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Retracing the centre of origin and evolutionary history of nutmeg *Myristica fragrans*, an emblematic spice tree species

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Identifying the centres of origin of cultivated plants is important for conservation and sustainable management, since this is where these species tend to be most genetically diverse. This research seeks to determine the centre of origin and evolutionary history of nutmeg (*Myristica fragrans*; Myristicaceae), an emblematic spice tree species traditionally believed to originate from the Banda Islands, South Moluccas, Indonesia. We explored nutmeg's genetic diversity and structure across the Moluccas archipelago using nuclear microsatellite markers and whole plastid genome sequences. Two primary intra-specific genetic clusters were found: one in the North Moluccas (Ternate, Tidore and Bacan islands) with higher genetic diversity and another in the South Moluccas (Banda and Ambon islands), which exhibited signs of a recent bottleneck. Although the North Moluccas showed higher genetic diversity, approximate Bayesian computation analyses supported South Moluccas as the centre of origin of *M. fragrans*. The species migrated from South to North Moluccas during the late Pleistocene to early Holocene period and experienced a recent bottleneck in the South. These findings suggest a naturally driven distribution influenced by migration and past climate changes. Human activities have further shaped these patterns, offering insights for developing targeted conservation strategies for nutmeg based on its genetic diversity.

1. Introduction

Agriculture developed independently in various parts of the world between 11 000 and 5000 years ago. Alphonse de Candolle was one of the first to question the geographical origin of cultivated plants using an integrated scientific approach [1,2]. He synthesized data from various disciplines (botany, plant biogeography, archaeology, palaeontology, history, linguistics, ethnology) to propose hypotheses on the geographical origin of 247 cultivated species. This work was later extended by Nikolaï Vavilov, who proposed main centres of origin for domesticated plants [3]. Vavilov's work has since been revisited and updated by others [4–10]. Vavilov's centres of cultivated plant origins were later confirmed by a number of archaeological finds [11,12]. More recently, the study of the geographical origin of cultivated species has greatly benefited from the use of genomic approaches [13]. However, the origins of many cultivated species are still poorly understood. This hinders the development of conservation strategies for their genetic resources.

Identifying the origin and biogeographic history of a cultivated species is essential for effective conservation and sustainable management. Genetic diversity within a species is usually uneven across its range, with centres of origin typically showing higher diversity than introduced populations due to genetic bottlenecks during propagation outside their native areas [14,15]. However, this expectation can be obscured by inter-specific gene flow with closely related species, a relatively frequent phenomenon in plants [16,17]. In fact, as cultivated species spread outside their native range, they may come into contact with closely related species, creating new opportunities for hybridization and increasing genetic diversity in the introduced populations. This process is recognized as a contributing factor to the adaptation of species to new environmental conditions during the propagation process outside their native range [18,19]. A second factor that can mask the expected pattern of higher diversity in the centre of origin is when that region also becomes a centre of early domestication or long-term cultivation, as human practices may markedly reduce local genetic diversity [20,21].

Nutmeg, *Myristica fragrans* Houtt., is one of the most emblematic spice tree species. Its fruit is the source of two spices that are highly valued: nutmeg and mace. The exact location of the centre of origin of the species is controversial in historical archives, with some authors suggesting it includes the entire Indonesian archipelago of the Moluccas (known as 'the Spice Islands'), while the vast majority mention only the Banda Islands—a group of small islands in the South Moluccas (figure 1A). The origins of nutmeg cultivation are shrouded in mystery, but this puzzle can hopefully be unravelled by integrating data from multiple disciplines.

Archaeological, textual and molecular evidence can illuminate the origins and history of cultivated plants. Archaeobotanical work in Indonesia is scarce; the only available study found nutmeg residue on Neolithic pottery from Pulau Ay in the Banda group, indicating the species's long-term presence in South Moluccas [22]. According to Rumphius, in his *Herbarii Amboinensis*, nutmeg is naturally distributed throughout the entire Moluccas [23], yet other historical sources later identified the Banda Islands as the primary centre of nutmeg cultivation by at least the early seventeenth century [24–26], shaping the long-standing assumption that the species originated there. This is presumably the result of the Dutch East India Company's (Vereenigde Oostindische Compagnie, VOC) strong monopolistic policies during the Dutch colonial period in Indonesia (*ca* 1600–1800), which were intended to ensure control over this important economic resource [25]. Other European nations, such as France and England, attempted to circumvent the Dutch monopoly by obtaining planting material from the highly controlled Banda Islands in order to cultivate the tree in their own tropical colonies [24,26]. While this historical prominence explains why Banda has traditionally been viewed as the cradle of nutmeg, the true native range of nutmeg has never been tested using genetic data.

Genetic studies based on extensive sampling across a species distribution can help identify its centre of origin and trace its biogeographical history [27]. To date, despite the socio-economic importance of nutmeg, no genetic studies have been carried out on the species. For non-model organisms with few genomic resources available such as nutmeg, two types of genetic markers are commonly used: nuclear microsatellites (nSSR) and chloroplast DNA (cpDNA). These markers are used to infer past demographic events and to test different demographic scenarios with temporal calibrations [28,29]. Moreover, by enabling the evaluation of both past and recent evolutionary processes, the combination of nuclear and chloroplast markers represents a comprehensive approach to understanding the evolutionary history of a species [30].

This study therefore aims to identify the most likely centre of origin of *M. fragrans* using genetic data collected across the Moluccan archipelago. To address this question and improve our understanding of the species's biogeographical history, we applied a population genetic approach. We sampled individuals of *M. fragrans* across five islands spanning the North and South Moluccas and characterized the genetic diversity and structure of the species using recently developed nSSR [31] and whole chloroplast genome data [32]. These data were then used to test alternative hypotheses regarding whether the species originated in the South Moluccas or in the North Moluccas. The data acquired provide a valuable opportunity to assess the historical influence of trading and cultivation events on the genetic diversity and structure of the species. It is hypothesized that nutmeg cultivation practices in the Banda Islands during the VOC monopoly may have resulted in a reduction of species genetic diversity. Indeed, the VOC often ordered the destruction of nutmeg trees to sell the spice at good prices. The geographical origin of the species and its evolutionary history have been clarified by the new data acquired.

2. Material and methods

(a) Study area: the Moluccas region

The Moluccas (figure 1A) constitute a natural biogeographical unit within the Wallacea region in the eastern part of Indonesia. They include two island groups: the North Moluccas (Maluku Utara province), which is part of a volcanic arc, and the South Moluccas (Maluku province) located on the Australasian continental plate.

(b) Study species: *Myristica fragrans*

Myristica fragrans Houtt. (Myristicaceae), or nutmeg, is a tropical tree native to Indonesia's Moluccas [23]. It thrives in warm, humid climates with over 150 cm annual rainfall and grows up to 1300 m elevation. Typically 5–15 m tall, it can occasionally reach 20–30 m. Trees begin fruiting about 8 years after planting, peak at 25 years, and can produce for over 60 years. Usually dioecious like other *Myristica* species, some cultivated trees are monoecious (J.K. 2026, personal observation). The species is mainly insect-pollinated by small generalist beetles, thrips and flies [33]. Natural populations often show male-biased sex ratios, varying with flowering cycles. The species is diploid ($2n = 44$ [34,35]). Seeds are dispersed naturally by frugivorous birds and mammals, but human-mediated dispersal has driven its spread across the tropics within and beyond its native range.

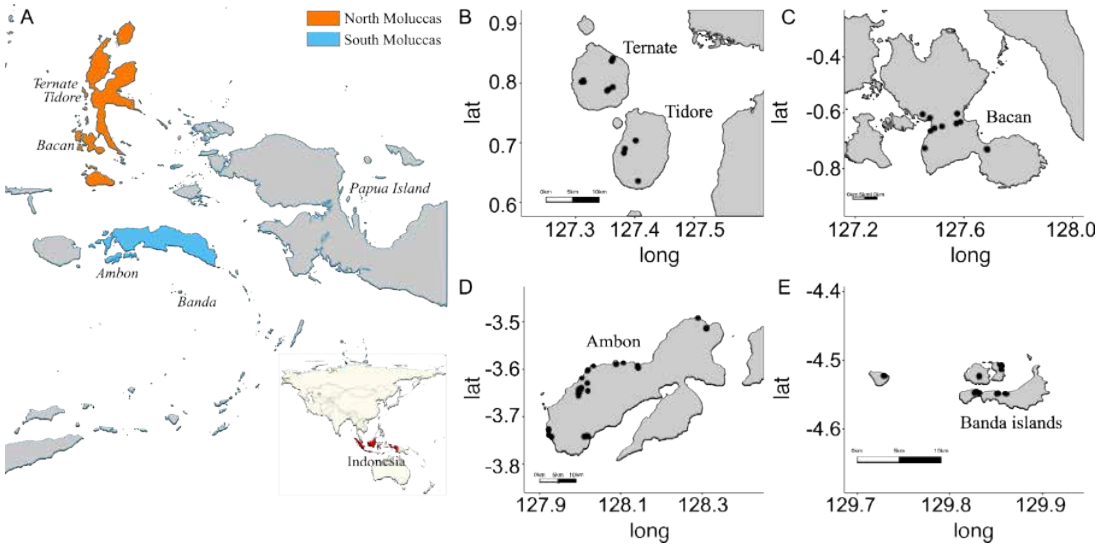

Figure 1. Sampling sites of nutmeg (*Myristica fragrans*) in the Moluccas. (A) Position of the Moluccas archipelago in Indonesia and subdivision into North Moluccas (orange colour) and South Moluccas (blue colour). The five islands that were sampled are (B) Ternate and Tidore island, (C) Bacan island, (D) Ambon island and (E) Banda archipelago. Black dots in (B–E) correspond to a sampled individual.

(c) Plant material

A total of 393 individuals of *M. fragrans* were collected at five different sites (Ambon, Banda Islands, Ternate, Tidore and Bacan) covering the geographic extent of the Moluccas archipelago from North to South (figure 1). This sampling scheme ensures that the potential natural distribution of *M. fragrans* is covered in a representative way. The Banda Islands are a group of ten volcanic islands: we sampled four of them (hereafter 'Banda' to refer to these sampling localities). Leaves of individuals were collected and stored in silica gel to dry rapidly for preservation until DNA extraction. We refer to each island as a 'population', and the different collecting sites within each island are referred to as 'subpopulations' (see electronic supplementary material S1 for details).

(d) DNA extraction, nSSR genotyping and cpDNA sequencing

DNA extraction. Total genomic DNA was extracted using the MATAB protocol and chloroform separation with slight modifications following Mariac *et al.* [36]. We checked DNA quality and quantity using a NanoDrop One spectrophotometer (Thermo Scientific).

nSSR genotyping. All individuals were genotyped with 14 polymorphic nSSR markers following PCR conditions described in Kusuma *et al.* [31]. One primer pair (Myr42) amplified two distinct genomic regions and was therefore scored as two separate loci (Myr42a and Myr42b), yielding a final dataset of 15 diploid loci per individual. Fragment analysis was performed on an ABI 3500 XL capillary sequencer (Applied Biosystems) at CIRAD (Montpellier, France) using 1 µl PCR product, 12 µl Hi-Di Formamide (Applied Biosystems) and 0.3 µl GeneScan 500 LIZ size standard (Applied Biosystems). Allele calling was carried out with the automated pipeline in Geneious Prime v. 2022.2.2 [37] and subsequently checked and corrected manually.

cpDNA sequencing. We selected 3–5 individuals per subpopulation for genomic library construction (n = 90; see electronic supplementary material S1) plus four individuals of the sister species *Myristica argentea* (Papuan nutmeg; Fakfak, Papua) used as an outgroup in phylogenetic network analyses (n = 94 total; electronic supplementary material S1). Library preparation, chloroplast enrichment, multiplexing and sequencing followed the protocols of Mariac *et al.* [38], and sequence processing followed Scarcelli *et al.* [39]. We excluded INDELS and SSRs to focus only on SNP in our cpDNA analyses as SNPs are generally more stable and informative sites in population genetic studies (See electronic supplementary material S2 for details).

(e) Genetic diversity and population structure of *M. fragrans* at nSSR loci

The distribution of genetic diversity in *M. fragrans* (n = 393 individuals) was characterized at the population level (N_{POP} = 5) by estimating the following indices using SPAGeDi v. 1.5 [40]: the number of alleles (N_A), observed and expected heterozygosity (H_O and H_E, respectively), rarefied allelic richness (AR) and inbreeding coefficient (F_{IS}).

Population structure was inferred with a Bayesian clustering approach implemented in Structure v. 2.3.4 [41] under the admixture model with sampling location as a prior and independent allele frequencies. We tested K = 1–10 with 10 replicate runs per K, each consisting of 20 000 burn-in iterations followed by 100 000 MCMC iterations. The most likely K was identified using Structure Harvester [42]. Replicate outputs were aligned with CLUMPP [43] and visualized using CLUMPAK [44]. As a complementary approach, we also estimated the optimal K using generalized thermodynamic integration (GTI) implemented in `rmaverick` [45], applying the same run parameters as for Structure.

(f) Genetic diversity and population structure of *M. fragrans* at cpDNA loci

Using the cpDNA SNP dataset from 94 individuals (90 *M. fragrans*, 4 *M. argentea*), we characterized geographic chloroplast diversity. Haplotype number (H), segregating sites (S) and nucleotide diversity (π) were estimated in DnaSP v. 6.12.03 [46]. Populations were grouped regionally, Ambon and Banda as South Moluccas and Ternate, Tidore and Bacan as North Moluccas. Genetic structure was assessed by AMOVA in Arlequin v. 3.5 [47] with significance tested over 1000 permutations.

(g) Haplotype network reconstruction

We assigned cpDNA SNPs to different haplotypes using the *pegas* R package v. 1.1 [48]. We constructed the haplotype network using the maximum parsimonious tree method [49] available in PopART v. 1.7 [50], with a 95% statistical parsimony criterion. To test for phylogeographic signal, we calculated N_{ST} and G_{ST} [51], using Permut v. 1.2.1 applying 1000 permutation tests [52].

(h) Inference of population size change in *M. fragrans*

Past demographic events in *M. fragrans* populations from the Moluccas were inferred using approximate Bayesian computation (ABC; see electronic supplementary material, methods). ABC estimates posterior distributions by comparing observed and simulated summary statistics [53,54]. We implemented the skyline analysis using the nSSR dataset in DIYABC Skylineplot [55] to reconstruct temporal changes in effective population size. To assess the robustness of these inferences, we complemented ABC with a maximum-likelihood importance-sampling approach implemented in Migraine [56].

(i) Reconstructing population history of *M. fragrans*

We inferred the ancestry and divergence time of the genetic clusters defined by Structure (see Results section), using DIYABC Random Forest v. 1.1.1 [57]. Populations assigned to a given genetic cluster according to Structure results were pooled as a single genetic group to reduce demographic model complexity. For these analyses, we only kept individuals with a cluster assignment probability higher than 0.85.

We first performed the analysis on each dataset (nSSRs and cpDNA) separately to understand the behaviour of confidence intervals on the posterior distribution of demographic parameters. We then combined the two datasets and analysed them together to assess the robustness of the analyses.

We used demographic and historical model parameters with their prior distributions to define the range of biologically realistic values for each scenario. Priors were set to encompass plausible effective population sizes (N_e), divergence times, migration rates and potential demographic changes (e.g. expansion or bottlenecks). Detailed values for these priors are described in electronic supplementary material, table S1. We then used two scenarios of species population divergence were tested with historical demographic parameters drawn from the prior distribution (electronic supplementary material, table S1; File S3), with no admixture event included in the analysis (electronic supplementary material, figure S1).

In Scenario 1, the South Moluccas populations were considered as ancestral and the North Moluccas populations diverged at time t, before a reduction in population size in the South at time tc. In Scenario 2, the northern populations were considered as ancestral and the southern populations diverged at time t, resulting from a colonization event with a reduction in genetic diversity (founder event). We also linked this demographic prior distribution according to historical text of *M. fragrans* distribution in the Moluccas as stated by Hanna [58] and Lape [59] to infer the ancestry and divergence time of the genetic groups.

Posterior distributions of demographic parameters were then estimated in DIYABC Random Forest. For each scenario, simulated datasets were generated from the prior distributions and compared with the observed genetic data using summary statistics. The closest simulations were retained to approximate posterior probabilities of scenarios and parameter distributions. Scenario selection was based on posterior probability, and parameter estimates were summarized using posterior means and 95% credibility intervals. Robustness was evaluated through cross-validation and posterior predictive checks.

3. Results

(a) Genetic diversity and population structure of *M. fragrans* at nSSR loci

We found a total number of 210 alleles using the 14 nSSR (corresponding to 15 diploid loci, see above), with the lowest number observed in Banda (N_A = 68) and the highest in Bacan (N_A = 176). No private alleles were detected in the South Moluccas, but we identified 15 private alleles exclusive to populations in the North Moluccas, 11 of which are unique to Bacan Island. The mean number of alleles per population (N_M) ranged from 4.53 to 11.73 across the five populations (table 1). We found lower genetic diversity in Ambon and Banda than in Ternate, Tidore and Bacan, as shown by the rarefied allelic richness statistics ($AR_{(k = 46)}$, table 1). The inbreeding coefficient (F_{IS}) values were found to be significantly greater than zero in Ambon, Ternate and Bacan, indicating a signal of inbreeding.

Table 1. Genetic diversity in *M. fragrans* populations at 15 polymorphic microsatellite loci.

populations	N	N_P	N_A	N_M	$AR_{(k=46)}$	H_O	H_E	F_{IS}
Ambon	161	7	75	5.00	3.85	0.512	0.547	0.068*
Banda	72	4	68	4.53	3.84	0.587	0.606	0.038
Ternate	55	6	154	10.26	8.63	0.711	0.770	0.086*
Tidore	30	3	154	10.26	9.74	0.764	0.812	0.076
Bacan	75	9	176	11.73	8.98	0.668	0.776	0.147*

Number of individuals analysed (N), number of subpopulations in the population (N_P), number of alleles (N_A), mean number of allele per populations (N_M), rarefied allelic richness for $k = 46$ gene copies ($AR_{(k=46)}$), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}) calculated overall loci on each population, where an asterisk indicates values significantly different from zero with $p < 0.01$ [60].

The global genetic structure among populations as measured by F_{ST} was 0.069. Meanwhile, the pairwise F_{ST} between populations ranged from 0.012 (between Ternate and Bacan) to 0.182 (between Ambon and Tidore). The genetic structure within populations (F_{ST} among sub-populations) was globally relatively low (F_{ST} values from 0.008 in Bacan to 0.040 in Tidore; see details in electronic supplementary material, tables S2 and S3).

Bayesian clustering analyses suggest that the most likely number of intra-specific genetic clusters within our dataset is two, as indicated by both the Evanno method and the GTI method (electronic supplementary material, figure S2). Individuals from Ambon and Banda are assigned to a first genetic cluster, referred as the 'South Moluccas cluster' hereafter, whereas individuals from Ternate, Tidore and Bacan are generally assigned to a second genetic cluster, which we name the 'North Moluccas cluster' (figure 2; $F_{ST} = 0.089$ between the two clusters). A part of these individuals show variable admixture proportions (probability of assignation to a cluster between 0.2 and 0.9) with the South Moluccas cluster (31%, 4% and 26% respectively for Ternate, Tidore and Bacan).

(b) Genetic diversity and population structure of *M. fragrans* at cpDNA loci

Of the 94 individuals analysed for whole cpDNA genome data, 10 were discarded as they had more than 25% missing data. Of the remaining 84 individuals (with the four *M. argentea* individuals included), we obtained a total of 146 SNPs (109 SNPs if *M. argentea* individuals are excluded). We obtained a total of 30 haplotypes in *M. fragrans* and three additional haplotypes found exclusively in *M. argentea*. Within *M. fragrans*, we observed one common haplotype (*Hap*3, approx. 60% of the individuals) that was present in all populations throughout the Moluccas archipelago (figure 3; electronic supplementary material, figure S4). Two other common haplotypes (*Hap*4 and *Hap*17) were present only in the North Moluccas. Unique haplotypes were found in all populations (three in Ternate, four in Tidore, seven in Bacan, seven in Ambon and six in Banda). The most common haplotype is placed in the centre of the phylogenetic network (figure 3). We also observe that *Hap*3 differs from the *M. argentea* haplotypes by 48 mutations. Diversity statistics obtained for the cpDNA dataset (number of segregating sites, nucleotide diversity Π) suggest a higher level of diversity in Bacan and Ternate (table 2). At the cluster level, the nucleotide diversity is relatively lower in the South Moluccas cluster ($\Pi = 0.122$) than in the North Moluccas cluster ($\Pi = 0.280$). The AMOVA shows that the genetic variance is mainly explained by the cluster ($\Phi = 41.50\%$ of the total variation, $p < 0.001$; electronic supplementary material, table S4) and the sub-population (52%) levels. We found no signal of phylogeographic structure within our dataset ($N_{ST} = 0.462 < G_{ST} = 0.532$; $p < 0.05$).

(c) Inference of population size changes in *M. fragrans*

The DIYABC Skylineplot analyses show no evidence of significant population change over time in Ternate, Tidore and Bacan populations, with a Bayes factor (BF) [61] of 0.53, 0.45 and 0.34, respectively (figure 4). Migraine revealed a population expansion in Ternate, with $\theta_\mu > \theta^{anc}{}_\mu$. However, Ambon and Banda exhibit a strong relatively recent bottleneck ($BF = 2.17$ and $BF = 141$, respectively). Similar patterns of population size reduction in Ambon and Banda were also shown by our MIGRAINE analyses. The ratio of scaled population sizes $\theta_{ratio} = \theta_0 / \theta_A$ (see electronic supplementary material, table S7) indicates a recent reduction in population size in Ambon and Banda populations.

(d) Reconstructing population history of *M. fragrans*

Model selection according to DIYABC Random Forest using all three datasets (nSSR, cpDNA, and both nSSR and cpDNA) favoured Scenario 1 as the best supported scenario, with a posterior probability of 0.73, 0.88 and 0.79 (electronic supplementary material, figure S1A, table S5). Based on Jeffreys's scale [61], the corresponding Bayes factors ($BF = 2.7$–7.3) indicate substantial to strong support of population size change for Scenario 1 over Scenario 2 (electronic supplementary material, table S5). This indicates that simulations generated under this scenario more closely matched the observed summary statistics than those from Scenario 2. In particular, the summary statistics showed the highest variable importance in distinguishing among scenarios and were more compatible with Scenario 1. In Scenario 1, the divergence time (t) between the two genetic clusters of *M. fragrans*

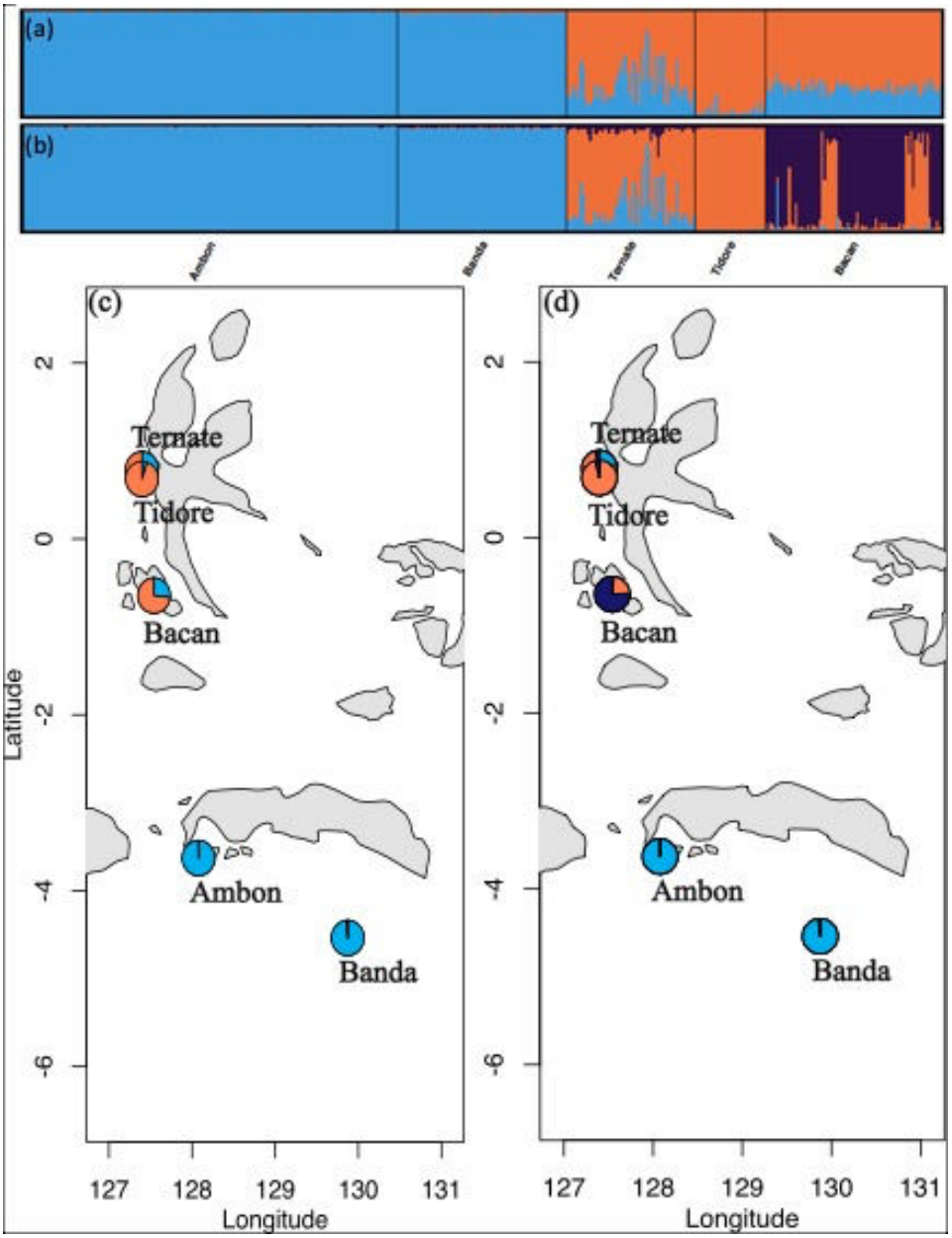

Figure 2. Intra-specific genetic structure of nutmeg (*Myristica fragrans*) across the Moluccas, Indonesian archipelago, inferred from Bayesian clustering of 15 nuclear microsatellite (nSSR) loci. (a) Individual admixture proportions at $K = 2$ and (b) at $K = 3$, as estimated by Structure. (c) Geographic distribution of the inferred genetic clusters for $K = 2$ and (d) for $K = 3$, shown as pie charts showing the proportion of individuals in each cluster on each island. See electronic supplementary material, figure S3 for further explanation.

occurred around 2159–8231 generations ago, and the population bottleneck in the South Moluccas cluster occurred around 299–402 generations ago (electronic supplementary material, table S6).

4. Discussion

We aimed to identify the centre of origin of the Indonesian nutmeg, *M. fragrans*. We applied a population genetic approach and used genetic data obtained from nSSR genotyping and whole plastid genome sequencing. Our results suggest that *M. fragrans* originated from the South Moluccas and colonized North Moluccas islands well before the management of the species by humans (Middle, Late Pleistocene). The species was thus present across the entire Moluccas at the start of species trading history.

We found two different intra-specific genetic clusters in the Moluccas, one in South Moluccas (Banda and Ambon) and the other in North Moluccas (Ternate, Tidore and Bacan). The presence of a third genetic cluster in Bacan suggests additional genetic structuring that needs further investigation, notably through additional sampling in this region. The South Moluccas cluster showed lower diversity at nSSRs and cpDNA markers than the North Moluccas cluster. According to the hypothesis that the centre of origin of a species presents higher genetic diversity, this suggests that the North Moluccas would actually be the centre of origin of the species. However, our ABC analyses supported the South Moluccas as the centre of origin rather than the North Moluccas.

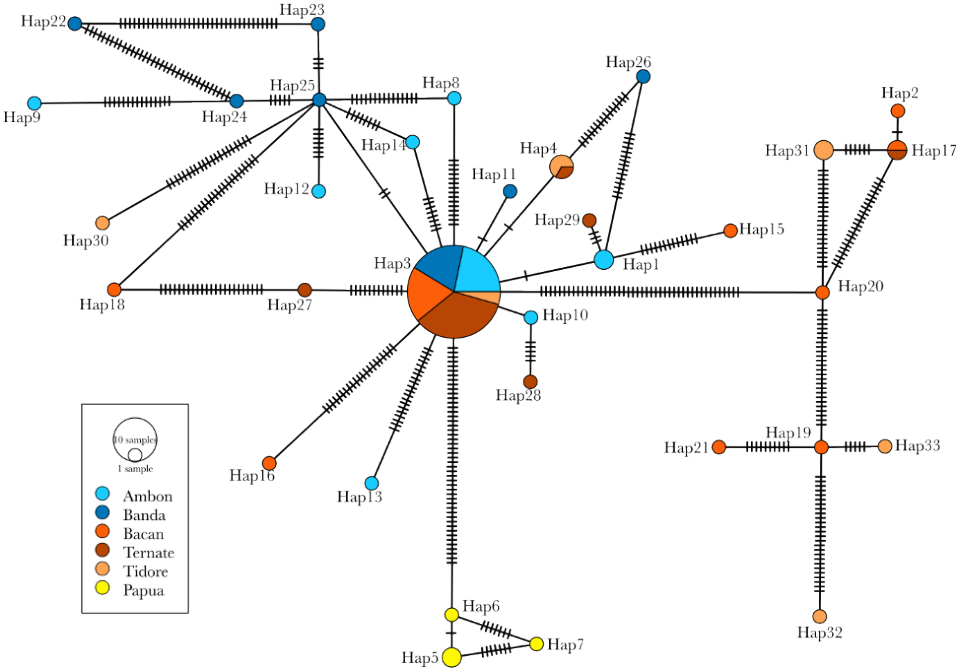

Figure 3. Maximum parsimony network of chloroplast DNA (cpDNA) haplotypes in nutmeg (*Myristica fragrans*). Each circle represents a distinct haplotype, with colours indicating the population of origin (Ambon, Banda, Bacan, Ternate and Tidore; island names in the Moluccas, Indonesian archipelago). Hash marks on connecting branches denote mutational steps. Haplotypes *Hap*5, *Hap*6 and *Hap*7 (shown in yellow) correspond to *M. argentea*, included as an outgroup.

Table 2. Genetic diversity in *M. fragrans* populations at cpDNA loci.

populations	*N*	*H*	*Π*	*S*	*P*
Ambon	20	8	0.116	56	14
Banda	15	7	0.117	50	10
Ternate	20	5	0.312	90	45
Tidore	8	6	0.188	59	0
Bacan	19	10	0.277	96	65
cluster level	***N***	***H***	***Π***	***S***	***P***
South Moluccas	35	14	0.122	82	23
North Moluccas	47	17	0.280	113	77

Number of individuals analysed (*N*), number of haplotype (*H*), nucleotide diversity (*Π*), number of segregating sites (*S*), number of parsimony-informative sites (*P*).

The discrepancy between the observed levels of genetic diversity and the centre of origin supported by the ABC analyses can probably be explained by the management history of the species in South Moluccas and/or the presence of inter-specific gene flow in North Moluccas (see below for a discussion of these aspects). The best-supported scenario further supports a colonization of *M. fragrans* from South to the North Moluccas between 2159 and 8231 generations ago and a demographic bottleneck in South Moluccas populations 299–402 generations ago. Assuming a generation time of 50 years in *M. fragrans*, species migration from South to North would have thus occurred *ca* 411–108 ka ago (corresponding to the Middle/Late Pleistocene), and the demographic bottleneck would have occurred *ca* 20–15 ka ago (Late Pleistocene). It is worth noting that the dating of demographic events resulting from ABC analyses should be interpreted with caution [55], particularly for long-lived species, as estimating generation time is challenging [62,63].

The first individuals that colonized North Moluccas were probably carrying the cpDNA haplotype *Hap*3. Actually, the *Hap*3 haplotype is frequent and widespread across the entire Moluccas region and was also inferred to be ancestral, being directly connected to the outgroup (*M. argentea*) and having a central placement in the phylogenetic network. Most of the other haplotypes are endemic to a specific island or group of islands and appeared to have diverged from *Hap*3. Also, the South and North Moluccas haplotypes tend to be in two different groups in the haplotype network, which is in line with the North/South genetic divide observed from nSSRs. Under this scenario, we would expect the presence of a phylogeographic signal, which is not the case. Recent human-driven dispersal of the species has potentially blurred this signal.

M. fragrans likely migrated northward via animals or sea dispersal, as no land bridges have linked the North and South Moluccas since their emergence in the Oligocene/Miocene, even during glacial sea-level lows [64–66]; this supports observed differences between the general flora of the North and South Moluccas [67]. The origin of the Asian genus *Myristica* has been dated around the Late Miocene based on plastid data [68–70], at a time when both North and South Moluccas were already

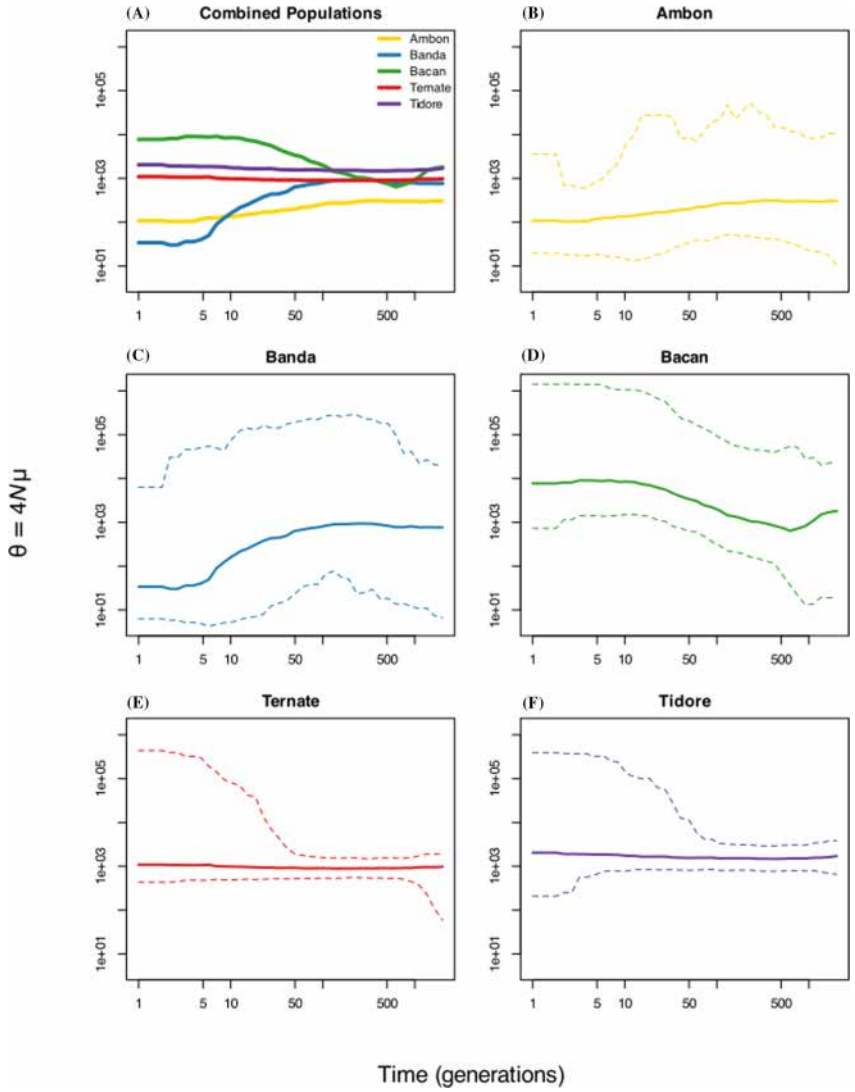

Figure 4. Demographic history of nutmeg (*Myristica fragrans*) in the five islands under study using DIYABC skylineplots (A). The figures show changes in population size through time for Ambon (B), Banda (C), Bacan (D), Ternate (E) and Tidore (F). Each plot displays the median estimate of population size (solid coloured line) from past (right) to present (left), with 95% highest posterior density (HPD) intervals indicated by dashed lines.

present. The geological history of the North and South Moluccas islands and the timing of colonization obtained in our analyses thus suggest that the dispersal of *M. fragrans* was probably mediated by animals or ocean currents as opposed to rafting across tectonic terranes. Hornbills (Bucerotidae) are known to be involved in seed dispersal of Myristicaceae [71]. These big birds potentially allow for long-dispersal events, although we cannot exclude that marine dispersal played a role in the demographic expansion of these species. It has also been demonstrated that seeds can be dispersed by marine currents over long geographic distances, and *M. fragrans* is no exception [72]. If some seeds kept their viability after marine dispersal, this might have also contributed to the dispersal of the species, as has been shown for other tree species [73,74]. It has also been suggested that the sea currents in the Moluccas during the Pleistocene flowed northwards [75], allowing seed dispersal from South Moluccas to North Moluccas.

Since our demographic analyses suggest that *M. fragrans* colonized the North Moluccas during the Pleistocene, they support the presence of the species all across the Moluccas before the arrival of Europeans. We found a number of historical accounts supporting this hypothesis [76–78] (see also electronic supplementary material S3). It is thus striking that at that time, most Europeans were focused on getting material from the Banda Islands to circumvent the Dutch monopoly and propagate the species in their tropical colonies [79,80]. Why was the focus initially on getting material from the strictly controlled islands of Banda and Ambon, if plantation material was more easily accessible in the North Moluccas? We do not have a definitive answer to this question. It seems that Europeans were in search of the mysterious historical place of cultivation of nutmeg (i.e. the place where nutmeg was cultivated before being imported to Europe along a complex network of different traders and nations). The North Moluccas were known for the cultivation of cloves [81] and the South Moluccas for the cultivation of nutmegs [82,83]. The search for this 'golden place' and the particular focus on the South Moluccas where the species was first grown *en masse* probably impeded them realizing that the species could be present elsewhere. Here, we can speculate that historical information on the distribution of the species was strictly controlled by the VOC. This is supported by the embargo set by the VOC on the publication of Rumphius 'Herbarium amboinense', a document that includes information about the trade and cultivation of the species [84,85].

During the human-managed evolutionary history of *M. fragrans*, it is likely that the North Moluccan gene pool remained undisturbed in contrast to the South Moluccan stock that was strongly impacted. We observed higher levels of genetic diversity both for the SSR and cpDNA in the North Moluccan genetic cluster than for the South Moluccas. The lowest level of genetic diversity observed in the South is probably due to the reduction in *M. fragrans* population size during the Dutch colonization period in the seventeenth and eighteenth centuries. In point of fact, the Dutch secured a monopoly on the production [86] and trade of nutmeg by adopting a strong policy of resource control (extirpation of trees, destruction of a part of the production to keep prices high) [24]. Such management practices certainly negatively impacted the genetic diversity of the species. This pattern is consistent with global observations reported by Fuller *et al.* [87], who found that domesticated plant populations often experience a loss of genetic diversity in their historical centres of origin due to long-term cultivation and commercialization.

A reduction in population size in the South is supported by our demographic analyses, with a (relatively recent) bottleneck signal observed in Banda and a less-marked one in Ambon. In contrast, the demographic tests tend to support a constant population size in the North Moluccan islands. The dating of the population bottleneck is a little older than the Holocene period, but dating recent bottlenecks is almost impossible. Moreover, it is worth noting that it is extremely difficult to apply a time calibration in demographic analyses that use generation time as time unit for long-lived species [62]. Here, we have set an arbitrary generation time of 50 years, which implies the detection of a bottleneck event before the Holocene period. Even though our analyses were based on only 15 nSSR, our results are roughly in agreement with the knowledge we have on the historical management of the species. However, we need to keep in mind that time estimates in demographic analyses are expressed in generations and carry inherent uncertainty, often spanning an order of magnitude. While we used a generation time of 50 years to approximate timing in calendar years, this value serves only to provide a rough order of magnitude. The real uncertainty lies in the posterior distribution, and further precision would be misleading given the limits of resolution in population genetic inference for long-lived species. Furthermore, demographic inferences based on a limited number of loci, especially with arbitrary assumptions on generation time, may lack precision and should be interpreted with care. The timing and intensity of demographic events (such as bottlenecks) remain sensitive to these parameters, and our estimates should be seen as approximations rather than exact reconstructions.

The observed pattern of higher genetic diversity in the North Moluccan cluster might also be the result of inter-specific gene flow [16,17]. The potential for hybridization of *M. fragrans* with other *Myristica* species present in these islands is not known. According to de Wilde [88], 20 *Myristica* species are present in the Moluccas, which suggests that a number of *Myristica* sister species can be found in sympatry with *M. fragrans*. The radiation of *Myristica* species is probably quite recent, as demonstrated by the high rate of transferability of nSSR markers from *M. fragrans* to sister species [31]. A recent radiation implies that inter-specific gene flow may occur. It is worth noting that morphologically, *M. fragrans* individuals sampled in these islands are, to the best of our knowledge, similar to *M. fragrans* in South Moluccas. That would imply that if inter-specific gene flow occurred, it might have had only a small effect on the phenotypic diversity of *M. fragrans*. In the absence of additional genetic data on other *Myristica* species present in the region, we cannot support or rule out this hypothesis, which deserves further investigation.

(a) Perspectives for conservation and sustainable management and use

Our results bring insights that will be important for conserving and managing the genetic diversity within *M. fragrans*. Genetic differentiation observed between the North and South Moluccas in this study should be integrated into conservation strategies and management practices for this species. The genetic diversity in Banda and Ambon has been particularly impacted by past human practices, with potential consequences for the adaptive potential of the species in these islands. To date, this lower level of genetic diversity does not seem to have caused any noticeable reduction in nutmeg production or susceptibility to pests and diseases, but such impacts may appear in the near future resulting from indirect drivers of change, particularly climate change.

Banda and Ambon islands were, and still are, the main sources of planting material introduced to other parts of Indonesia and across all major tropical regions of the world [89,90]. Given the low genetic diversity on these islands, the limited number of male trees maintained on farms and the common practice of sourcing seeds from a single mother tree, it is likely that the genetic diversity introduced to other regions is also low.

The best-known variety is the Banda Island nutmeg, but it is unclear whether its popularity is due to historical cultivation centred around the Banda Islands, intentional selection for resilience to environmental factors (e.g. soil properties), genetic differences or a combination of the above. Testing differences in the quality of the nuts by conducting common garden experiments would be needed to inform strategies of genetic resource management [91]. If no significant differences exist, it would be interesting to consider the sourcing of additional material from North Moluccas in order to increase the level of genetic diversity and thus the potential resilience of introduced populations.

We cannot exclude that additional original genetic resources are present elsewhere. Here, we have sampled only a representative part of the Moluccas islands. This sampling was sufficient to infer the native range of the species, but not for conservation purposes. The presence of a third genetic cluster in Bacan island is interesting as it outlines an additional genetic structuring. We would need additional samples from the whole North Moluccas area (Halmahera, Sula, Obi, Misool in particular) to better interpret this result and get a more comprehensive view of the spatial genetic diversity of *M. fragrans*. Conducting an exhaustive sampling in a complex archipelago such as Indonesia is particularly complicated and time consuming (approx. 1000 islands for the Moluccas only). This probably explains why the local flora remains largely undocumented. Concerning *M. fragrans*, we cannot rule out that some additional unique resources exist somewhere else in the Moluccas, such as in the more southerly islands (Kai, Aru, Tanimbar, etc.), but to resolve this, a much more intensive sampling is needed.

Ethics. This study was authorized by Indonesian National Research and Innovation Agency (BRIN) with research permit to J.D. (144/SIP/FRP/E5/Ditk.KI/V/2018) and collecting permit to J.K. (B-3382/IPH.1/KS.02.04/IX/2019 and B-75/IV/KS.01.04/3/2022).

Data accessibility. The dataset titled 'Retracing the center of origin and evolutionary history of nutmeg Myristica fragrans, an emblematic spice tree species' has been reviewed by a curator and approved for publication. It is publicly accessible at Dryad repository [92].

Supplementary material is available online [93].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.K.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, software, visualization, writing—original draft, writing—review and editing; M.C.: formal analysis, validation; P.R.G.: supervision, validation, writing—review and editing; M.d.N.: methodology, validation, writing—review and editing; N.S.: conceptualization, funding acquisition, supervision, validation, writing—review and editing; J.D.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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