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Ancient DNA from lentils (*Lens culinaris*) illuminates human - plant - culture interactions in the Canary Islands

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ABSTRACT

The intimate relationship between humans and crop plants means that traces of human cultural practices become embedded in the crop genome. Genetic analyses of archaeological crop remains thus allow cultural consequences of societal change to be studied. The Canary Islands have a unique cultural history where the Hispanic colonization in the 15th century led to eradication of the indigenous culture, partial replacement of the human gene pool and a rapid transformation of the islands into a globalization hub between the Old and the New World. Although many aspects of these events are well known, the interconnections between the cultural turnover and cultivated crops have rarely been studied.

In this study full genome sequencing and KASP genotyping have, for the first time, been successfully carried out on millennium old seeds of lentil (*Lens culinaris*). Comparisons with present day lentils reveal that indigenous lentils were kept in continuous cultivation on the Canary Islands until the present. We suggest that this was facilitated by a gendered division of agricultural responsibilities and inheritance as well as adaptation to the local climate. We confirm a previously suggested long-term inter-island isolation prior to the arrival of Europeans and demonstrate continuous lentil cultivation also on islands where they were believed lost prior to the arrival of Europeans. The results furthermore hint to a role of Canarian lentils in the cultivation and consumption of lentils on the European mainland. To conclude, this first analysis of ancient lentil DNA show how understudied archaeological plant remains can reveal aspects of past cultures not documented in written records.

1. Introduction

Crop plants have been the companions of humans since the dawn of agriculture. The intimate relationship between humans and crop plants means that traces of human cultural practices, e.g. seed exchange or differing end-uses, have become embedded in the crop genomes (Kui et al., 2020; Leino et al., 2013). Thus, the genetic analysis of archaeological crop remains allows past human - plant - culture interconnections, for example cultural consequences of societal upheavals and climate change, to be studied (Larsson et al., 2021; Pressoir and Berthaud, 2004). Such challenges are particularly interesting when occurring in an island setting where isolation limits the opportunities available to the inhabitants.

The Canary Islands are located only 100 km west of Africa (Fig. 1a–c). The archipelago was permanently settled by Amazigh/Berber farmers from North Africa between the 1st and the 3rd century of the common era (CE) (Fregel, et al., 2009b, 2019; Maca-Meyer et al., 2004; Santana et al., 2024). The Amazigh/Berber colonizers brought with them a crop package consisting of *Hordeum vulgare* ssp. *vulgare* (six-row hulled barley), *Triticum durum* (durum wheat), *Lens culinaris* (lentil), *Vicia faba* (broad bean), *Pisum sativum* (pea) and *Ficus carica* (fig) (Morales, et al., 2017, 2023), and the crops were subsequently introduced to the different islands of the archipelago.

After its colonization, the archipelago is believed to not only have

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lost contact with the mainland but also among islands (Morales et al., 2009; Serrano et al., 2023). Crop diversity declined on the different islands (Morales et al., 2023), likely as a result of crop failure and only on Gran Canaria was the full crop package retained. Here, the indigenous farmers excavated silos from the porous volcanic rock (Fig. 1d) and used them as cave-granaries for long-term storage of part of the harvest (Henríquez-Valido et al., 2020; Morales et al., 2014).

In the fourteenth century, European sailors encountered the archipelago and towards the end of the fifteenth century the Hispanic conquest of the islands was completed. This brought profound changes to the people inhabiting the islands. The indigenous population was decimated through war, starvation and slavery (Adhikari, 2017) and the survivors admixed with immigrants from Europe and enslaved people from Africa (Pino-Yanes et al., 2011; Santana et al., 2016). After the European arrival to the Americas, the Canary Islands became a globalization hub for trade between the Old and the New World (Macleod, 1999). The use of the traditional cave-granaries was, in most cases, discontinued shortly after the conquest of Gran Canaria. However, archaeological remains in the form of seeds and grains can still be found in the silos. Thanks to the excellent storage conditions these archaeobotanical remains are not only exceptionally well-preserved (Fig. 1e), but also retain DNA of sufficient quality to allow genetic analyses (Hagenblad, et al., 2017, 2024; Oliveira et al., 2012).

Among the pulses found in the Canarian archaeobotanical record the most common one is lentil, *Lens culinaris* (Morales et al., 2023). Archaeological remains of lentils have been found on the islands of Fuerteventura (dating to 5th - 8th century), Gran Canaria (6th - 16th century) and La Palma (3rd - 13th century) (see Morales et al., 2023 and references therein). Written 15th-16th century sources, however, do not mention the cultivation of lentils by the indigenous population, suggesting that at the time lentil cultivation was rarely practiced or absent from most islands (Morales et al., 2023). Whether present-day Canarian landraces, unimproved domesticated varieties preserved in genebanks, descend from indigenous lentils or from lentils introduced after the Hispanic conquest is not known.

Here we report a study of more than a thousand-year-old archaeological lentils from Gran Canaria, to our knowledge the first ever study of aDNA in lentil. By comparing the genetic diversity of archaeological and extant, still viable, genebank lentils from the Canary Islands, Morocco and Spain we investigate the history of lentil cultivation in the archipelago, from the original settlement until the present. More specifically we wanted to 1) investigate whether aDNA could be successfully analysed from legume remains found in the Canarian cave-granaries; and if so 2) quantify the extent to which lentils currently cultivated on the Canary Islands share a genetic identity with prehistoric lentils, indicative of continuous lentil cultivation; and 3) pinpoint a geographic origin of lentils brought to the Canary Islands.

2. Materials and methods

2.1. Archaeological specimens and extraction of aDNA

The archaeological material consisted of 14 lentil seeds, preserved by desiccation, with a chronology spanning from the 7th to the 20th century cal CE. The seeds originated from five different archaeological sites (Table 1, Appendix A.1), all being indigenous cave granaries, excavated in the rock and located in the mountainous region of Gran Canaria (Fig. 1c).

DNA extraction and library preparation were performed in dedicated, clean lab facilities at the Paleogenomics Lab at University of La Laguna (Tenerife, Spain). To avoid contamination with modern DNA, archaeological samples were irradiated with UV (0.120 J/cm^2) for 5 min. DNA extraction was performed following Wales and Kistler (2019). Briefly, whole decontaminated seeds were incubated in lysis buffer and extracts were purified using a phenol-chloroform protocol. Ancient DNA was then extracted using a silica-based protocol (Dabney et al., 2013)

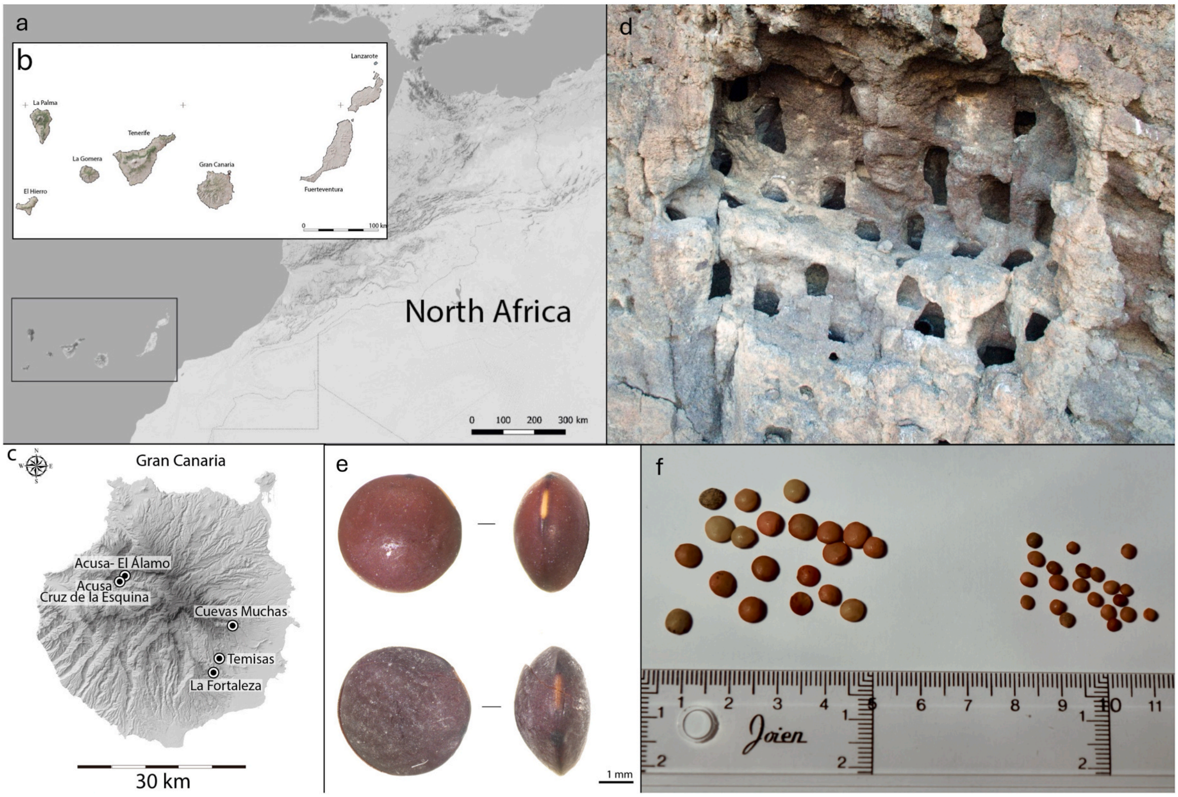

Fig. 1. a) Location of the Canary Islands and b) the different islands of the archipelago. c) Location of the archaeological sites on Gran Canaria. d) Example of cave granaries. e) Example of archaeological lentils and f) extant lentils CBT01398 (left) and CBT01390 (right).

Table 1
Description of archaeological specimens used in the study and sequencing and genotyping statistics.

ID	Sampling information	Dating	DNA concentration (nM)	Mapped reads	Mean fragment length (bp)	3′ G to A	coverage (X)	KASP genotyping success rate
PGULL-1725.1	La Fortaleza, Silo 2	1024–1155 cal CE	48.9	865 839	47.1	0.049	0.009	0.072
PGULL-1725.2	La Fortaleza, Silo 2	1024–1155 cal CE	51.1	32 966 470	42.5	0.031	0.347	0.374
PGULL-1725.3	La Fortaleza, Silo 2	1024–1155 cal CE	5.8	11 847	64.9	0.068	2.1×10^{-4}	0.072
PGULL-1725.4	La Fortaleza, Silo 2	1024–1155 cal CE	8.8	438 603	52.6	0.083	0.006	0.194
PGULL-1726.1	Acusa, El Alamo, Silo 10	1682–1955 cal CE	18.5	50 380	51.2	0.078	0.001	0.129
PGULL-1726.2	Acusa, El Alamo, Silo 10	1682–1955 cal CE	31.2	63 691	47.2	0.081	0.001	0.137
PGULL-1727.1	Cuevas Muchas, Silo 1	1456–1634 cal CE	46.8	214 662	46.6	0.068	0.003	0.086
PGULL-1728.1	Acusa, Cruz de la Esquina, Silo 9	1300–1624 cal CE	2.3	1 258	72.5	0.066	2.6×10^{-5}	0.058
PGULL-1728.2	Acusa, Cruz de la Esquina, Silo 9	1300–1624 cal CE	1.0	1 823 217	57.0	0.080	0.022	0.058
PGULL-1729.1	Acusa, Cruz de la Esquina, Cueva funeraria	664–770 cal CE	65.8	5 803 317	49.6	0.060	0.073	0.194
PGULL-1729.2	Acusa, Cruz de la Esquina, Cueva funeraria	664–770 cal CE	57.1	4 656 460	49.4	0.069	0.055	0.122
PGULL-1730.1	Temisas, Silo 10	1326–1444 cal CE	55.5	2 816 147	48.6	0.048	0.035	0.252
PGULL-1731.1	Temisas, Silo 1	1290–1410 cal CE	19.5	689 209	50.6	0.038	0.009	0.655
PGULL-1732.1	Temisas, Silo 18	1219–1280 cal CE	86.9	13 785 549	43.8	0.056	0.145	0.094

and built into double-stranded libraries following Kircher et al. (2012).

2.2. Reference material and extant DNA extraction

As a reference material, 29 extant (still viable, Fig. 1f) lentil landraces were obtained from the genebanks International Center for Agricultural Research in the Dry Areas (ICARDA, prefix IG, eight landraces), Centro Nacional de Recursos Fitogenéticos (CRF, prefix BCU, seven landraces), Centro de Conservación de la Biodiversidad Agrícola de Tenerife (CCBAT, prefix CBT, twelve landraces) and Jardín Botánico Canario Viera y Clavijo (prefix CMC, two landraces) (Table 2). From each extant landrace, DNA was extracted from dried vegetative tissue or from ungerminated seeds from six individuals using the QIAGEN DNeasy DNA extraction kit according to the manufacturer's instructions.

Table 2
Extant, present day genebank accessions used in the study, their origin, genetic diversity and clustering.

Accession number	Origin	Latitude (N)	Longitude (W)	Collection year	Nei's h	Clustering group
CBT02700	La Palma	28.828768	−17.802538		0.000	IV
BCU001206	La Palma	28.79722	−17.75861	1978	0.026	I
IG4928	La Palma	28.7833	−17.75	1980	0.013	I
CBT01453	La Gomera	28.099444	−17.279444	2007	0.039	I
CBT01447	La Gomera	28.179080	−17.264944	2007	0.085	I
CBT01296	Tenerife	28.343333	−16.876944	2007	0.007	II
CBT02876	Tenerife	28.099800	−16.679083	2014	0.089	I
CBT02680	Tenerife	28.076111	−16.654722		0.069	III + IV hybrid
CBT01242	Tenerife	28.236111	−16.455833	2007	0.057	IV
CBT00490	Tenerife	28.340556	−16.396667	2005	0.184	III (mixed)
CMC169	Gran Canaria	27.927095	−15.552318	2007	0.192	III (mixed)
CMC147	Gran Canaria	27.910386	−15.540052	2006	0.155	III (mixed)
BCU001353	Fuerteventura	28.39583	−14.08667	1991	0.184	III
BCU001914	Fuerteventura	28.52667	−13.99056	1991	0.004	II
CBT01390	Fuerteventura	28.435556	−13.973611	2007	0.002	II
BCU001913	Fuerteventura	28.60944	−13.92639	1991	0.094	III
CBT01376	Fuerteventura	28.55638	−13.83416		0.002	II
BCU001509	Lanzarote	28.96667	−13.71667	1995	0.011	III
BCU001952	Lanzarote	28.96028	−13.55139	2000	0.162	III
BCU001967	Lanzarote	29.08083	−13.53	2005	0.190	III
CBT01397	Lanzarote	29.158611	−13.493333	2007	0.129	III
CBT01398	Lanzarote	29.195833	−13.480556	2007	0.221	III
IG71435	Morocco	32.35	−8.85	1987	0.147	
IG111986	Morocco	32.1681	−6.52833	1994	0.000	
IG71429	Morocco	35.1667	−5.26667	1987	0.158	
IG4927	Spain, mainland	37.7833	−5.28333	1980	0.244	
IG4936	Spain, mainland	39.5919	−3.04167	1980	0.212	
IG4948	Spain, mainland	40.5833	−2.15	1980	0.000	
IG4940	Spain, mainland	38.95	−1.43333	1980	0.270	

2.3. *Sequencing and genotyping*

Two sets of ancient DNA libraries were constructed from each lentil seed. The first was initially sequenced to determine the percentage of endogenous DNA. Sequencing was carried out on an Illumina NextSeq 500 platform at Sistemas Genómicos S.L. (Valencia, Spain), using a 2 × 75 bp paired-end protocol and aiming to obtain approximately 5 million reads per sample. The same set of libraries was also sequenced with Illumina NovaSeq XPlus 10B-300 at the Science for Life Laboratory, Royal Institute of Technology (Stockholm, Sweden) to obtain additional sequence depth.

Adapters were removed from raw sequence reads using AdapterRemoval (v 2.3.1) (Lindgreen, 2012) with the setting –minquality 15. Reads were aligned to the CDC Redberry reference genome (Lcu.2RBY, https://knowpulse.usask.ca/genome-assembly/Lcu.2RBY) (Ramsay et al., 2021) using BWA aln (v 0.7.17) (Li and Durbin, 2009) and SAMtools (v 1.14) (Li et al., 2009). Reads were filtered using the settings -q 30 and -minlen 30. Sequence damage was assessed with mapDamage (v 2.0.9) (Ginolhac et al., 2011) and duplicates marked with the MarkDuplicates tool of picard (v 2.23.4, http://broadinstitute.github.io/picard/). Variant calling was carried out with freebayes (v 1.3.2, https://doi.org/10.48550/arXiv.1207.3907) using the setting QUAL >10 with no filtering for known present-day variants. VCF files were constructed using vcftools (0.1.16) (Danecek et al., 2011) and the setting –minQ 20. Since lentil is a predominantly self-fertilizing species (Horneburg, 2006), heterozygosity is expected to be negligible and hence a single allele was allowed at each locus.

Publicly available sequence reads from 24 western Mediterranean individuals (Liber et al., 2021) were downloaded from https://www.ebi.ac.uk/biostudies/arrayexpress/studies/E-MTAB-9222/sdrf (Table A.2). These were analysed as described above except that adapter removal was not needed. Exploratory Principal Component Analysis (PCA) showed that the individual PI 612265 from Morocco was genetically an outlier and it was hence excluded from further analysis.

The second set of ancient DNA libraries from the 14 archaeological specimens was, together with DNA extracts from 174 extant individuals, genotyped for 139 SNP markers, developed from Sharpe et al. (2013), using KASP genotyping (LGC genomics, UK). For each plate of 96 samples a negative control was included and DNA from the same extant individual (BCU001952.6) was genotyped on both plates of 96 individuals. Genotype calls were manually inspected and corrected when considered necessary. Since lentil is a predominantly self-fertilizing plant, the few heterozygous loci detected were recoded as missing data before used for downstream analysis.

2.4. *Population genetic analyses*

Specimens yielding low quality data were removed from downstream analysis (Appendix A.3). Genetic diversity, determined as Nei's h (Nei, 1973), and F_{ST} values, calculated according to Wright (1949), were computed using purpose-written Perl scripts (available upon request). Genetic structuring among the different contexts was investigated through PCA using the *prcomp* command in RStudio (v 2023.09.0 + 463) (RStudio Team, 2022). PCAs based on sequence data were only carried out on datasets not containing any missing data. Structuring was further explored with the software Structure (v 2.3.4) (Falush et al., 2003; Pritchard et al., 2000) using the haploid setting, as suggested for pre-dominantly self-fertilizing species by Nordborg et al. (2005), and allowing for admixture. Structure was run with a burn-in length of 40 000 iterations followed by 100 000 iterations for parameter estimation, with 10 repeated runs at each level of predetermined clusters (K) ranging from 1 to 10. The software CLUMPP (v 1.1.2) (Jakobsson and Rosenberg, 2007) was used to compare the outcome of individual runs with the Greedy algorithm for $4 < K < 6$ and with the LargeKGreedy algorithm for $K \geq 6$. The number of clusters best describing the data was evaluated from the CLUMPP H' values and ΔK calculated according to Evanno et al. (2005). Results were visualized using DISTRUCT (v 1.1) (Rosenberg, 2004). Statistical testing was carried out in RStudio using the *cor.test* command.

3. Results

3.1. *Genetic structure in sequence data*

Of the 14 analysed archaeological specimens only two failed to yield useful sequence data (Table 1). The successfully sequenced DNA showed the signs of degradation (deamination and fragmentation) typical for aDNA. The level of DNA degradation was not associated with the age of the specimen and may instead depend on the storage conditions of the different silos (Appendix B.1). Among the twelve successfully sequenced archaeological specimens, PCA of the genetic diversity in shared SNPs ($N_{SNP} = 63$) showed no clustering with respect to either age of the specimen, nor the excavation site (Fig. 2a, Figure B.2).

An additional PCA was carried out based on the allele frequencies at SNPs shared between the two archaeological specimens with the highest sequence coverage (PGULL-1732.1 and PGULL-1725.2) and publicly available sequences from extant mainland lentils, preserved in genebanks (Liber et al., 2021) (Table A.2, $N_{SNP} = 556$). PC1 separated the archaeological specimens from all extant lentils while PC2 separated lentils from North African countries from south European ones (Fig. 2b).

3.1.1. *Genetic structure in SNP data*

We used a SNP dataset derived from KASP genotyping of 174 individuals from 29 extant accessions to calculate within-accession and within-island genetic diversity (Table 2, Appendix B.5; Table B.6). We also used the SNP data together with data from KASP genotyping of the archaeological specimen PGULL-1731.1 to further explore geographic structure. In a PCA based on per accession allele frequencies ($N_{SNP} = 139$), PC1 separated most of the Canarian accession (PC1 values above 0) from those from the mainland (PC1 values below 0) with the Spanish accessions falling in between those from Moroccan and the Canary Islands (Fig. 3a). The group with most of the Canarian accessions also included the archaeological specimen PGULL-1731.1, leading us to designate the accessions it contained "True Canarians". PC2 separated the remaining Canarian accessions from all other lentils with the Spanish accession IG40927 having an intermediate location among the other groups (Fig. 3a).

When per accession allele frequencies from only the True Canarian lentils were used for PCA three groups were identified along PC1; group I consisted of accessions from La Palma, La Gomera and an accession from Tenerife; group II consisted of accessions from Fuerteventura and an accession from Tenerife and the more diffuse group III contained accessions from Lanzarote, Fuerteventura, the extant Gran Canarian accessions and an accession from Tenerife (Fig. 3b). The archaeological specimen PGULL-1731.1 (a single seed with more than 30 % missing data) clustered with group I along PC1 but was separated from all other accessions (consisting of the allele frequencies of 6 individuals, the majority of which had less than 5 % missing data) along PC2.

When restricting the analysis to the most successful KASP markers (< 20 % missing data, $N_{SNP} = 38$) additional archaeological specimens could be analysed (PGULL-1725.2, PGULL-1725.4, PGULL-1726.2, PGULL-1729.1, PGULL-1730.1 and PGULL-1731.1 with less than 40 % missing data) alongside the 114 extant True Canarian individuals. In PCA archaeological specimens tended to fall within group II, both when analysed as a single population and when analysed individually (Fig. 3c–d).

When the full KASP dataset ($N_{SNP} = 139$, only the archaeological specimen PGULL-1731.1) was analysed using the software Structure, Delta K values were highest for $K = 8$ groups as were *CLUMPP H* values, although with almost equally high values for $K = 2$ (Figure B.3). The True Canarian groups I (orange in Fig. 4), II (violet) and III (pink, with the blue accession BCU001913 clustering with the remaining group III

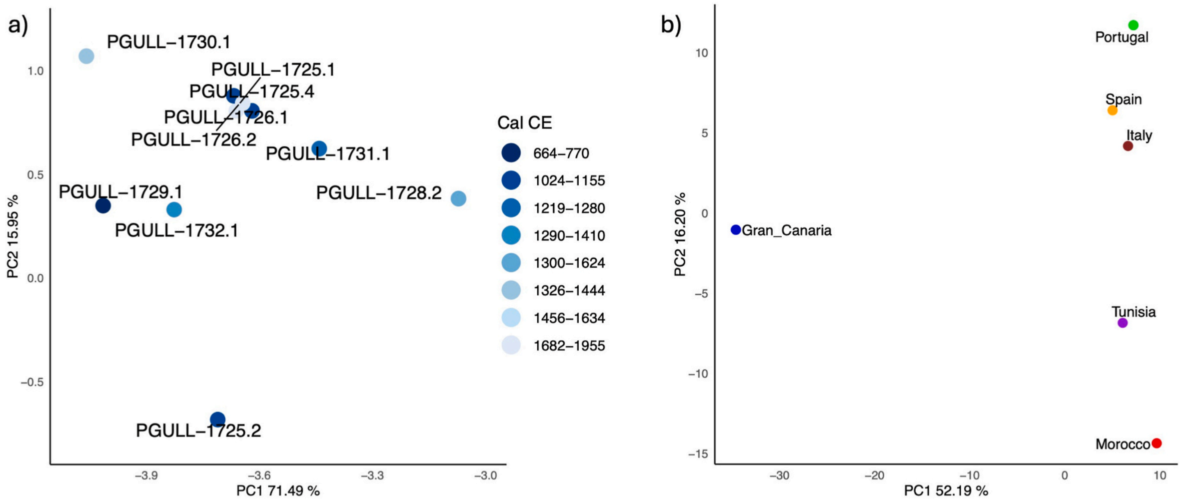

Fig. 2. Results from principal component analysis of SNPs called from sequence data of a) individual archaeological specimens only ($N_{SNP} = 63$ loci) where darker shades of blue denote older specimens and b) population allele frequencies for extant mainland accessions and the two most successful archaeological specimens ($N_{SNP} = 556$ loci, blue: archaeological specimens from Gran Canaria, green: Portugal, orange: Spain, brown: Italy, purple: Tunisia and red: Morocco). In a) jitter has been added to separate overlapping symbols.

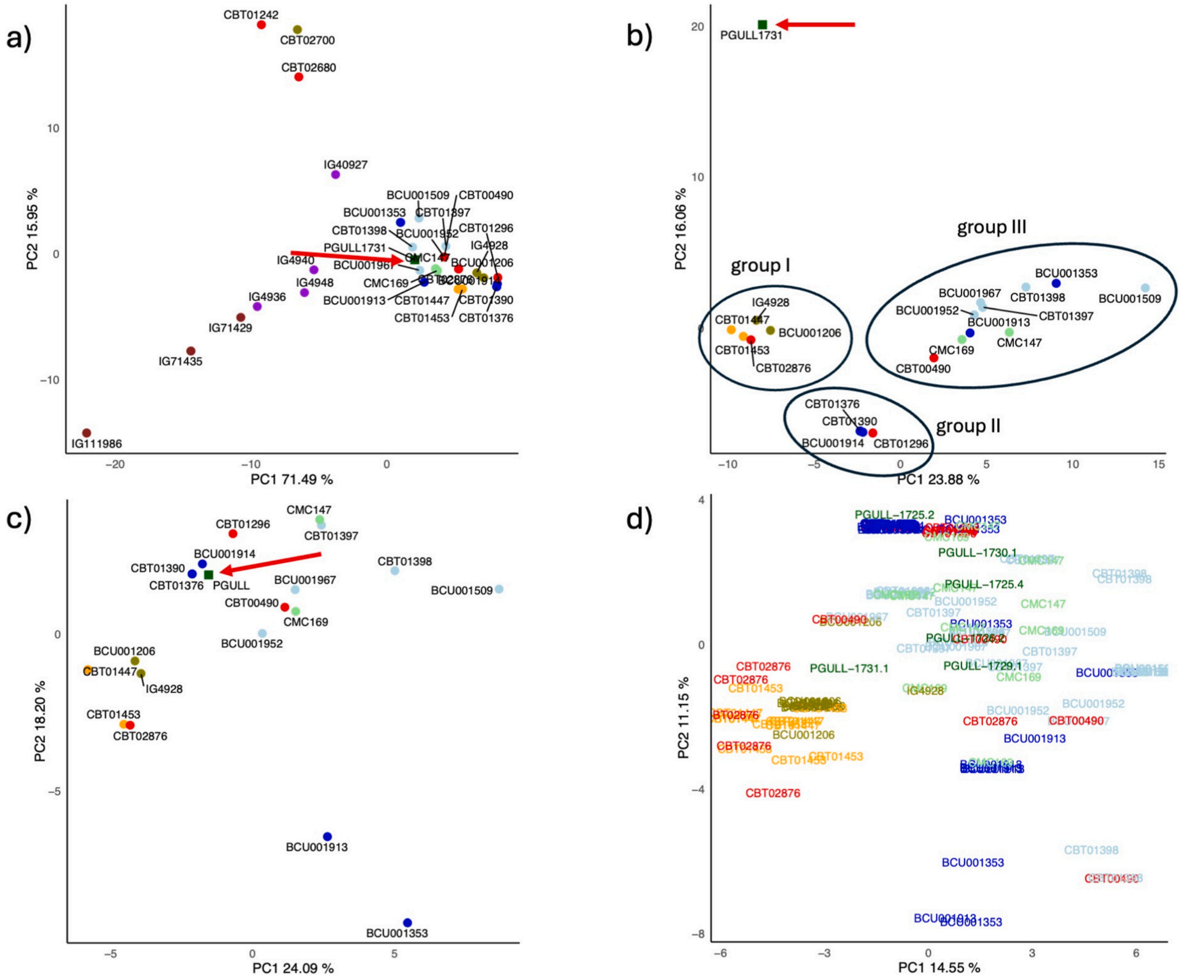

Fig. 3. Results from principal component analysis of KASP genotyped SNPs for a) all extant accessions studied and the archaeological specimen PGULL-1731.1 ($N_{SNP} = 139$), b) True Canarian accessions and PGULL-1731.1 ($N_{SNP} = 139$), c) restricted dataset including True Canarian accessions and the six most successful archaeological specimens ($N_{SNP} = 38$) and d) same dataset as in c) analysed for population allele frequencies. Colours denote origin of the accessions: dark green: archaeological specimens from Gran Canaria, light green: extant accessions from Gran Canaria red: Tenerife, olive: La Palma, light blue: Lanzarote, blue: Fuerteventura, orange: La Gomera, purple: Spain, brown: Morocco. Squared symbols and red arrows indicate the position of the archaeological specimens in a) - c).

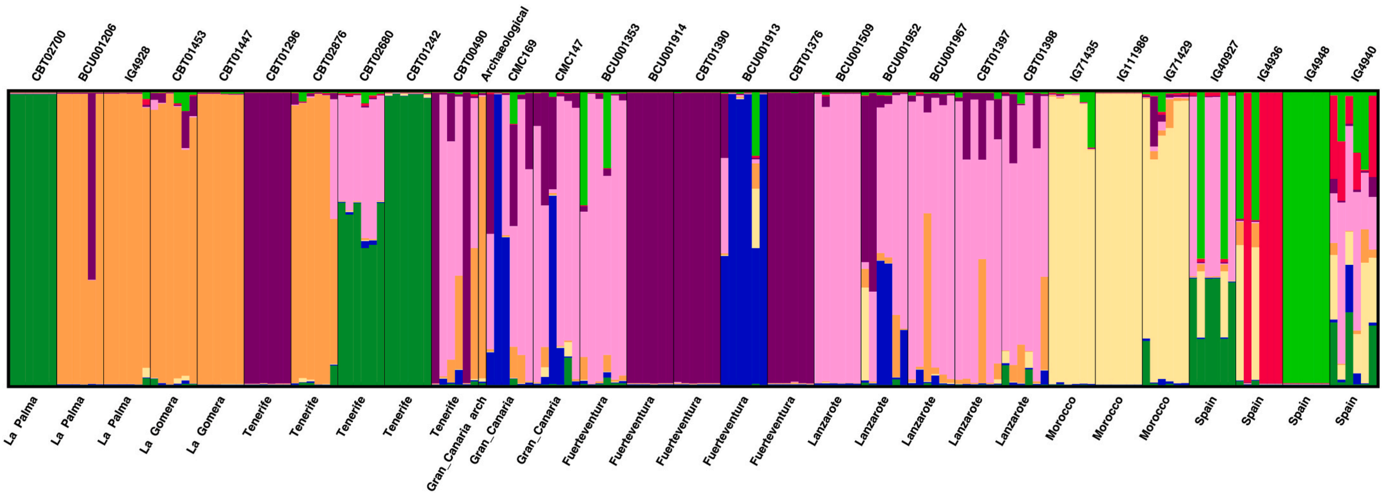

Fig. 4. Results of Structure analysis of KASP genotyped SNPs in extant accessions and the archaeological specimen PGULL-1731.1 at K = 8. Each individual is represented by a vertical line where different colours represent the proportion of the individual belonging to that cluster. Accessions are separated by black lines and sorted in a west - easterly order based on their longitude of origin.

accessions up until K = 7, Figure B.3), were all recovered at K = 8. The remaining Canarian accessions (originating from Tenerife and La Palma) formed a separate cluster (group IV, green). The individuals of group I, II and IV almost completely belonged to a single group, while mixed ancestry could be seen in individuals primarily belonging to group III, in particular the accessions from Tenerife and Gran Canaria. At K = 8 the Moroccan accessions formed a separate cluster (yellow) while the Spanish accessions showed a mixed ancestry, with individuals in IG40927 and IG4940 partially clustering with group III and group IV.

Genetic differentiation among accessions was quantified by calculating pairwise F_{ST} values for the full KASP dataset (Figure B.4). The F_{ST} values, most of which were significant, ranged from 0 (between CBT001376 and CBT001390) and 1 (all three pairwise comparisons of the Spanish accession IG4948, the Moroccan IG111986 and CBT002700 from La Palma). Non-significant values were found both in within-island and between-island comparisons, but in all cases these were between accessions from the same group.

4. Discussion

4.1. Well-preserved DNA in desiccated lentils

Desiccation has been identified as the superior preservation state with respect to aDNA in plants and many of the oldest plant DNAs analysed come from archaeobotanical remains preserved in a desiccated state (Li et al., 2011; Mascher et al., 2016; Palmer et al., 2009; Wales et al., 2019). Here, we confirm the excellent storage conditions of the indigenous grain silos on Gran Canaria, previously shown by successful aDNA analyses in wheat and barley (Hagenblad, et al., 2017, 2024; Oliveira et al., 2012) and add lentil to the growing list of plant species for which genetic analyses of archaeological remains have been successfully carried out. The current study is one of very few aDNA studies of legumes, and support results from sequencing of ancient common beans (*Phaseolus vulgaris*) (Trucchi et al., 2021), suggesting that legume seeds in general can provide high quality aDNA, if the seeds have been preserved under favourable climatic conditions. These findings are encouraging for future analyses of ancient legumes and broaden the scope for genetic studies of pre-historic crops which has so far had a strong focus on cereals.

The sequence coverage obtained from the archaeological specimens varied by multiple orders of magnitude. The cause of the differences in sequencing success is unknown and specimens yielding both high and low sequence coverage could originate from the same context (e.g. La Fortaleza, Silo 2, Table 1). At present it is unfortunately not possible to predict sequencing success prior to the destructive analysis.

Only a very low number of shared SNPs were recovered from the successfully sequenced archaeological specimens and based on these, no clustering by age or site could be detected. Given the low number of SNPs analysed, the lack of clustering does not necessarily mean archaeological lentils have been genetically homogenous. It is possible that the number of SNPs available is insufficient for resolving population structure. Indeed, in archaeological barley from Gran Canaria, age-related genetic structuring was detected when using a much larger number of SNPs (Hagenblad et al., 2024). Comparisons of sequence data from archaeological and extant lentils did result in the expected separation of European and North African countries, but with the Canarian archaeological specimens not being more similar to extant lentils from either continent. Degradation of the aDNA may have introduced sequence variation to the Canarian specimens, but with the level of genetic diversity (Nei's h = 0.006) being a third of one found in the extant lentils (mean Nei's h = 0.018) it is unlikely to have had a large effect on the results (Table B.6). Instead, loss of genetic diversity during the founding and isolation of the Canarian lentil population, and selection for adaptation to cultivation in the insular climate, may have caused the development of a lentil gene pool unique to the Canary Islands, a similar to the development of 'Bere' barley on Orkney (Drosou et al., 2022).

4.2. Continuous lentil cultivation in the Canary Islands

Following the Hispanic conquest of the Canary Islands, people of European and African origin largely replaced the indigenous population (Flores, et al., 2001, 2003; Fregel, et al., 2009a, 2021; Pino-Yanes et al., 2011). On Gran Canaria, existing indigenous agricultural infrastructure was repurposed for growing new crops, brought to the archipelago from both the old and the new world (Aznar Vallejo, 2009; Díaz-Sierra, 2022). The archaeological specimens analysed here show a clear similarity with the majority of the lentils cultivated on the archipelago today (groups I through III, Figs. 3b and 4, Figure B.3) that can only be explained by continuous cultivation of indigenous lentils on the Canary Islands. It demonstrates that lentils cultivated on the Canary Islands today almost exclusively, directly descend from lentils brought to the archipelago almost two millennia ago by the original colonizers, similar to what has been found in barley (Hagenblad, et al., 2017, 2024).

On the Canary Islands, intermarriage of immigrant men and indigenous women was common following the Hispanic conquest, as shown by the more widespread presence of matrilineally inherited mitochondria (≈45 %) than patrilineally inherited Y-chromosomes (<10 %) among present day Canarians (Fregel et al., 2009a; Santos et al., 2010). The True Canarian lentils support that, alongside the cash crops and other novel produce introduced (Aznar Vallejo, 2009), immigrants continued the cultivation of indigenous lentils, and replacement of already existing crop species with their mainland counterparts seems not to have been widespread. In ethnographic interviews, Canarian women have displayed more knowledge about crops used for the family's food than have men (Gil González, 2011). Preadaptation to the local climate is likely to have played a part in the continued cultivation of indigenous crops, but in the presence of a gendered immigration bias, a tradition of women managing, preserving and inheriting the food crops, similar to the case in Rwanda (Howard, 2003), may have been instrumental for the local preservation of Canarian crops.

4.3. *Inter-insular isolation*

Early Europeans encountering the Canarian archipelago reported that the inhabitants did not possess the means to travel between islands (Mederos Martín and Escribano Cobo, 2005). With crop plants being intrinsically a part of human culture, inter-island isolation must have resulted in a cessation of seed exchange and gene flow within crops among islands, genetic differentiation and a geographic clustering of genetic diversity among the islands. The existence of an eastern (group III) and a western group (group I) among the present-day True Canarians (Fig. 3a and c), partly reflects the east - west divide reported from indigenous human populations (Serrano et al., 2023) and barley (Hagenblad et al., 2017; Hagenblad and Morales, 2020). Although continuous seed exchange within the lentil groups and inter-island contacts not resulting in seed exchange among groups cannot be excluded, results are consistent with cultural isolation between eastern and western islands during the pre-Hispanic period.

Archaeological finds of lentils are currently only recorded from Gran Canaria, La Palma and Fuerteventura (Morales et al., 2023). It should be noted that systematic sampling aiming to collect archaeological seeds has not been applied to all the sites on the islands, and a lack of lentil records may well be due to a methodological bias (Morales et al., 2023). However, cultivation of lentil by the indigenous population is not mentioned in written contemporary sources at the time of contact with Europeans, suggesting that lentil production was reduced or abandoned during this time of crisis. The genetic differentiation between group I and III supports that lentils have been continuously cultivated on either La Palma, La Gomera or both islands from prior to the arrival of the Europeans until the present, and that if the crop was lost on one island, it must have been restocked from the other. On Lanzarote, if lentil cultivation was indeed lost, it has likely been restocked from Fuerteventura. With the current dataset it is not possible to confirm continuous cultivation on Tenerife or Gran Canaria, as has been the case in barley (Hagenblad et al., 2017).

4.4. *Lentil currently cultivated in the Canary Islands*

Compared with previously studied barley from the Canary Islands, using a similar number of SNP markers (Hagenblad et al., 2017), lentil accessions seem to be more homogenous with similar clustering of the individuals within most accessions (Fig. 4). Historically, barley was subject to taxation on the Canary Islands while lentils were not (Santana Pérez, 1995). A difference in purpose between the two crops, with barley being to a larger extent a traded crop while lentils were cultivated more for household use (Santana Pérez and Santana Pérez, 1998), may have led to a smaller amount of seed exchange among lentils resulting in more homogeneous populations.

Following the Hispanic conquest, the smaller Canary Islands mainly produced cereals, legumes and other crops for export to Tenerife and Gran Canaria, where cash crops such as sugar and grapes for wine dominated the agricultural sector from the 16th century onwards (Santana Pérez, 1995). Export of lentils from Lanzarote to Gran Canaria and Tenerife is known from the mid 17th century (Santana Pérez, 2001) and during the mid-20th century, lentil production in Lanzarote was large, exporting to the bigger islands (Gil González et al., 2005). The mixed ancestry of CMC169, CMC147 (both from Gran Canaria) and CBT00490 (from Tenerife) suggest they could partially be the result of post conquest imports from Lanzarote, overstamping any existing pre-Hispanic signals of inter-island isolation.

We suggest that group IV is a recent introduction from an unknown source. We have been unable to find any historical sources describing import of lentils to the archipelago after the Hispanic conquest and hence do not know when or from where this import could have happened. Our results do not give any clear indication of a possible origin (Figs. 3a and 4), and although the genetic diversity of lentils has been investigated in a number of articles (Alo et al., 2011; Khazaei et al., 2016; Liber et al., 2021; Lombardi et al., 2014; Pavan et al., 2019; Rajendran et al., 2021; Wong et al., 2015), to the best of our knowledge, none of the accessions from group IV has been compared with mainland accessions before. Additional genotyping of mainland accessions from a larger geographic region, together with accessions from group IV, will be needed to identify the geographic origin of these lentils.

4.5. *Relationships among Canarian and mainland lentils*

Multiple lines of evidence support the suggested Amazigh/Berber origin of the indigenous Canarian settlers, their crops and animals (Farrujia de la Rosa et al., 2010; Hagenblad et al., 2017; Maca-Meyer et al., 2004; Morales et al., 2023). However, although the introduction of the True Canarian lentils clearly predates the Hispanic conquest (as evidenced by their similarity with the archaeological specimens), the current study fails to add support to a North African ancestry. Only a small number of mainland lentils were included and the choice of accessions naturally affects the clustering of the included accessions. Nevertheless, we expected the Canarian lentils to exhibit more genetic similarity with the Moroccan lentils than the Spanish ones but instead found the opposite (Figs. 2b, 3a and 4, Figure B.3, B.4).

Closer examination of the Spanish accessions suggests a tantalizing explanation to this conundrum. Individuals in the Spanish accessions IG40927, IG4940 and IG4936 partially cluster with the eastern True Canarian group (pink in Fig. 4, Figure B.3). Historical archives indicate export of lentils from the eastern islands to mainland Spain since at least the mid-17th century CE, although the volume of this trade was limited (Santana Pérez, 2001), and during the mid-20th century lentils from Lanzarote were exported to mainland Spain (Gil González et al., 2005). Today, lentils labelled as of "Lanzarote type" ("Lenteja tipo Lanzarote") are sold in supermarkets in both the Canary Islands and mainland Spain. These are not produced on Lanzarote but allude to the consumers' memories of the quality of Lanzarote lentils. Our results tentatively suggest that lentils from Lanzarote may, in fact, have contributed to the early development of Spanish lentil varieties, not only in name, but also genetically. With the changing climate, Canarian lentils, adapted to cultivation in hot and dry conditions, may again play an important role for the development of future lentil cultivars.

5. Conclusions

With this, the very first genetic analysis of archaeological lentil specimens, we show how the genetic diversity of archaeological crop remains, when evaluated together with data on within-population genetic diversity of landraces preserved in gene banks until the present, can be used to shed light on aspects of past human cultures that are not documented in written records. We add support to an extended pre-Hispanic inter-island isolation in the Canarian archipelago and the adoption of indigenous crops by immigrant farmers on the Canary Island after the Hispanic conquest. Local adaptation and a gendered division of farming responsibilities have likely been drivers for the continuous cultivation of local landrace lentils.

CRediT authorship contribution statement

Jenny Hagenblad: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jacob Morales:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition, Conceptualization. **Rosa Fregel:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **Pedro Henríquez-Valido:** Writing – review & editing, Resources. **Matti W. Leino:** Writing – review & editing, Writing – original draft, Methodology. **Amelia C. Rodríguez-Rodríguez:** Writing – review & editing, Funding acquisition. **Jonathan Santana:** Writing – review & editing, Resources, Project administration, Funding acquisition.

Data accessability

The sequence data generated in this study is available at the European Nucleotide Archive (ENA, https://www.ebi.ac.uk/ena/browser/home) with the accession number XXX. [To be submitted upon acceptance.] Results of KASP genotyping are available in Appendix C.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2025.106360.

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