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Whole genome population structure of North Atlantic kelp confirms high-latitude glacial refugia

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Abstract

Coastal refugia during the Last Glacial Maximum (~21,000 years ago) have been hypothesized at high latitudes in the North Atlantic, suggesting marine populations persisted through cycles of glaciation and are potentially adapted to local environments. Here, whole-genome sequencing was used to test whether North Atlantic marine coastal populations of the kelp *Alaria esculenta* survived in the area of southwestern Greenland during the Last Glacial Maximum. We present the first annotated genome for *A. esculenta* and call variant positions in 54 individuals from populations in Atlantic Canada, Greenland, Faroe Islands, Norway and Ireland. Differentiation across populations was reflected in ~1.9 million single nucleotide polymorphisms, which further revealed mixed ancestry in the Faroe Islands individuals between putative Greenlandic and European lineages. Time-calibrated organellar phylogenies suggested Greenlandic populations were established during the last interglacial period more than 100,000 years ago, and that the Faroe Islands population was probably

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established following the Last Glacial Maximum. Patterns in population statistics, including nucleotide diversity, minor allele frequencies, heterozygosity and linkage disequilibrium decay, nonetheless suggested glaciation reduced Canadian Atlantic and Greenlandic populations to small effective sizes during the most recent glaciation. Functional differentiation was further reflected in exon read coverage, which revealed expansions unique to Greenland in 337 exons representing 162 genes, and a modest degree of exon loss (103 exons from 56 genes). Altogether, our genomic results provide strong evidence that *A. esculenta* populations were resilient to past climatic fluctuations related to glaciations and that high-latitude populations are potentially already adapted to local conditions as a result.

KEYWORDS
Alaria esculenta, brown algae, Last Glacial Maximum, Phaeophyceae, population genomics, whole genome sequencing

1 | INTRODUCTION

Marine coastal systems in the Northern Hemisphere have survived a dynamic history of climatic fluctuations. Cycles of Pleistocene glaciations over the past 2.6 million years are widely accepted to have left a significant imprint on the genetics of marine coastal populations, with refugia scattered throughout the Atlantic providing periodic sanctuary from the expansion and contraction of ice-sheets (Assis et al., 2018; Maggs et al., 2008). Today, marine coastal populations face the challenge of a warming and increasingly volatile climate (IPCC, 2021). Warming has been particularly pronounced at high latitudes, with Arctic warming progressing at three times the global average (IPCC, 2021; Miller et al., 2010). October 2019 to September 2020 represented the second warmest 12-month period of observed surface air temperatures over Arctic land during the last century (Ballinger et al., 2020), and trends suggest a decoupling of Earth's climate from Pleistocene climatic cycles (Berger et al., 2016). Changes observed in today's oceans will therefore persist over geological timescales (IPCC, 2021), and include declining perennial ice cover, ocean acidification, altered circulation patterns, and changes to sea-surface temperatures and salinity (Renaud et al., 2015; Stroeve et al., 2012; Thornalley et al., 2018). More than ever, a robust understanding of marine ecosystem responses to climate change is needed, a need that inherently depends on a comprehensive and accurate view of biodiversity, the recent history of marine ecosystems within the context of Earth's climate, and ultimately the potential for populations to adapt to a new climatic regime.

Among the most important components of coastal ecosystems are marine forests, the dynamic underwater seascapes formed by macroalgae. Kelps (Laminariales), in particular, are canopy-forming species that provide crucial ecosystem functions and societal services (Bringloe, Starko, et al., 2020; Bruno & Bertness, 2001; Dayton, 1985; Schiel & Foster, 2006; Teagle et al., 2017; Wernberg et al., 2019). Kelps are globally distributed, occupying an estimated 36% of the world's coastlines with highest occurrences in cold-temperate and Arctic waters (Jayathilake & Costello, 2021; Starko, Wilkinson, & Bringloe, 2021). Kelp forests provide foraging and nursery grounds for numerous fish and invertebrate species (Bégin et al., 2004; Teagle et al., 2017), and may play an important role in carbon sequestration (Krause-Jensen & Duarte, 2016; Ortega et al., 2019). Global analyses highlight wide variability in kelp ecosystem trends, with local-scale variation exceeding a small global average decline in abundances (Krumhansl et al., 2016). Polar regions may experience expansion of some kelp species as sea-ice retreat opens new habitat (Bringloe et al., 2022; Krause-Jensen et al., 2020), while in other regions, warming threatens to extirpate cold-adapted flora in favour of warm-adapted turf-forming species, with accompanying changes to ecosystem function (Filbee-Dexter & Wernberg, 2019; Filbee-Dexter et al., 2020; Pessarrodona et al., 2021; Vergés et al., 2016). Safeguarding kelp and the accompanying services they provide will require genomic insights to unravel details about past evolution, the historical environmental processes that underpin current biogeographical patterns, dispersal and exchange of genomic information among populations, and ultimately the capacity for genetic adaptation of populations in a changing climate.

Our current phylogeographical understanding of coastal marine ecosystems remains limited to relatively coarse-resolution genetic data sets. Marine coastal ecosystems in the North Atlantic and Arctic were historically viewed as depauperate extensions of southern European refugial populations following the Last Glacial Maximum (LGM; 21 thousand years ago [ka]). This scenario is known as the "tabula rasa" hypothesis (Dunton, 1992; Ingolfsson, 1992; Lee, 1973) and is a view that continues to serve as the basis for interpretations of evolution and adaptation in North Atlantic and Arctic populations (e.g., Liesner et al., 2020). Genetic studies have since supported the idea of refugia in other areas of the Atlantic, including the Northwest (Bringloe & Saunders, 2018; Li et al., 2015; Maggs et al., 2008; Neiva et al., 2018; Wares & Cunningham, 2001) and high-latitude areas encroaching on the Arctic environment (Bringloe, Verbruggen, & Saunders, 2020; Guzinski et al., 2020;

Figure 1a). Species distribution modelling studies incorporating climatic data have pointed to further scattered refugia during the LGM in the North Atlantic, helping to forward the hypothesis of refugia at previously unconsidered high latitudes, specifically along the southwestern tip of Greenland (Assis et al., 2018; Bringloe, Verbruggen, & Saunders, 2020). The view of high-latitude North Atlantic and Arctic refugia persisting through cycles of glaciation has important implications for understanding the adaptation history of species/populations to their respective environments. The above research, however, relied on Sanger sequencing of organellar markers, microsatellite data or reduced capture methods (i.e., RADseq), and while their use has been critical to furthering our understanding of the population history and phylogeography of marine populations, their resolution to resolve past events remains coarse. The increasing accessibility of genomic data sets has made it possible to leverage single nucleotide polymorphism (SNP) data sets orders of magnitude greater in resolution for all genomic compartments concurrently (organellar and nuclear), along with functional genomic information, thus opening new possibilities to understand past events (Oleksiak & Rajora, 2020).

Among the marine species hypothesized to have survived at high latitudes during the LGM, particularly along the southwest corner of Greenland, is the kelp species *Alaria esculenta* (Linnaeus) Greville (Assis et al., 2018). The genus *Alaria* is distributed throughout cold-temperate waters in the northern hemisphere, and is a kelp of aquaculture interest (Kraan, 2020). *A. esculenta* is the only Atlantic species, with most of its diversity present in the Northwest Pacific. Being a kelp, *A. esculenta* alternates its life history with a conspicuous sporophyte, with a characteristic midrib and sporophylls at the base of the blade (Figure 1d,e), and a microscopic gametophyte stage. Short-range dispersal is believed to be primarily achieved through spores, but gametophytes are hypothesized to grow indiscriminately, and are known to grow as endophytes in other seaweeds (Bringloe et al., 2018), which potentially facilitates dispersal mediated through other marine species. *A. esculenta* is considered perennial, with the maximum age of plants estimated at 7 years (Baardseth, 1956), and tend to grow on exposed shorelines subtidally or at the low tide mark (Figure 1e). Genetic studies in *A. esculenta* are generally limited to *cox*I data sets (Bringloe & Saunders, 2018; Bringloe, Verbruggen, & Saunders, 2020) and point to trans-Atlantic divergence pre-dating the LGM. Whole genome sequencing data sets for a limited number of individuals were also recently published by Bringloe et al. (2021), which identified that specimens from the Canadian Arctic do not represent *A. esculenta*, but rather a separate species with a history of hybridization with Northeast Pacific species.

Here, whole genome sequencing (WGS) data sets were used to revisit questions about the phylogeographical history of North Atlantic *A. esculenta*. Our primary objective was to test the hypothesis that high-latitude marine glacial refugia occurred in the area of southern Greenland during the LGM, the null hypothesis being that *A. esculenta* was established in this area within the past 20 ka. We tested three sets of predictions to determine if the null hypothesis is true. (1) If the null hypothesis is true, we expect low levels of phylogenetic differentiation and nucleotide divergence (i.e., F_{ST} values) in Greenlandic populations relative to potential source populations that postdate the LGM (21 ka). (2) If the null hypothesis is true, we expect several signatures of recent recolonization to be present in Greenlandic populations of *A. esculenta*, namely low nucleotide diversity, low levels of heterozygosity, high levels of linkage disequilibrium and a cline in minor allele frequencies relative to potential source populations (i.e., the Northwest Atlantic or European populations; Peter & Slatkin, 2013). (3) If the null hypothesis is true, we expect Greenlandic populations to be functionally similar to potential source populations, as evidenced by consistent levels of read coverage for exon regions. This study is among the first broad-scale analyses of whole genome population patterns in kelp, and showcases the rich source of information provided by whole genomes that can be utilized to unravel recent phylogeographical history in marine populations, along with potential functional consequences of localized evolution.

2 | MATERIALS AND METHODS

2.1 | Drafting the *Alaria esculenta* genome

To generate a draft genome of *A. esculenta*, we generated ~4.6 million Pacbio SequelII Continuous Long Reads (67.89 Gb) from a single individual collected in Oyragjógv, Faroe Islands. The long reads were assembled using WTDBG2 version 2.5 (Ruan & Li, 2020), obtaining a first draft genome of ~845 Mb, containing 11,327 contigs and an N50 of 560 kb. The assembly was polished once with NEXTPOLISH version 1.3.1 (Hu et al., 2020), using long reads and short reads (34 Gb of data representing ~114 million DNBSEQ-G400 150-bp paired-end reads) from the same individual. This first assembly was subjected to two additional rounds of NEXTPOLISH. Because the *A. esculenta* individual used for the assembly is not axenic and contains the *Alaria* holobiont of its original location, we employed a two-step approach to remove contigs of probable bacterial origin.

First, using the assembly itself, we filtered contigs based on their GC (i.e., guanine–cytosine) content and coverage. We calculated the GC content and k-mer coverage of each contig using KAT version 2.4.1 (Mapleson et al., 2017). We found two GC peaks, one with ~30% GC content, and the other with higher coverage with ~50% GC content. Given that we expect the coverage of the genome to be high overall, and that the genomic GC content of other brown algae is ~50% (Cock et al., 2010; Liu et al., 2019; Shan et al., 2020), we selected contigs with a GC content >35% and <75%, as well as a k-mer coverage >10 as probably "true" *A. esculenta* contigs. The selected contigs were extracted from the assembly using the SEQTK toolkit version 1.3.

Second, we used the entire data set (the coverage per contig of the short read data of all samples used in this study) to further filter contigs of probable contaminant origin. For this, we calculated the coverage per contig of each sample, and normalized by the median coverage of all contigs in the sample (a value >1 or <1 indicates that

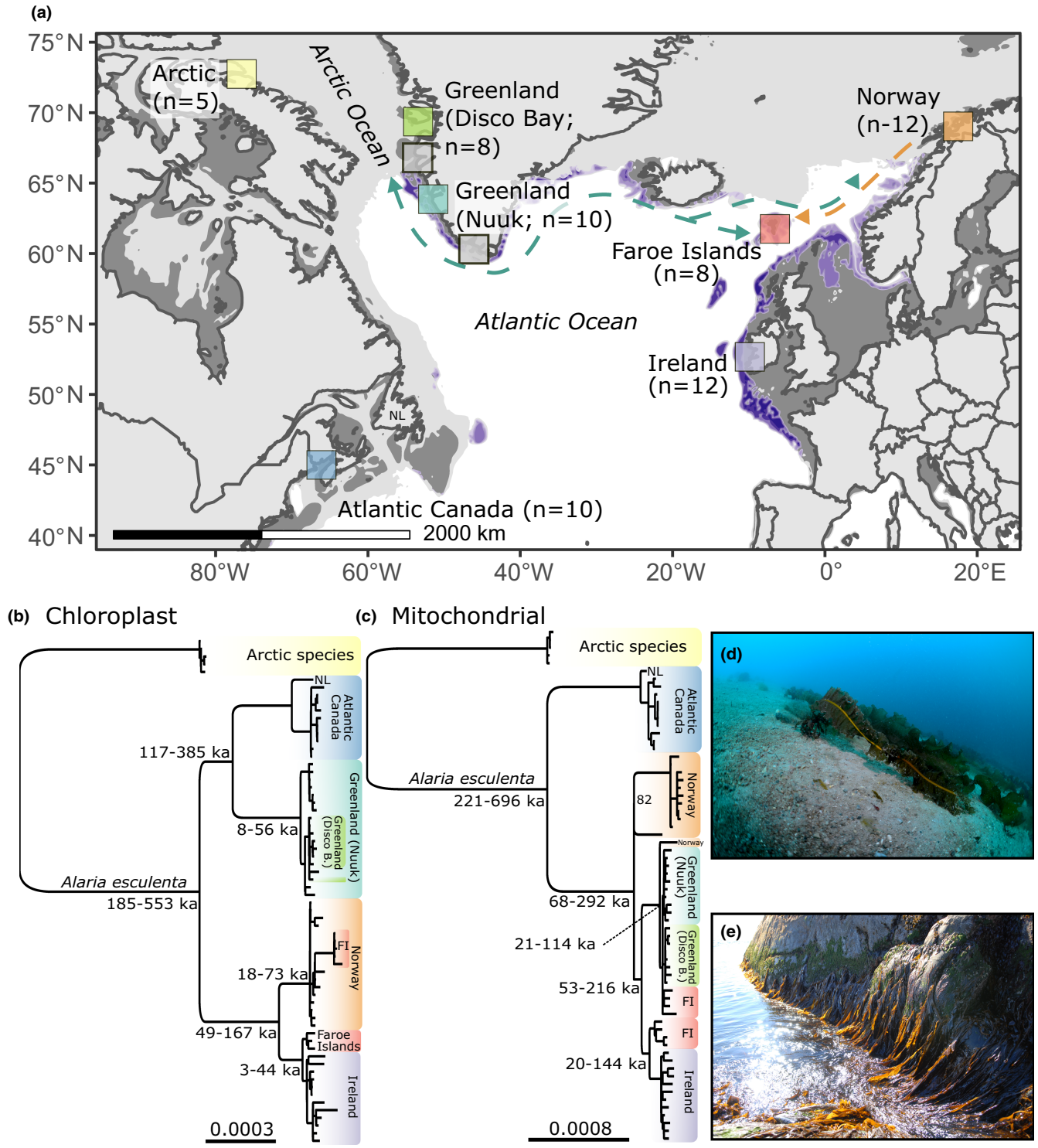

FIGURE 1 Sampling locations for populations of *Alaria esculenta* and maximum-likelihood trees based on organellar genomes. (a) Map of the North Atlantic and sampling locations. Conditions during the LGM (21 ka) are depicted, including exposed land mass in dark grey due to lower sea levels, persistent oceanic ice cover in light grey and suitable macrophyte habitat in purple (adapted from Bringloe, Verbruggen, & Saunders, 2020). The faded grey boxes represent areas of long-term persistence inferred by species distribution models presented by Assis et al. (2018). Putative migration pathways during the Pleistocene inferred in the current study are depicted with dashed arrows. (b) Chloroplast and (c) mitochondrial trees based on 605 and 698 SNPs respectively. Bootstrap support was 100% at all internal nodes and highlighted clusters unless otherwise indicated. Times estimates for divergences in thousands of years are indicated (NL = Newfoundland Canada; FI = Faroe Islands. (d) Outgroup species Arctic *Alaria*, which is hypothesized to represent a species distinct from *A. esculenta* (Bringloe et al., 2021) growing below the ice-scour of Southampton Island, Nunavut, Canada (photo courtesy of Ignacio Garrido). (e) *A. esculenta* beds growing in the low intertidal of Godthåbsfjorden, Greenland (photo courtesy of Dr Peter Bondo Christensen). Scale bars represent number of substitutions/site. See Figure S3 for Bayesian time-calibrated trees.

the contig's coverage is higher or lower than that of the median coverage of all contigs in the sample, respectively). Then, we calculated the normalized median coverage of each contig across all samples in the data set. Only contigs with a median normalized coverage >0.30 were kept. As these contigs are well represented in all samples, we reasoned they probably belong to the *A. esculenta* genome. Discarded contigs are contigs with a poor representation across all samples, which probably belong to bacterial and/or eukaryotic contaminants, the rationale here being that contaminating species are likely to vary between samples of widely different geographical origin, leading to uneven contig coverage across samples.

To confirm the validity of the filtering steps described above, we assessed the purity of the assembly using BLOBTOOLS version 1.1.1 (Laestch & Blaxter, 2017). Pre- and post-filtration assemblies were used as queries against the NCBI nt database, as well as the Uniprot Reference Proteome database. Taxonomic assignment of contigs based on BLASTN and BLASTX results, respectively, was performed using BLOBTOOLS. The results showed that the filtering steps removed all obvious contaminating contigs (assigned as *Flavobacteriales*, *Hyphomicrobiales*, *Pirellulales*, *Cellvibrionales* and undefined bacteria; Figure S1), without compromising the amount of *Laminariales*-assigned contigs (Figure S2). The final draft assembly shows that 447/487 Mb (91%) are taxonomically assigned to *Laminariales*, with a further 5 Mb assigned as *Ectocarpales* and 3 Mb assigned as *Fucales*. Altogether, these filtering steps removed 357 Mb of the original assembly and did not lead to a decrease in BUSCO scores (v.5.1.0; Seppey et al., 2019), which were 76.5% for Eukaryota and 83% for Stramenopiles. Therefore, we postulate that the final assembly presented here is a good representation (albeit probably incomplete) of the *A. esculenta* nuclear genome.

For genome annotation, we first created a custom repetitive elements library for *A. esculenta* using REPEATMODELER2 version 2.0.1 (-LTRStruct enabled) (Flynn et al., 2020), and used the repeat library created to mask repeats in the draft genome with REPEATMASKER version 4.1.2 (Smit et al., 2013). Approximately 58% of the genome was masked using the custom repeat library. Next, we used the masked genome for gene prediction using the BRAKER2 pipeline version 2.1.6 (Brůna et al., 2021) in -etp mode. The prediction used the "all proteins" file from orthodb version 10 (Kriventseva et al., 2019) as the protein database, and RNA sequencing (RNA-seq) data of *A. esculenta* gametophytes from KU-791(female) and KU-792 (male), mapped onto the masked genome using STAR version 2.7.8 (Dobin et al., 2013). The RNA-seq data were generated by extracting RNA from gametophyte cultures using a Qiagen RNeasy Plant Kit. Extractions were sent to BGI (Hong Kong) where libraries were generated using standard BGI protocols and sequenced on the BGISEQ-500 platform (30 million reads per sample). Finally, predicted protein-coding genes were functionally annotated using a combination of INTERPROSCAN (Zdobnov & Apweiler, 2001) and BLASTP (Protein–Protein BLAST) against the Swissprot and TrEMBL (restricted to *Phaeophyceae*) databases (The UniProt Consortium, 2021), with a minimum e-value of $1\times e^{-5}$ (referring to the expected number of random hits for a given alignment score). INTERPROSCAN and BLAST hits were combined into a single gff3 file using AGAT version 0.6.0 (Dainat, 2021). The final assembly and annotations are available via FigShare (https://doi.org/10.6084/m9.figshare.16712797.v1).

2.2 | Whole genome sequencing of populations and variant-calling

Blades of *Alaria* sporophytes were collected from Atlantic Canada (n = 12), Southwest Greenland (n = 10 for Nuuk, n = 8 for Disco Bay populations), Faroe Islands (n = 8), Norway (n = 12) and Ireland (n = 12; Table S1). Generally, specimens were collected haphazardly by divers or by rake from a boat, from 5–10 m depth and 10 m apart. Gametophyte samples were additionally sourced from the Kobe University Macroalgal Culture Collection (KU-MACC) for RNA-seq; whole genome data for five Arctic individuals and a single New Foundland gametophyte culture were also included in some of our analyses. Total genomic DNA was extracted either using a modified CTAB protocol (Cremen et al., 2016), a magnetic beads protocol (Fort et al., 2018), or a Qiagen DNeasy Plant Kit. Extracted DNA was sent to either GENEWIZ (Suzhou, China), where libraries were generated using the Illumina VAHTS Universal DNA Library prep kit and protocols, and sequenced on the NovaSeq System (paired-end, 150-bp reads, ~15–30 Gb of data per specimen), or BGI, where libraries were generated using standard BGI protocols, and sequenced on the DNBSEQ-G400 platform (paired-end, 150-bp reads, ~20–30 Gb of data per specimen). In total, 68 specimens were sequenced, representing over 1.6 TB of data and over 6.4 billion paired reads. Prior to analysis, all reads were trimmed using TRIMMOMATIC version 11.0.2 (Bolger et al., 2014), with a hard trim of the first 15 bp, trimming bases with a quality score below 10 from the 3′ end, and keeping reads with an average read quality score of 20 and minimum length of 75 bp.

Organellar genomes were de novo assembled for all samples using default settings in NOVOPLASTY version 3.7.2 (Dierckxsens et al., 2017). Read coverage typically exceeded 1000× for the organelles. SNPs for the organellar genomes were called by aligning organellar genomes using the MAUVE alignment (Darling et al., 2004) plugin in GENEIOUS PRIME version 2021.1.1 (Kearse et al., 2012). In order to infer the timing of diversification events within *A. esculenta*, we generated time-calibrated phylogenies for plastid and mitochondrial genomes using BEAST version 1.10.4 (Drummond et al., 2012). We produced concatenated alignments of all protein-coding and ribosomal genes from each genome and identified optimal partitioning schemes (based on gene identity and codon position) in PARTITIONFINDER2 (Lanfear et al., 2017). We conducted separate analyses on each alignment and used a single calibration point aimed at capturing the timing of the split between *A. esculenta* and *Alaria crispa* Kjellman as previously inferred by Bringloe et al., 2021 (mean age = 0.9, SD = 0.15). Two to five MCMC (Markov chain Monte Carlo) chains (for mitochondrial and plastid alignments, respectively) were run for 10,000,000 generations, phylogenetic tree sets from each chain were combined and log files were checked to ensure convergence

(Effective Sample Size >200 for all parameters). The trees are presented in Figure S3.

In order to call nuclear SNPs, reads for each specimen were mapped to the draft genome described above, using score min parameters of L, −0.6, −0.3 in BOWTIE2 version 2.3.4 (Langmead & Salzberg, 2012), which represented a 5% divergence threshold for mapping reads. SAM files were then converted to BAM format and sorted using SAMTOOLS version 1.9 (Li et al., 2009). BCFTOOLS version 1.9 (Danacek et al., 2021) was used to compile all the sorted bam files into variant call format (VCF) and call variant and invariant positions. The data set was filtered in a series of steps. First, repeat regions were removed using VCFTOOLS version 0.1.16 (Danecek et al., 2011). Second, BCFTOOLS version 1.9 was used to set genotypes to missing based on the following criteria: allelic balance/ratio of heterozygous SNPs >5 or <0.2 (reference:alternate allele), genotyping score (GQ) of ≤30 (i.e., 1/1000 chance of a genotyping error), read depth <10, read depth >100 and 1 bp proximity to indels (i.e., SNPs adjacent to indels). Indels and SNPs with more than three genotypes were also removed. The variant+invariant sites data set represented 203,209,555 positions (i.e., ~42% of the genome). Third, the data set was then filtered at the site level using VCFTOOLS version 0.1.16 (Danecek et al., 2011) according to the following criteria: max missingness per site of 15%, minimum site quality score of 30 (i.e., 1/1000 chance of a calling error), minor allele frequency of 0.01 (i.e., singleton SNPs were removed) and bi-allelic sites were retained (i.e., invariant positions removed). Individuals with >15% missingness were also removed using VCFTOOLS version 0.1.16 (Danecek et al., 2011). The site filtering parameters retained 1,897,988 sites for analysis. Fourth, we used PLINK version 1.9 (Purcell et al., 2007) to remove linked sites using a 25-kb window and an r^2 value of .25, which retained 172,554 sites. The workflow used here is depicted in Figure S4. The full set of command lines and justifications for the parameter choices are available at https://github.com/tbringloe/WGS-NOVAC.

2.3 | Population genomic analyses

Relationships among populations based on organellar genomes were first visualized as maximum-likelihood trees, generated using the GTRGAMMA model in RAXML version 8.2.12 (Stamatakis, 2014), and using an undescribed sister species as an outgroup (Bringloe et al., 2021). Using the data set pruned for correlated sites (i.e., 172,554 positions analysed), nuclear SNPs were first visualized as a network, which was done by converting the VCF file to fasta format using PGDSPIDER version 2.1.1.5 (Lischer & Excoffier, 2012) before importing into SPLITSTREE version 5.2.24 (Huson & Bryant, 2006). Population structure of the nuclear genome was then visualized in ADMIXTURE plots using a combination of PLINK and ADMIXTURE version 1.3.0 (Alexander & Lange, 2011) at *k* values of 2–5. The values of *k* were evaluated based on 5-fold cross-validation error.

Several statistics were calculated for each population using the nuclear SNP data set prior to filtering for linked sites (i.e., 1,897,988 positions analysed). Population statistics included nucleotide diversity (π), Weir and Cockerham's F_{ST}, heterozygosity and minor allele frequency spectra. The R package POPGENOME version 2.7.5 (Pfeifer et al., 2014) was used to calculate π for organellar genomes, while VCFTOOLS was used to calculate heterozygosity and minor allele frequencies for the nuclear SNPs. To correct for missing data in the diversity statistics (nucleotide diversity and F_{ST}) for nuclear SNPs, we used PIXY version 1.2.6 (Korunes & Samuk, 2021) on the variant+invariant sites VCF, employing a 25-kb genomic window. Windows with fewer than 100 SNPs were discarded for plotting F_{ST} values. A fundamental assumption of our analysis is that individuals are not related, and thus for each population we presented, as heatmaps, an unadjusted genetic relationship (A_{jk}) following the calculation of Yang et al. (2010), and the kinship coefficient (Φ_{ij}) following Manichaikul et al. (2010) using VCFTOOLS. A_{jk} is 0 (or negative) for unrelated individuals, while Φ_{ij} is 0.5 (individual-self) and decays to 0 for unrelated individuals. No concerns were raised regarding relatedness of individuals, and results for relatedness are presented in Figure S5. Linkage disequilibrium was also calculated using POPDECAY version 3.40 (Zhang et al., 2018).

Populations were also scanned for exon loss and expansion using read coverage information from all samples and our genome annotations. Average read coverage for all exons was calculated using VCFTOOLS. We then calibrated read coverage for exons using average read coverage for single-copy orthologues, as these should be devoid of gene loss or expansion. We used ORTHOFINDER (Emms & Kelly, 2019) to identify single-copy orthologues in reference genomes produced from *Alaria* gametophyte samples and a single *Laminaria solidungula* J. Agardh gametophyte sample (provided by the Phaeoexplorer consortium). The single-copy orthologues identified from the ORTHOFINDER analysis were used to create a custom protein database, against which we blasted our diploid *A. esculenta* assembly to identify matches with a minimum e-value of 1e-40. We then extracted positional information for the single-copy exons based on these matches and calculated per-sample coverage using the –depth function in VCFTOOLS; average coverage across samples was ~19×. These values were used to calibrate read coverage across all exons for each sample, where 1 = expected read depth, 0 = missing exon and departures >1 indicate exon expansions/duplications; for expansions, we conservatively set a calibrated coverage threshold of 4× expected read coverage (based on coverage of single-copy orthologues). Note, because reads can map to multiple locations, Faroe Islands (i.e., location of the reference genome) was expected to display higher coverage sites, which we interpreted as potential recent gene/exon expansions. In order to differentiate gene/exon expansion from mapping artefacts (e.g., due to collapsed loci in the reference genome, repetitive protein motifs), we limited our interpretations to expansions specific to a single population, under the assumption these differences are more likely to be driven by biological processes (i.e., gene/exon duplications).

Figures for the above analyses were generated in R using GGPLOT2, ggridges and pheatmap. Scripts are available at https://github.com/tbringloe/WGS-NOVAC. Resources used to carry out the project are listed in Table S2.

3 | RESULTS

3.1 | The first draft genome of *Alaria esculenta*

Using a combination of long and short read data, the genome of *A. esculenta* was resolved as 1931 contigs sharing similar features to previously published kelp genomes (Shan et al., 2020; Ye et al., 2015). Specifically, the genome was relatively large (487.8 Mb; N50 of 1,249,706 bp), with a GC content of 50.03%, 28,969 genes with an average length of 8619 bp, with an average of 6.18 exons per gene, and high proportion of repeat regions (57.18%), of which 10% were retroelements, 0.49% were DNA transposons and 43.16% were unclassified repeats. BUSCO scores indicated our draft genome to be 83% complete, suggesting the genome size could be upwards of 587.7 Mb.

3.2 | Population genomic patterns in *Alaria*

In order to test the hypothesis that populations of the kelp *A. esculenta* persisted through the LGM in Greenlandic refugia, we analysed the genomes of 54 individuals from Atlantic Canada, Greenland, Faroe Islands, Norway and Ireland. Using a total of 1.2 TB of data and over 4.8 billion paired-end reads mapped to an annotated reference genome, variant data sets were compiled for organellar and nuclear genomes, the latter of which consisted of 1,897,988 SNPs. Organellar genomes were ~39 kb for mitochondrial and ~130 kb for chloroplast genomes, with the full complement of genes typically reported for brown algal organellar genomes (Starko, Bringloe, et al., 2021).

Regarding prediction 1 (phylogenetic differentiation), phylogenetic signal differed across genomic compartments (Figures 1 and 2). The chloroplast genomes positioned Atlantic Canadian and Greenlandic specimens as sister populations diverging 117–385 ka, while Faroe Islands specimens shared closely related haplotypes with Norwegian and Irish populations with timeframes postdating the LGM (Figure 1b). Mitochondrial genomes, meanwhile, were generally differentiated, but Greenland, Faroe Islands and Norway shared closely related haplotypes diverging 21–114 ka (Figure 1c). Nuclear SNPs revealed varying degrees of differentiation among all populations (Figure 2). Based on F_{ST} values, the Canadian Atlantic population was strongly differentiated, while Greenland, Faroe Islands, Norway and Ireland populations were moderately differentiated from one another (Figure 2a). This differentiation was reflected in the phylogenetic network, but Faroe Islands individuals assumed an intermediate position sharing SNPs with Greenlandic and Norwegian individuals (Figure 2b). ADMIXTURE plots pointed to mixed ancestry proportions in the Faroe Island population at *k*-values of 3 and 4, the latter of which was best supported by cross-validation errors. The mixed ancestry of Faroe Islands individuals was associated with Greenlandic and Norwegian individuals. At higher *k*-values, all populations were differentiated, including Nuuk and Disco Bay populations ($k = 6$; Figure 2c).

Regarding prediction 2 (population statistics), three patterns were noted. First, Canadian Atlantic and Greenlandic populations featured lower levels of nucleotide diversity, flattened minor allele frequency spectrums, a lower level of linkage disequilibrium decay, but an excess of heterozygosity relative to Faroe Islands, Norwegian and Irish populations (Figure 3). Second, the Faroe Island population featured a high level of nucleotide diversity (including the highest levels in the organellar genomes), a somewhat truncated minor allele frequency spectrum favouring higher frequency alleles, a lower level of linkage disequilibrium decay and the lowest level of heterozygosity (Figure 3). Third, Norwegian and Irish populations featured high levels of nucleotide diversity, a normal minor allele frequency spectrum favouring low-frequency alleles, the fastest and greatest decay in linkage disequilibrium, and intermediate levels of heterozygosity relative to the other populations (Figure 3).

Regarding prediction 3 (functional differentiation as proxied by exon coverage), we identified 2201 exons corresponding to 988 genes that featured differing levels of read coverage across the populations analysed (Figure 4). These genes represented a small portion of the total predicted genes, with 96.6% of genes exhibiting expected read coverage. Of the exons with differing read coverage, putatively absent or expanded exons were inferred on the basis of 0 or >4× expected coverage. The function of these genes covered a wide range of basic biological functions, including, but not limited to, carbohydrate metabolism, protein ubiquination processes and phosphorylation, transmembrane transport, peptidase activity, oxidoreductase activity, binding activity (nucleic acids, proteins, metal ions, ATP, NAD and cellulose; FigShare: https://doi.org/10.6084/m9.figshare.16712797.v1), among many other genes with unknown function. Read coverage for Atlantic Canadian populations was considerably different compared to the other populations; unique to Atlantic Canada were 416 exons from 210 genes with no read coverage, and 218 exons from 130 genes with at least 4× the expected read coverage (Figure 4). Greenlandic populations were also differentiated at the exon level; this included 19 exons in 14 genes uniquely not recorded in both Greenlandic populations, including another 24 exons in 18 genes uniquely not recorded from Nuuk, and 60 exons in 24 genes uniquely not recorded from Disco Bay (Figure 4). Greenlandic individuals exhibited a larger number of exons with higher read coverage relative to other populations; 337 exons representing 162 genes had at least 4× the expected coverage (Figure 4). These numbers were comparably lower in Irish and Norwegian populations; 205 exons representing 83 genes were not recorded exclusively in the Ireland individuals, and 96 exons representing 56 genes had 4× the expected coverage; unique to Norway, eight exons in six genes had 0 read coverage, while 17 exons in 15 genes had 4× the expected coverage (Figure 4).

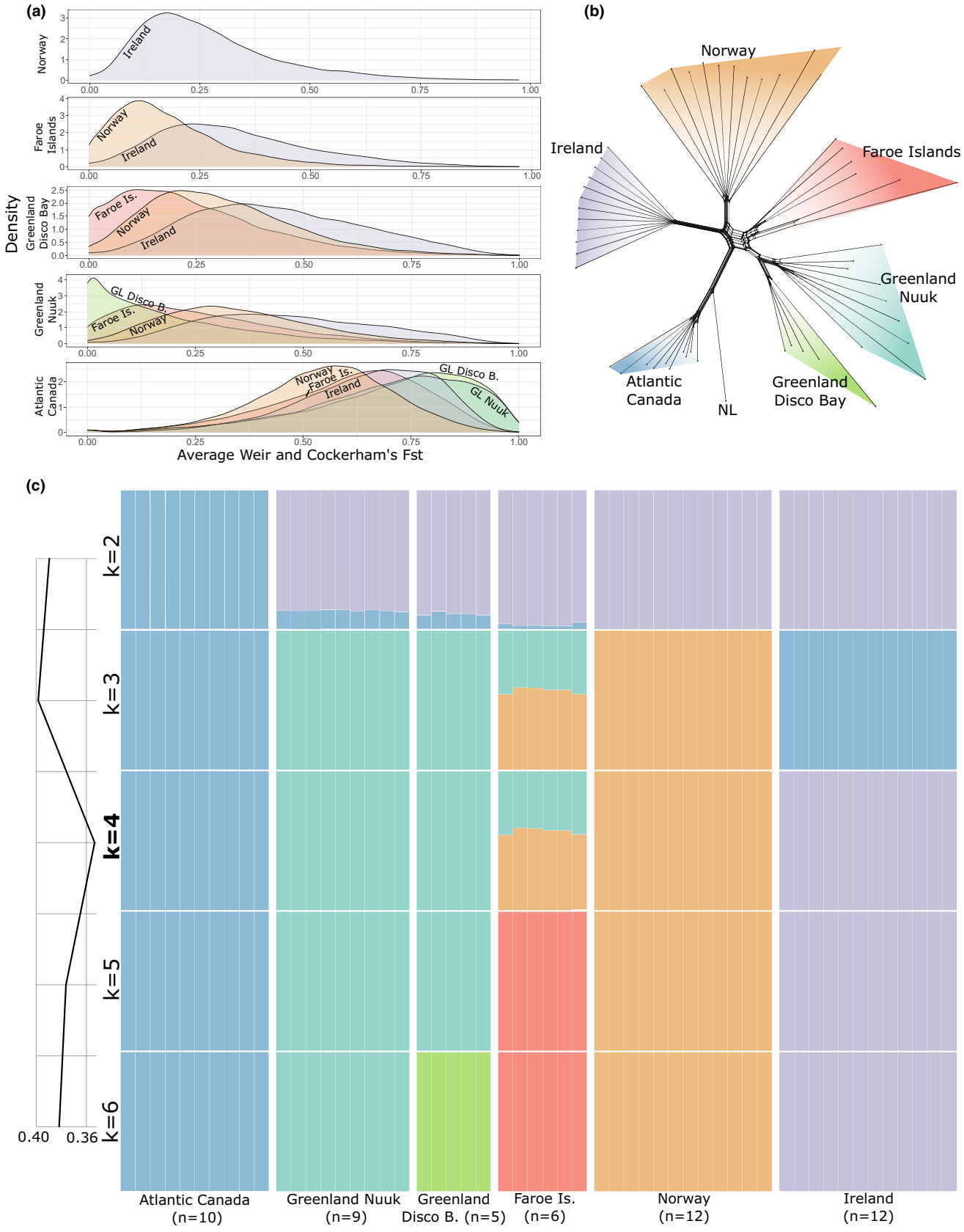

FIGURE 2 Phylogeographical structure of 172,554 unlinked nuclear SNPs in populations of *Alaria*, including (a) Weir and Cockerham's F_{ST} density plots (based on the nonsite-filtered data set, representing 203,209,555 positions), (b) phylogenetic network of uncorrected distances, and (c) ADMIXTURE plots at $k = 2$–6. The best supported value of k ($k = 4$), based on cross-validation error (depicted to the left), is in bold type. Note, for F_{ST} values (a), pairwise comparisons are between the population listed on the *y*-axis and plotted populations (colours correspond with panels b and c). Note also, Newfoundland (NL) is excluded from the ADMIXTURE analysis given $n = 1$; sample sizes also differ from Figure 1 due to filtering thresholds set for nuclear SNPs (see Methods).

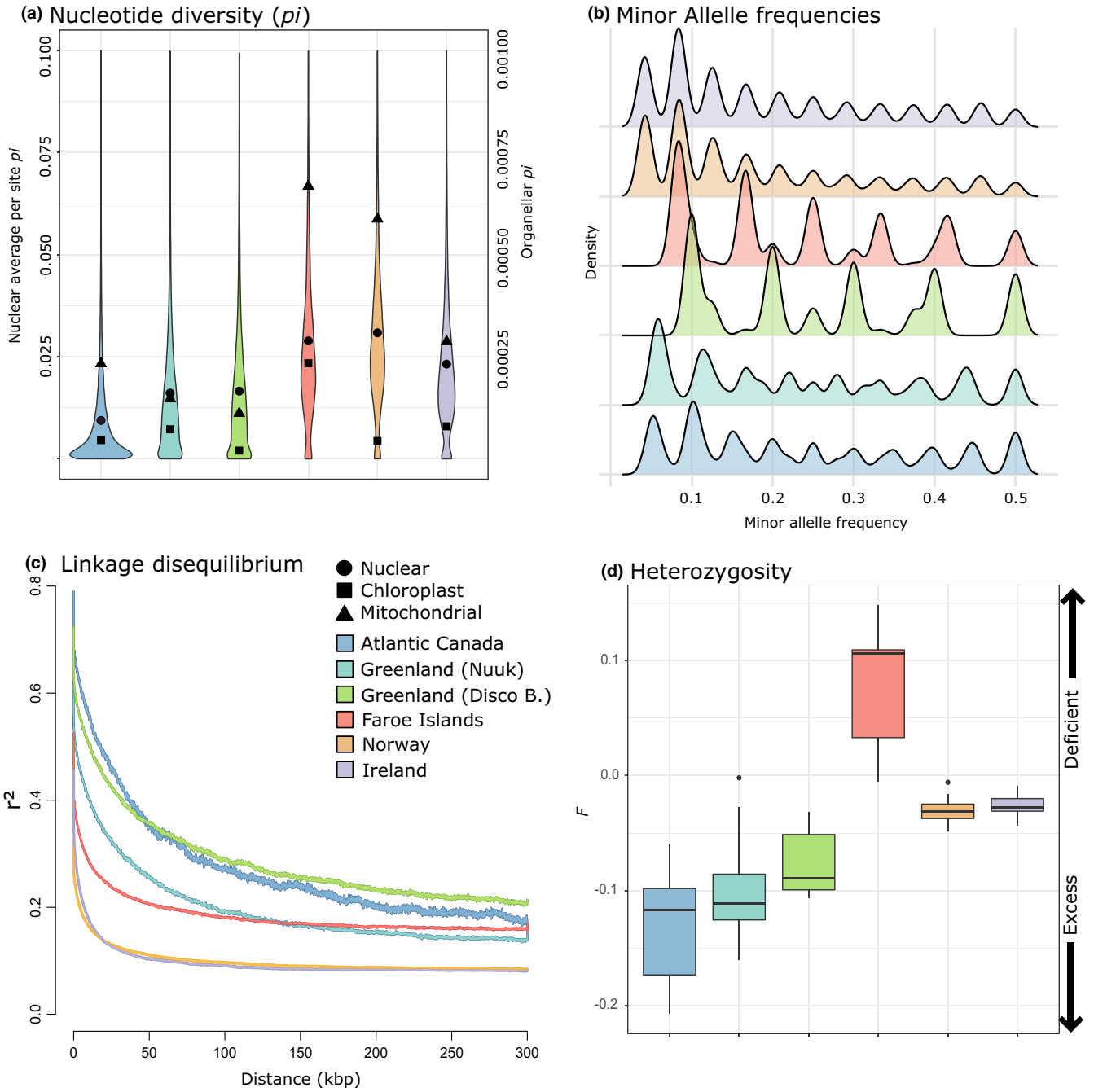

FIGURE 3 Population statistics in populations of *Alaria* based on 1,897,988 nuclear SNPs, including (a) nucleotide diversity based on 25-kb genomic windows (based on the nonsite-filtered data set, representing 203,209,555 positions), (b) minor allele frequencies, (c) linkage disequilibrium and (d) heterozygosity (*F*). Nucleotide diversity for nuclear (mean of windows), chloroplast and mitochondrial genomes are also displayed in (a).

4 | DISCUSSION

Phylogeographical investigations of North Atlantic marine coastal populations have improved considerably since hypotheses of refugial origins were forwarded several decades ago (e.g., Ingolfsson, 1992). Recently, the kelp *Alaria esculenta* was hypothesized to have survived the LGM in southern Greenland (Assis et al., 2018; Figure 1a), a putative refugial location for other coastal species (Bringloe, Verbruggen, & Saunders, 2020). Here, we tested this hypothesis using WGS data sets. Our results supported the view that populations have persisted through cycles of glaciation at high latitudes, including Greenland and Norway, and further revealed populations have recently admixed in the mid-Atlantic (i.e., Faroe Islands). Not only were populations genetically differentiated, but the underlying genomes also showcased functional differentiation, as evidenced by missing or expanded exons/genes. The insights from this study are a considerable improvement on current genetic data sets for *A. esculenta*; previous studies resolved <10 SNPs from standard DNA

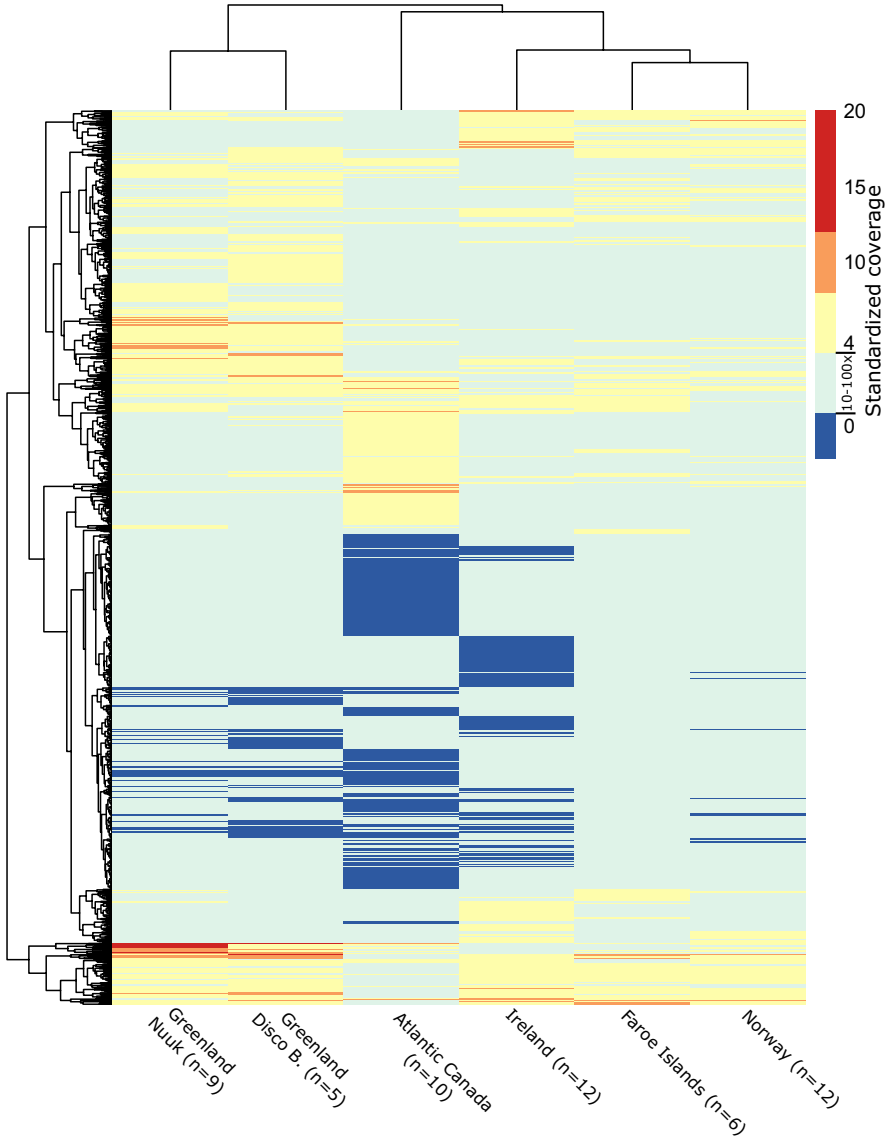

FIGURE 4 Average standardized read coverage for exons in *Alaria esculenta*. Only exons with standardized coverage of 0 or >4 in at least one population are depicted (2200/167,154). A value of 1 indicates expected coverage based on average coverage of single-copy orthologues (see Methods). The dendograms correspond to clustering based on heatmap functions in R. Note, the reference genome used for mapping was derived from a Faroe Islands individual.

barcode markers (Bringloe & Saunders, 2018; Bringloe, Verbruggen, & Saunders, 2020), whereas here we have resolved ~1.9 million SNPs from nuclear and organellar genomes. As such, our work also showcases the power of WGS to resolve previously intractable details about phylogeographical history, and serves as a template for further genomic investigations of marine populations.

4.1 | Genomic patterns confirm high-latitude refugia

The hypothesis of high-latitude glacial refugia in southwest Greenland was supported by WGS data. Put differently, we rejected the null hypothesis that this area was recolonized within the past 20 ka. Our first prediction of the null hypothesis, that Greenlandic populations would be weakly differentiated from potential source populations in the Northwest or Northeast Atlantic, was generally not supported by the phylogenetic results. The chloroplast genomes of Greenlandic populations were highly differentiated, corresponding to 117–385 ka of divergence from its sister Canadian Atlantic population (Figure 1b). The mitochondrial genomes provided a different perspective, with recent shared ancestry among Greenland, Faroe Island and Norwegian populations potentially postdating the LGM (Figure 1c). This pattern pointed to some recent migration across the Atlantic in *A. esculenta*, but did not offer much insight into the direction of migration. Noteworthy, however, was the scattered phylogenetic signal of the Faroe Islands population, with haplotypes grouping with Norway and Ireland in the chloroplast phylogeny, and haplotypes grouping with Greenland/Norway and Ireland populations in the mitochondrial phylogeny (Figure 1b,c). These patterns suggested the Faroe Island population either seeded the other populations, or was recently established from several distinct populations consistent with evidence of admixture (Figure 2c). Also noteworthy were the differing topologies of the organellar genomes, which are the basis for most of our current phylogenetic and population genetic understanding (Bringloe, Verbruggen, & Saunders, 2020; Maggs et al., 2008; Neiva et al., 2018). The resolution and comprehensive nature of WGS serves as a reminder that

true population history is often obscured by uniparental inheritance, and that larger scale nuclear SNP data sets are needed to make sense of conflicting patterns presented by organellar genomes (e.g., Bringloe et al., 2021).

The nuclear SNP data sets revealed the source of incongruent patterns in the organellar phylogenies. The phylogenetic network and ADMIXTURE plots of nuclear variants confirmed historical mixing in the Faroe Islands population, with ancestry derived from lineages associated with Greenlandic and Norwegian populations (Figure 2b,c), and Irish populations to some extent, given the organellar phylogenetic results (Figure 1b,c). This result is among our strongest pieces of evidence supporting the presence of high-latitude refugia in the area of Greenland during the LGM, as the occurrence of two phylogenetically distinct migration vectors meeting midway in the Atlantic would not be possible otherwise. It could be argued that Canadian Atlantic populations seeded the Greenlandic populations before this migration vector continued its journey to the Faroe Islands. F_{ST} values, however, indicated the Canadian Atlantic populations are highly differentiated relative to the other sampled populations (Figure 2a), with the Greenlandic and European populations moderately differentiated, ruling out Atlantic Canada as a recent source for the establishment of Greenlandic populations. Furthermore, the time calibration results indicated that divergence in the Atlantic Canadian and Greenlandic populations exceed the timeframe of the LGM (Figure 1b,c). These results support many genetic studies that showcase trans-Atlantic differentiation of populations pre-dating the LGM (e.g., Bringloe & Saunders, 2018; Li et al., 2015; Maggs et al., 2008; Neiva et al., 2018; Wares & Cunningham, 2001), highlighting the unique history of Northwest Atlantic populations. It is worth noting, however, that Greenlandic populations probably interacted with Atlantic Canadian populations early in their evolution, as evidenced by the ADMIXTURE results at $k = 2$ and the conflicting organellar phylogenies; it is possible the chloroplast genome of Atlantic Canadian populations introgressed into the Greenlandic populations, which continued to maintain a mitochondrial genome more closely aligned with European populations. Reconciling the exact series of events will require further geographical sampling of populations.

4.2 | Kelp genomes reflect differences in the severity of glacial conditions throughout the North Atlantic

Our second prediction followed the logic outlined by Peter and Slatkin (2013), who state that range expansions leave several signatures in newly colonized areas, namely low nucleotide diversity, low levels of heterozygosity, high levels of linkage disequilibrium, and a cline in minor allele frequencies relative to potential source populations (see also Alachiotis & Pavlidis, 2018; Koropoulis et al., 2020). Our results were somewhat conflicting in this regard. Our first observation was that Canadian Atlantic and Greenlandic populations featured lower levels of nucleotide diversity, flattened minor allele frequency spectrums and a lower level of linkage disequilibrium decay, which suggested these areas have been recently recolonized. The excess of heterozygosity relative to Faroe Islands, Norwegian and Irish populations, however, provided contradictory evidence (Figure 3). Given the phylogenetic results (see above), we interpreted that these patterns reflect harsh glacial conditions that probably reduced these populations to small effective population sizes during the LGM, pockets of refugia that differentiated and admixed locally following glaciation. Our results therefore substantiate the idea that glaciation was harsh for marine macrophytes in the Northwest Atlantic and at high latitudes surrounding Greenland (Figure 1a), but reject the view that glaciation conditions entirely extirpated populations from these areas (Ingolfsson, 1992; Maggs et al., 2008; Wares & Cunningham, 2001).

We also observed that the Faroe Island population featured a high level of nucleotide diversity (including the highest levels in the organellar genomes), a somewhat truncated minor allele frequency spectrum favouring higher frequency alleles, a lower level of linkage disequilibrium decay and the lowest level of heterozygosity. These results also seemed somewhat contradictory, however, the phylogenetic results clearly demonstrated that Faroe Island populations are a clash of two phylogenetically distinct parental populations. Given this scenario, nucleotide diversity is expected to be high (as both parental genomes are represented in Faroe Island individuals). If the merger of populations on Faroe Islands is recent, potentially since the LGM as suggested by the time calibration analyses (Figure 1b,c), then we would expect the other observed patterns, namely minor allele frequencies to favour higher frequency alleles, higher levels of linkage disequilibrium and reduced heterozygosity. Given admixture between distinct populations, lower levels of heterozygosity must also be reconciled. If the Faroe Islands population was established from a small set of individuals, as expected of kelp dispersal, then inbreeding or selfing is likely to have been high initially. If true, high levels of nucleotide diversity would have been segregated into homozygous alleles, leading to the patterns observed in our data sets. Overall, the population patterns support our view that Faroe Islands individuals were established following the last glaciation.

Our third observation was that Norwegian and Irish populations exhibited patterns consistent with long-term persistence at large effective population sizes, namely high levels of nucleotide diversity, minor allele frequencies favouring low-frequency alleles, rapid decay of linkage disequilibrium and nondivergent levels of heterozygosity. While survival in southern European refugia (i.e., near Ireland) is not surprising, genetic and modelling work has yet to forward northern Norway as a refugial location for coastal populations during the LGM (e.g., Assis et al., 2018; Bringloe, Verbruggen, & Saunders, 2020). It is possible that large populations were contiguous throughout Europe during the LGM (Figure 1a), with differentiation between north and south populations through cycles of glaciation. Differentiation in northern European kelp populations has also been reported for *Saccharina latissima* (Linnaeus) C. E. Lane, C. Mayes, Druehl & G. W. Saunders (Guzinski et al., 2020). Overall, these results point

to recent glacial conditions that were less severe in the Northeast Atlantic relative to the North (i.e., Greenland) and Northwest (i.e., Atlantic Canada).

4.3 | Functional differentiation in Greenlandic populations

Our third prediction of the null hypothesis was that Greenlandic populations will be functionally similar to potential source populations, as evidenced by consistent levels of read coverage for exon regions. Here, we interpret zero and high (4×+) coverage exons as loss or duplication events, respectively, unique to specific populations, which are potentially driven by functional benefits of reducing or augmenting the number of gene copies in the underlying genome. Analogous interpretations were presented by Iha et al. (2021); the genome of the endolithic green alga *Ostreobium* lacks several genes for photoprotection and photoreceptors, but has expanded light harvesting complex genes, which the authors attributed to adaptations to a low-light environment. Here, our results showcased considerable differences among populations regarding exon coverage, including a high number of putative expansions in the Greenlandic populations. Interestingly, the two populations sampled from Greenland also differed in exon coverage (Figure 4), suggesting they may be derived from separate refugia. Assis et al. (2018) forward two areas of long-term persistence for *A. esculenta* in Greenland, which roughly corresponded to the areas sampled here (Figure 1a). Some exon expansions in the Nuuk population were especially notable (Figure 4), greatly exceeding read coverage in the other populations (including Disco Bay). While most of the genes were *Ectocarpus* orthologues of unknown function, genes with functional information were related to ADP binding and kinesin complexes, and methyltranferases (note, data tables with read coverage and associated functional annotations are available via FigShare: https://doi.org/10.6084/m9.figshare.16712797.v1). Among the expanded genes unique to the Greenlandic populations was an uncharacterized *Ectocarpus* orthologue linked to PC-Esterase (InterPro: IPR026057), which includes cold acclimation regulator proteins such as ESK1 described from *Arabidopsis* (Xin et al., 2007).

In contrast, missing exons were prominent in the lower latitude populations, including Atlantic Canada and Ireland. In particular, Atlantic Canadian individuals had missing exons related to metallopeptidase activity, microtubule motor activity, protein deubiquination, DNA repair and a heat shock protein, while Irish individuals had missing exons related to carbohydrate biosynthesis, glycosyltransferase activity, transmembrane transport and manganese ion binding. Any patterns regarding functions specifically gained or lost in these populations are purely speculative at the moment; besides needing a more comprehensive formal analysis, the function of many genes will remain biased towards housekeeping genes or otherwise unknown for the time being. Nonetheless, functional differentiation of populations will be an exciting avenue to explore for future work, and potentially highly relevant for predicting climate change responses (Bringloe et al., 2022) and informing global kelp/marine forest restoration strategies (Coleman et al., 2020).

Several studies hint at the possibility that species and populations are adapted to high-latitude conditions. Transcriptomic profiles in the kelp *Saccharina latissima* are markedly different between Arctic and temperate populations, with notable differences in gene expression for cell wall adjustments (Monteiro et al., 2019). Differences in biochemical compositions in response to temperature and partial pressure of CO_2 have also been reported between Arctic and temperate populations (Olischläger et al., 2014), with Arctic populations potentially better adapted for projected climate change (Olischläger et al., 2017). Modest differences in the timing and magnitude of thermal stress responses were recorded in cold and warm range edge populations of *Laminaria digitata* (Hudson) J. V. Lamouroux (Liesner et al., 2020). The Arctic kelp *Laminaria solidungula* completes most of its annual growth under ice cover (Chapman & Lindley, 1981; Dunton & Schell, 1986), and species distribution modelling also indicates that ice cover best predicts global ranges in species with distributions restricted to the Arctic basin (Bringloe et al., 2022; Goldsmit et al., 2021). In contrast, *A. esculenta* cultures from Svalbard have reduced reproductive success under continuous light regimes (Martins et al., 2022), which speaks to the pressures of adapting phenology to high-latitude conditions. The high number of exon/gene expansions detected in the Greenlandic populations potentially reflects a history of augmented evolutionary pressures, tailoring these populations to the polar environment (Figure 4). Note, however, the same level of functional differentiation was not observed in the Norwegian population, which assumed approximately the same latitude as the Greenlandic populations but does experience considerably higher temperature regimes owing to the Gulf Current. Nonetheless, adaptations to the polar environment, which are made possible when populations persist at high latitudes over evolutionary timescales (as inferred here), are an interesting prospect. There is no knowledge of the genomic features that allow some species of seaweed to flourish in the Arctic where others cannot, and as far as we know, there are no studies confirming whether potential adaptions to polar environments are reflected in the underlying genomes of Arctic seaweeds.

Several caveats of our exon analysis warrant mentioning. Coverage information was inferred relative to the reference genome derived from a Faroe Islands individual. As such, we cannot necessarily differentiate whether an exon was lost in one population or gained in the other(s). Annotated reference genomes from all populations of interest, along with ancestral information from a closely related species (i.e., Arctic *Alaria*; Bringloe et al., 2021), will be needed to ascertain the exact chain of events leading to contemporary exon/gene content. Moreover, read coverage was dependent, in part, on mapping thresholds set in our workflow (Figure S4), meaning that reads from highly divergent genes would not have mapped to our reference genome, and would have appeared as missing or lost exons in our analysis; the "missing" exons reported here may equally represent pseudogenization or advanced sequence evolution retaining some function. As

such, prediction 3 (functional differentiation), as outlined in the Introduction, is not independent of prediction 1 (population nucleotide differentiation). This issue would similarly be resolved by assembling genomes from the populations of interest. On a final note, we predicted >28,000 genes in the reference genome for *A. esculenta*, while putative loss or expansion of exons were limited to at most 218 genes for any given population, and 988 genes overall. It is worth considering quantitatively how differentiated these populations are from one another when 96.6% of the genes appeared to be stable across all sampled individuals.

5 | CONCLUSIONS

Here, we have tested the hypothesis that *A. esculenta* survived in southern Greenland during the LGM, a hypothesis initially forwarded by modelling (Assis et al., 2018) and DNA barcoding surveys (Bringloe, Verbruggen, & Saunders, 2020). Our genomic data supported this hypothesis. The dynamic scenario of survival, ancient mixing and potential functional differentiation across Atlantic populations presented here represents a substantial shift from simple recolonization hypotheses, and absolves the persistent view that marine coastal populations were unable to survive recent periods of glaciation. Our work also pushes the field of marine phylogeography forward by upscaling the resolution of genetic data sets, by incorporating functional genomic information to better understand potential biological differences among populations, and by synthesizing interpretations across fully resolved genomic compartments, thereby increasing the tractability and confidence with which past events can be inferred. Among the next steps are to broaden the geographical scope of the data sets presented here; dimensions in the SNP data set came at the expense of sequencing fewer individuals, a gap that will hopefully be filled in future work. Another potential next step will be to utilize this information to assess the resilience of marine populations to anticipated environmental changes, and determine how best to mitigate losses. Comparative genomic analyses, within the context of both whole genomes and gene expression profiles, will therefore continue to be an invaluable asset for understanding past and modern pressures driving evolution in marine coastal populations of the Atlantic.

AUTHOR CONTRIBUTIONS

Trevor T. Bringloe, Heroen Verbruggen, Antoine Fort and Ronan Sulpice conceived the study; Agnes Mols-Mortensen, Cliodhna Ní Ghriofa, Karen Filbee-Dexter, Dorte Krause-Jensen, Birgit Olesen, Christophe Vieira, Hiroshi Kawai and Takeaki Hanyuda provided specimens; Trevor T. Bringloe, Antoine Fort, Masami Inaba, Ronan Sulpice, Christophe Vieira, Hiroshi Kawai and Takeaki Hanyuda generated the sequence data; Trevor T. Bringloe, Antoine Fort, and Samuel Starko conducted the analysis; Trevor T. Bringloe and Antoine Fort wrote the manuscript; Ronan Sulpice, Agnes Mols-Mortensen, Cliodhna Ní Ghriofa, Karen Filbee-Dexter, Dorte Krause-Jensen, Birgit Olesen, Christophe Vieira, Hiroshi Kawai, Takeaki Hanyuda, Samuel Starko, and Heroen Verbruggen edited the manuscript.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

Raw sequencing reads were deposited through the National Center for Biotechnology Information database under the BioProject accession code PRJNA675898. Assembled and annotated organellar

genomes are deposited on GenBank, with accessions provided in Table S1. The *A. esculenta* genome and annotations, and a table of standardized exon coverage, are deposited on FigShare: https://doi.org/10.6084/m9.figshare.16712797.v1. Command line arguments for population genomic analyses are available on github: https://github.com/tbringloe/WGS-NOVAC.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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