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Human-Mediated Dispersal Routes Structure Sahara Mustard Genomics

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ABSTRACT

Humans have facilitated the spread and evolution of invasive species, a pattern that has accelerated with the globalisation of trade and societal development. Consequently, the invasiveness of a species may be determined not only by how many propagules and which genotypes are introduced, but also by its evolutionary history and how humans have interacted with it. Here, we document the population structure and movement of Sahara mustard (*Brassica tournefortii*) within its native range and its invaded U.S. and Australian ranges. We evaluated 312 individuals spanning 31 sites. We found that Sahara mustard has likely undergone substantial mixing within its native range, with genotypes from Egypt potentially representing a human-created connection between North African, European and West Asian genotypes. Our results suggest Egypt—and perhaps closely related populations in Morocco and France—as the likely origin of invasive U.S. populations. Australian accessions appear most closely related to those from Qatar and may have acted as a bridgehead and potential source of the most-recently introduced U.S. population. Further, agricultural varieties from Pakistan and India represent a mix of genotypes from the western part of the species' native range and the eastern site in Qatar. We also identified evidence of mixing of some accessions of crop wild relatives. Nearly all populations sampled display excess heterozygosity and negative inbreeding coefficients, likely indicative of selection and potential admixture with other cultivated *Brassica* species. Overall, we reconstructed the probable invasion history of Sahara mustard, inferring significant human-mediated movement of the species within and beyond its native distribution.

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1 | Introduction

Invasive species have been transplanted around the world intentionally and unintentionally with increasing globalisation (Hobbs and Mooney 2005; Hulme 2009). The resulting economic and ecological damages (Pimentel et al. 2000; Bradshaw et al. 2016; IPBES 2023) further constrain already limited resources to control and manage undesirable outcomes (e.g., Wittenberg and Cock 2005). At the same time, invasion opportunities are increasing as native ecosystems are modified by human and agricultural development (Sax and Brown 2000; McNeely 2006) and impacted by climate change (e.g., Merow et al. 2017; Shabani et al. 2020). As a result, land managers face significant challenges in responding to existing and newly introduced invasives. Identifying the origin(s) and transport pathways of invasive populations is oftentimes the critical first step for developing effective approaches to species control (e.g., Lodge et al. 2006; Mehta et al. 2007; Estoup and Guillemaud 2010). Land managers require targeted, accessible, and relevant information to develop solutions needed to effectively mitigate negative ecological impacts from invasives (e.g., Beaury et al. 2020). Reconstructing invasion routes also contributes to understanding the interaction of environmental and evolutionary factors that may enable the success of invasive species (Kolar and Lodge 2001; Beer et al. 2024; Liu et al. 2025).

Classical genetic theory predicts that founding events deplete genetic variation in invading populations, leading to lower genetic diversity compared to native range populations (Nei et al. 1975; Barrett et al. 2008). While some invasives exhibit this pattern (e.g., Ciosi et al. 2008), others have shown unexpected increases in genetic variation and competitive ability owing to forces including admixture and outcrossing (e.g., Barker et al. 2019; Smith et al. 2020), selection and local adaptation (e.g., Stuart et al. 2021), and polyploidization (Mandáková et al. 2019; Cheng et al. 2020), among other genetic effects (C. E. Lee 2002). Additional studies show some invasives maintain genetic diversity levels similar to their native range, suggesting that existing genetic diversity partly determines invasiveness (e.g., Kang et al. 2007). Outcrossing is another evolutionary process that can elevate genetic diversity in populations. For example, agricultural varieties often hybridise with their wild relatives (termed Crop Wild Relatives, CWRs), introducing novel genetic variation into CWR populations (Ellstrand et al. 2010; Turcotte et al. 2017). As a result, human agricultural practices can unintentionally modify wild plant genomes, increasing genetic variation within CWR populations (Mitton 1998; Pujol et al. 2005; Mittell et al. 2020) and potentially conferring an evolutionarily competitive advantage that enhances invasiveness (Ridley and Ellstrand 2009; Vigueira et al. 2013). Compared to Earth's long history, human activities can rapidly break down dispersal barriers for invasive species, potentially leading to increased gene flow that reduces genetic differentiation and homogenises native and source populations (Zarlenga et al. 2014; Campbell et al. 2016; Cristescu 2016; Arredondo et al. 2018; Östergren et al. 2021). Characterising genetic diversity across native and introduced ranges is an important first step in uncovering invasion mechanisms, a method that can reveal insights into the precise interaction among these different evolutionary forces.

The introduction and subsequent spread of an invasive species commonly results from a small number of propagules that arrive once, or on multiple occasions, to a novel environment (Lockwood et al. 2005; Cristescu 2016). High propagule pressure and multiple introductions can facilitate invasive species establishment by preventing genetic bottlenecks (e.g., Rosenthal et al. 2008; Vavassori et al. 2022), ensuring sufficient diversity for the evolution of traits selected in new environments (e.g., Sun and Roderick 2019), and enabling invasive species to outcompete native taxa (e.g., Holle and Simberloff 2005). Subsequent invasion processes such as bridgehead events—whereby already established invasive populations are introduced to new locations—may further enhance invasive success by increasing standing genetic diversity in the new range (Lombaert et al. 2010; Barker et al. 2017; but see Bertelsmeier and Keller 2018). These various genetic and demographic phenomena are likely to act in tandem to determine invasive potential, and their interaction may accelerate invasion when repeated introductions combine with divergence through mixing or mutation.

Sahara mustard (*Brassica tournefortii* Gouan) has been introduced to the United States (U.S.) and Australia, causing negative impacts on agricultural and protected native systems over the past century (Florin 2024). The species has continued to expand its range in the U.S. and Australia, and more recently invaded systems in Chile, New Zealand, South Africa, and South Korea (De Villiers et al. 2003; Heenan et al. 2004; Teillier et al. 2014; Kang et al. 2022). Recent distribution models suggest the species has high potential to further expand its range in North America (Rodriguez et al. 2024). Sahara mustard is thought to be native to northern Africa, southern Europe, and western Asia where, in some regions, it is an important historic agricultural crop and is still wild-collected for use in traditional cuisines (Rivera et al. 2006; Singh et al. 2015). It is an annual species that typically germinates earlier than native species within its invaded range, exhibits trait plasticity across distinct environments, and possesses chemical defences to defend itself from herbivory (Horn and Vaughan 1983; Winkler et al. 2018; Tlili et al. 2022; Alfaro and Marshall 2023). Diversity and abundance of native plant and animal communities have declined in invaded areas because of its exceptional competitive ability (Esque and Schwalbe 2002; Marushia et al. 2010; Schneider and Allen 2012; Hulton VanTassel et al. 2014).

Previous work has shown that Sahara mustard was introduced multiple times in the U.S. and exists as three genetically distinct populations, two of which are known from only one or a few localities across the southwest U.S. (Winkler et al. 2019). Since the native origins of these populations are unknown, identification and testing of potential biological control methods have been limited (Hajek and Eilenberg 2018). This further complicates management of this species, which is known to be resistant to common herbicides (Boutsalis et al. 1999). The species was purportedly introduced as a contaminant of date palm (*Phoenix dactylifera* L.) agricultural imports (Sanders and Minnich 2000; USDA 2021). This contaminant hypothesis is supported by two key observations: First, the earliest observations of Sahara mustard in both the U.S. and Australia coincide with the historical development of modern agriculture in arid regions. For example, the earliest U.S. record is from 1927 near Palm Springs in California's Coachella Valley, a center of date palm cultivation. Second, Sahara mustard and date palm co-occur across much of their native ranges. Given that date palm shows substantial genetic evidence of admixture throughout its cultivated native range (Hazzouri et al. 2015; Gros-Balthazard et al. 2018; Flowers et al. 2019), it is plausible that Sahara mustard exhibits similar genetic patterns if it coevolved or hitchhiked with date palm during its historical selection and movement (e.g., Drew et al. 2010; Faria and Kitahara 2020).

In this study, we reconstruct the dispersal routes of Sahara mustard from its native range into the U.S. and Australia using population genetic analyses of a genome-wide single nucleotide polymorphism (SNP) dataset. We first assessed the population structure of the species across much of its native range and contemporary invaded U.S. and Australian ranges. We tested three key hypotheses: First, the native range of Sahara mustard exhibits genetic population structures indicative of admixture and gene flow, consistent with the influence of human activities such as historical trade routes. Second, geographically distinct invasive populations of Sahara mustard are genetically derived from multiple native range populations, supporting a scenario of multiple dispersal events via agricultural trade pathways. Third, agricultural varieties of Sahara mustard and wild populations influenced by cultivation or trade exhibit genetic signatures of human-mediated mixing and selection, particularly elevated heterozygosity which is hypothesised to contribute to invasive success. Overall, we reconstructed the invasion history of the species and described the likely pathways of spread across multiple continents over more than a century, while inferring the likely human-mediated movement of the species within its native range.

2 | Methods

2.1 | Species

Sahara mustard (Brassicaceae: *Brassica tournefortii*) is a facultative autogamous (i.e., primarily self-fertilising but with the potential to outcross) diploid annual native to southern Europe, northern Africa, and western Asia (Aldhebiani and Howladar 2013; Prain 1898; Thanos et al. 1991). It is an agricultural pest in parts of its native range (Ahmed et al. 2015; El-Saied et al. 2015; Salisbury et al. 2018), but it is also cultivated for traditional dietary uses with localised economic value (Guarrera and Savo 2016; Singh et al. 2015). Sahara mustard is a prolific invasive weed throughout seasonally dry regions of Australia (Chauhan et al. 2006), South Africa (McGeocha et al. 2009), Chile (Teillier et al. 2014), and western North America (Li et al. 2015). Its genome is approximately 791 Mbp (Arumuganathan and Earle 1991) and, although it may be most closely related to *B. rapa* (Kumar et al. 2015), it has also been shown to be divergent from most other species in the *Brassica* lineage (Pradhan et al. 1992; Li et al. 2011).

After its introduction, Sahara mustard historically remained confined to the Coachella and Imperial Valleys of the Sonoran and Mojave Deserts, where it established locally (Musil 1948, 1950; Robbins et al. 1951). It appeared to have spread rapidly throughout the southwest U.S. in the 1980s (Sanders and Minnich 2000), which suggests a potential lag phase prior to range expansion; however, corrected observational data suggested linear expansion over time throughout the southwest U.S. (Winkler et al. 2019).

2.2 | Sample Collection

We sampled multiple individuals in four distinct manners. First, we sampled 7–20 individuals each from 52 locations in the invaded U.S. range and 15 individuals from one location in the invaded Australian range (hereafter 'invaded range'; 775 individuals total; Figure S1 and Table S1; Winkler et al. 2019). Second, we sampled 5–28 individuals each from 16 locations in the native range (hereafter 'native range'; 207 individuals total), including from Egypt, France, Israel, Italy, Morocco, Turkey and Qatar (Table S1). Third, we obtained an additional 11 historical invasion samples from herbaria at the New York Botanical Garden, Rancho Santa Ana Botanic Garden, San Diego State University, and the University of Arizona (hereafter 'historical invasion'; Table S2). Finally, we sampled germinated agricultural seeds sourced from the United States Department of Agriculture's Germplasm Resources Information Network, including 27 samples from India, Israel, France, Morocco, Pakistan and Spain (hereafter 'agricultural varieties'; Table S3).

2.3 | DNA Extraction

We preserved samples by desiccation in silica gel prior to DNA extraction. We extracted DNA from 1020 individuals using QIAGEN DNeasy Plant Mini Kits (Qiagen). We estimated DNA concentrations via fluorometry (Qubit 2.0 Fluorometer, Invitrogen, Life Technologies) and tested DNA quality for a subset of samples via 1% agarose gel electrophoresis. We generated single nucleotide polymorphism (SNP) data via nextRAD (Nextera-tagmented reductively amplified DNA) sequencing after libraries were prepared and sequenced by SNPsaurus LLC (Russello et al. 2015). NextRAD uses short oligonucleotide primers to amplify arbitrary loci across genomic samples. Primers were integrated into the Nextera library preparation protocol (Illumina Inc), which ligates short adapter sequences to the ends of the DNA fragments. DNA fragments with one of the primers matching the adapter sequence were then amplified, and pooled samples were barcoded before being purified and size selected to 350–500 bp. Multiplexed segments were sequenced on an Illumina HiSeq2000 platform (Genomics Core Facility, University of Oregon) producing 100 bp single read lengths.

As in Winkler et al. (2019), sequence data were processed by SNPsaurus using Trimmomatic software (Bolger et al. 2014) to remove adapter sequences and sequences less than 50 bp. Sequences were then quality-filtered using the program *process_radtags* in STACKS (Catchen et al. 2011, 2013). We retained sequences with 15–2500× coverage that were present in at least 10% of samples. This excludes low-coverage sequences that have low read confidence, and high-coverage sequences, which can include artefacts such as mapping from paralogs. To remove potential paralogs, we removed loci with more than two alleles in a sample in more than 5% of a sampling locality (Hare 2001; Russello et al. 2015). We then mapped sequences to a de novo reference pseudo-genome created using reads across the combined set of samples using BBmap v.35.40 (http://sourceforge.net/projects/bbmap; *sensu* Russello et al. 2015). We then took 1000 reads randomly from each sample and compared them to known sequences in the NCBI database via BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to test for contamination from species other than Sahara mustard, using default parameters. No plausible contamination was detected in the test reads (Appendix S1).

We performed data processing in Python 3.12 and analyses in R 4.3.3 (R Core Team 2022). We selected a representative subset of samples from the contemporary invaded U.S. populations to represent the population structure presented in Winkler et al. (2019). This subset of invaded U.S. samples included individuals from each of the three genetically distinct Sahara mustard populations identified in Winkler et al. (2019), including samples from a distinct population in Nipomo, California (hereafter, Nipomo, CA); a distinct population in Palm Springs, California showing admixture with individuals from Parker, Arizona (hereafter, Palm Springs, CA + Arizona); and representatives from a large population originating in Malibu, California with individuals also in Texas, and Utah (hereafter, Malibu, CA + Texas + Utah). In each case, we included all samples from the site nearest the centroid of each population identified in Winkler et al. (2019). We filtered this representative subset with PLINK 2.0 to exclude SNPs that significantly departed from Hardy–Weinberg equilibrium at $p < 1 \times 10^{-50}$ and with a minor allele frequency ≥1%. We performed linkage disequilibrium pruning with a 50 variant window, step size of 10 variants, and $r^2 > 0.2$ threshold. Our final data subset included 284 individuals with 1258 SNPs across 188 native, 82 U.S., and 14 Australian samples. We added agricultural variety samples and historical invasive samples and reran the above filtering step for analyses that included these samples, resulting in 26 agricultural variety samples and 2 historical invasive samples for a total of 312 individuals and 1159 SNPs.

2.4 | Population Structure

We used the *snmf* function in the 'LEA' 3.14.0 package (Frichot and François 2015) to estimate ancestry coefficients across the sampled ranges of Sahara mustard. This approach is similar to the Bayesian clustering program Structure but instead uses a sparse non-negative matrix factorization algorithm to facilitate working with large datasets. We identified the optimal number of ancestral populations (K) based on the lowest cross-entropy criterion value identified from 1 to 20, with 100 repetitions for each K tested. We then assessed genetic structure of native, contemporary invaded, historical invaded, and agricultural variety samples with a Discriminant Analysis of Principal Components (DAPC) implemented in the 'adegenet' 2.1.11 package (Jombart 2008). DAPC is a useful tool to understand potentially complicated systems as it makes few assumptions of underlying population genetic processes (e.g., linkage disequilibrium, Hardy–Weinberg equilibrium; Mittell et al. 2020). We selected the optimal number of discriminant functions for analyses by comparing the BIC values of successive K-means with clusters from 2 to 40 for the native range samples. We then performed cross validation to determine the ideal number of principal components to include in our final model (*sensu* Jombart et al. 2010). We selected the number of PC axes that produced the highest proportion of successful predictions after 1000 repetitions (Figure S2).

We also tested the correspondence of genetic relatedness inferred from principal components analysis to the geography of the sampled native range using the *dubi.pca* and *procrustes* functions in the 'ade4' 1.7.23 and 'MCMCpack' 1.7.1 packages (Dray and Dufour 2007; Martin et al. 2011). This approach projects the first two principal components in relation to their geographic location. Next, we constructed an unrooted distance tree using maximum likelihood in the 'phangorn' 2.12.1 package (Schliep 2011) to graphically illustrate genetic relationships among native, contemporary invaded, historical invaded, and agricultural variety samples. We identified the best substitution model, GTR + G(4), by AICc using *modelTest*. We performed maximum likelihood optimization of model parameters and branch lengths under the selected model using the *pml_bb* function and ran 1000 bootstrap replicates to assess topologies.

2.5 | Genetic Diversity

We calculated genetic diversity indices for each locality using the 'hierfstat' 0.5.11 package (Goudet 2005), including mean observed heterozygosity (H_O), mean within population gene diversity (H_S), overall gene diversity (H_T), and inbreeding coefficients (F_{IS}). F_{IS} coefficients were calculated in 'hiefstat' following Nei (1987). We then calculated pairwise F_{ST} coefficients for each pair of sampling sites including those in the native range, invaded ranges, and agricultural varieties following Weir and Cockerham (1984) using 'hiefstat'. Pairwise F_{ST} coefficients for native and invaded range sites were visualised using the *heatmap* function in R.

3 | Results

3.1 | Population Structure

Ancestry coefficients revealed a structured genetic landscape across sampled ranges of Sahara mustard, with distinct patterns in native, U.S. invaded, and Australian invaded populations (Figure 1). Twelve genotypic clusters were identified within the native range. Notably, most native sites formed distinct genetic clusters, even when geographically proximate. This was evident in the marked differentiation between the Puglia South and North sites in Italy, and similarly between the Camargue South and Camargue North sites in France. An exception to country-level distinctiveness was observed with Carnon, France, and Boudiar, Morocco, which shared assignment to the same genotypic cluster. While some admixture was evident among distinct populations within native countries (e.g., France, Morocco), it often appeared unidirectional, such as the presence of Camargue South ancestry in Carnon, France, and Guercif ancestry in Boudiar, Morocco (Figures 1 and S3).

Ancestry coefficients further suggested the invaded U.S. and Australian samples were genetically distinct from the native

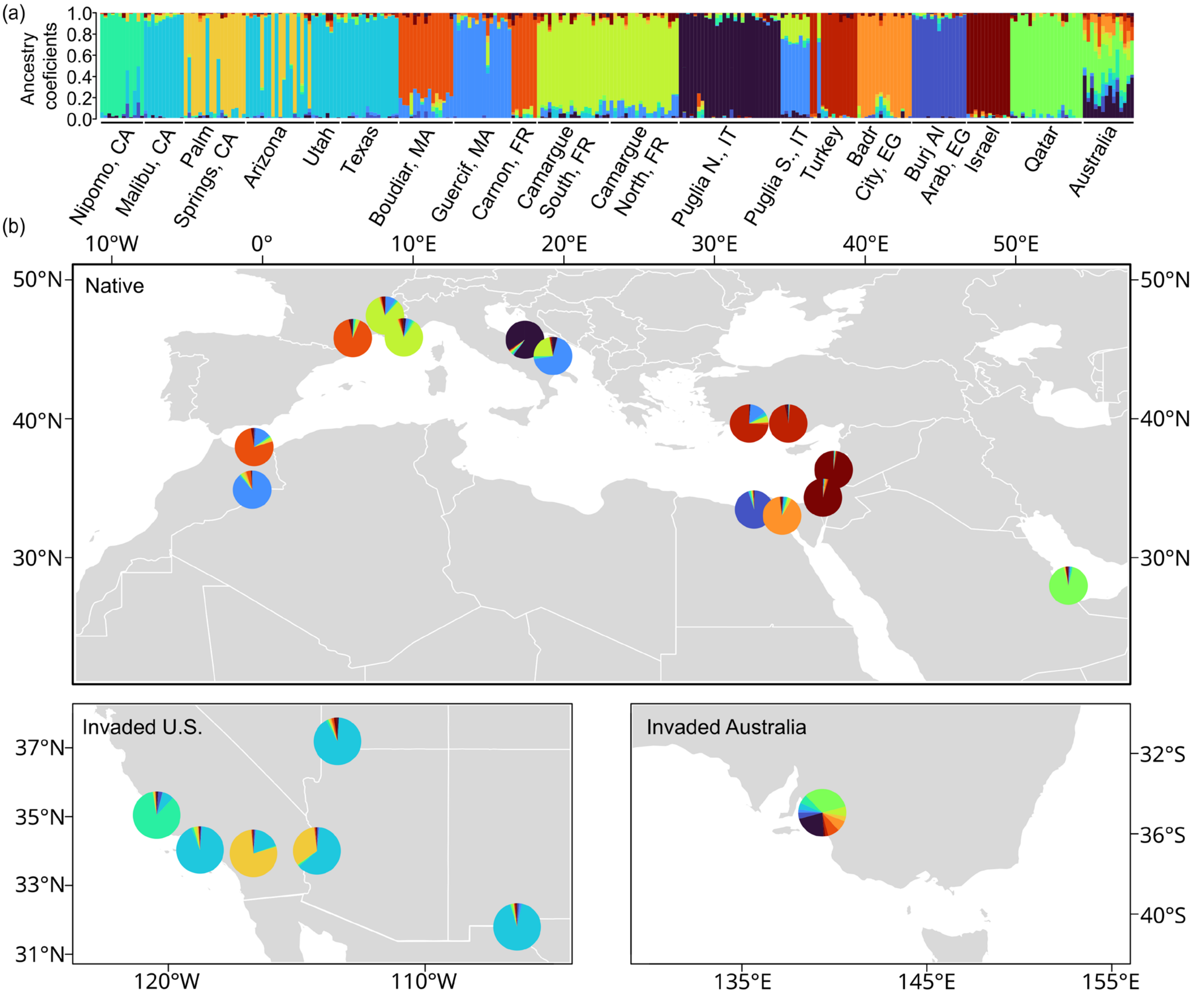

FIGURE 1 | (a) Estimated ancestry coefficients based on 1258 SNP loci of Sahara mustard (*Brassica tournefortii*) native range and invaded sampling sites. Bar plots are averaged across 40 iterations of the highest likely number of clusters predicted to be $K = 12$. Bar plots with ancestry estimated for $K = 2$–15 are provided in Figure S2. (b) Maps illustrating pie charts of average site assignment probabilities to each cluster in the native (upper panel), invaded US (lower left panel), and invaded Australian (lower right panel) ranges.

range populations. The largest U.S. cluster encompassed the Malibu, CA + Texas + Utah group, which also included several individuals from the Palm Springs, CA + Arizona group. Nipomo, CA largely formed a distinct genetic group, though a minority of individuals showed partial ancestry from other U.S. clusters, and, to a lesser extent, from the Qatar, Badr City, Egypt, and Australian clusters (Figure 1). Australian samples generally displayed admixed ancestries across various clusters at all K values but consistently shared a significant ancestral component with samples from Qatar, with this shared assignment becoming more pronounced at lower K values (Figures 1 and S3).

Discriminant Analysis of Principal Components (DAPC) revealed distinct population structure across native and invaded ranges, and with agricultural varieties and historical invaded samples (Figure 2). At least 2–3 distinct genetic clusters separated along the first DF axis, and at least 4 clusters appeared along the second DF axis. Samples from Israel (Caesarea, IL; Tel Aviv, IL) and Turkey (Cirali, TU; Demre, TU) generally separated from all other native samples along the first DF axis and clustered near two agricultural varieties (France1991 and Israel1991; Figure 2 inset). Contemporary invaded range samples generally clustered together with native range samples and some agricultural varieties along the second DF axis. Invaded U.S. samples from the Malibu, CA + Texas + Utah cluster and the Palm Springs, CA + Arizona cluster formed marginally distinguishable groupings along both axes, though overlap among some invaded sites was evident and alignment with native range sites varied. Notably, contemporary invasive samples generally clustered with native samples from Morocco, Egypt, and Qatar, and agricultural varieties from Morocco, Spain, and France. Agricultural varieties from Pakistan and India separated from most clusters along the second DF axis but aligned with the largest cluster along the first DF axis. The two historical invaded samples clustered closest to an agricultural variety sample from Morocco, contemporary native samples from Burj Al Arab, Egypt, and one invasive sample from Australia along the second DF axis,

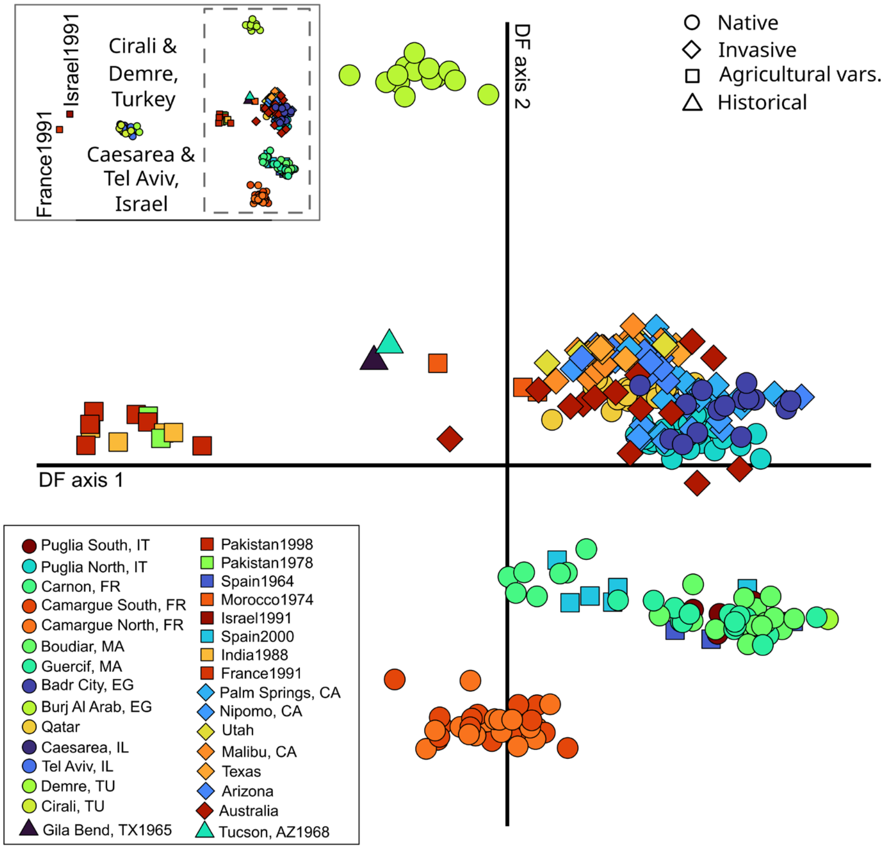

FIGURE 2 | Discriminate Analysis of Principal Components (DAPC) showing genetic similarity between sampling sites in Sahara mustard's (*Brassica tournefortii*) native range (circles); invaded range samples (diamonds); agricultural varieties (squares); and two historic invasive samples (triangles). Panel inset in the upper left shows the complete samples included in the analysis and the dashed lines indicate the portion of the plot enlarged. See Table S2 for additional details on historical samples. See Table S3 for additional accession details for agricultural samples. Country codes are abbreviated according to the International Organisation for Standardisation: France (FR); Israel (IL); Turkey (TU); Italy (IT); Morocco (MA); Egypt (EG).

and most contemporary invasive samples along the first DF axis (Figure 2). DAPC analyses of only native range samples showed similar patterns to the full dataset, highlighting the tight clustering of Badr City, Egypt to Moroccan, French and Italian sites and, to a lesser extent, Qatari samples (Figure S4).

Procrustes analysis of native range samples demonstrated that while geography broadly influences Sahara mustard genetics, several notable exceptions highlight complex evolutionary relationships (Figure 3). Qatari and Egyptian populations, despite their geographic distance, showed closer genetic affinity to Moroccan, French, and Italian individuals than physical proximity alone would suggest. Conversely, Israeli and Turkish samples exhibited greater genetic divergence from most other populations, forming distinct clusters, with the exception of a subset of samples from Puglia North, Italy, which showed some relatedness. Furthermore, Moroccan, French, and Puglia South, Italy samples were genetically more similar than anticipated based purely on geographic distance, indicating either shared ancestry or gene flow that transcends simple geographic isolation.

Pairwise F_{ST} analyses revealed clear differentiation between native and invaded range sites (Figure 4; Table S5). A pattern of extremely low differentiation was observed among invaded U.S. sites, particularly the Malibu, CA, Texas, and Utah group, which exhibited F_{ST} values at or near zero. Samples from sites previously identified as likely introduction points, including Palm Springs and Nipomo, CA, as well as samples from Australia, showed greater genetic differentiation from the main U.S. invaded cluster (Malibu, CA + Texas + Utah). Further, samples from Nipomo, California and Australia appear least differentiated from native samples, corresponding to Puglia North, Italy and Qatar, respectively.

Within the native range, samples generally exhibited lower differentiation when comparing sites within countries (e.g., Demre, Turkey and Cirali, Turkey show very low F_{ST} values; Figure 4; Table S5). An exception was seen between samples from Puglia South, Italy, which are genetically closer to sites in Morocco (Guercif and Boudiar) and France (Camargue North and South) than they are to sites in Puglia North, Italy. This is also visually apparent in the hierarchical clustering, where Puglia South, Italy clusters more closely with sites in Morocco and France than with Puglia North (Figure 4).

Phylogenetic reconstruction illustrated distinct genetic relationships among native and invaded range Sahara mustard samples, agricultural varieties, and historic invaded range samples

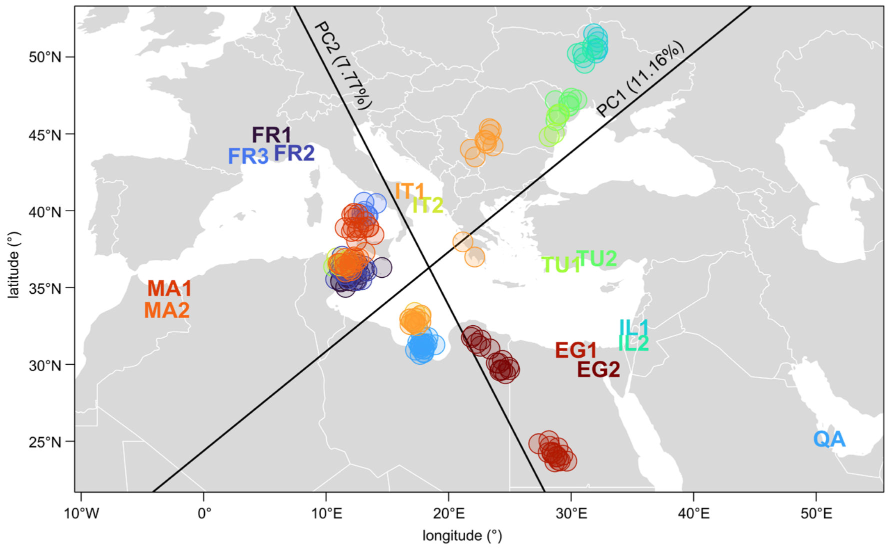

FIGURE 3 | Sahara mustard (*Brassica tournefortii*) native range sampling localities (text abbreviations described below) with individual samples (circles) graphed along two principal component axes based on a Procrustes analysis that included 10 PCs retained in the best model. PC axes account for 18.93% of the genetic variation (PC1 = 11.16% and PC2 = 7.77%). Circle colours correspond to abbreviated sampling site names: Boudiar, Morocco (MA1); Guercif, Morocco (MA2); Carnon, FR (FR3); Camargue North, FR (FR1); Camargue South, FR (FR2); Puglia North #1, IT (IT1); Puglia North #2, IT (IT2); Puglia South, IT (IT3); Demre, TU (TU1); Cirali, TU (TU2); Tel Aviv, IS (IL1); Caesarea, IS (IL2); Burj Al Arab, EG (EG1); Badr City, EG (EG2); and Qatar (QA).

(Figure 5). All major branches were supported by bootstrap values >80% except the Australia–Puglia North–Qatar–Morocco 1974 clade (62.6%), where the basal Australian sample switches with the Australia–Morocco 1974 group in some topologies. While deep branches show clear separation among native range samples by site, a direct relationship with geographic distance is not consistently apparent. For example, most Puglia North, Italy samples grouped more closely with Australian and Qatari samples than with samples from Puglia South, Italy, with which they are geographically closer. Conversely, Puglia South, Italy samples showed closer phylogenetic affinity to French and Moroccan samples. A distinct subset of Puglia North, Italy samples formed a clade closely related to Israeli and Turkish samples. Invaded U.S. range samples largely separated into their own clade and appear closest to a smaller, neighboring clade of samples from Egypt, and the larger clade of samples from Australia, Qatar, Puglia North, Italy, and the agricultural variety from Morocco. Agricultural varieties from India and Pakistan appear on the clade most distant from invasive samples and are closer to samples from Turkey and the smaller subset of Puglia North, Italy samples. Agricultural varieties from Israel and France clustered together with contemporary samples from Israel (Figure 5).

3.2 | Genetic Diversity

Observed heterozygosity (H_O) was generally higher than the mean within-population gene diversity (H_S) in both contemporary native (mean $H_O = 0.20$; $H_S = 0.16$) and invaded range samples (mean $H_O = 0.28$; $H_S = 0.20$; Table 1). This translated to negative inbreeding coefficients (F_{IS}) in both native (mean $F_{IS} = -0.26$) and invaded (mean $F_{IS} = -0.40$) ranges and most localities sampled (native range $F_{IS} = -0.44$–0.10; invaded ranges $F_{IS} = -0.62$–0.05; Table 1). Only 3 of the 14 localities in the native range had positive F_{IS} values (Caesarea and Tel Aviv, Israel; Demre, Turkey; Puglia North, Italy). All invaded sites had negative F_{IS} values (Table 1). Gene diversity (H_T) was, on average, 1.25× higher in invaded range samples (mean $H_T = 0.20$) compared to the native range ($H_T = 0.16$), though this might be driven by sample size differences and, in particular, the samples from Israel that had the lowest gene diversity values ($H_T = 0.08$; Table 1). Agricultural varieties had similar observed levels of heterozygosity (mean $H_O = 0.20$; Table S4) and inbreeding (mean $F_{IS} = -0.26$) as the native range, though no positive F_{IS} values were observed. Pairwise F.

4 | Discussion

Globalisation will continue to remove natural dispersal and gene flow barriers (Clavel et al. 2011), promote the homogenization of floras and genomes (e.g., Gámez-Virués et al. 2015), and provide a means for unwanted global hitchhiking of invasives (Cristescu 2016). Three essential goals toward controlling invasions are determining where non-native introductions occur, what dispersal routes they followed, and which ecological or evolutionary processes promote or inhibit their success (e.g., Ascunce et al. 2011; Fitzpatrick et al. 2012; Colautti and Barrett 2013). Combined with previous work in this system (Winkler et al. 2019), our study addresses these goals by demonstrating how Sahara mustard has likely been moved by humans throughout its native range (intentionally and/or unintentionally) and that multiple genotypes have been introduced into the U.S. and at least one genotype into Australia. We show that despite potential founder effects, characteristics such as genetic mixing and high heterozygosity have likely contributed to its successful spread throughout its invaded ranges. Below we describe the probable scenarios of human-mediated movement in

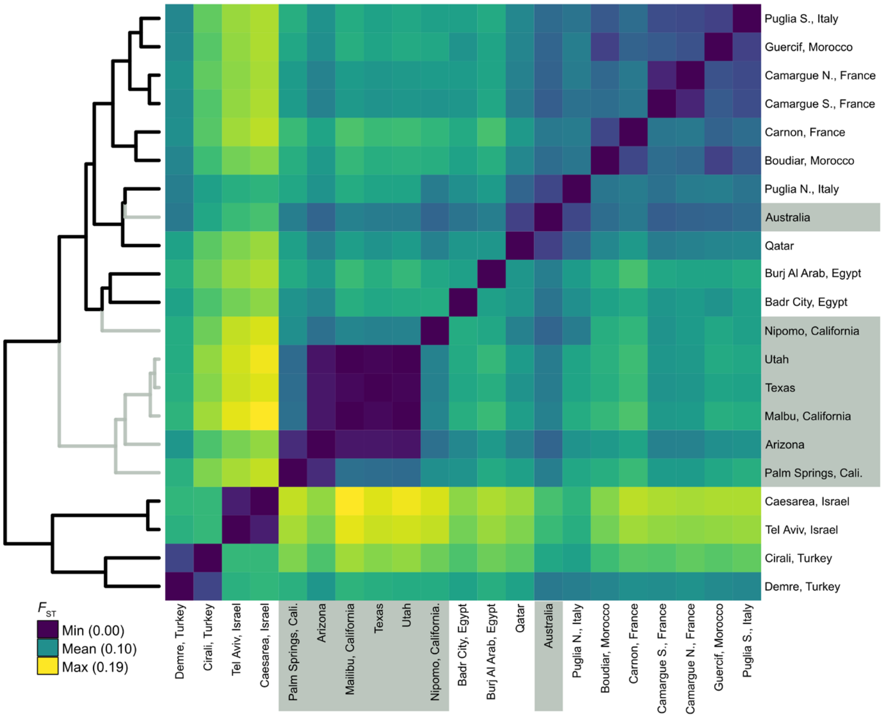

FIGURE 4 | Heatmap with hierarchical clustering of pairwise F_{ST} coefficients following Weir and Cockerham (1984) for Sahara mustard (*Brassica tournefortii*) native range and invaded range sampling sites. Grey branches and text boxes denote invaded range sampling sites. Minimum ($F_{ST} = 0$; blue) to maximum ($F_{ST} = 0.19$; yellow) genetic differentiation is colour coded in the heatmap.

both the native and invaded ranges, highlighting genetic shifts that may have enabled this species' invasive success.

Homogenization of biotic communities is commonplace with globalisation and development (McKinney 2006; Groffman et al. 2014; Valtonen et al. 2017) and can occur in the form of declines in community diversity (Clavel et al. 2011), conversion to invasive dominated systems (Holway and Suarez 2006), and reductions in the genetic diversity of native species (Rhymer and Simberloff 1996). Invasive species also can carry homogenised genotypes to places they colonise (C. E. Lee 2002) while simultaneously aligning phenotypes across environmental gradients in invaded areas (e.g., Marchini et al. 2018; Dematteis et al. 2020). Native range samples showed distinct population structure (Figure 1), yet consistently exhibited evidence of admixture across all genotypic analyses. Samples from Egypt appear to represent a potential historical hybrid zone between North African and European (primarily Morocco and France and, to a lesser extent, Italy) and west Asian (Qatar) genotypes. This pattern is also evident in clustering analyses (Figures 1 and S3) and DAPC analyses (Figure S4). Additionally, fixation indices (F_{ST}) among native range sites suggest most sites are less differentiated from their nearest geographic neighbours, except Egyptian sites that appear generally differentiated at equal levels to most other native sites sampled (Figure 5 and Table S5). Egypt as the confluence of multiple geographic genotypes is notable not only as a potential hybrid zone for Sahara mustard but also as a recurring pattern in other biological systems that have been influenced by trade and human migration in the region (e.g., Smith et al. 1991; Flowers et al. 2019). Combined, these data support our first hypothesis, indicating that human activities, likely historical trade routes, have significantly shaped the genetic landscape of Sahara mustard within its native range.

Intercontinental agricultural trade is the most likely cause of Sahara mustard's introduction in the U.S. and Australia, and, to date, the species is purported to have been introduced as an unexpected contaminant of date palm agriculture (Sanders and Minnich 2000; USDA 2021). While DNA quality limited comprehensive analysis of our earliest herbarium specimens, DAPC analyses that included two historical invaded samples from the 1960s show genetic proximity to contemporary Egyptian (Burj Al Arab) and 1974 Moroccan agricultural varieties (Figure 2). Crucially, contemporary samples from the U.S. also cluster near and are less differentiated than Egyptian samples (Figures 2 and 5), indicating that Egyptian genotypes likely represent the most probable origin of the two largest U.S. populations of Sahara mustard (Malibu, CA + Texas + Utah; Palm Springs, CA + Arizona; Winkler et al. 2019). These data directly support our second hypothesis that invasive U.S. populations originate primarily from specific native range populations, consistent with human-mediated dispersal associated with agricultural trade. Despite this, Egyptian sites themselves are likely of mixed ancestry and show signs of admixture with Moroccan, French, and Qatari populations (Figures 5 and S3; Table S5). This may be unsurprising since global trade and human migration are known to facilitate the spread of invasives and their influence has varied temporally with agricultural development, expansion of historical empires, and more recently via colonialism (Hulme 2009; Banks et al. 2015; Secord 2016; Lenzner et al. 2022).

Sahara mustard co-occurs with date palm throughout much of its North African and West Asian range and, outside of

FIGURE 5 | Unrooted maximum likelihood tree for Sahara mustard (*Brassica tournefortii*) contemporary native and invaded range sampling sites, historical invaded range samples, and agricultural varieties. Branches are colour coded by sampling site. Historical invaded range samples are labelled with the sampling site and year the sample was collected (see Table S2 for additional details on historical samples). Agricultural varieties are labelled with the origin country and year the accession was collected (see Table S3 for additional accession details).

Mediterranean systems in Europe and coastal North Africa, cultivated date palm oases form the ecological foundation for plant communities that include Sahara mustard (e.g., Zuaran 1972; Gazer 2011; Moussouni et al. 2017; Balah 2019). Past molecular studies of date palm reveal three strikingly similar genomic features to Sahara mustard in our present study. First, date palm genomics show a major separation between North African and West Asian varieties, with notable admixture in Egypt (Hazzouri et al. 2015; Flowers et al. 2019). We found a highly analogous pattern in Sahara mustard's native range, with Egypt serving as a genetic bridge between distinct western and eastern genotypes (Figures 1 and S3). Second, Egyptian and Moroccan date palms appear to have been intentionally moved and mixed multiple times and remain genetically similar relative to other local agricultural varieties (Elhoumaizi et al. 2006; Chaluvadi et al. 2019; Sallon et al. 2020; Gros-Balthazard et al. 2021). Again, we observed similar patterns in Sahara mustard, with samples from Badr City, Egypt clustering nearer to Moroccan, French, and Italian samples than to other Egyptian samples (Figures 2, 3 and S4). Third, date palms have been intentionally outbred for centuries and the resulting genomic structure of most varieties displays excess heterozygosity that corresponds to inbreeding avoidance seen in negative F_{IS} values (e.g., Elshibli and Korpelainen 2009; Bodian et al. 2012; Moussouni et al. 2017). We see similar excess heterozygosity and corresponding negative F_{IS} values in Sahara mustard's native range and elevated levels in the invaded U.S. samples as would be expected with potential recent founder effects and/or admixture of previously isolated genotypes (Table 1; Fitzpatrick et al. 2012). That we see these levels in both native and invaded range samples suggests the possibility of overdominance (either true or associative) leading to these heterozygote excesses that appear to be maintained in both wild and cultivated populations (Tables 1 and S4; Smith and Haigh 1974; Mitton 1989; Stoeckel et al. 2006).

Date palms were introduced to the U.S. for agricultural development primarily in the late 19th and early 20th centuries. Date palms were largely imported as offshoots from locations in what is now Morocco, Algeria, Tunisia, Iraq, Oman, and Egypt (Swingle 1900; D. R. Lee 1963; Rivera et al. 2013). The date palm offshoots were often wrapped in leaf sheath remnants that were tough, coarse-matted fibers taken from between the bases of date palm stalks and trunks (Swingle 1900; Mason 1915). These wrappings were placed around offshoots and stuffed with wet soil, moss, or sometimes sawdust to prevent desiccation during travel (Wright 2016). It is possible these offshoots carried Sahara mustard seeds from their sources to the U.S. Indeed, Sahara mustard first appears in U.S. historical herbaria records in the late 1920s at a time when tens of thousands of date palm offshoots had been imported to the Coachella Valley of California and thousands more were being imported annually (Popenoe 1913; Nixon 1950; Wright 2016). Date palms were also introduced to Australia during agricultural development periods in the late 19th and early 20th centuries (Brown 1884) and were sourced from Algeria, Tunisia, Iraq, Morocco, Saudi Arabia, and Pakistan, among others (Swingle 1900; Al-Najm et al. 2016). Sahara mustard is purported to have been introduced to the Australian flora in the early 20th century and first appears in herbaria records in 1929 when it was collected near Southern Cross in Western Australia

TABLE 1 | Genetic diversity of Sahara mustard (*Brassica tournefortii*) contemporary native and invaded range samples based on 1258 SNPs. F_{IS} coefficients are calculated following Nei (1987).

Source	n	H_O	H_S	H_T	F_{IS}
Nipomo, California	12	0.27	0.19	0.19	−0.40
Malibu, California	11	0.31	0.19	0.19	−0.62
Palm Springs, California	18	0.29	0.22	0.22	−0.33
Arizona	19	0.29	0.23	0.23	−0.25
Utah	7	0.30	0.19	0.19	−0.56
Texas	15	0.28	0.18	0.18	−0.56
Australia	14	0.23	0.22	0.22	−0.05
Boudiar, Morocco	15	0.21	0.17	0.17	−0.26
Guercif, Morocco	16	0.22	0.17	0.17	−0.33
Carnon, France	7	0.23	0.16	0.16	−0.44
Camargue N., France	19	0.25	0.17	0.17	−0.44
Camargue S., France	20	0.25	0.18	0.18	−0.42
Puglia North, Italy	28	0.20	0.22	0.22	0.10
Puglia South, Italy	8	0.22	0.16	0.16	−0.40
Cirali, Turkey	8	0.17	0.13	0.13	−0.32
Demre, Turkey	5	0.21	0.22	0.22	0.06
Badr City, Egypt	15	0.19	0.14	0.14	−0.33
Burj Al Arab, Egypt	15	0.21	0.16	0.16	−0.31
Caesarea, Israel	7	0.09	0.08	0.08	−0.15
Tel Aviv, Israel	5	0.08	0.08	0.08	0.03
Qatar	20	0.21	0.15	0.15	−0.38

Abbreviations: F_{IS} = inbreeding coefficient, H_O = mean observed heterozygosity, H_S = mean within-population gene diversity, H_T = overall gene diversity.

before likely spreading via the transcontinental railroad where it reached South Australia less than a decade later (Kloot 1987). This historical context, combined with our genomic data, provides compelling evidence consistent with Sahara mustard's introduction as a contaminant in the date palm trade. Our genotypic analyses demonstrate that Sahara mustard's native range populations, while distinct, show clear signs of human influence connecting populations across historical and contemporary trade regions, such as Morocco, France, and Egypt (Figure S4). This reinforces the plausibility of seed hitchhiking during extensive human-mediated transport.

Beyond the correlative relationship of date palm and Sahara mustard population histories, humans have cultivated Sahara mustard for hundreds of years and its use in traditional cooking may have both influenced its current genomic structure (Heywood et al. 2007; Fuller and Lucas 2017; Turcotte et al. 2017) and potentially its invasiveness (e.g., Ellstrand et al. 2010). Sahara mustard is described as an agricultural pest in parts of its native range (e.g., Egypt; Ahmed et al. 2015) and is also delineated as currently rare in other parts of its range (e.g., Malta; Sicily; Rivera et al. 2006; Casha 2009). This juxtaposition may reflect the large and varied habitats Sahara mustard occupies as well as regional, sometimes shifting, uses humans have for the species. For example, Sahara mustard was once common in cultivated date palm oases in Tunisia, and likely elsewhere in North Africa, but modern varieties of other species have become increasingly common, displacing Sahara mustard (Pistrick et al. 1994). In some oases, Sahara mustard was relatively abundant and cultivated as recently as the 1990s (El-Ghani 1994) but has likely been extirpated since (El-Saied et al. 2015). Further, the species is restricted entirely to agricultural areas in parts of its range (e.g., the United Arab Emirates; Brown and Feulner 2023) and may be largely dependent on agricultural irrigation in others (e.g., Egyptian oases; Thanheiser et al. 1994). It is possible humans have selected the species through control methods in agricultural settings (Kreiner et al. 2022) while simultaneously influencing populations through overuse of wild populations (Heywood et al. 2007). Our analysis of agricultural varieties, sourced from both 'wild' and cultivated fields, showed overall genetic diversity comparable to most contemporary native sites (Table S4). Notably, seed accessions from Pakistan and India (1970s–80s) show closer genetic relatedness to many contemporary African and European native sites than geographic distance would suggest (Figure 4). This suggests these agricultural varieties were sourced from, or developed with, these African and European populations (e.g., Mabry et al. 2021). Combined with the pervasive excess heterozygosity observed across nearly all native range sites (Table 1), these results suggest potential admixture of cultivated genotypes into wild Sahara mustard populations. This phenomenon is common in agricultural species and crop wild relatives including multiple *Brassica* species (Mabry et al. 2023). For example, feral individuals of the congeneric *B. oleracea* appear to have spread from agriculture and mixed with wild populations in multiple locations throughout the species' native range, resulting in excess heterozygosity in all wild populations sampled (Mittell et al. 2020).

Agricultural varieties from France and Israel also provided evidence of human influence, with the France accession appearing indistinguishable from both the agricultural variety collected from Israel as well as those sourced from the contemporary native range in Israel (Figures 2 and 4). In fact, this was likely suspected by the USDA, which maintains these seed collections as crop wild relatives and agricultural conservation resources and noted that the French accession was sourced from France but maintained in Israel before it was donated to the USDA (Table S3; USDA 2023). These patterns are mostly identical to those observed in contemporary native range samples. This striking similarity to patterns in date palms (Bodian et al. 2012; Khouane et al. 2020) is often attributed to farmer breeding and cultivation techniques that actively select for heterozygous individuals (Moussouni et al. 2017). This has also been observed in studies of wild tree populations, suggesting that foresters select heterozygotes, thereby influencing population genetic structure (Mitton 1998). If Sahara mustard moved along trade routes with date palms, it is possible its own cultivation (Singh et al. 2015) or other influences by date palm farmers led to the observed excess heterozygotes observed in the present study. For example, Pujol et al. (2005) show that excess heterozygotes appear in cultivated cassava because of selection by farmers and unintentional hybridization with weedy volunteers. This mechanism, seen in crops like cassava (Pujol et al. 2005) and artichoke (Sonnante et al. 2007), and even *Brassica* species like *B. rapa* (Sammour et al. 2020) and *B. napus* (El-Esawi 2015), directly supports our third hypothesis regarding human-mediated selection and mixing in agricultural varieties and influences wild populations.

It is possible the observed heterozygosity levels and negative inbreeding coefficients we report in the current study, particularly in the invaded U.S. range, may suggest some level of self-incompatibility in Sahara mustard (e.g., Stoeckel et al. 2006) and, perhaps, an evolutionary shift toward asexual reproduction (e.g., Menken et al. 1995) that requires further investigation. This is counter to earlier results that suggested self-fertilisation appeared to be a dominant strategy in the species' invaded U.S. range (Winkler et al. 2019) and was discussed as a potential methodological artefact (Hedrick 2020; Winkler et al. 2020), likely related to utilising a limited dataset and without native range samples. As mentioned, these heterozygosity levels could also result from mixing with cultivated varieties of Sahara mustard or even with closely related congenerics. For example, Sahara mustard has been used as a cytoplasmic donor in hybridization breeding programs in canola (*B. napus*) and Chinese mustard (*B. juncea*) crops (Yamagishi and Bhat 2014) and has been shown to have partial genome homeology with *B. rapa* (Kumar et al. 2015). This suggests potential interspecies mixing, a common occurrence among many *Brassica* crops and their crop wild relatives (Saban et al. 2023). Given that breeding technologies for *B. napus* and *B. oleracea* maintain excess heterozygosity across generations (Fu and Gugel 2010; Ciancaleoni et al. 2014), and that gene flow between crops and wild relatives is ongoing (Mittell et al. 2020), our observed elevated heterozygosity throughout Sahara mustard's range strongly points to human-mediated mixing with non-wild populations (Saban et al. 2023), further supporting our third hypothesis.

Given that Sahara mustard was likely introduced to the U.S. multiple times within the last century (Winkler et al. 2019), it is possible the species did not undergo a severe enough genetic bottleneck to prevent or limit its colonisation (Vavassori et al. 2022). In fact, we observed overall gene diversity (H_T) levels that were mostly similar, and sometimes elevated, when compared to the contemporary native range sites (Table 1). Furthermore, our clustering analyses indicate that the Australian population is an admixed combination of native range populations (Figures 1 and S3) and may also represent an unsampled native source. This highlights a critical need for future studies to comprehensively document the population structure of Sahara mustard across its entire invaded Australian range.

Today, humans are spreading invasive species via multiple modes (e.g., Ladin et al. 2023), with potentially larger influences than natural dispersal mechanisms such as wind, water, or non-human animals (e.g., Horvitz et al. 2017). Our findings demonstrate that human movement and mixing of Sahara mustard within its native range, its agricultural utilisation, and artificial selection have all shaped its invasive success. Invasives growing around ports and human development can have higher genetic diversity than elsewhere, suggesting multiple introductions and mixing among invasive populations may be the norm (e.g., Baird et al. 2020; Mairal et al. 2022). Controlling this highly problematic species remains challenging, given its herbicide resistance (Boutsalis et al. 1999) and its role in providing a competitive advantage for other invasive species including the agricultural pest *Bagrada hilaris* (Lillian et al. 2018, 2019). Despite this, the identification of the most likely sources of Sahara mustard in its invaded ranges can support the design of effective management strategies that control further spread while preventing additional invasions (Lodge et al. 2006). This includes informing classical biological control by guiding the survey and identification of host-specific natural enemies in source populations (e.g., Borowiec and Sforza 2022). Future studies focused on the demographic history within Sahara mustard's native range as well as its chemical defense strategies will likely provide opportunities to identify and test potential controls given the results presented here. Further, directly testing sexual and asexual reproductive strategies in the species may reveal important mechanisms by which invasive species like Sahara mustard are capable of rapidly colonising novel habitats. Last, given the species' historical use in agriculture and its relationship with congeneric crop species, additional genomic work to uncover the evolutionary history and selection of Sahara mustard throughout its range may provide tremendous insight into human forcings on natural systems in our increasingly globalised world.

Author Contributions

D.E.W. conceived of and designed the project with help from T.E.H., K.J.C., J.D.G. and L.S. D.E.W., K.J.C., W.M.A., M.A., M.-C.B., M.C., J.K., F.M., and R.S. collected samples. D.E.W., K.J.C., and M.-C.B. carried out laboratory work. K.J.C. and D.E.W. processed data and performed analyses. D.E.W. wrote the manuscript with contributions from all authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Molecular data used in these analyses are available as NCBI's sequence read archive (BioProject for *B. tournefortii*: PRJNA534338), subject to a 5-month embargo period post publication. Python and R scripts are publicly available on the GitHub repository at https://github.com/chapinkj/mustard.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** BLAST results using 1000 randomly-selected reads from each sample and compared them to known sequences in the NCBI database via BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). **Data S1:** mec70176-sup-0002-Supinfo.pdf.