Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome

Lara M. Cassidy\textsuperscript{a,1}, Rui Martiniano\textsuperscript{a,1}, Eileen M. Murphy\textsuperscript{b}, Matthew D. Teasdale\textsuperscript{c}, James Mallory\textsuperscript{b}, Barrie Hartwell\textsuperscript{b}, and Daniel G. Bradley\textsuperscript{a,2}

\textsuperscript{a}Smurfit Institute of Genetics, Trinity College, Dublin 2, Ireland; and \textsuperscript{b}School of Geography, Archaeology and Palaeoecology, Queen’s University Belfast, Belfast BT7 1NN, Northern Ireland

Edited by Montgomery Slatkin, University of California, Berkeley, CA, and approved November 18, 2015 (received for review September 18, 2015)

The Neolithic and Bronze Age transitions were profound cultural shifts catalyzed in parts of Europe by migrations, first of early farmers from the Near East and then Bronze Age herders from the Pontic Steppe. However, a decades-long, unresolved controversy is whether population change or cultural adoption occurred at the Atlantic edge, within the British Isles. We address this issue by using the first whole genome data from prehistoric Irish individuals. A Neolithic woman (3343–3020 cal BC) from a megalithic burial (10.3× coverage) possessed a genome of predominantly Near Eastern origin. She had some hunter–gatherer ancestry but belonged to a population of large effective size, suggesting a substantial influx of early farmers to the island. Three Bronze Age individuals from Rathlin Island (2026–1534 cal BC), including one high coverage (10.5×) genome, showed substantial Steppe genetic heritage indicating that the European population upheavals of the third millennium manifested all of the way from southern Siberia to the western ocean. This turnover invites the possibility of accompanying introduction of Indo-European, perhaps early Celtic, language. Irish Bronze Age haplotype similarity is strongest within modern Irish, Scottish, and Welsh populations, and several important genetic variants that today show maximal or very high frequencies in Ireland appear at this horizon. These include those coding for lactase persistence, blue eye color, Y chromosome R1b haplotypes, and the hemochromatosis C282Y allele; to our knowledge, the first detection of a known Mendelian disease variant in prehistory. These findings together suggest the establishment of central attributes of the Irish genome 4,000 y ago.

ancient DNA | genomics | population genetics

The oldest Gaelic literature describes the origins of the Irish people as a series of ancient invasions, and the archaeological record in Ireland, as elsewhere in Europe, exhibits several horizons where major cultural shifts are apparent (1). The two most transformative are the arrival of agriculture (∼3750 BC) followed by the onset of metallurgy (∼2300 BC). The Neolithic package characterized by animal husbandry, cereal crops, ceramics, and timber houses reached the shores of Ireland some 5,000 years after its beginnings in the Near East. The second great wave of change starts with the appearance of copper mines, associated with Bell Beaker pottery, which are quickly followed by Bronze tool-making, weaponry, and gold-working, with distinct Food Vessel pottery succeeding from the earlier beakers (2). This period coincides with the end of the large passage graves of Neolithic Ireland in favor of single burials and smaller wedge tombs.

Twentieth-century archaeology was dominated by two non-mutually-exclusive paradigms for how such large scale social change occurs (3). The first, demic diffusion, linked archaeological change with the displacement and disruption of local populations by inward migrations. However, from the 1960s onwards, this assertion was challenged by a paradigm of cultural diffusion whereby social change happened largely through indigenous processes.

High-throughput sequencing has opened the possibility for genome-wide comparisons of genetic variation in ancient populations, which may be informatively set in the context of extensive modern data (4–10). In Europe, these clearly show population replacement by migrating farmers from southwest Asia at the onset of the Neolithic with some retreatment of the earlier Mesolithic genome at later stages (5–9, 11, 12). Three longitudinal genome studies have also shown later genome-wide shifts around the beginnings of the Bronze Age in central Europe with substantial introgression originating with the Yamnaya steppe herders (7, 9, 10). However, replacement coupled to archaeological horizons is unlikely to be a universal phenomenon, and whether the islands of Britain and Ireland, residing at the temporal and geographical edges of both the Neolithic and steppe migrations, were subject to successive substantial population inflows remains an open and debated question. For example, a recent survey of archaeological opinion on the origins of agriculture in Ireland showed an even split between adoption and colonization as explanatory processes (13).

Recent archaeological literature is also divided on the origins of the insular Bronze Age, with most opinion favoring incursion of only small numbers of technical specialists (1, 2, 14, 15).

To address this controversy, we present here the first, to our knowledge, genome-wide data from four ancient Irish individuals, a Neolithic woman (3343–3020 cal BC) from Ballynahatty, Co. Down, found in the context of an early megalithic passage-like grave, and three Early Bronze Age men from a cist burial in Rathlin Island, Co. Antrim (2026–1534 cal BC) with associated Food Vessel pottery (16) (SI Appendix, Section S1).

Significance

Modern Europe has been shaped by two episodes in pre-history, the advent of agriculture and later metallurgy. These innovations brought not only massive cultural change but also, in certain parts of the continent, a change in genetic structure. The manner in which these transitions affected the islands of Ireland and Britain on the northwestern edge of the continent remains the subject of debate. The first ancient whole genomes from Ireland, including two at high coverage, demonstrate that large-scale genetic shifts accompanied both transitions. We also observe a strong signal of continuity between modern day Irish populations and the Bronze Age individuals, one of whom is a carrier for the C282Y hemochromatosis mutation, which has its highest frequencies in Ireland today.

Author contributions: D.G.B. designed research; L.M.C. and R.M. performed research; E.M.M. contributed new reagents/analytic tools; L.M.C., R.M., M.D.T., and D.G.B. analyzed data; and L.M.C., R.M., E.M.M., M.D.T., J.M., B.H., and D.G.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. Freely available online through the PNAS open access option.

Data deposition: The sequences reported in this paper have been deposited in the European Nucleotide Archive (project accession no. PRJEB11995).

1L.M.C. and R.M. contributed equally to this work.

2To whom correspondence should be addressed. Email: dbradley@tcd.ie.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1518445113/-/DCSupplemental.
Results
DNA Extraction, Sequencing, and Uniparental Haplotypes. DNA was extracted (SI Appendix, Section S2) from the petrous portion of the temporal bone (7) yielding high levels of endogenous content (38–68%) for all samples (Table 1). Two individuals, Ballynahatty and Rathlin1, were shotgun sequenced to high coverage (10–11x), whereas the two remaining Bronze Age samples, Rathlin2 and Rathlin3, were sequenced to 1.5x and 0.75x, respectively (SI Appendix, Section S3). Data authenticity was assessed by using several approaches (SI Appendix, Section S5). Molecular damage patterns were found to be consistent with those of ancient DNA (SI Appendix, Fig. S5.1). Contamination estimates were found to be low from negative controls (0.07–0.16%), as well as heterozygosity of the mitochondrial genome (0.36–0.50%) and the X chromosome in males (0.688–1.646%).

Molecular sex determination agreed with archaeological results (SI Appendix, Section S7), and whole mitochondrial chromosome haplogroups were assigned (Table 1 and SI Appendix, Section S7). The Neolithic individual, Ballynahatty, belongs to HV0, a clade with highest frequencies seen in Early and Middle Neolithic (MN) groups from Germany and France (9, 17, 18) and which has not been identified in any Mesolithic Europeans. The Bronze Age individuals belonged to the haplogroups U5 and J2b. Notably, the three Bronze Age males each belong to the Y chromosome haplogroup R1b1a2a1a2c (SI Appendix, Section S8). This lineage is characterized by a modern east–west frequency gradient in the British Isles, and is almost fixed (94%) in the West of Ireland (19, 20). R1b haplotypes have been argued as first appearing with steppe incursion in the central European Bronze Age (9).

Principal Component Analysis and ADMIXTURE. A projection principal component analysis (PCA) was used to investigate the genetic affinities of our four ancient Irish genomes, alongside 78 published ancient samples (SI Appendix, Table S9.1; selection criteria detailed in SI Appendix, Section S4) (5–10, 21–26) using 677 modern individuals from Western Eurasia (8) as a reference population (Fig. 1A and B and SI Appendix, Sections S9.1 and S10). In Fig. 1A, we see a clear division between hunter–gatherer and early farmer individuals, with the Ballynahatty female plotting with five other MN samples from Germany, Spain, and Scandinavia. However, a large shift in genetic variation is seen between Ballynahatty and the three Irish Early Bronze Age samples, Rathlin1, Rathlin2, and Rathlin3, who fall in a separate central region of the graph along with Unetice and other Early Bronze Age genomes from Central and North Europe. These plots imply that ancient Irish genetic affinities segregate within European archaeological horizons rather than clustering genetically within the island.

Model-based approaches allow the decomposition of individuals into coefficients contributed by a set number (K) of ancestral populations. We investigated this by using ADMIXTURE (Version 1.23) (27) with ancient individuals included in the analysis alongside 1,941 modern samples from diverse worldwide populations (8) (SI Appendix, Section S11). Fig. 1C shows the plot of estimated ancestry proportions for each ancient genome at a value of K = 11. These partition similarly to previous analyses (7, 9, 10), with three major ancestral coefficients manifesting in west and central Europe. The first (colored red) forms the near totality of ancestry in hunter–gatherer samples, and admixes with a second (orange) component found at high levels in Neolithic and also modern Near Eastern populations (SI Appendix, Section S11.1). Ballynahatty is similar to other MN samples with a majority orange “early farmer” component but with an elevated level of the red “hunter–gatherer” component compared with Early Neolithic genomes. The ancestry of Yamnaya, Early Bronze Age herders from the Pontic Steppe, is evenly divided between this same red component and the third major European coefficient, colored in green, which has been identified with a Caucasus origin (28). This Caucasus component is encountered subsequently, introduced via Yamnaya, in Late Neolithic and Bronze Age samples in central Europe (9, 10) and features in the three Irish Early Bronze Age samples within profiles similar to continental Bronze Age genomes.

Neolithic Origins. D and f statistics (29, 30) (Dataset S1 and SI Appendix, Section S12) support identification of Ballynahatty with other MN samples who show a majority ancestry from Near Eastern migration but with some western Mesolithic introgression. Outgroup f2 statistics indicated that Ballynahatty shared most genetic drift with other Neolithic samples with maximum scores observed for Spanish Middle, Epicardial, and Cardial Neolithic populations, and the Scandinavian individual Gok2 (SI Appendix, Section S12.1). D statistics confirmed these affinities. Interestingly, both the Spanish MN individuals and Gok2 also belong to Mega-lithic passage tomb cultures. Along with other MNs, Ballynahatty displays increased levels of hunter–grouther introgression compared with earlier farming populations. D statistics revealed that, out of the three Mesolithic hunter–gatherer groupings from Haak et al. (9), eastern hunter–grouther (EHG), Scandinavian hunter–grouther (SHG), and western hunter–grouther (WHG), Ballynahatty shares the most alleles with WHG and furthermore has the strongest preference for WHG over EHG and SHG out of all contemporaneous Neolithic individuals so far sampled. However, Ballynahatty forms a clade with other MN genomes to the exclusion of WHG and, symmetrically, WHG genomes form a clade to the exclusion of Ballynahatty. Of the three WHG individuals, Ballynahatty appeared to share the least amount of affinity with LaBranca (Spain) and the largest amount of affinity with Loschbour (Luxembourg). To gauge the proportion of Ballynahatty's ancestry derived from WHG, we used the f2 ratio, f2(Mbuti, Loschbour; Ballynahatty, Dai)/f2(Mbuti, Loschbour; K01, Dai) (29), to estimate a hunter–grouther component of 42 ± 2% within a predominantly early farmer genome. Thus, we deduce migration has a primary role in Irish agricultural origins.

Bronze Age Replacement. Prior studies (7, 9, 10) convincingly demonstrate that Central European genomes from the late Neolithic and Early Bronze Age differ from the preceding MN due to a substantial introgression originating with Steppe herders linked to cultures such as the Yamnaya. Accordingly, we used a series of tests to gauge whether the ancestries of the Rathlin Early Bronze Age genomes were subject to this influence. D statistics confirmed that Ballynahatty and other MN individuals form clades with each other to the exclusion of these Irish Bronze Age samples. Specific disruption of continuity between the Irish Neolithic and Bronze Age is clear with significant evidence of both Yamnaya and EHG introgression

Table 1. Sequencing results from four ancient Irish individuals

<table>
<thead>
<tr>
<th>Sample</th>
<th>Date, cal BC</th>
<th>Archaeological context</th>
<th>Final endogenous DNA content, %</th>
<th>Mean genome coverage, X</th>
<th>Genetic sex</th>
<th>mtDNA haplogroup</th>
<th>Y chromosome haplogroup</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ballynahatty</td>
<td>3343–3020</td>
<td>Middle to Late Neolithic</td>
<td>67.86</td>
<td>10.27</td>
<td>Female</td>
<td>HV0 +195</td>
<td></td>
</tr>
<tr>
<td>Rathlin1</td>
<td>2026–1885</td>
<td>Early Bronze Age</td>
<td>60.74</td>
<td>10.50</td>
<td>Male</td>
<td>U5a1b1e</td>
<td>R1b1a2a1a2c1g</td>
</tr>
<tr>
<td>Rathlin2</td>
<td>2024–1741</td>
<td>Early Bronze Age</td>
<td>38.15</td>
<td>1.49</td>
<td>Male</td>
<td>U5b2a2</td>
<td>R1b1a2a1a2c1</td>
</tr>
<tr>
<td>Rathlin3</td>
<td>1736–1534</td>
<td>Early Bronze Age</td>
<td>61.42</td>
<td>0.75</td>
<td>Male</td>
<td>J2b1a</td>
<td>R1b1a2a1a2c</td>
</tr>
</tbody>
</table>
into Irish Bronze Age samples when placed in a clade with any MN. However, like other European Bronze Age samples, this introgression is incomplete, as they also show significant MN ancestry when placed in a clade with Yamnaya. The highest levels of MN ancestry were observed when either Ballynahatty or Gok2 (Scandinavian) was the sample under study. However, when paired with central European Bronze Age populations, the Rathlin samples show no trace of significant introgression from Ballynahatty, suggesting that earlier Irish populations may not have been a source of their partial MN ancestry.

These analyses, taken with the PCA and ADMIXTURE results, indicate that the Irish Bronze Age is composed of a mixture of European MN and introgressing Steppe ancestry (9, 10). To estimate the proportion of Yamnaya to MN ancestry in each Irish Bronze Age sample, we took three approaches. First, from ADMIXTURE analysis (Fig. 1), we examined the green Caucasus ancestry component. We presume an ultimate source of this as the Yamnaya where it features at a proportion of 40% of their total ancestry. In our three Irish Bronze Age samples, it is present at levels between 6–13%, which, when scaled up to include the remaining 60% of Yamnaya ancestry, imply a total of 14–33% Yamnaya ancestry and therefore 67–86% MN in the Irish Bronze Age. Second, for each Bronze Age Irish individual, we calculated the proportion of MN ancestry by using the ratio $f_4$ (Mbuti, Ballynahatty; X, Dai)/$f_4$ (Mbuti, Ballynahatty; Gok2, Dai), which gave estimates between 72 ± 4% to 74 ± 5%, implying a substantial Yamnaya remainder. Third, we followed the methods described in Haak et al. (9), which use a collection of outgroup populations, to estimate the mixture proportions of three different sources, Linearbandkeramik (Early Neolithic; 35 ± 6%), Loschbour (WHG; 26 ± 12%), and Yamnaya (39 ± 8%), in the total Irish Bronze Age group. These three approaches give an overlapping estimate of ~32% Yamnaya ancestry.

Runs of Homozygosity. We coanalyzed Ballynahatty, Rathlin1, and the four other ancient Europeans sequenced to high coverage (7, 8) to estimate the fraction of each genome under runs of homozygosity (ROH) (SI Appendix, Section S13). This approach may be useful to inform on past demography; long contiguous homozygous segments indicate recent endogamy, whereas shorter runs result from older restrictions in ancestral population size (31, 32). Fig. 2 plots these
ROH estimates in a background of data from modern genomes of diverse origins (33, 34). The single ancient hunter–gatherer genome in this analysis, Loschbour, shows extremely high levels of ROH, indicative of a restricted ancestral population size. However, Ballynahatty and the two early Neolithic genomes, Stuttgart and NE1, each show levels of ROH comparable to those seen in modern East Asians. This pattern argues against a genetic bottleneck, such as that due to a narrow pioneer colonization, in the ancestry of this Irish Neolithic genome and supports the idea of large-scale Neolithic migration rather than assimilation of farming by local hunter–gatherers. The Bronze Age genomes, Rathlin1 and BR2, both show further reductions of ROH, producing distributions similar to each other and to that of modern Europeans.

Haplotype-Based Resolution of Continuity. Haplotype-based approaches are more powerful than those using unlinked genetic loci in identifying fine genetic structure, such as that displayed among Europeans, and are relatively robust to bias from marker ascertainment (35, 36). We ran ChromoPainter in fineSTRUCTURE (Version 2) (35) to decompose each ancient genome into a series of haplotypic chunks, and identified which modern individuals from a diverse set of Eurasian populations (37) shared the same, or most similar, haplotype at each given chunk. In each analysis showing highest levels of chunk copying. However, some differences are discernable; the Hungarian and Stuttgart Neolithic genomes tend toward higher values in eastern Mediterranean (Sicilian, Italian, and Greek samples; Fig. 3 and SI Appendix, Fig. S14.1), and the Irish Neolithic has highest values in the west (Sardinian and Spanish). A further difference lies in the comparison of each to the affinities shown by the Luxembourg WHG, Loschbour, which shows no correlation in its modern affinities with the earlier continental Neolithics but does show a significant relationship (P = 5.4 × 10−3) with those of Ballynahatty, undoubtedly because of greater WHG admixture in her ancestry.

The most striking feature of the haplotype sharing by the Irish Bronze Age genome is its high median donation levels to Irish, Scottish, and Welsh populations (Fig. 3). In regression with results from the other ancient genomes, these insular Celtic populations, and to a lesser degree the English, show an excess of sharing with Rathlin1, suggesting some level of local continuity at the edge of Europe persisting over 4,000 y. The Hungarian Bronze Age genome shows more affinity with central European populations. Interestingly, for both Bronze Age genomes, the modern Basque population displays outlying low-affinity scores compared with neighboring western European samples, supporting recent findings that suggest a continuity between the Basques and Iberian Chalcolithic groups (25).

Phenotypic Analysis. Ireland is unusual in displaying world maximum frequencies of a number of important genetic variants, particularly those involved in lactase persistence and two recessive diseases: cystic fibrosis and hemochromatosis (38–41, 42, 43). Interestingly, both the high coverage Neolithic and Bronze Age individuals were heterozygous for the hemochromatosis alleles H63D and C282Y, respectively. Modern Irish allele frequencies are 15% and 11% for these variants, with the latter, more penetrant variant responsible for a world maximum of this disease in Ireland (44, 45). Additionally and in accordance with other data suggesting a late spread of the lactase persistence phenotype not yet prevalent in western Europe (7, 10), the Neolithic Ballynahatty was homozygous for the nonpersistent genotype and Rathlin1 was heterozygous and thus tolerant of drinking raw milk into adulthood.

We were able to deduce that Neolithic Ballynahatty had a dark hair shade (99.5% probability), most likely black (86.1% probability), and brown eyes (97.3% probability) (46). Bronze Age Rathlin1 probably had a light hair shade (61.4%) and brown eyes (64.3%). However, each Rathlin genome possessed indication of at least one copy of a haplotype associated with blue eye color in the HERC2/ OCA2 region.

Discussion

The advent of farming in Ireland lies at the temporal and geographical terminus of several thousand years of transition across
Europe and seems to occur rapidly ~3750 BC (47). The nature of this transition remains a long-standing archaeological controversy between proposals of migration by incoming farmers versus those of adoption of agriculture by indigenous Mesolithic populations (48–51). The Irish MN female farmer (3343–3020 cal. BC) from a Megalithic tomb in Ballynahatty near Belfast affords, to our knowledge, a first direct genetic view of the transition at Europe’s western edge. She displays predominant ancestry from early farmers that ultimately originated in migrating agriculturalists from the Near East. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.

From examination of the fraction of her genome, which is under ROH, she seems similar to other ancient Neolithic, suggesting that she belonged to a large outbreeding population. This analysis argues against a marked population bottleneck in Ireland. This derivation is attested by her PCA and ADMIXTURE profile, her correlated allele frequencies with other Neolithic genomes, reflected in D statistics, and by her haplogetic affinity with modern southern Mediterranean populations such as Sardinians. Her early European farmer coefficient is estimated at ~60%; an ancestry which is difficult to reconcile with extensive indigenous adoption of agriculture in Ireland only several hundred years earlier. She shares higher levels of genetic drift with Early and MN samples from Spain rather than those from Germany, supporting a link between the early farming cultures of Atlantic Europe and arguing for the possible passage of farming to Ireland via a southern coastal route rather than via the migrations through central Europe (2). A high affinity to Scandinavian farmers, Gök2, is more difficult to interpret as it is associated with the TRB (Funnelbeaker) culture whose origins are generally derived from Central European farming cultures but perhaps it is noteworthy that this latter sample is also recovered from a Megalithic context.
(ERC) Investigator Grant 295729-Codex. We acknowledge Science Foundation Ireland (SFI) ERC Support Award 12ERC/B2227, Valeria Mattiangeli, and TrinSeq for MiSeq support. We acknowledge the DJE/DES/HR/HEA Irish Centre for High-End Computing for the provision of computational facilities and support.