Early Neolithic sites. Particularly striking are two directly-dated Irish cattle (*Bos taurus*) samples placing their arrival at the end of the 5th millennium BCE, slightly ahead of other Irish Neolithic evidence: while this isolated data should be treated cautiously, it may imply occasional late Mesolithic introduction of cattle or early false starts to Neolithic colonization (73). In any case, such animals were a dramatic addition to Ireland's resource landscape given the absence till then of large ungulates for dairying, meat, tool-making or clothing (unlike Britain which had red deer and wild auroch populations). Cattle remain the dominant livestock for much of the Irish Neolithic, with a slight increase in pig (*Sus domesticus*) during the later Neolithic and sheep/goat (*Ovis aries*, *Capra aegagrus hircus*) only a minor component (73). In Britain the picture is similar (74-76), albeit with the impression of considerable variety in the northern and western Scottish islands and a higher prominence there of early sheep/goat (65). Dairying seems to have been the main function of Early Neolithic livestock herds, as seen in both organic residues and faunal mortality profiles, with meat seemingly secondary and wool production unlikely given the nature of Neolithic sheep fleeces and the absence of loom weights or spindle whorls (75-78).

Overall, Early Neolithic agriculture in England and Ireland appears quite different to more familiar European subsistence systems from later historical periods. There is an absence of obvious storage pits, extremely limited evidence for glume bases indicative of routine dehusking, a continued prominence of wild food remains, and only sparse evidence for querns and sickles (70,79-81). Weed assemblages suggest a dominant role for small, intensively-managed horticultural plots (66,83-84). A few stone enclosure walls from Ireland and Scotland, may conceivably indicate Neolithic field systems, but they are challenging to date and renewed debate about the well-known fields at Céide, Mayo is an example of current uncertainties (85-86). Ard-marks at a number of sites suggest simple hoe-like ploughs pulled by yoked animals, but without implying large-scale arable fields, and with the likelihood that many plots were hoed by hand.

The Middle and Late Neolithic sees a shift in the archaeobotanical and zooarchaeological evidence that has previously been linked to possible population downturn and increased reliance on wild food resources and pastoralism, in England and Ireland especially (7,65-66,74). While domesticated cattle and pig are still present after ~3400 BCE and in particular impressive numbers at sites such as Durrington Walls, Wiltshire (87), there are relatively few sheep/goat remains from mainland England and Ireland until ~2000 BCE. Directly dated samples confirm this discrepancy, with rapidly rising proportions of animal dates versus starch plant dates in the later Neolithic (figure 4D, main text) of which cattle are the most obvious (figure S4A). Scotland in contrast presents a more complex picture, with continued evidence for barley cultivation, especially at island and coastal sites, as well as the continued importance of sheep/goat (88-89). These regional trends now need to be set within the context of the aggregate radiocarbon time series, in which England, Wales and Ireland see major population downturns in the period ~3500-3000 BCE, coincident with deteriorating climate and with direct dates suggesting sequential shifts towards increased barley cultivation, then increased hazelnut collection as population declines or stagnates and further moves to stock-keeping as population rebounds. Scotland in contrast stands out as a region whose inferred population appears stable through the Middle Neolithic, only declining after ~3000 BC, and for having a more persistent mix of plant and animal evidence, probably suggesting the continued resilience of a very specific, local subsistence strategy in certain Scottish island and coastal areas.

Alongside the inferred overall increase in British and Irish population from ~2500-2000 BCE, both direct dates and the wider archaeological record demonstrates a slow return to cereal crops in southern Britain (predominately barley and some emmer). In Ireland, such Chalcolithic evidence for cereals continues to remain rare or absent until much later. More significant developments are visible in both regions after ~2000 BCE and especially from ~1650 BCE onwards with the arrival of a slightly wider set of crops (e.g. first dated instances of spelt wheat, *Triticum spelta* and Celtic bean, *Vicia faba*), the clear reappearance of Irish cereal agriculture, and the uptake of many elements of what are later viewed as key features of full-scale agriculture, such as the common use of saddle querns for cereal processing; metal sickles for harvesting, above- and below-ground granaries, and extensive mixes of roundhouses and field systems over large tracts of south-east England especially (44,70,90-94). The main crops are barley, emmer and spelt wheat, with the latter increasing in prominence in many parts of England, but rare in Ireland and Scotland throughout this period (95-97). Free-threshing wheats are largely or totally absent. While evidence for spelt wheat's greater ecological tolerance remains equivocal, one possibility suggested by the study of weed ecologies is that it was nevertheless being cultivated on more marginal soils, intercropped with emmer and/or spring-sown (98).

Starting in the Early Bronze Age, but especially from the Middle Bronze Age (~1500 BCE, figure S4B), there is also a rising prominence of sheep throughout much of the British Isles, which is likely related to wider patterns of field enclosure (to keep such animals in or out) and agricultural expansion into new upland landscapes. The presence of spindle whorls and loom weights on many later Bronze Age British sites suggests wool production and new breeds with wool-producing fleeces (99) in keeping with wider European evidence (100). Wild animals contribute little if anything to subsistence in the later Bronze Age and this too appears to be part of a wider European phenomenon (99), with deer in the Scottish islands an interesting exception [101]). The Bronze Age also probably marks the final extinction of many once endemic wild species, including beaver and auroch in Britain, but the introduction of domestic horses (at least to eastern England [102]).

A striking landscape change at the end of the Bronze Age and start of the Iron Age is the apparent abandonment of many upland Bronze Age enclosed field systems ~1000-800 BCE (90,93-94,103-104). This phenomenon, if correctly dated, is coincident with the aggregate radiocarbon evidence presented here for population downturn and also is plausible in terms of deteriorating climate. As noted in the main text, direct dates on food samples suggest switches to barley or sharply-reduced wheat cultivation in Ireland and some areas during this period, but continued wheat production in others. From the wider archaeological record, commentators have also argued for crop diversification in the final stages of the 2nd and beginning of the 1st millennium BCE (both in Britain and also nearby continental Europe [105]). For example, Celtic bean becomes more obvious in multiple assemblages in south-eastern England over the Late Bronze Age/Early Iron Age transition, including some near pure caches of thousands of specimens (106), with pea (*Pisum sativum*) also very visible. Together these two plants suggest possible new or newly-prioritised cultivation strategies, at least in south-eastern England, where cereals might be intercropped or placed in rotation with nitrogen-fixing leguminous plants.

As overall archaeological evidence becomes more substantial again and inferred population rises from ~400 BCE, spelt wheat, emmer and 6-row hulled barley continue to be present, but with spelt again dominant over much of south-central England, emmer more common in other parts of England and hulled barley dominant in Ireland and Scotland (95,107-109). Free-threshing wheat remains uncommon. The Middle and Late Iron Age also sees the emergence of newly organised fields systems and further developments such as the introduction of rotary querns (70) and more centralised storage practices that suggest a reorganisation of production with a view to larger-scale efficiencies. Domesticated animals from England and to some extent Scotland are often dominated by sheep and goat (110) with pigs less common except at certain kinds of site (e.g. trading centres [111]). Whilst fish bones are not common on Iron Age sites, they are noticeable on Scottish island and coastal sites (63,112).

Romano-British agrarian and stock-keeping practice exhibits general continuity from the Iron Age, but with clear evidence for the further establishment of field systems (113) and increased market exchange within southern Britain and with continental Europe. Spelt and six-row hulled barley remain the most prominent cereal crops, with the latter still more important in Scotland and Ireland (107,114). Free-threshing wheats are still rare, except in certain well-connected towns such as London (115-116), while there is also the first conclusive evidence for domesticated rye (*Secale cereale*) and oats (*Avena sativa* [95-96,117]). Various plants used as condiments or edible fruits become more common on Romanised sites but are likely to have been imported rather than grown locally (e.g. fig, pine nut and olive), with the exception being grape (*Vitis vinifera*) which may have been cultivated in England (107,118-120). Other developments include the introduction of corn-drying ovens (121), and closely associated with them, the likely introduction of malting and brewing, predominately using spelt wheat. Changes in milling technologies also occurred in this period with both greater numbers of watermills and a gradual increase in quern stone size suggesting more complex installations operated by animals or multiple people (70,120,122). Coulters found near more Romanised settlements suggest improved ploughs that would have facilitated cultivation of heavier soils (123), but it is likely that, for many, the simple ard remained the main form of animal-assisted tillage (122). Romano-British sites also exhibit a varying mix of sheep/goat, cattle and pigs, often in that order of frequency, and with evidence for wild game being very rare (111). More significant perhaps is a possible change in butchery techniques, again especially in Romanised settlements, with the introduction of cleavers and other heavy bladed tools implying market-led changes in the way meat products were supplied, at least to more nucleated settlements (124).

These Roman period developments typically suggest local technological adoptions, rather than the impact of migrant farmers, and also highlight the role of nucleated towns and market-led incentives. However, they probably only had an impact in a portion of Britain and Ireland and in contrast, it is the ensuing Early Medieval period that sees a more marked shift in agricultural practices, probably the most significant since the Middle Bronze Age with changes clearly felt at every level of society (125-126). Stock-keeping is arguably a relatively stable component amidst these changes, with Anglo-Saxon faunal assemblages, for example, dominated by cattle, pig and sheep (127), and Irish ones suggesting continued dominance of cattle for dairying up to ~800 CE and greater balance of cattle, pig and sheep thereafter (128). For cereals, however, there is continued cultivation of barley but a relatively sudden move from spelt wheat (*Triticum spelta*) to free-threshing bread wheat (*Triticum aestivum*, also a first example of *Triticum turgidum*), with varieties of hulled wheat now rapidly becoming negligible crops. Likewise, rye and oats, which before were occasionally found on Romanised sites, gradually become agricultural mainstays starting in the Early Medieval period but clearer still by 1000 CE (129-130). In Early Medieval Ireland and Scotland, hulled barley continued to be dominant along with occasional instances of free-threshing bread wheat, but oats now also became more common alongside a small amount of rye (107,131). Fruits, condiments, lentils and wild foods are all reasonably well represented on English sites, especially from 9th century CE onwards, and more widely across Britain and Ireland, so too are pea, bean and flax (130-131). These crop changes must also be seen in the context of changes to both agricultural technology and landscape organisation. For example, watermills become more obvious from ~600-800 CE in both England and Ireland, even if primarily associated with royal/monastic initiatives (132). More importantly, there is piecemeal introduction of heavier, more complex ploughs (with coulters and sometimes also mouldboards), such as the early example found at Lyminge, Kent from the first half of the 7th century CE (133) and as implied by weed species assemblages, early ridge-and-furrow fields and (by the later tenth–eleventh century CE) illuminated manuscripts (128). In Ireland, ploughs with coulters seem likely by the 10th century CE, with the mouldboard perhaps only introduced in the Anglo-Norman period (128,134). Despite these changes, there continues to be considerable diversity of landscape organisation and agricultural practice, with certain areas of England, Scotland and Ireland retaining more traditional forms of cultivation (with hoes and simple ards) right up until the late 19th and early 20th century CE. Medieval field systems reinforce this impression of diversity of behaviour and property rights, with the well-known 'three-field' Medieval agricultural system still not well-understood (126,135), but likely to have roots in England prior to the Domesday tax census (1086 CE), consistent with the wider Early Medieval evidence for more complex ploughs, oats and rye and more legumes suitable for crop rotation and/or multiple sowings (136). In Ireland, rath/cashel landscapes are associated with field systems, albeit ones with less clear organization (134). Medieval Scottish island sites also are useful in demonstrating clear diversity in the use of marine resources with organic residues and isotopes both suggesting specialised marine products on Shetland, but a continued dominance of dairying at Bornais on South Uist, Outer Hebrides (137-138).

Our understanding of food production strategies in the later Medieval period is considerably enhanced by the presence of detailed documentary evidence in England, Wales and Ireland. These records, especially from manorial estates, stress detailed agronomic knowledge, rapid responsiveness to both weather and cereal market prices, as well as complex decision-making about crop mixes, spring versus winter sowings, manuring, labour intensification, field rotation, etc. (27). They and wider ethnohistorical evidence (139) also emphasise that impacts from agrarian famines differ depending on regionally-varying land and livestock tenure structures, differential social status and local patterns of labour organisation. Although outside the chronological scope of this paper, it is worth emphasising that the post-Black Death era saw very substantial changes to stock-keeping, enclosure systems, labour productivity and crop choices, with larger or more productive animal breeds, additional nitrogen fixing crops such as clover or turnip, a series of imported New World cultivars such as potato, as well as new ways of preserving and transporting food (140-142). The cereal and other mono-cultures produced on British and Irish fields in the post-Industrial period are a further development linked closely to strongly integrated market economies, increasingly nucleated settlements and highly mechanised labour.

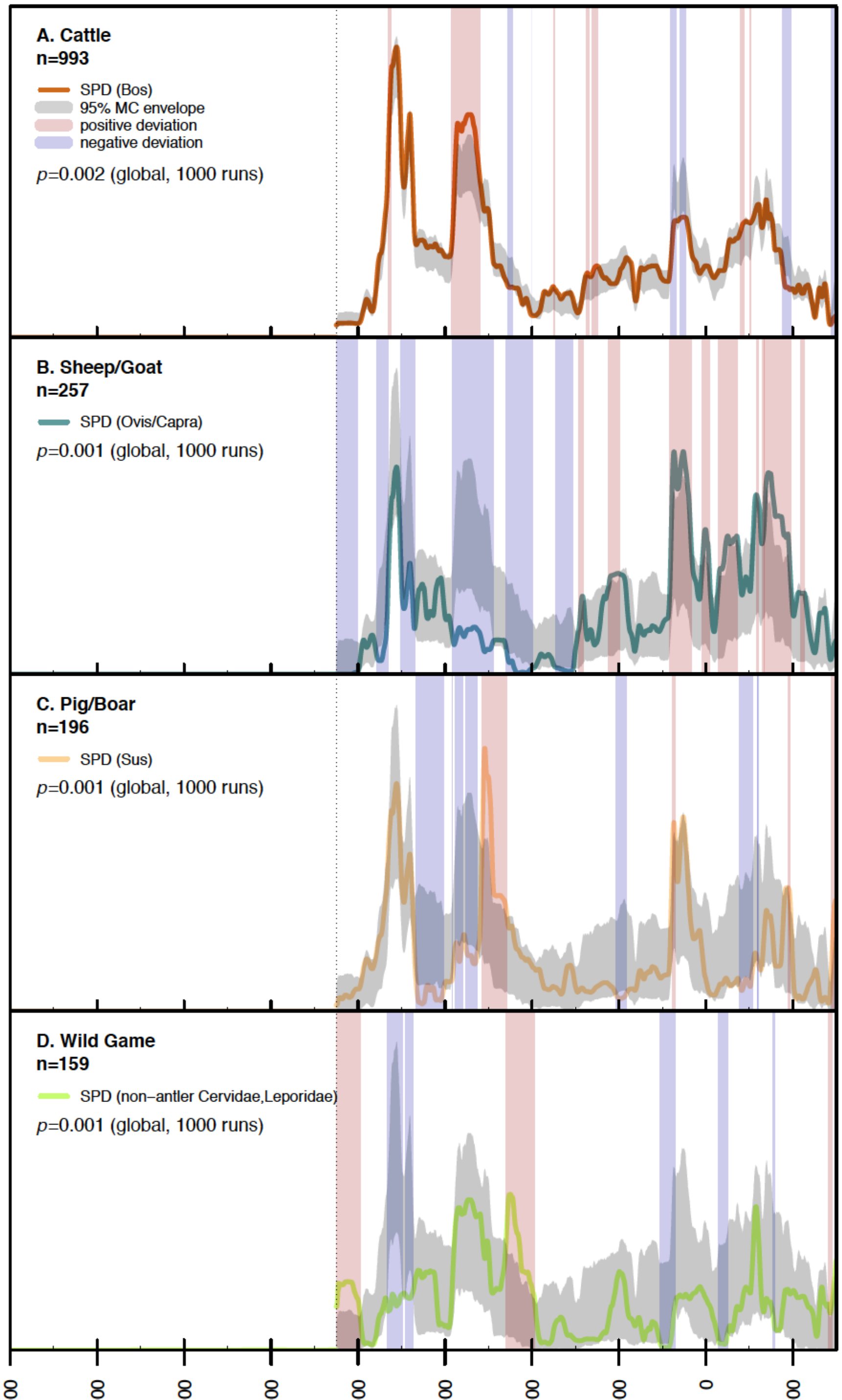


Figure S5. Permutation tests of animal species. The observed data (coloured line) is plotted on top of a 95% critical envelope produced by random relabelling of the species assigned to each date over 1000 simulations. Positive and negative deviations indicate greater than expected or less than expected quantities of dates belonging to the species/category in question. Only dates after ~4250 BCE are tested here.

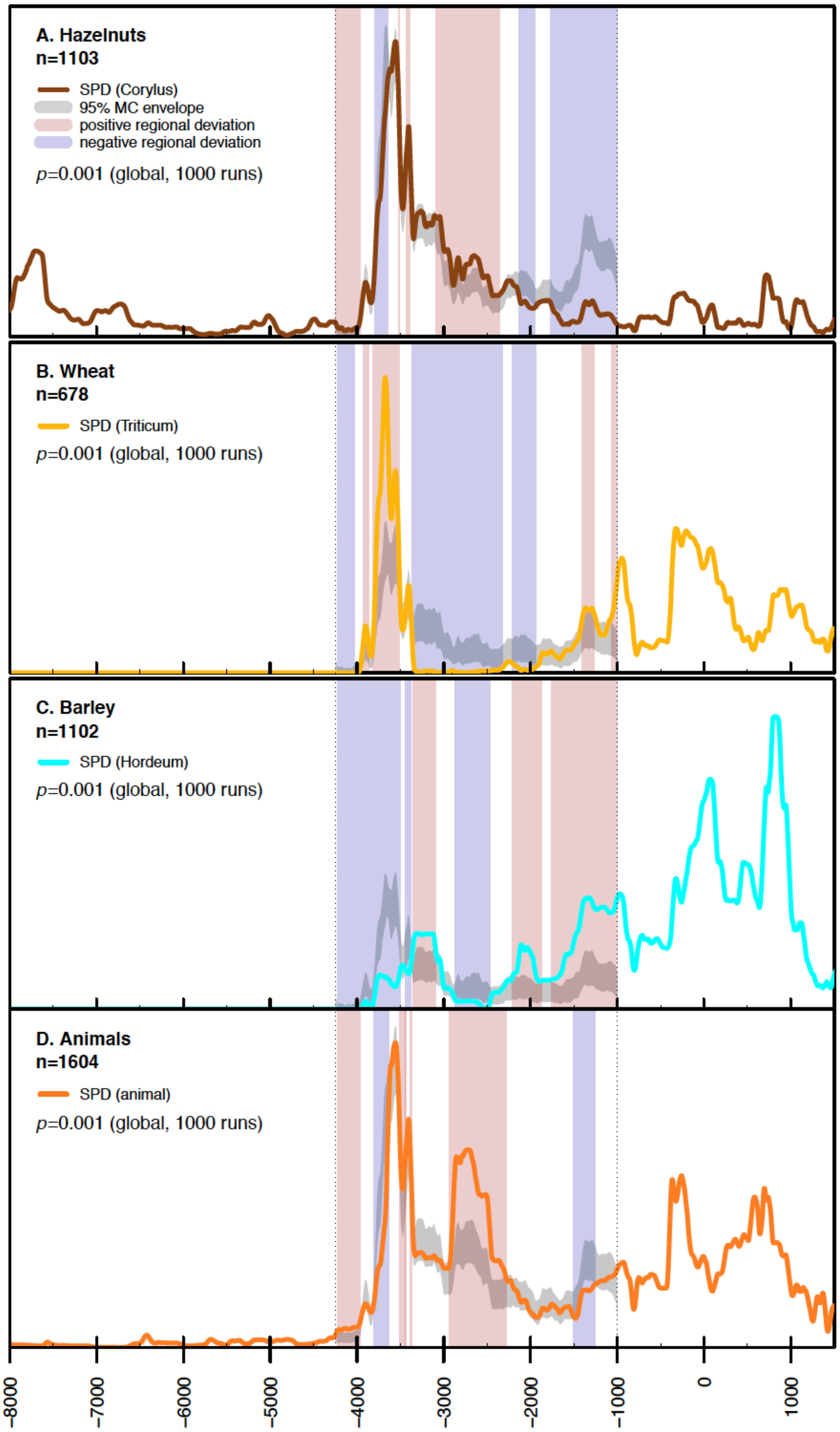


Figure S6. Permutation tests of plant species, earlier period. The observed data (coloured line) is plotted on top of a 95% critical envelope produced by random relabelling of the species assigned to each date over 1000 simulations. Positive and negative deviations indicate greater than expected or less than expected quantities of dates belonging to the species/category in question. Only dates after ~4250 BCE and before ~1000 BCE are tested here.

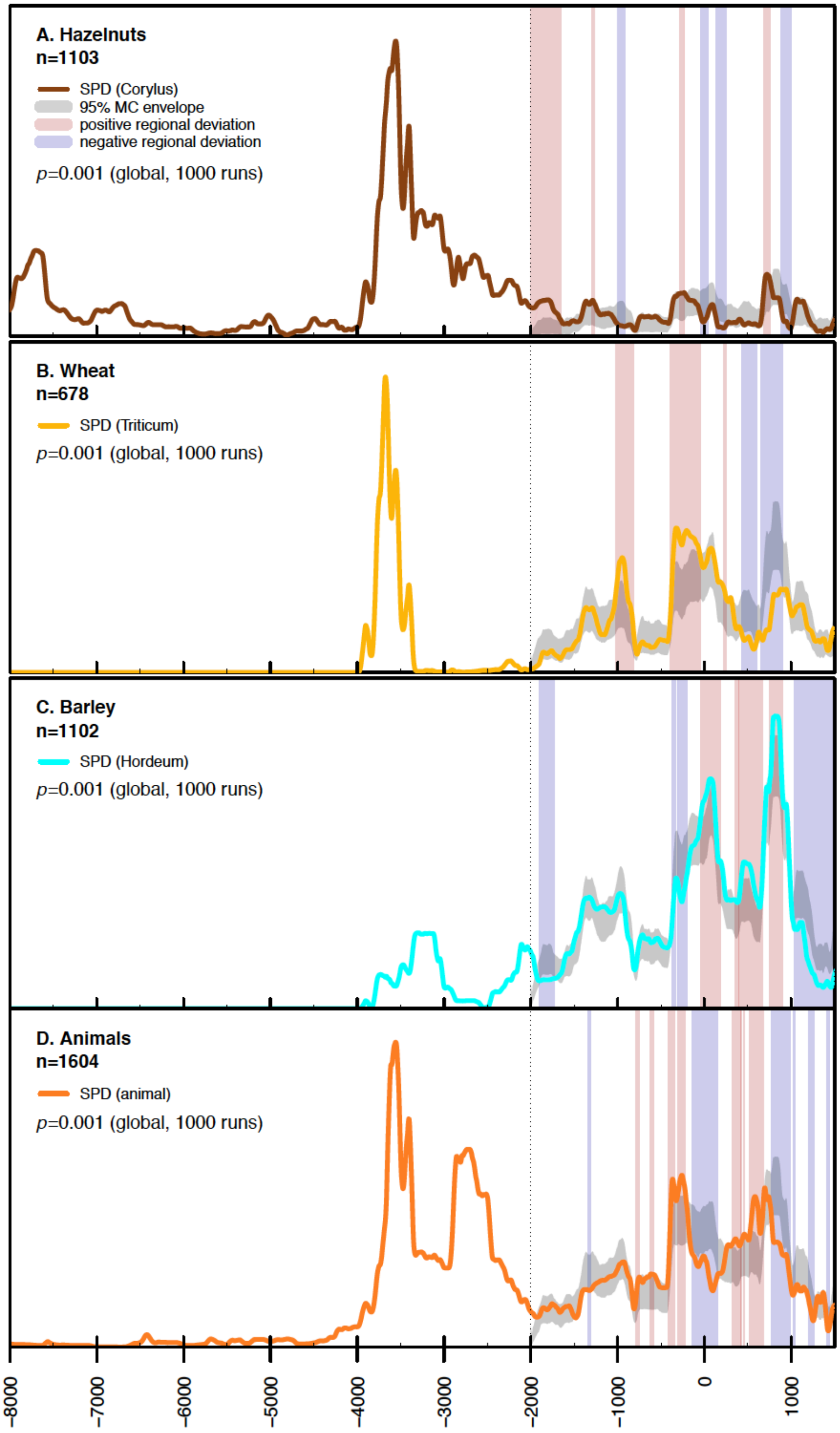


Figure S7. Permutation tests of plant species, later period. The observed data (coloured line) is plotted on top of a 95% critical envelope produced by random relabelling of the species assigned to each date over 1000 simulations. Positive and negative deviations indicate greater than expected or less than expected quantities of dates belonging to the species/category in question. Only dates after ~2000 BCE are tested here.

Crop	Presence						Growing conditions /Ecological Tolerances				
	Neolithic	*Bronze Age*	*Iron Age*	*Romano-British*	*Saxon-Medieval*	*Post-Medieval*	*Growing Season*	*Wet Climates*	*Cold Climates*	*Low Nutrient*	*Yields Returns*
Hulled Barley (6-row)	x	x	x	x	x	x	short	medium	good	good	medium
Naked Barley (6-row)	x	x	o	o	o	x	short-med	poor	v.good	good	medium
Barley (2-row)	-	-	-	-	-	x	medium	medium	good	good-v.good	poor
Einkorn	o	-	-	-	-	-	long-v.long	?good*	v.poor	v.good	poor
Emmer Wheat	x	x	x	x	o	?	long	good	med-poor	medium	medium
Spelt Wheat	-	x	x	x	x	x	long	med-poor	med-good	medium	med-good
Free-threshing Wheat (tetraploid)	x	?	?	?	?	x	long	poor	poor	poor	good
Free-threshing Wheat (hexaploid)	-	?	o	o	x	x	med-long	poor	medium	poor	good
Oats	-	-	-	o	x	x	short-med	good	good	v.good	med-poor
Rye	-	-	-	o	x	x	long-v.long	med-good	v.good	v.good	poor

Table S1. The main cereal crops and the main periods in which they are recorded across Britain and Ireland along with their main ecological attributes (Sources: 143-155)
Presence: x present / o restricted presence / - absent / ? uncertain
Growing season: The relative length of the crops growing season (spring to spring varieties, autumn to autumn varieties) relative to other crops. The effect of growing season will be very much dependent on what varieties, e.g. spring or autumn, were present in the past. It seems reasonable to assume that spring varieties of barley were present from earliest periods, but this may not have been the case for emmer, spelt or free-threshing wheat.
Wet Climates/Cold Climates: How the crop performs within wetter and colder climatic conditions.
Low nutrients: How the crop performs under low nutrient conditions. It should be noted that in colder climates due to the shorter period in which soil organisms are active that without adequate manuring they are likely to be on average more nutrient poor.
Yield returns: are the general relative return of each cereal for a fixed land unit if planted within relatively normal or average conditions.
***** Due to its general association with drier climates, einkorn has also been suggested to have poor tolerance in wetter climates

4. Palaeoecological Audit

A variety of palaeoecological proxies exist that complement the evidence present in the main text for climate change in key periods of the British and Irish later Holocene. Rising European lake levels or glacial advances have been proposed as direct proxies of cooler, wetter conditions and linked with observed societal changes while multi-proxy studies of bog-surface wetness curves provide centennial-scale indicators of a precipitation-evaporation balance, related to both summer precipitation and temperature, using testate amoebae, macrofossils, peat humification, stable isotopes or a combination of these (156-161). Increasingly, records from multiple sites are combined and compared to differentiate autogenic signals (noise) from more regionally consistent climate patterns (e.g. stacked-and-tuned testate amoebae records [161]), even if British and Irish peatland-derived records rarely extend beyond ~2500 BCE (for exceptions see Walton Moss [162] and Sluggan Bog [163]). The high-resolution speleothem record from Crag Cave in Ireland further provides a proxy record for temperature over much of the Holocene (164). These more localised records can be useful alongside the broader North Atlantic records, but it is also clear that they both exhibit considerable variation and suffer from varying degrees of dating uncertainty.

Despite these caveats, there is good corroborating evidence for unstable, then colder, wetter conditions in north-western Europe coincident with the three main phases of suggested population downturn considered in the main text. Amongst others, the later 4th millennium downturn finds support from changing Swiss lake levels and shifts to wild game hunting in Swiss lake villages (156,165), peat formation, pine recolonisation and bog oak tree-rings in Ireland (166-168), extreme storm events in coastal sediment archives in Brittany (169), and aggregate archaeological radiocarbon, south German tree-rings and north German microalgae (170). In contrast, another often discussed hemisphere-scale climatic episode in the second half of the Holocene is the proposed “4.2 ka event” in the later 3rd millennium BCE which has considerable support from Mediterranean and Middle Eastern sequences (171-172). However, there is no sign of population impact in the aggregate radiocarbon proxy for Britain and Ireland presented here, nor in most palaeoecological archives from north-western Europe (168). The earlier 1st millennium BCE climate downturn has previously been identified as a major wet phase across north-western Europe (104,173-177). In particular, Armit et al. (160) have compared Irish bog wetness for this phase with archaeological radiocarbon dates and suggest that, because observed decline in the former appears to post-date the observed decline in the latter, climate change cannot be causal. However, it is not at all clear (a) that we can assign such chronological priority in this notoriously flat part of the calibration curve, or that bog wetness indices might not lag atmospheric climate changes. For the Medieval period, we have the further benefit of documentary sources that identify stormy, increasingly cold weather (the beginning of what is known as the Little Ice Age) over the period ~1270-1420 BCE, and major contemporary European crises in human, animal and crop mortality, such as the European Great Famine (1314-22), Bovine Pestilence Epidemics (1315-21) and Black Death (1348-51 [178-181]) all with plausible mechanisms for how they might be climate-related. Downturns in Icelandic population and the abandonment of Norse Greenland settlements are also further well-known pieces of evidence that have been linked to deteriorating North Atlantic conditions in this period, even if the mitigating or exacerbating role played by human action clearly varied (181-182).

We can also compare the demographic changes inferred from archaeological radiocarbon date density to records of land-cover change, as reconstructed via pollen analysis and age-depth modelling from sedimentary sequences. Britain and Ireland have a long tradition of pollen analysis and over 2000 palynological sequences are known (169). There are a variety of qualitative or semi-quantitative ways to infer land cover and land use from pollen sequences (183-184), but the best quantitative estimates of land cover for individual pollen taxa use mechanistic models of the pollen-vegetation relationship and correct both for a non-linear relationship that exists between pollen and vegetation and for inter-taxonomic differences (185-186). Here we use a REVEALS model that validation has shown produces good estimates of actual vegetation cover from modern pollen assemblages (187-194) and draw upon pollen count data for Britain and Ireland from the European Pollen Database, filtered for those 94 sites that have good chronological control (191-193). The model uses parameters and methods described in Fyfe et al. (193) and Trondman et al. (195) with the exception that sedges (*Cyperaceae*) have further been excluded to avoid local vegetation bias. Mean values for the key plant taxa are calculated for contiguous 200-year time windows from 8000 BCE to present. Figure S8, compares the REVEALS results to the summed archaeological radiocarbon distribution and several regional climatic proxies. Overall woodland cover is stable at around 60-70% throughout the earlier Holocene up to ~4200-4000 BCE, but then open ground taxa increase approximately coincident with the increase in archaeological radiocarbon at the start of the Early Neolithic (196). Specifically, there is a suggested doubling of the amount of grassland (in particular *Poaceae*) at the start of the Early Neolithic from 12% to 24% land area, with clearance of shade-intolerant woodlands (e.g. hazel: *Corylus*) and areas of elm (*Ulmus*). Following the radiocarbon-inferred population peak at ~3700 BCE, grassland appears to decrease, followed by a period between 3600-2200 BCE, when vegetation remains broadly stable. There is no clear signal in the vegetation cover data for any abrupt ~3250 BCE ('5.3/5.2ka') climatic event (167-168), but gradual increase in heathland likely reflects a regional expansion of peatland, while growing cover of ash (*Fraxinus*, a secondary succession species) possibly indicates some woodland regrowth (for a proposed link with later Neolithic demographic decline and woodland regrowth in south Germany, see Lechterbeck et al. [197]).

From ~2200 BCE, grassland starts to increase again from ~20% to 35% cover at 1400-1200 BCE which is in step with the broader pattern observed across Europe by several recent semi-quantitative and quantitative studies (183,195,198). The expansion of grassland matches an increase in archaeological date densities but with a clear lag consistent with the earliest phases of Chalcolithic demographic expansion continuing to be more reliant on livestock, dairying and gathered foods, with cereal agriculture only building in intensity more slowly up to a Middle Bronze Age peak (which saw the first definite evidence for enclosed fields: figure S2). The increasing visibility of the common pasture weed *Plantago lanceolata* supports the assertion of improved grassland and intensified land use (184) and the peak of openness at 1400-1200 BCE coincides with peaks both in pollen-inferred cereal coverage and the proportion of summed radiocarbon dates on cereals. There is no suggestion in the pollen, or the radiocarbon data, of a climatic deterioration at ~2250 BCE ('4.2 ka') which is consistent with wider evidence that this suggested episode is more visible in Mediterranean and Middle Eastern sequences than in north-west European ones (168,172,199-200).

The Late Bronze Age/Early Iron Age population decline inferred from radiocarbon coincides with a period of observed stasis in woodland clearance/grassland expansion and a decline in the areal extent of cereals, in step with the climatic deterioration observed in local proxies (161,177) as well as evidence for agrarian restructuring (see above). From the Iron Age ~500 BCE there is sudden expansion of grassland cover and increases in cereal pollen, consistent with the recovery visible in the directly dated radiocarbon cereal samples and also evidence for the increasing importance of sheep and goats (main text figure 4, figure S4B). After a period of relative vegetation stability during the Roman period, the post-Roman period sees a replacement of grassland with heathland until 800-1000 CE, at which point grassland re-expands at the expense of all woodland cover. There appears to be far less of a clear relationship between the expansion of grassland and demography, which might reflect more complex and different relationships between population and land cover than in prehistory perhaps due to technological changes, regional diversification and/or overall increased productivity.

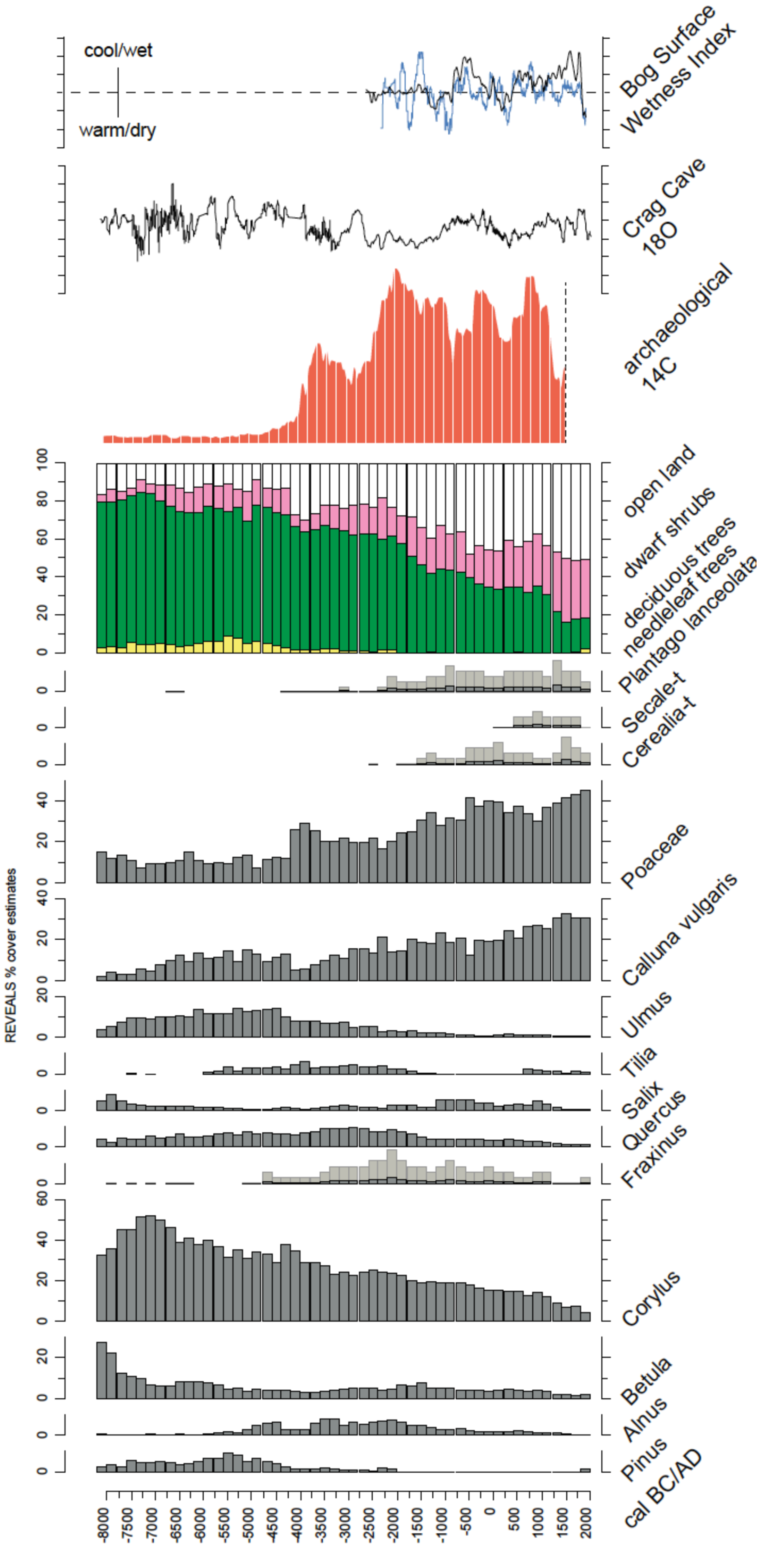


Figure S8. REVEALS-based percentage vegetation cover of Britain and Ireland (lighter grey bars indicate x5 exaggeration), compared with the archaeological date density summary for Britain and Ireland, and key UK/Ireland derived palaeoclimate indicators from Crag Cave (151), and compiled water table reconstructions from northern Britain (blue line, [148]) and Ireland (black line, [163]).