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The evolutionary relationship between bere barley and other types of cultivated barley

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Abstract We used genotyping-by-sequencing to investigate the evolutionary history of bere, the oldest barley variety still cultivated in Britain and possibly in all of Europe. With a panel of 203 wild and 401 cultivated barley accessions, including 35 samples identified as bere, we obtained filtered datasets comprising up to 1,946,469 single nucleotide polymorphisms (SNPs). The beres formed two genetically-distinct groups, the larger of which included beres from Orkney and the Scottish Western Isles, as well as varieties not identified as bere from the

Faroe Islands. This group of beres was distinct from other British barleys, but had a close genetic affiliation with Scandinavian accessions. Although the data were partly compatible with the traditional view that bere was introduced to Scotland by the Vikings during the eighth century AD, the evidence as whole suggested that the bere and Scandinavian barleys are sister groups descended from a more distant common progenitor, possibly dating to the Bronze Age when hulled barleys first become common in northern Europe. More recently, there has been gene flow from these beres into Polish barleys, possibly following export of grain to the Baltic region during periods when Orkney was under Norwegian or Danish rule. A second, smaller group of beres, which included a traditional Welsh variety, was genetically distinct from the main group and probably represents a more

Hayley Craig and Karren Palmer made equal contributions and are joint second authors.

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recent introduction of barley from central Europe. Our results emphasize the uniqueness of bere barley and its importance as a heritage crop and a potential source of germplasm for breeding programmes.

Keywords Agriculture · Barley · Bere · Crop evolution · Genotyping-by-sequencing

Introduction

Bere is a six-row, hulled landrace of barley (*Hordeum vulgare* L. subsp. *vulgare*) which was once extensively cultivated throughout Scotland but in recent years has only been grown on a small scale in Orkney, Shetland and the Western Isles (Scholten et al. 2011: pp. 26–74). Even in 1912, when many areas had ceased producing bere, the agricultural census (Board of Agriculture for Scotland 1913) documented 4228 ha of the crop in 36 of the 101 Scottish districts. Bere was also grown more widely in Britain, especially in northern or upland areas and on poor soils. An early English description of bere mentions that it was common in parts of Yorkshire and Durham (Gerard 1633: pp. 70–72) while in Wales a similar type of barley, Haidd Garw or ‘coarse barley’, was also grown (Jarman 1996). Bere was important in Ireland, too, where about 21,500 ha (18% of the total barley area) were returned in the 1848 census (Porter 1850). Improved types of bere, such as Victoria and Buchan bere, were also selected for wider distribution (Lawson and Son 1852: pp. 67–78). Bere was taken to North America, where European settlers on the East coast found that bere from Scotland grew better than two-row varieties (Briggs 1978: pp. 445–480), and the crop was probably also taken to Canada by Scottish settlers (Martin et al. 2009). However, the many historical references to bere or its various synonyms may not all refer to the landrace which is grown today, as the name was applied more widely to six-row barley by some authors (Jarman 1996).

Bere was well-suited to the crofting system of subsistence farming, as it gives reasonable yields on unimproved nutrient-poor soils (Scholten et al. 2009; Schmidt et al. 2019) and does not require a high level of inputs. It is spring sown and has a relatively high growth rate, resulting in a short period from sowing to harvesting which is an advantage in northern latitudes where there are long summer day lengths

but a short, cool growing season (Wright and Dalziel 2002). Under these conditions, bere can provide a greater grain yield than many modern cultivars (Riggs and Hayter 1975; Schmidt et al. 2019) and can often be harvested under more favourable weather conditions than later maturing varieties (Martin et al. 2010). Bere was an important staple, providing grain for both milling into flour (beremeal) and malting, with bere malt used for brewing and, from the sixteenth century, for whisky production (Martin et al. 2009). Small-scale private distilling was an important cottage industry, which provided an opportunity to add considerable value to bere (Hay 2012); although private distilling was made illegal at the end of the eighteenth century, illicit distilling using locally grown bere continued for several more decades.

Despite the adaptation of bere to the environmental and economic conditions of north and east Scotland, its cultivation declined from the nineteenth century following the introduction of improved agricultural practices such as new rotations, liming and drainage (Hay 2012). New, higher yielding two-row barley cultivars were also more attractive because of their shorter straw, which reduced the risk of lodging, and larger grains with lower nitrogen content which produces more efficient malt for brewing and distilling. Other factors which must have contributed to the decline of bere include a reduced dependence on bere as a food following the introduction of potatoes in the eighteenth century and the availability of cheap wheat flour from the early twentieth century. By the end of the twentieth century, only about 5–15 ha of bere were being grown annually in Caithness and Orkney (Jarman 1996) and about 25 ha in the Western Isles (Scholten et al. 2009).

During the last twenty years, interest in bere has revived, in particular on Orkney where the crop is looked on as an important part of the island’s cultural heritage (Mahon et al. 2016). Unlike modern barley cultivars, which on Orkney are grown mainly for animal feed, bere is grown for higher value products such as beremeal which is used in biscuits, bannocks and bread (Martin et al. 2009), and malt which is increasingly used in the production of niche market Scotch whiskies and beer (Martin and Chang 2008). There is also a growing recognition of the value of landraces as genetic resources for breeding programmes aimed at more sustainable production (Kumar et al. 2020). With barley,

manganese deficiency is one of the major factors limiting productivity on poor soils and can lead to complete crop failure if other environmental factors are unfavourable (Schmidt et al. 2013). The adaptation of some bere genotypes to northern Scottish conditions includes greater efficiency in the uptake of manganese and other trace elements on high pH soils, enabling growth and grain production under conditions that could not be tolerated by modern 'improved' barley cultivars (Schmidt et al. 2019).

The origins of bere barley are intriguing. It is a survivor of pre-industrial agriculture and is thought to be the oldest barley variety still cultivated in Britain and possibly in all of Europe (Scholten et al. 2009). Historical sources often refer to bere as *bygg*, the Old Norse for barley, and Jarman (1996) suggested that its origins might go back to the Norse and Danish invasions of the eighth century AD. However, results from a recent grain morphometrics study of bere and Scandinavian six-row landraces (Wallace et al. 2019) do not support this theory. Bere may therefore represent an earlier introduction of barley, possibly a remnant of the crops brought to Scotland when agriculture was first established in the region approximately 6000 years ago (Thorpe 1996; Lee and Thomas 2012; Thomas 2013), or a descendant of the hulled barleys that became predominant about 3000 years ago during the later Bronze Age (Bishop et al. 2009).

So far, there have only been limited genetic studies of bere and although these have revealed variations between accessions from different geographical regions, they have not enabled the evolutionary origins of the crop to be distinguished. Typing of 20 microsatellite markers placed bere accessions from Orkney and Shetland in a different cluster to those from the Western Isles, and revealed some distinctions between Orkney and Shetland beres (Southworth 2007). More comprehensive typing with 2312 single nucleotide polymorphisms (SNPs) showed a less clear distinction between beres from Orkney/Shetland and the Western Isles, but confirmed that there are genetic differences between bere and Scandinavian and British landraces (Wallace et al. 2019). A parallel study with a larger SNP dataset, comprising some 9000 markers, re-established the distinctiveness of Orkney, Shetland and Western Isles beres and again showed beres to be genetically different from barleys of Scandinavia and Britain (Schmidt et al. 2019).

In recent years, genotyping-by sequencing (GBS) methods have been developed which enable the rapid typing of thousands of SNPs in multiple accessions of a single species (Kim et al. 2016; Scheben et al. 2017). The detailed information on genotype variations that is provided by GBS enables the relationships between different populations of a species to be probed at great depth (Oliveira et al. 2020), potentially enabling a greater discrimination of the relationship between bere and other cultivated barleys than has been possible by the microarray-based SNP typing methods previously used (Schmidt et al. 2019; Wallace et al. 2019). Here we report the use of GBS to compare the genotypes of 35 bere accessions with those of 366 other barley landraces from all parts of Europe and the Near East.

Materials and methods

The study material comprised 203 wild barley accessions (*Hordeum vulgare* L. subsp. *spontaneum* (K. Koch) Thell) and 401 landraces and other cultivated barley varieties (Supplementary Table S1). The cultivated barleys comprised 35 samples identified as bere from mainland Scotland, Orkney, the Western Isles or of unknown Scottish provenance, and 366 other cultivated accessions not identified as bere, these including 32 accessions from Scandinavia (which we define as Norway, Sweden, Denmark, the Faroe Islands and Finland), ten accessions from Britain, and 324 accessions from elsewhere in Europe and the Near East. For most accessions, DNA was extracted from 1 to 3 dry seeds using the CTAB extraction protocol (Rogers and Bendich 1988). For some accessions that gave poor DNA yields with the CTAB method, seeds were vernalized for 2 days at 4 °C, grown for two weeks at room temperature in petri dishes covered with filter paper, and DNA extracted from first leaves using the Bioline Isolate II Plant DNA Kit. DNA was quantified by a Qubit dsDNA HS assay with a Qubit 2.0 Fluorometer and DNA integrity was checked by electrophoresis in 1% agarose gels.

Genotyping-by-sequencing (Novogene, following the procedure described by Elshire et al. 2011) yielded 2,670,738 reads. Unique sequence tags were identified from the FASTQ files by reference to the barley genome assembly of Mascher et al. (2017) using the *ref_map.pl* programme of STACKS v2.2

(Catchen et al. 2011, 2013). Following quality control with *process_radtags*, sequence tags were aligned to the reference genome with BWA v0.7.17 (Li and Durbin 2009) and the alignments sorted with SAMTOOLS v1.9 (Li et al. 2009). Fifty percent of the sequence tags mapped to unique positions in the barley reference genome, 47.8% mapped to multiple positions and 0.9% were unmapped. A SNP catalogue was then constructed from the resulting BAM files with the STACKS programme *gstacks*.

Three filtered datasets were prepared. Dataset 1 omitted barley accessions with >78% missing data and/or identified as possible wild-cultivated hybrids based on the smatpca analysis described below. This dataset was filtered to retain sites with <70% missing data, a probability of excess heterozygosity of <0.5 and minor allele count of ≥ 9 , yielding 1,946,469 SNPs for 584 accessions. Dataset 2 was then obtained by further filtering of dataset 1 to retain only those variants with >0.05 frequency in the cultivated barleys and absent in the wild accessions. This dataset, which is enriched for ‘post-domestication’ variants and hence less susceptible to the effects of ancestral lineage sorting, contained 63,265 SNPs in 401 cultivated accessions and a single wild genotype (the filtering collapses all of the wild accessions into a single ‘individual’). Dataset 3 was prepared with the entire set of accessions, applying a minimum mean depth filter of >7, and retaining biallelic sites with <20% missing data and minor allele frequency of >0.05, yielding 9719 SNPs.

Principal components analysis (PCA) was performed with TASSEL (Bradbury et al. 2007) and smartpca from the Eigensoft package (Patterson et al. 2006) and plotted as one- or two-dimensional graphs with Excel 14.7.3. Dendrograms were constructed by neighbour-joining (NJ) using TASSEL and the maximum likelihood (ML) method with IQ-TREE (Nguyen et al. 2015) and visualized with FigTree 1.4.4 (Rambaut 2014). IQ-TREE was run with ModelFinder (Kalyaanamoorthy et al. 2017) and the optimal substitutional model determined to be GTR + F + ASC + R₄ (general time-reversible model with empirical base frequencies, ascertainment bias correction and four rate change categories). Identity-by-state (IBS) was calculated using PLINK 1.9 (Purcell et al. 2007). Population structure was examined with the model-based clustering algorithm STRUCTURE 2.3.4 (Pritchard et al. 2000), with *K* values

between 1 and 20, 20,000 burnins, 40,000 MCMC repetitions and ten independent runs for each value of *K*. Likelihood values for different *K* were assessed with STRUCTURE HARVESTER 0.6.94 (Earl and vonHoldt 2012) and histograms illustrating population membership of individual accessions prepared with Excel 14.7.3. Geographical maps were drawn with ArcMap 1.0 of ArcGIS (ESRI 2011). The ABBA-BABA test (Patterson et al. 2012) was performed in Dsuite (Malinsky et al. 2020) and population splits and mixtures were inferred in TreeMix 1.13 (Pickrell and Pritchard 2012).

Fourteen accessions were processed as replicate DNA extracts. The eigenvalues obtained by PCA and the STRUCTURE Q-matrices were close to identical for the members of each set of replicates (Supplementary Table S2), indicating the reproducibility of the GBS method.

Results

Population structure was first examined by PCA with the filtered dataset 1 comprising 1,946,469 SNPs. The two-dimensional graph plotted from the first and second principal components (PCs) resulted in separation of the wild and cultivated accessions, with the latter group displaying limited diversity (Supplementary Fig. S1). This pattern is similar to previously-reported PCAs of barley SNP datasets obtained by exome sequencing (Russell et al. 2016; Civiň et al. 2021) and targeted resequencing of neutral loci and ones implicated in domestication and environmental adaptation (Pankin et al. 2018). A second PCA was then performed with dataset 3 comprising 9719 SNPs obtained with a minor allele frequency of >0.05. Application of this filter reduces the variation in the wild accessions (which have many rare variant sites) to a greater extent compared with the cultivated group (in which most variants have relatively high frequencies), and therefore achieves better resolution within the cultivated group. In the resulting graph (Fig. 1), the cultivated group as a whole is more spread out, with the bere accessions located in a single area adjacent to accessions from various parts of Europe, close to but not overlapping various Scandinavian accessions. Within this bere cluster, those accessions from Orkney (AI 35, 46, 52, 58, 93, 109, 110, 111 and PI 130740) are placed close to one another, as are those

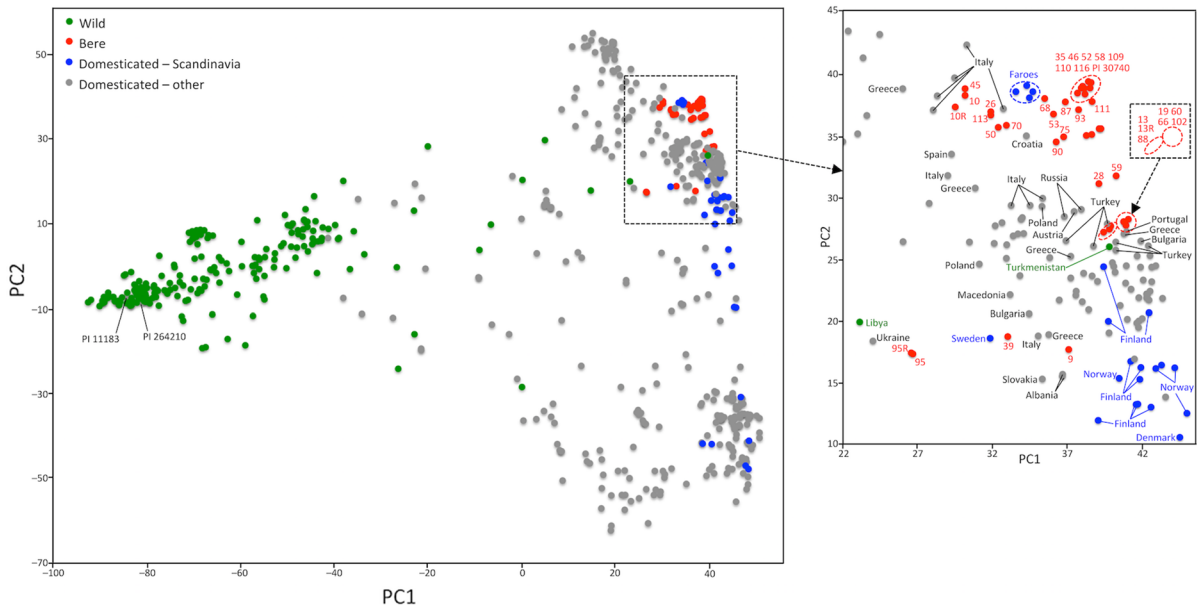


Fig. 1 PCA of 203 wild and 401 cultivated barley accessions, constructed from the 9719 SNPs in dataset 3. Replicate bere accessions are given the suffix 'R'. Two accessions identified as cultivated barleys by the germplasm collection (PI 11183 from Ethiopia, PI 264210 from Libya) locate within the wild

from the Western Isles (AI 10, 26, 45, 50, 53, 70, 75, 90 and 113). Three accessions from the Faroe Islands (the two replicates of AI 32, along with AI 119 and NGB 4701, which are independent samples of the Stjernebyg landrace) grouped closely together adjacent to the Orkney and Western Isles beres.

Dendrograms were constructed in order to explore the relationships between bere and other barleys in greater detail. An NJ tree of just the bere and Scandinavian accessions, based on the 9719 SNPs in dataset 3, divided the beres into two groups, the smaller Group 2 comprising samples AI 9, AI 39 and AI 95, and the larger Group 1 containing all the other beres (Fig. 2). Within Group 1, the beres from the Western Isles formed a separate subclade, as did those from Orkney, although the Orkney cluster also contained Scottish beres AI 87 and AI 116. The three Faroe Island accessions formed a subclade within the Group 1 topology, but the other Scandinavian accessions were located in the opposite half of the tree, along with the Group 2 barleys. The division of the beres into two groups was evident also in a NJ tree of all 401 domesticated accessions (Fig. 3) and a ML tree of dataset 2, comprising 63,265 SNPs in 402 accessions

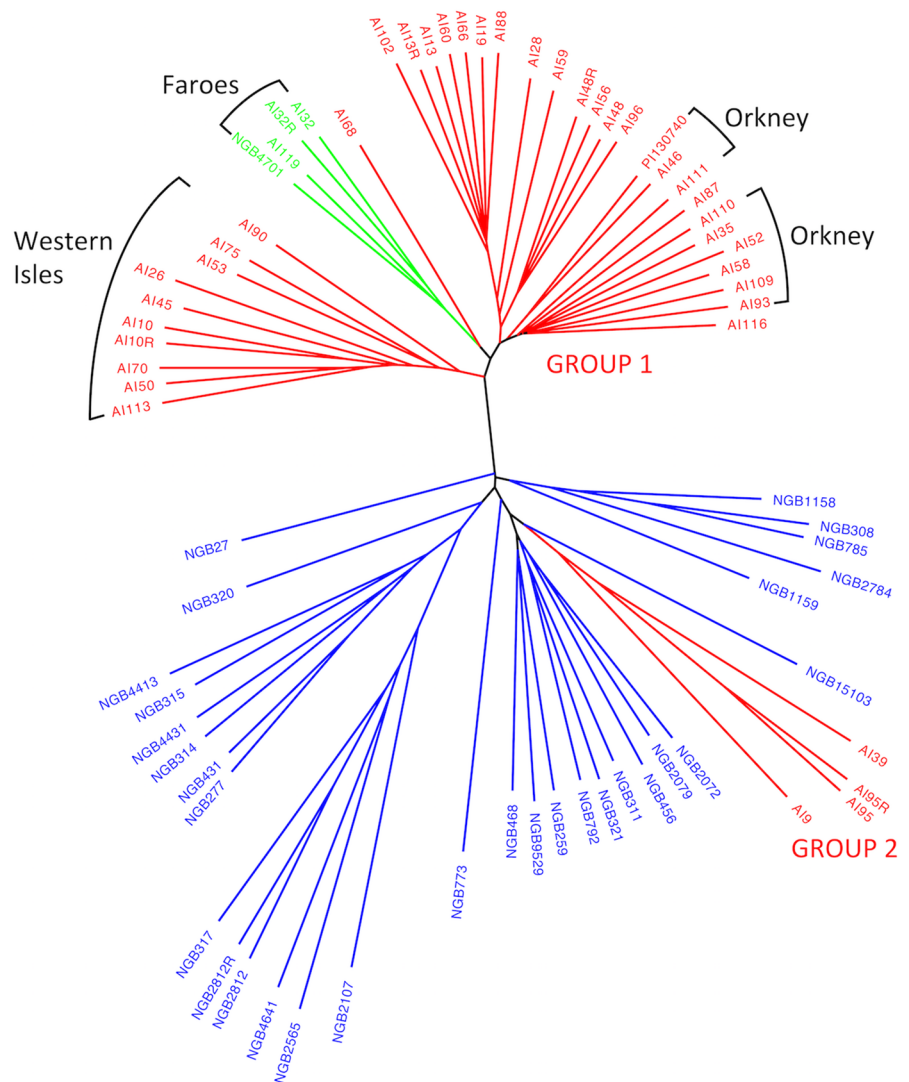
cluster and are probably misidentified. The four bere samples in the lower part of the inset (AI 9, AI 39, AI 95 and AI 95R) comprise the Group 2 accessions apparent in the subsequent analyses reported in this paper

(Supplementary Fig. S2), although the ML tree split the Group 2 barleys into two subgroups, with AI 39 in one subgroup and AI 9 and 95 in the other. The ML tree also placed two barleys from Poland (PI 129469, PI 129476) and one from Switzerland (HV 0242) within bere Group 1, and both trees revealed diversity among the Scandinavian accessions, some of these placed at positions distant from either bere group, including in regions of the tree also occupied by the non-bere British landraces.

The distinctiveness between the Group 1 and 2 barleys was further studied by IBS measurements using the 1,946,469 SNPs in dataset 1 (Fig. 4). The Group 1 beres collectively showed similar IBS patterns, with the Faroe Islands accessions showing the closest relationship, followed by the Scandinavian barleys. The Group 2 barleys, in contrast, displayed closest similarity to European accessions from outside of Scandinavia.

The individual PCs from the PCAs were then plotted to assess the extent of the difference between the Group 1 bere barleys and the Scandinavian accessions (Fig. 5). The eigenvalues of the Faroes accessions consistently lay within the range of the Group 1 beres

Fig. 2 NJ tree constructed from dataset 3 for the bere (red), Faro Islands (green) and other Scandinavian (blue) accessions. Replicate accessions are given the suffix ‘R’



for each of PCs 1–10 calculated from the filtered SNP datasets 1 and 3. There was less similarity between the Group 1 beres and the other Scandinavian barleys, with no overlap in the variance for these two sets of accessions for PCs 3, 6 and 7 (7.2% of the total variability) generated from dataset 1, nor for PCs 2, 3, 8 and 10 (14.6% of variation) for dataset 3. The bere accessions fell entirely within Scandinavian range only for PC 9 (1.4% of variation) with dataset 1 and PCs 4, 5 and 7 (8.7% of variation) for dataset 3. In a separate analysis, the mean and standard deviation was calculated for each of the top ten eigenvalues for the Group 1 beres, based on the dataset 1 PCA. Each accession was then assigned a Z-score to indicate its

distance from this mean (Supplementary Table S3). The Z-scores show that, when all the variation represented by the top ten eigenvalues is combined, there is no overlap between the Group 1 beres and the non-Faroese Scandinavian barleys. In fact there is a sharp disjunction, with the Group 1 and Faro Islands Z-scores in the range 0.06–0.38, and the other Scandinavian barleys in the range 1.34–2.42, with no accessions occupying the intervening space. More detailed examination of dataset 1 showed that, when considering SNPs that has been typed in at least ten Group 1 accessions and ten Scandinavian accessions, there were 124,169 positions that were variable in both the Group 1 and Scandinavian accessions (i.e.

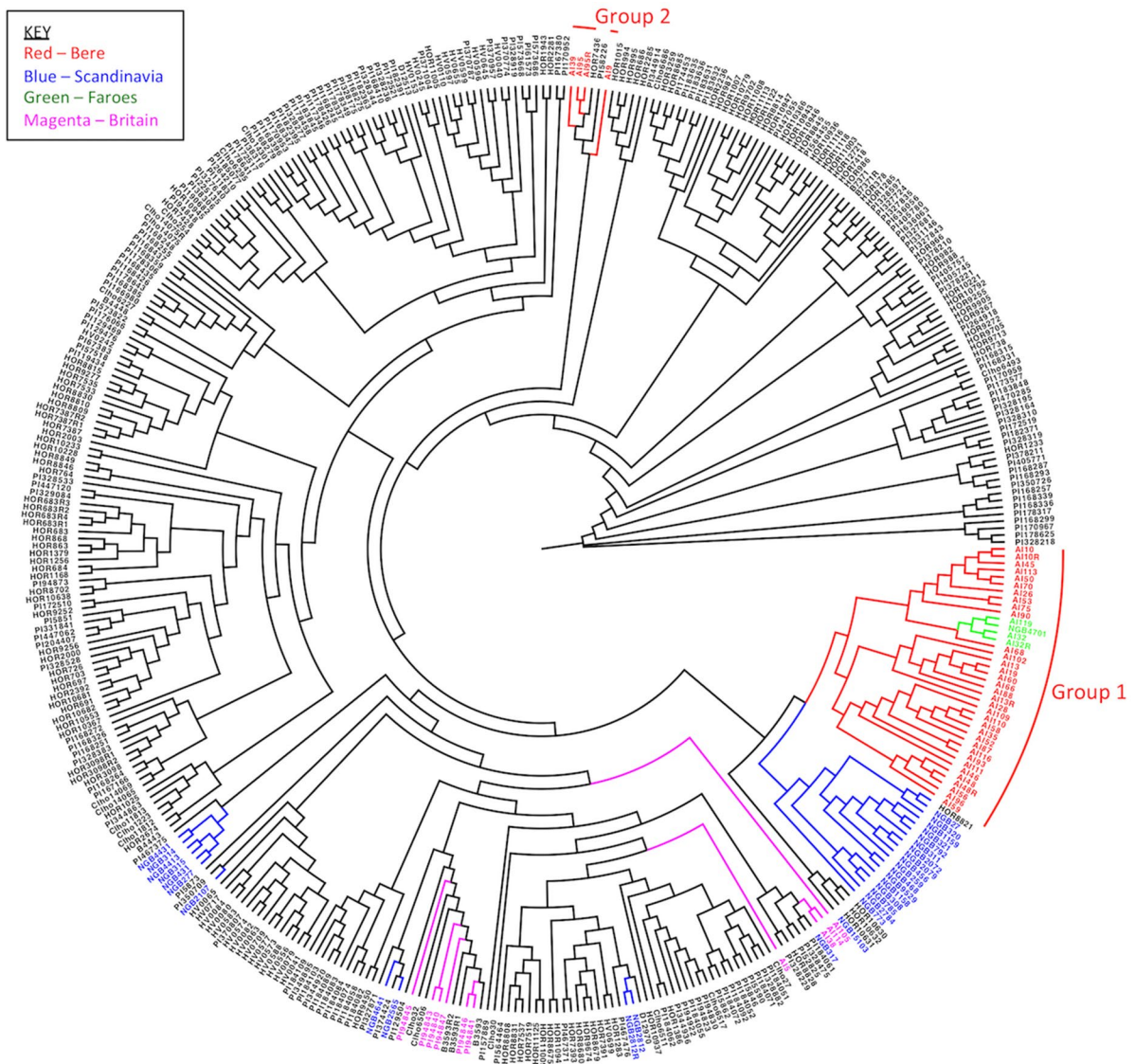


Fig. 3 NJ tree constructed from dataset 3 for 401 cultivated barley accessions. Bere accessions are shown in red, those from the Faroe Islands are green, other Scandinavian acces-

sions are blue, and other British accessions are magenta. Replicate accessions are given the suffix 'R'

shared variants) compared with 314,517 SNPs that were variable in only one of these sets of accessions or were differentially fixed (i.e. unshared variants).

STRUCTURE analysis of dataset 3 was used to place the barleys in populations and to assess admixture between those populations. A ΔK analysis (Evanno et al. 2005) indicated that the most significant values of K were 2, 3 and 16 (Supplementary Fig. S3). At $K=2$, the wild and cultivated accessions

were separated. At $K=3$, the cultivated barleys were split into two populations (Fig. 6A, B), both comprising accessions from all over Europe although with one population (population 2) more greatly represented in the Mediterranean countries and Iberia. The beres were all placed in population 2 (Table 1), and the Scandinavian accessions were distributed in both populations 2 and 3. At $K=16$, the wild accessions were divided into five populations (A–E) and

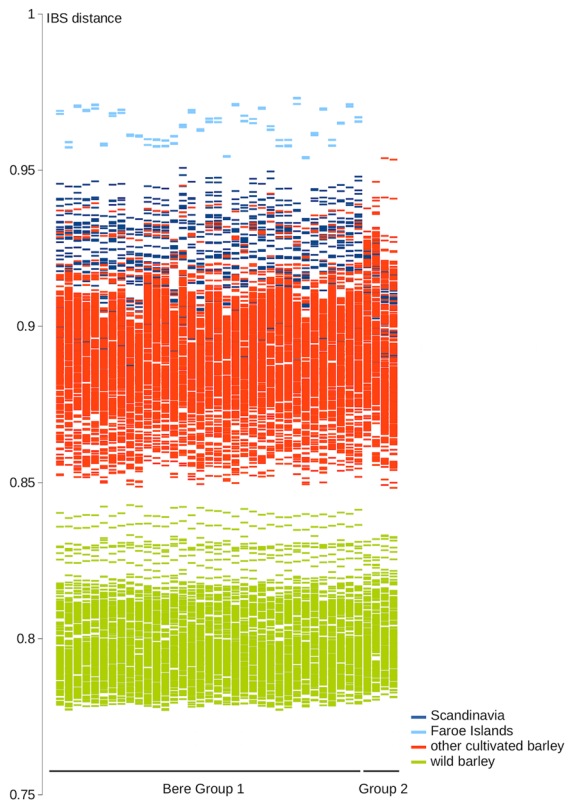


Fig. 4 Isolation-by-state (IBS) analysis of dataset 1, comprising 1,946,469 SNPs in 584 accessions. Each column represents a single Group 1 or 2 barley and the lines indicate the IBS distance of that barley to the other accessions, the latter colour-coded according to their geographical origin

the domesticated barleys into 11 populations (F–N). Bere Group 1 was placed in population F, along with the Faroe Islands accessions, 17 other Scandinavian accessions, three from Poland (HOR 8821, PI 129469, PI 129476), and one each from Switzerland (HV 0242) and Austria (HOR 10630) (Fig. 6C). The majority of these accessions were six-row, hulled barleys with a spring growth habit, exceptions being the Swiss specimen which was two-row, three Finnish accessions which were either two-row or reported to have mixed spikelet morphologies, and two of the Polish barleys, which had naked caryopses (Supplementary Table S4A). The bere and Faroes accessions displayed relatively little admixture (Table 1), whereas the other members of population F were admixed with 2–6 other populations (Fig. 7A). The Group 2 barleys formed part of population G, with 68 other accessions with broad distribution throughout

central and eastern Europe, including one accession from Sweden and one from Finland (Fig. 6D). Most of the population G accessions were six-row, hulled, spring barleys, but four (two from Turkey, one from Romania, and one from Germany) were two-row, and thirteen, mainly from southern Europe, were described as winter growth habit (Supplementary Table S4B). Within population G, the Group 2 barleys displayed a relatively high degree of admixture with up to nine other populations (Table 1; Fig. 7B).

The remaining ten Scandinavian barleys, comprising seven accessions from Finland and one each from Denmark, Norway and Sweden (Supplementary Table S4C), were placed in population H at $K=16$. Each of these Scandinavian accessions were two-row, hulled, with a spring growth habit, and were positioned away from the main Scandinavian cluster in the NJ and ML trees (Fig. 3, Supplementary Fig. S2). Population H had a total of 92 members, the non-Scandinavian ones predominantly from southeast, central and eastern Europe (nine from Russia/USSR; eight from Serbia, six from each of Bosnia, Italy and Poland; five from Slovakia; four from each of Croatia, Czech Republic, Germany, Turkey and Ukraine).

The relationships between the Group 1 beres and other barleys was also examined by considering only those SNPs in dataset 1 that are close to fixation (frequency > 0.95) in Group 1 but rare (frequency < 0.1) in the other accessions. The resulting IBS values (Supplementary Table S5) show that, other than the Group 1 beres themselves and the Faroes Islands barleys, the accessions with the highest proportion of these group-specific variants were not from Scandinavia, but instead are the two Polish (PI 129469, PI 129476) and one Swiss (HV 0242) accessions that clustered within Group 1 in the ML tree, followed by seven other Polish accessions (HOR 8815, HOR 7535, HOR 9277, HOR 7533, HOR 8809, HOR 8810, HOR 8830) and one from Czechia (HOR 7387). All of these are two-rowed naked barleys, except the Swiss accession which is a hulled variety. To understand more fully the relationship of the Group 1 beres to these various accessions, an ABBA-BABA test (Patterson et al. 2012) and TreeMix analysis (Pickrell and Pritchard 2012) were carried out with the nine Polish barleys listed above, the twelve Scandinavian accessions with the closest affiliation to Group 1 according to the PCA of dataset 1, and wild barley as the outgroup. The ABBA-BABA test of the

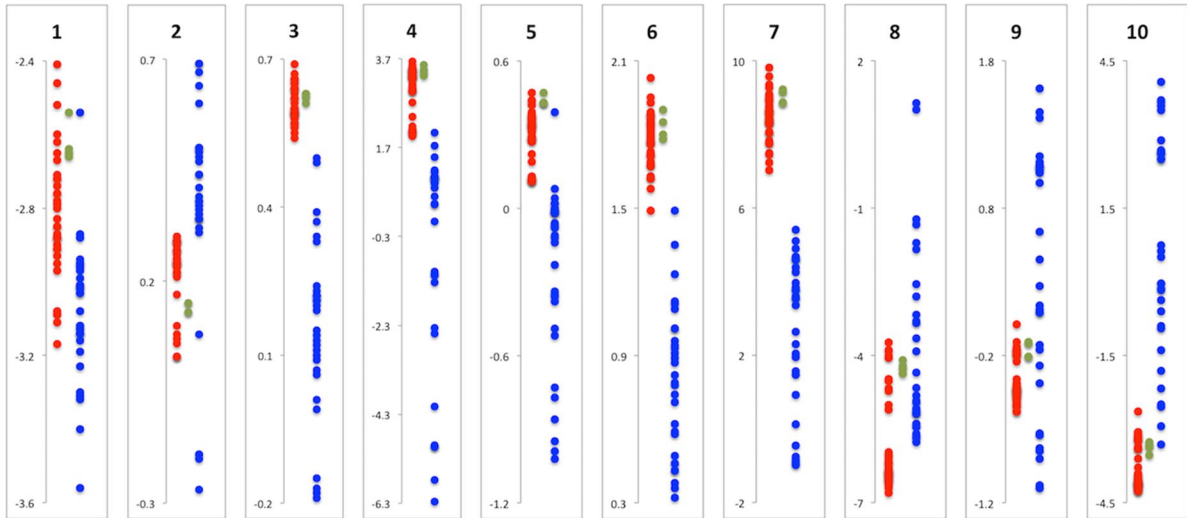
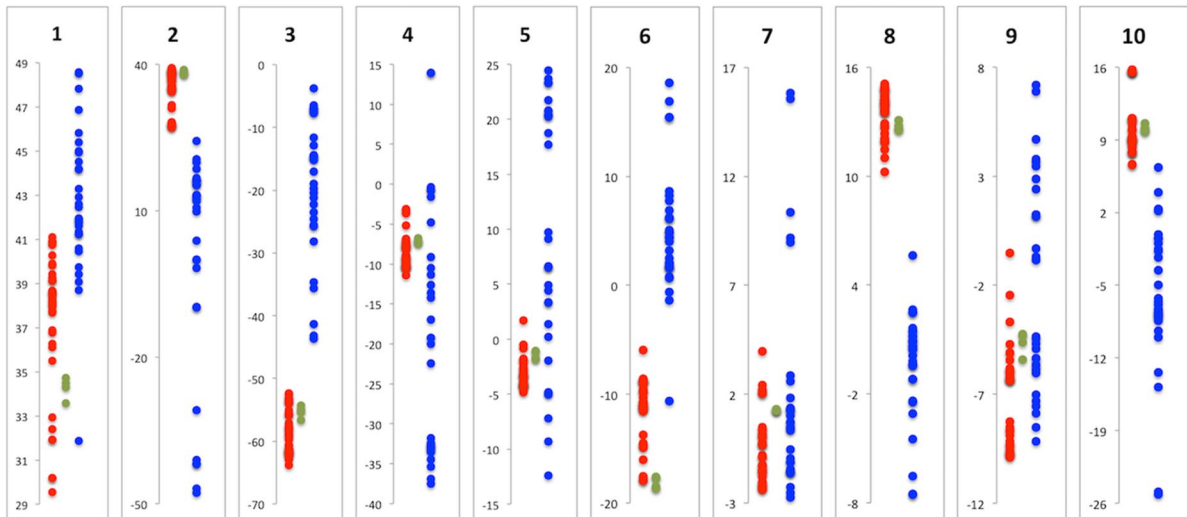
(A) Dataset 1**(B)** Dataset 3

Fig. 5 Single-dimensional plots of the first ten PCs for the Group 1 bere barleys (closed red circles), the Faroes Islands accessions (green circles) and the other Scandinavian accessions (blue circles). PCs generated from **A** dataset 1 com-

prising 1,946,469 SNPs for 584 wild and cultivated barley accessions, and **B** dataset 3 comprising 9719 SNPs for 604 accessions

tree (((Scandinavian, Polish), Group 1), wild barley) gave a D-statistic of 0.143, Z-score of 3.193 and p -value 0.0007 (Supplementary Table S6), indicative of introgression between the Polish and Group 1 barleys. This conclusion was supported by the TreeMix analysis (Supplementary Fig. S4) which showed gene flow from the Group 1 beres into the family of Polish accessions.

Discussion

Relationships among the bere barleys

Analysis of the GBS data by tree-building, IBS and genetic clustering divided the bere accessions into two groups. These groups appear to be genetically distinct as they occupied different positions in the NJ

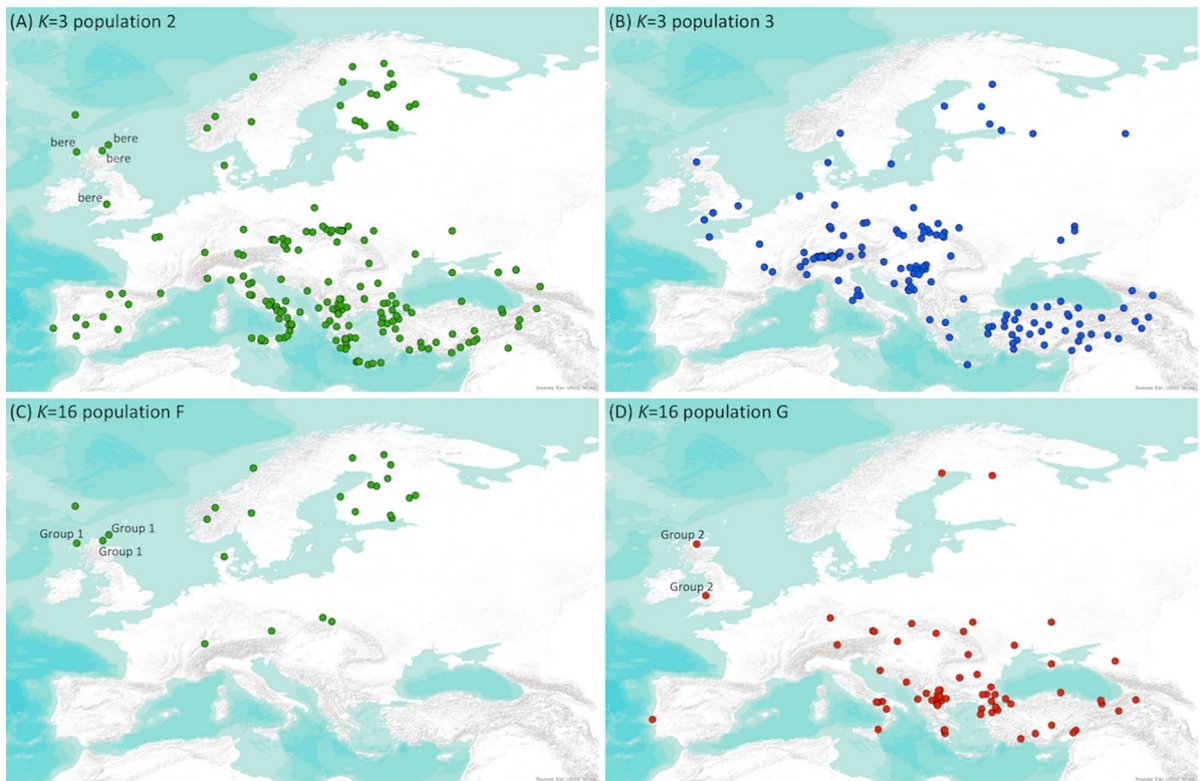


Fig. 6 Geographical distributions of populations of cultivated barley identified by STRUCTURE analysis of dataset 3. **A** Population 2 identified at $K=3$; **B** $K=3$ population 3; **C** $K=16$ population F; **D** $K=16$ population G

and ML trees (Fig. 3, Supplementary Fig. S2), were affiliated with different groups of accessions according to the IBS analysis (Fig. 4) and were also placed in different populations as identified by STRUCTURE at $K=16$ (Table 1, Fig. 7). The division into two groups was not highlighted by either of the three previous genetic studies of bere barley. Southworth (2007) typed microsatellite markers in bere accessions from Orkney, Shetland and the Western Isles, and although she did not compare the bere genotypes with those of other types of barley the results she presents indicate that her set of accessions were closely similar in genetic terms. Using larger SNP datasets, Schmidt et al. (2019) and Wallace et al. (2019) did make comparisons between bere and other barleys, and both placed the bere accessions that were typed into a single monophyletic cluster in the trees that they report. Because of some commonality in the accession sets used, it is clear that this previously-reported monophyletic cluster is equivalent to the Group 1 beres identified in our study.

Within our Group 1, the Orkney and Western Isles accessions were placed in separate subclades, in agreement with the variance between the bere barleys from different island groups first described by Southworth (2007) and apparent also in the results presented by Schmidt et al. (2019) and Wallace et al. (2019). The only exceptions were the presence within the Orkney subclade of AI 87 (Scots Bere Golspie Mill 02), which was collected from Golspie Mill in Sutherland on the Scottish mainland, and AI 116 (Bere SASA 820), whose passport data do not identify its place of collection. The apparent anomaly with AI 87 is probably explained by the use of Orkney grain as the seed stock when Golspie Mill was renovated after a period of inactivity between 1953 and 1992. AI 87, which is morphologically very similar to Orkney bere varieties, is therefore quite probably the descendent of Orkney bere that was recently transferred to the Scottish mainland. We have less information about AI 116. Although Wallace et al. (2019) describe Bere SASA 820 as having ‘unknown’

Table 1 Q-matrices for the bere barleys at K values of 3 and 16

Accession	Description	Origin	$K=3$			$K=16^*$											
			Pop1		Pop2	Pop3	PopA	PopB	PopF	PopG	PopH	PopI	PopJ	PopK	PopL	PopM	PopN
			Wild	Culti- vated	Culti- vated	Wild	Wild	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated
Bere group 1																	
AI 10	Bere 13 Balashere	Western Isles	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
AI 10R	Bere 13 Balashere replicate	Western Isles	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
AI 13	Scots Bere K17253	Scotland	0	0.916	0.084	0	0	0	0	0	0	0	0	0	0	0	0
AI 13R	Scots Bere K17253 replicate	Scotland	0	0.93	0.07	0	0	0	0	0	0	0	0	0	0	0	0
AI 19	Bere JIC 8466	Scotland	0	0.935	0.065	0	0	0	0	0	0	0	0	0	0	0	0
AI 26	Bere Sample 2 North Uist 5/3/04 2 Clachan Sands	Western Isles	0	1	0	0	0	0	0.883	0.028	0	0	0	0	0	0	0.088
AI 28	Scots Bere Clho 5003	Scotland	0	0.986	0.014	0	0	0	0.972	0.027	0	0	0	0	0	0	0
AI 35	Bere 33 Orkney	Orkney	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 45	Bere 5 Barra Isles	Western Isles	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 46	Bere Clho 6478 (PI130740) Orkney	Orkney	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 48	Bere JIC 8143 Scot- land	Scotland	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 48R	Bere JIC 8143 Scotland replicate	Scotland	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0

Table 1 (continued)

Accession	Description	Origin	K = 3			K = 16*												
			Pop1	Pop2	Pop3	PopA	PopB	PopF	PopG	PopH	PopI	PopJ	PopK	PopL	PopM	PopN		
			Wild	Culti- vated	Culti- vated	Wild	Wild	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	Culti- vated	
Bere group 1																		
AI 50	Scots Bere Clachan Farm	Western Isles	0	1	0	0	0	0	0	0.999	0	0	0	0	0	0	0	0
AI 52	Bere 36 Eday	Orkney	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 53	Bere 16 Bernaray	Western Isles	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 56	Scots Bere 7035	Scotland	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 58	Scots Bere SASA Bere Shortland	Orkney	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 59	Bere JIC 4843	Scotland	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 60	Scots Bere 20,562	Scotland	0	0.932	0.068	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 66	Scots Bere 7045	Scotland	0	0.931	0.069	0	0	0	0	0.999	0	0	0	0	0	0	0	0
AI 68	Bere JIC 24,268	Orkney?	0	1	0	0	0	0	0	0.953	0	0	0	0	0	0	0	0.046
AI 70	Scots Bere Clachan Sands	Western Isles	0	1	0	0	0	0	0	0.999	0	0	0	0	0	0	0	0
AI 75	Bere 8 South Uist	Western Isles	0	1	0	0	0	0	0	0.999	0	0	0	0	0	0	0	0
AI 87	Scots Bere Golspie Mill 02	Scotland	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AI 88	Scots Bere (Origin Denmark)	Scotland	0	0.921	0.079	0	0	0	0	0.999	0	0	0	0	0.001	0	0	0

Table 1 (continued)

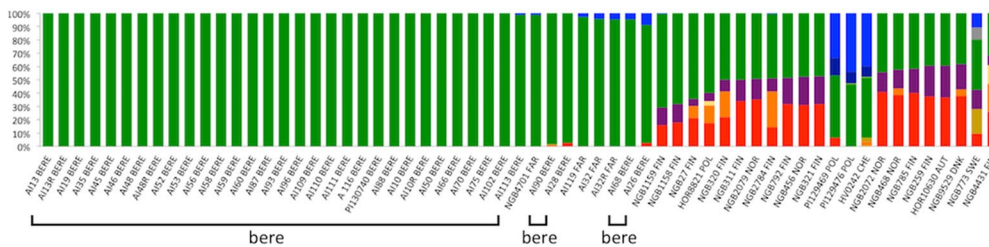
Accession	Description	Origin	K = 3			K = 16*												
			Pop1 Wild	Pop2 Culti- vated	Pop3 Culti- vated	PopA Wild	PopB Wild	PopF Culti- vated	PopG Culti- vated	PopH Culti- vated	PopI Culti- vated	PopJ Culti- vated	PopK Culti- vated	PopL Culti- vated	PopM Culti- vated	PopN Culti- vated		
AI 90	Bere Sample 4 North Uist 5/3/04 Clachan Farm	Western Isles	0	0.999	0.001	0	0	0	0.984	0	0.013	0.003	0	0	0	0	0	0
AI 93	Scots Bere SASA Bere Challoner	Orkney	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
AI 96	Scots Bere (Clho 8327) (Collected From France)	Scotland	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
AI 102	Scots Bere 7673	Scotland	0	0.943	0.057	0	0	0.999	0	0	0	0	0	0	0	0	0	0
AI 109	Bere SASA 818 Mr Barnsley Orkney OSTS 2414	Orkney	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
AI 110	Bere Eday 35 2004	Orkney	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
AI 111	Bere Rousay 32 2004	Orkney	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
AI 113	Bere 1 Tiree	Western Isles	0.001	0.999	0	0	0	0.99	0	0	0	0	0	0	0	0	0	0.01
AI 116	Bere SASA 820	Scotland	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
PI 130,740	Bere from Hoy, Ork- ney Islands	Orkney	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Table 1 (continued)

Accession Descrip- tion	Origin			K = 16*												
	Pop1	Pop2	Pop3	PopA	PopB	PopF	PopG	PopH	PopI	PopJ	PopK	PopL	PopM	PopN		
Bere group 2	Wild	Cultivated	Wild	Wild	Wild	Cultivated	Cultivated	Cultivated	Cultivated	Cultivated	Cultivated	Cultivated	Cultivated	Cultivated		
AI 9	Bere JIC 3962	Scotland	0.016	0.9	0.084	0.018	0	0.133	0.619	0.003	0.014	0.017	0.028	0.132	0.001	0.035
AI 39	Scots Bere 4828	Scotland	0.038	0.924	0.038	0	0	0.053	0.637	0	0	0.068	0	0.17	0.072	0
AI 95	Scots Bere Haidd Garw K17470	Wales	0.096	0.812	0.092	0.009	0.067	0.003	0.723	0	0	0.137	0	0.001	0.054	0.006
AI 95R	Scots Bere Haidd Garw K17470 replicate	Wales	0.093	0.811	0.096	0.01	0.067	0.001	0.728	0	0	0.139	0	0.001	0.053	0.001

* At $K = 16$, those populations that make no contribution to the listed accessions are omitted

(A) Population F



(B) Population G

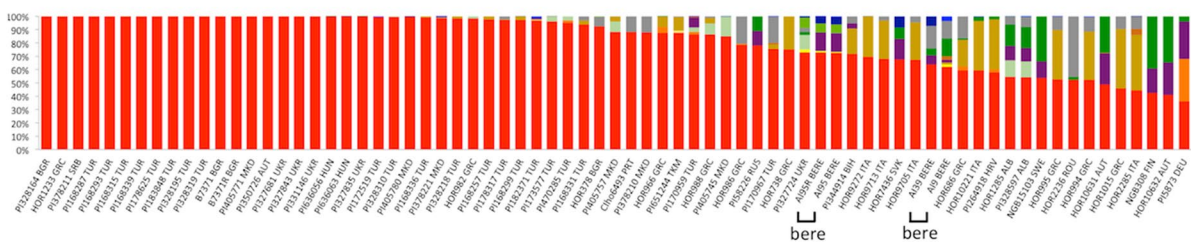


Fig. 7 Histograms of the Q-matrices at $K=16$ for the members of **A** Population F (including the Group 1 bere barleys) and **B** Population G (including the Group 2 barleys)

provenance, Schmidt et al (2019) list it as an Orkney variety, though it is not clear if this is based on passport data or the position of the accession in their NJ tree.

The Group 1 cluster also includes three barley accessions from the Faroe Islands: the two replicates of AI 32 (Langaks), along with AI 119 and NGB 4701, which are independent samples of the Stjernebyg landrace. The morphology of Langaks is very similar to that of bere grown on Orkney, and although Stjernebyg plants are shorter in height, both of the Faroes accessions have early heading dates, similar to bere, and both tend to have a prostrate first leaf, like many beres. Additionally, the geometric structures of the grain are sufficiently similar to group Langaks and Stjernebyg with bere (Wallace et al. 2019). These two accessions clustered with bere barleys in the two previous SNP analyses (Schmidt et al. 2019; Wallace et al. 2019), with the closest relationship with Shetland beres, which are absent from the accession set that we studied. In our NJ trees (Figs. 2, 3) Langaks and Stjernebyg are most closely affiliated with AI 68 (JIC 24268), which has been described as a Shetland accession (Schmidt et al. 2019; Wallace et al. 2019) but which we believe is more likely to be

an Orkney bere, possibly from the most northern part of the archipelago (Supplementary Table S1 footnote d). Both Faroes accessions, but especially Stjernebyg, are similar to AI 68 in having relatively short heads compared with most other beres. Wallace et al. (2019) suggested that Langaks and Stjernebyg are descendants of bere barleys introduced into the Faroes from the Scottish Northern Islands (Orkney and/or Shetland) during the nineteenth and early twentieth centuries by fishermen, these informal imports being used to renew seed stocks after poor harvests. An earlier introduction is also possible as there is evidence for the cultivation of six-row hulled barley in the Faroes from the time of the Norse settlement (Church et al. 2005), and even before this (Church et al. 2013). With a significant proportion of Norse settlers in the Faroes coming from Scotland/Ireland (Arge et al. 2005; Als et al. 2006), ancestral types of today's bere may have been taken by them to the Faroes in the early period of settlement and may have survived until barley cultivation was abandoned after the second world war (Brandt 1996).

The second group of bere barleys that we identify comprises three accessions, AI 9, 39 and 95. The last of these is a 'coarse barley' variety from Wales,

Haidd Garw, which was incorrectly classified as a two-rowed ‘UK landrace’ by Schmidt et al. (2019) and took up a position outside of the bere group in the NJ tree constructed from their genetic data. Schmidt et al. (2019) also include a second member of Group 2, Scots Bere 4828 (AI 39), in the list of accessions that they studied, but unfortunately did not obtain SNP data from this variety and hence could not determine its position in their NJ tree. Each of the three Group 2 accessions have some morphological characteristics that place them at the extreme of the ranges found in more typical bere accessions (Supplementary Note). The positioning of Group 2 relative to Group 1 in both the NJ and ML trees, along with their membership of different populations as defined by STRUCTURE at $K=16$, suggest that there is significant genetic difference between these two groups.

Relationships between bere and other European barleys

Absence of relationship with other British barleys

The traditional view, supported by some historical records, is that bere is derived from barleys that were introduced into northern Scotland from Scandinavia by the Vikings during the eighth century AD (Fenton 1978; Jarman 1996; Theobald et al. 2006; Martin and Wishart 2007). However, Wallace et al. (2019) argue that the morphometric differences between the grain of bere and Scandinavian landraces are sufficiently great to make such a recent introduction from Scandinavia unlikely, unless the progenitor Scandinavian lines are now extinct and hence not represented in the modern collections that have been studied. They suggest that more plausible hypotheses are that bere is derived from landraces originally grown in other parts of Britain or that bere evolved in Scotland from barleys that were introduced into that country during a period predating the Viking era.

Our data provide no support for the hypothesis that either the Group 1 or Group 2 barleys are derived from varieties grown historically in other parts of mainland Britain. The non-bere British accessions in our dataset are not positioned close to Groups 1 or 2 in the two-dimensional PCA (Fig. 1) nor the NJ tree or ML trees of all cultivated accessions (Fig. 3, Supplementary Fig. S2). Furthermore, in the STRUCTURE output at $K=3$ the Group 1 and Group 2

barleys are members of population 2 (Fig. 6A) and the other British barleys are placed in population 3 (Fig. 6B). On this basis, we believe that a British origin for either the Group 1 or Group 2 barleys can be discounted.

Relationship between the Group 1 beres and other European barleys

If the Group 1 or 2 barleys are not themselves closely related to other British varieties, then can we use the GBS data to understand their origins? With Group 1, the data emphasize a close similarity with a set of 6-row, hulled Scandinavian barleys, the bere and Scandinavian groups forming sister clades in the NJ and ML trees (Fig. 3, Supplementary Fig. S2), the Scandinavian barleys having the closest IBS distances to the Group 1 accessions (Fig. 4) and the two sets of accessions falling within population F as identified by STRUCTURE at $K=16$ (Supplementary Table S4A). The STRUCTURE results also suggest that within this population the Group 1 beres are relatively homogeneous and non-admixed (Table 1, Fig. 7A), which could be interpreted as indicating that the bere barleys have undergone a recent reduction in diversity as occurs during a founder event. If this interpretation is correct, then it could be inferred that the Scandinavian barleys, being the closest relatives, form the parent group from which these beres were taken. As all the Scandinavian accessions in population F display at least some admixture with other European barleys (Fig. 7A), one assumption would have to be that the founder effect that gave rise to the bere barleys sampled only a relatively small part of the Scandinavian diversity, in such a way that the component of the Scandinavian genepool resulting from admixture with other European barleys was not extensively carried over to the bere group, or was lost from the beres by drift and genetic inbreeding since their establishment as a distinct type of barley.

The above line of reasoning supports the traditional view that bere was introduced into Scotland by the Vikings, but other aspects of the data analysis are less compatible with this interpretation. Examination of the SNP genotypes for the Group 1 accessions and the Scandinavian barleys reveal a greater number of unshared compared to shared variants (314,517 vs 124,169 SNPs), and single-dimension graphs of the individual PCs (Fig. 5) show that the

variation accounted for by those PCs which do not overlap when the Group 1 and Scandinavian accessions are compared (7.2% and 14.6%, depending on the SNP dataset that is used) is greater than the variation contained in the PCs where there is overlap (1.4% or 8.7%). The distinctiveness between Group 1 and Scandinavian barley revealed by these analyses is arguably greater than would be expected if bere is a relatively recent introduction from Scandinavia. Additionally, the Group 1 beres and Scandinavian barleys form separate clusters in the two-dimensional graph of PCs 1 and 2 (Fig. 1), occupy different coordinate spaces when the variation contained in the top ten eigenvalues is combined (Supplementary Table S3), and form separate clades in the trees (Figs. 2 and 3, Supplementary Fig. S2). These results are contrary to the expectation that if the beres arose from a recent founder event then they would most likely still be positioned within the Scandinavian cluster/clade in the PCAs and trees. In contrast, the three Faroese barleys, whose origin from bere Group 1 via a more recent founder event has been suggested (Wallace et al. 2019), are located within the bere cluster in the PCA and do form a subclade within the bere group in each of the trees.

The ambiguity in the genetic data regarding the possibility that bere is a Viking introduction from Scandinavia, together with the morphometric evidence against this hypothesis (Wallace et al. 2019), prompts us to ask if the GBS data are compatible with the alternative explanation, that bere is derived from an older introduction of barley into Scotland. In fact, all of the aspects of the data analysis listed above in support of a Viking introduction can equally be used as evidence that the Group 1 beres and the Scandinavian accessions are sister groups descended from the same progenitor. This interpretation is fully compatible with the PCA and STRUCTURE results, the latter suggesting that following divergence from a common ancestral barley the Group 1 bere population remained genetically pure due to long-term isolation in northern Scotland, whereas the Scandinavian barleys acquired diversity via hybridization after mixing with landraces from adjacent regions of northern Europe. Furthermore, if the Group 1 beres and Scandinavian barleys are sister groups derived from a less recent parent population, the amount of shared variance revealed by the PC comparisons (Fig. 5, Supplementary Table S3) would not be unusual, and there

would be no expectation that morphological features such as grain geometries should be conserved.

At $K=3$, STRUCTURE divided the barleys into three populations, one of these comprising the wild accessions and the other two made of cultivated barleys. Both cultivated populations display a broad distribution throughout Europe, but population 2, which contains the Group 1 beres and those Scandinavian barleys with closest affinity to bere, is more greatly represented in Iberia (Fig. 6A). A shared cultural influence stretching from Iberia to northern Britain and southern Scandinavia during 4500–3500 BC, the period when agriculture was first developing in north-west Europe, is indicated by the presence of megalithic burial tombs of similar construction at sites in these regions (Scarre 2007; Schulz Paulsson 2017). Agricultural affinities along the Atlantic façade have also been suggested by genetic similarities between cultivated rye landraces from Iberia, western France and the Scottish Western Isles (Hagenblad et al. 2016). The presence of barleys from Scotland, Scandinavia and Iberia in the same population at $K=3$ could be a further indication of these early agricultural links. However, the archaeobotanical records for Scotland and Scandinavia indicate that the first types of barley to be grown in these areas were not hulled barleys similar to bere, but the alternative naked type, where the grain is less enclosed within the surrounding bracts (Clayton 1990; Sørensen and Karg 2014). These original naked introductions were not greatly supplanted by hulled barley until the later Bronze Age, c.1000 BC, when field-based agriculture first appears. The dichotomy between the cultivation of naked and hulled forms is most apparent in Scandinavia, where hulled barley is largely absent in those pre-Bronze Age assemblages that have been studied (Grabowski 2011). In Scotland, the picture is less extreme, as hulled barley is not entirely absent prior to the Bronze Age, and makes up a significant component of the crop package at some Neolithic sites (Bishop et al. 2009). Indeed, it has been suggested that the crop assemblages at the Neolithic sites of Tofts Ness and Pool on the Orkney island of Sanday show an earlier transition from the use of naked to hulled barley in Orkney than elsewhere in Britain (Bond 2007a, 2007b). The transition from naked to hulled barley was a Europe-wide phenomenon (Lister and Jones 2013), and the origin of the hulled barley that becomes common during the later Bronze Age

in Scotland and Scandinavia has not yet been traced in the archaeobotanical record. However, the more widespread use of hulled barley in Orkney during the Neolithic period, along with the genetic similarity between the Group 1 bere and Scandinavian landraces, suggests that the latter might in fact be descended from earlier Scottish hulled varieties. The direction of the relationship between bere and Scandinavian barley might therefore be the reverse of that indicated by the traditional Viking hypothesis.

Although the Scandinavian barleys are consistently identified as the closest European relatives to the Group 1 beres when all of the SNP data are considered, a different picture is seen when the analysis is limited to those SNPs that have a frequency >0.95 in Group 1 but <0.1 in other accessions. Now the closest affiliates are nine Polish accessions and one from each of Switzerland and Czechia (Supplementary Table S5). Two of the Polish accessions and the one from Switzerland cluster within the Group 1 clade in the ML tree (Supplementary Fig. S2) and are members of population F, as identified by STRUCTURE at $K=16$, along with the Group 1 beres and the related Scandinavian barleys (Fig. 7A). The other Polish accessions and the Czech barley occupy more distant positions in the trees and are placed in STRUCTURE population N. The greater degree of distinction between Group 1 bere and Scandinavian barleys apparent in this analysis is most likely due to the variants with high frequency in Group 1 being predominantly those that have emerged specifically in the bere population after the split between bere and Scandinavian barley. The ABBA-BABA test and TreeMix analysis (Supplementary Table S6, Supplementary Fig. S4) indicate that these variants have been acquired by the Polish accessions by gene flow from the bere population. As early as the twelfth century, bere grain was being exported from Orkney to Iceland and Norway (Barrett et al. 2000), and until the early nineteenth century, bere was often exported to Leith, Shetland and Norway when there was surplus production (Thomson 2001). Trade links between Orkney and northern Europe were especially strong as Orkney was under Norwegian and Danish rule for several hundred years before becoming part of Scotland in 1469. There was also considerable Scottish emigration to Poland in the sixteenth and seventeenth centuries and Scottish agronomists helped to rehabilitate Polish agriculture following the Napoleonic wars

(Bartyś 1967). With these strong North Sea–Baltic trade networks and a very significant Scottish presence in Poland, it would not be surprising if bere was taken to the region and grown at some point. Natural crossing between this material and local barley strains would explain the occurrence of markers for bere in Polish accessions. In Orkney, hybrid plants often occur in fields planted with farm-saved seed derived from modern two-row barley cultivars that were grown adjacent to bere (unpublished results, UHI Agronomy Institute), suggesting that natural crossing might be quite common.

Relationship between Group 2 and other European barleys

Less can be said about the relationship between Group 2 and other European barleys. Group 2 is positioned relatively closely to Scandinavian barleys in the two-dimensional PCA (Fig. 1), but the NJ and ML trees of all cultivated accessions (Fig. 3, Supplementary Fig. S2) suggest that the relationship is more distant. In the trees, the Group 2 barleys are more closely affiliated with a large group of European-wide accessions, as illustrated by the geographical distribution of population G identified by STRUCTURE at $K=16$, which includes Group 2 (Fig. 6D, Supplementary Table S4B). Within population G, the Group 2 barleys display admixture with up to nine other populations (Fig. 7B, Table 1), suggesting a complex evolutionary history. Population G has representatives in Scandinavia, but among our accession set these were limited to Finland and northeast Sweden, which are not obvious sources for introduction of barley into Scotland, by the Vikings or anyone else. The distribution of population G is more consistent with a central European origin for Group 2, and the admixed nature of these barleys suggests a relatively recent transfer to Scotland and Wales, with insufficient time having elapsed to enable the genotypes to become entirely distinct from their progenitor population.

Conclusion

Our results show that although the nature of the relationship between the Group 1 beres and Scandinavian barleys is open to different interpretations, the most plausible explanation of the genetic data is that bere

has a long history of cultivation in Scotland stretching back to the Bronze Age and possibly earlier. Its importance as a heritage crop is therefore emphasized, as is its value as a potential source of genetic alleles that are absent from or under-represented in other types of European barley, and which might therefore be used as an important resource in breeding programmes, especially those aimed at improving the productivity of modern cultivars when grown in marginal environments.

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Author contributions KD: methodology, investigation, formal analysis, data curation, writing – review and editing; HC, KP: equal contributions to investigation, writing – review and editing; SLK: investigation, writing – review and editing; JW: resources, writing – review; HRO: investigation, formal analysis, writing – review and editing; PC: methodology, investigation, formal analysis, writing – review and editing; PM: conceptualization, resources, investigation, writing – review and editing, funding acquisition; TAB: conceptualization, formal analysis, writing – original draft, writing – review and editing, supervision, project administration, funding acquisition.

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Declarations

Conflict of interest The authors declare that they have no financial or competing interests.

Availability of data and material The GBS data are available at the European Nucleotide Archive, study PRJEB41083.

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