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Genetic diversity and population structure of *Juniperus foetidissima* in Arasbaran: Implications for conservation using SCoT markers

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ABSTRACT

Foetid juniper (*Juniperus foetidissima*) is an important species within the Cupressaceae family, possessing considerable ecological and biological value. In Iran, *J. foetidissima* is found exclusively in the Arasbaran Biosphere Reserve. This study evaluated the genetic diversity and structure of eight *J. foetidissima* populations in the Arasbaran forest using six polymorphic SCoT markers, aiming to select genetically diverse individuals for establishing a seed orchard. A total of 118 polymorphic bands were generated using the six SCoT primers, indicating a 100% polymorphism rate and an average of 19.6 polymorphic bands per primer. The number of polymorphic bands per primer ranged from 13 to 29, with SCoT10 and SCoT11 amplifying the highest and lowest numbers of bands, respectively. The average polymorphic information content (PIC) across primers was 0.321, with SCoT41 exhibiting the highest PIC value of 0.378 and SCoT10 the lowest at 0.279. The average values of genetic diversity parameters—including the number of alleles (Na), effective number of alleles (Ne), Shannon's information index (I), and expected heterozygosity (He)—were 1.23, 1.29, 0.287, and 0.184, respectively. Analysis of molecular variance (AMOVA) revealed that 87% of the observed genetic variation occurred within populations, while 13% was distributed among populations, indicating that genetic diversity within populations is more substantial than that among populations. The UPGMA clustering method grouped the 48 individuals from the eight populations into five distinct clusters. These findings provide valuable insights for the conservation, breeding, and management strategies of *J. foetidissima*.

Key words: Arasbaran biosphere reserve, Conservation genetics, Genetic variability, *Juniperus foetidissima*, SCoT markers.

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INTRODUCTION

The Arasbaran Forest, located in northwest Iran, is one of nine designated Biosphere Reserves in the country. According to existing literature, this area is home to 1,067 identified plant taxa, 18 of which are endemic to Iran (Hamzeh *et al.*, 2010).

The genus *Juniperus*, belonging to the Cupressaceae family, comprises approximately 68 species worldwide. These aromatic, drought-resistant plants are typically found in mountainous regions of the Northern Hemisphere, at altitudes ranging from 500 to 3,000 meters. Some species are also present in Africa (Adams, 2014). In Iran, the *Juniperus* genus primarily includes five species: *J. communis*, *J. oblonga*, *J. sabina*, *J. foetidissima*, and *J. excelsa* (Emami et *al.*, 2007).

Juniperus foetidissima is a dioecious, wind-pollinated, evergreen coniferous tree with a conical shape that can grow up to 20 meters tall. Its scale-like leaves are relatively thick, measuring approximately 1.5 mm, especially when compared to closely related *Juniperus* species (Figure 1). The seed cones are globular, ranging from 7 to 12 mm in diameter, and typically take two years to mature, usually containing only one or two seeds (Farhat *et al.*, 2023). *J. foetidissima* is unique to the Arasbaran forest and exhibits diversity through several factors, including genetic variation within populations, adaptation to varying environmental conditions, and distinctive genetic traits. The European Medicines Agency has recognized the antimicrobial, antiviral, antioxidant, and anti-inflammatory properties of *Juniperus* berries and their associated essential oils (Mertiri *et al.*, 2024). The diverse therapeutic properties of *Juniperus* are attributed to its extensive chemical composition, which includes 279 unique compounds such as terpenoids, lignans, flavonoids, coumarins, and other constituents identified to date (Pan *et al.*, 2024). Beyond its economic and medicinal importance, *J. foetidissima* holds significant ecological value. It is often the only tree species capable of thriving in semi-arid environments, playing a crucial role in soil protection and climate regulation (Douaihy *et al.*, 2011).

Assessing genetic variation and its distribution within and among populations is fundamental for obtaining the necessary data to develop strategies for breeding and conserving genetic resources in plant species (Bruschi *et al.*, 2003; Meloni *et al.*, 2006). Genetic studies on woody plant populations reveal a significant level of diversity within populations (Hao *et al.*, 2018; Motahari *et al.*, 2021; Buer *et al.*, 2022).

The genetic polymorphism observed in plant populations arises from the interplay of evolutionary forces. As a dioecious species, *J. foetidissima* is obligately outcrossing—a reproductive strategy that typically promotes high levels of heterozygosity and genetic diversity within populations by preventing self-fertilization and reducing biparental inbreeding. The primary sources of this variation include mutation, which introduces new alleles, and gene flow (migration) through pollen or seed dispersal from other populations, which can introduce novel genetic material and counteract genetic drift (Andrews, 2010). However, the isolated nature of the Arasbaran habitats may restrict gene flow, potentially leading to population differentiation. To elucidate the impact of these forces, principles of population genetics are essential. Hardy-Weinberg Equilibrium (HWE) tests will be employed to detect significant deviations, such as heterozygote deficits, which could indicate non-random mating, selection, or genetic drift. Furthermore, diversity indices such as the Shannon Index and Nei's gene diversity will be calculated to quantitatively assess the level of polymorphism within and among populations. These analyses will be used to formulate and test

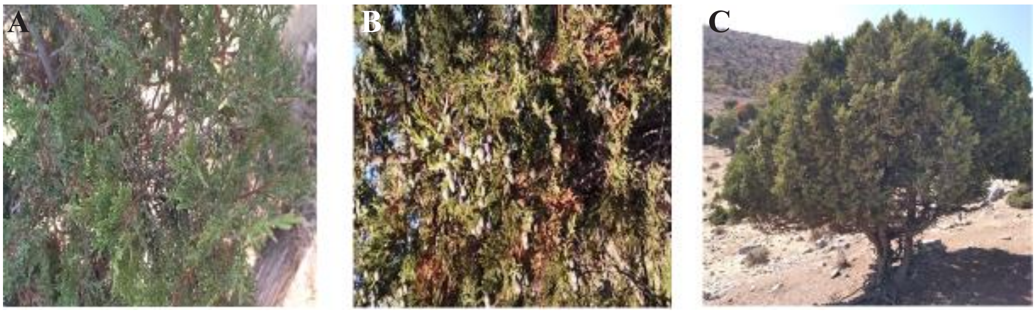

Figure 1. Morphological characteristics of *Juniperus foetidissima* in the Arasbaran region: **A:** Foliage and leaf arrangement, **B:** Mature seed cones, and **C:** General tree growth habit.

hypotheses regarding the relative roles of mutation, gene flow, and genetic drift in shaping the population structure of *J. foetidissima* in this unique biosphere.

To date, no comprehensive molecular studies have been conducted on different populations of *Juniperus foetidissima* in Iran. However, several molecular investigations have been carried out on *Juniperus excelsa* (Kermani *et al.*, 2010; Khoshal Sarmast *et al.*, 2018; Rahimian Boogar and Salehi, 2021).

Despite being the most widely distributed conifer genus globally, genetic research on *Juniperus foetidissima* remains limited. Most extensive genetic studies on junipers have focused on the phylogeny and phylogeography of the genus, investigating differentiation among and within species using cpDNA and ITS markers. Only a few juniper species have been analyzed for their within-species genetic variability (Terrab *et al.*, 2008; Douaihy *et al.*, 2011; Yücedağ and Gailing, 2013; Korshikov and Nikolaeva, 2013; Teixeira *et al.*, 2014; Kim *et al.*, 2018; Evren and Kaya, 2021; Ju *et al.*, 2022; Lu *et al.*, 2022; Yermagambetova *et al.*, 2023; Jadwiszczak *et al.*, 2024), revealing significant levels of genetic diversity within these species.

The Start Codon Targeted (SCoT) marker, initially proposed by Collard and Mackill (2009) in rice, is a molecular marker based on a single-primer amplification reaction. This marker targets specific genes and involves genome amplification using a single primer designed according to the conserved nature of the ATG translation initiation codon and the flanking sequences of plant genes. The objective of this approach is to identify a high percentage of dominant polymorphic markers within candidate functional gene regions through a straightforward procedure. Compared to other commonly used markers such as RAPD, AFLP, SSR, and ISSR, SCoT markers have demonstrated greater efficiency and effectiveness in identifying trait-linked markers, making them valuable tools in molecular marker-assisted breeding (Buer *et al.*, 2022). SCoT markers are widely recognized as preferred markers for studying intraspecific genetic variation and genetic structure.

To date, no studies have assessed the genetic variability of *J. foetidissima* populations across Iran or globally. Therefore, this research aimed to investigate the genetic diversity and structure within and among different populations of *J. foetidissima*, as well as to develop conservation strategies. This data is crucial for understanding the historical processes that have shaped genetic diversity and for designing effective conservation and reforestation programs. The results of this study can also support the establishment of a *J. foetidissima* seed orchard in Arasbaran.

MATERIALS AND METHODS

Plant material and DNA extraction

In this study, young leaves were collected from 48 GPS-marked individuals of *Juniperus foetidissima* across eight populations in the Arasbaran forest, located in northwest Iran. Each population was represented by six individuals (Figure 2 and Table 1). Samples were collected with a minimum spacing of 50 meters between individuals, and the leaves were immediately frozen at -80°C before analysis. Genomic DNA was extracted from 50 mg of young leaves using a modified CTAB protocol (Saghai-Maroof *et al.*, 1984). The quantity and quality of the extracted DNA were assessed using spectrophotometry (Thermo Fisher Nanodrop 2000) and 1% TAE agarose gel electrophoresis.

ScoT amplifications

Twenty-nine SCoT primers were selected based on previous research (Luo *et al.*, 2010; Vivodik *et al.*, 2019) and synthesized by Metabion (Germany). From these, six highly polymorphic and reproducible SCoT primers were chosen for the analysis of 48 individuals. PCR reactions were performed in a total volume of 10 µL, containing 5 µL of red mastermix (Ampliqon, Denmark), 1 µL of SCoT primer at a concentration of 10 pmol, 1 µL of genomic DNA (20 ng), and 3 µL of nuclease-free water. Amplification of the SCoT fragments was conducted using a Mastercycler Gradient Thermal Cycler (Eppendorf, Germany) with the following program: an initial denaturation at 95 °C for 5 minutes, followed by 40 cycles of denaturation at 95 °C for 1 minute, annealing at the specific primer temperature for 1 minute, extension at 72 °C for 90 seconds, and a final extension at 72 °C for 5 minutes. PCR products were separated on 2% agarose gels in TBE buffer, stained with Safe Stain, and visualized under UV light. A 100-bp DNA ladder (SMOBIO, Taiwan) was used to determine band sizes. To ensure the absence of contamination, a negative control PCR reaction without genomic DNA was included in each run.

Genetic analyses

The polymorphic information content (PIC) of the markers indicates the discriminatory power of each primer pair. This measure of marker detection power depends on both the number of polymorphic markers detected by each primer and the frequency of each marker. The PIC parameter was calculated using Excel.

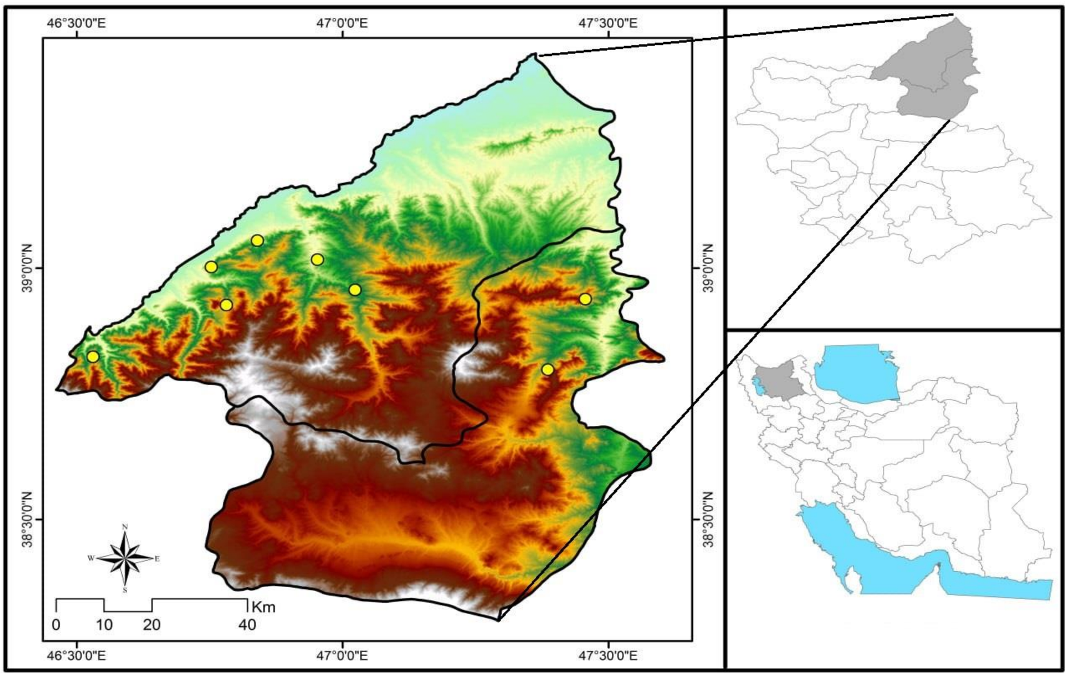

Figure 2. Geographic distribution map showing the locations of the eight sampled populations of *Juniperus foetidissima* within the Arasbaran Biosphere Reserve, Northwest Iran.

Table 1. Geographical coordinates and characteristics of eight natural populations of *Juniperus foetidissima* sampled from the Arasbaran Biosphere Reserve, Iran.

Population name	Longitude	Latitude	Elevation (m)
K	N38°55' 35"	E46°46' 53"	1345
L	N39°00' 07"	E46°45' 11"	358
M	N39°03' 16"	E46°50' 23"	593
N	N39°01' 00"	E46°57' 10"	618
O	N38°57' 24"	E47°01' 24"	805
P	N38°47' 53"	E47°23' 09"	1158
Q	N38°56' 18"	E47°27' 23"	1300
R	N38°49' 25"	E46°31' 50"	1226

In this study, we conducted a comprehensive analysis of genetic diversity parameters to gain insights into the genetic structure and differentiation both among and within populations. The parameters we focused on include the number of alleles (Na)—calculated based on the presence or absence of bands, where genotypic and gene frequencies at each locus in each population were determined, and the mean number of alleles per population was computed using GenAlEx software—the effective number of alleles (Ne), Shannon's information index (I), expected heterozygosity (He), and unbiased expected heterozygosity (uHe). These parameters provide a robust measure of genetic diversity, reflecting both the richness and evenness of alleles within a population.

The software GenAlEx version 6.5 (Peakall and Smouse, 2012) was used to estimate these parameters. GenAlEx is a powerful tool for population genetic analyses, offering a wide range of options for exploring and analyzing genetic data. In addition to these parameters, we also calculated Nei's genetic distances among populations and performed a cluster analysis of the eight populations using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). These analyses were conducted using NTSYS-pc version 2.10 (Rohlf, 2000), a widely used program for multivariate statistical analysis in ecology and systematics.

Furthermore, we conducted an Analysis of Molecular Variance (AMOVA) to evaluate genetic differentiation both among and within populations.

Table 2. Genetic polymorphism parameters generated by six SCoT markers across 48 individuals of *Juniperus foetidissima.*

Primer name	Primer sequence	AT (°C)	PIC Value	PB
SCoT4	5' CAACAATGG CTA CCACCT3'	54	0.288	14
SCoT8	5'CAACAATGGCTACAACGT3'	54	0.330	22
SCoT10	5'CAACAATGGCTACCAGCC3'	56	0.279	29
SCoT11	5'AAGCAATGGCTACCACCA3'	54	0.366	13
SCoT23	5'CACCATGGCTACCACCAG3'	58	0.287	22
SCoT41	5'CAATGGCTACCACTGACA3'	54	0.378	18

AT: Annealing temperature, PB: The number of polymorphic bands, PIC: Polymorphic information content.

AMOVA is a statistical method that partitions genetic variance across hierarchical levels and quantifies genetic differentiation. This analysis is crucial for understanding the distribution of genetic diversity within and among populations, as well as determining whether significant differences exist in this distribution.

Principal coordinate analysis (PCoA) was performed to visualize the genetic relationships among populations and individuals. This method reduces complex genetic data into a few key coordinates, which can be plotted in two or three dimensions to illustrate the clustering or grouping of populations or islands. By simplifying the genetic data into principal coordinates, researchers can visually represent the genetic relationships between different populations or groups. Plotting these coordinates in two or three dimensions facilitates the observation of how populations cluster based on their genetic similarities. This approach provides valuable insights into genetic diversity, relatedness, and evolutionary history, offering a clear understanding of the genetic composition and historical connections among different groups.

RESULTS AND DISCUSSION

SCoT polymorphism analysis

In this study, twenty-nine Start Codon Targeted (SCoT) primers were applied to individuals of *Juniperus foetidissima*. Of these, six primers produced distinct, high-resolution polymorphic bands (Table 2). These bands were used to assess the genetic structure and variation among the populations and individuals of *J. foetidissima.*

The amplification process produced 118 bands that were scored. All of these bands (100%) were polymorphic, with an average of 19.6 polymorphic bands per primer. This high level of polymorphism indicates substantial genetic variation within the *J. foetidissima* population.

Table 3. Polymorphism information of 6 SCoT primers in 48 individuals of *J. foetidissima*.

Population label	N	Na	Ne	I	He	uHe
K	6	1.203	1.271	0.272	0.174	0.190
L	6	1.347	1.284	0.292	0.184	0.200
M	6	1.347	1.312	0.311	0.199	0.217
N	6	1.178	1.330	0.302	0.199	0.217
O	6	1.169	1.294	0.279	0.181	0.197
P	6	1.220	1.332	0.305	0.200	0.218
Q	6	1.229	1.266	0.274	0.173	0.189
R	6	1.144	1.268	0.264	0.169	0.184
Mean	6	1.23	1.29	0.287	0.184	0.201

N: Sample size, Na: The number of alleles, Ne: The effective number of alleles, I: Shannon's information index, He: Expected heterozygosity, uHe: Unbiased expected heterozygosity.

Among the six SCoT primers, SCoT10 produced the highest number of bands (29), while SCoT11 generated the fewest (13). The Polymorphic Information Content (PIC) parameter, which ranges from zero to 0.5 in dominant markers, was also calculated. A higher *PIC* value indicates a greater frequency of polymorphism at that locus within the studied populations and a stronger ability to discriminate genetic differences among individuals. In this study, the highest PIC value was 0.378 (corresponding to SCoT41), and the lowest was 0.279 (corresponding to SCoT10).

For genetic diversity parameters, the Na values produced by the six SCoT primers ranged from 1.144 to 1.34, with a mean of 1.23; the Ne values ranged from 1.226 to 1.332, with a mean of 1.29; the I values ranged from 0.264 to 0.311, with a mean of 0.287; and the He values ranged from 0.169 to 0.200, with a mean of 0.184 (Table 3).

These results offer a comprehensive understanding of the genetic diversity and differentiation within and among *J. foetidissima* populations. The high level of polymorphism observed indicates substantial genetic variation, which is crucial for the long-term survival and adaptability of the species. The findings from this study can inform conservation efforts and contribute to the development of effective management strategies for *J. foetidissima*.

Genetic differentiation

The Nei similarity matrix generated by the GenAlEx program indicated that genetic similarity ranged from 0.916 to 1.00, with an average of 0.957, suggesting a low level of genetic diversity within the *J. foetidissima* population (Table 4). Populations P and Q, as well as Q and R, were found to be the most similar. In contrast, the lowest genetic similarity was observed between populations K and Q.

The Analysis of Molecular Variance (AMOVA) quantifies genetic variation within and among populations. The PhiPT values obtained from this analysis indicate that a significant proportion (87%) of the genetic variation exists within populations, reflecting a high level of genetic diversity within each population. In contrast, only 13% of the genetic variation is attributed to differences among populations. This suggests that, although some genetic differentiation occurs among populations, the majority of genetic diversity is contained within individual populations (Table 5).

Phylogeographical analyses

Using Nei's (1972) genetic distance values to construct a UPGMA dendrogram for examining relationships among populations, one cluster was identified (Figure 3). The resulting dendrogram divided the individuals into five groups. The first group includes individuals K1, L1, L2, K4, L4, K5, K6, K2, K3, M5, M6, N1, Q6, and Q5. The second group includes L5, M1, M2, M3, M4, N2–N6, O1–O5, and L6. The third group includes O6, P1, P5, P6, Q1, Q2, Q4, R4, P2, P3, R1–R3, and R5–R6. The fourth group includes two individuals, P4 and Q3. Finally, the fifth group includes L3.

A two-dimensional Principal Coordinate Analysis (PCA) was conducted, and a scatter plot was generated to illustrate the dispersion of individuals based on differentiation parameters. The PCA revealed that the first three principal coordinate components accounted for 59.55% of the total variation. However, a two-dimensional representation using the first two principal coordinates (PCA 1=24.92% and PCA 2=18.19%) did not differentiate individuals according to geographic patterns (Figure 4).

A collection of SCoT primers was effectively used to evaluate the genetic diversity of Arasbaran *J. foetidissima* populations. All primers produced polymorphic bands, demonstrating the effectiveness of these SCoT primers in assessing genetic variability both among and within *J. foetidissima* populations. The successful application of SCoT markers to investigate genetic diversity has been confirmed in woody plants such as *Juniperus procera* (Al-Yasi and Al-Qthanin,

Table 4. Matrix of pairwise genetic identity and genetic distance (based on Nei, 1978) among eight populations of *Juniperus foetidissima* in the Arasbaran forest.

K	L	M	N	O	P	Q	R	
1.000								K
0.966	1.000							L
0.936	0.943	1.000						M
0.936	0.953	0.937	1.000					N
0.940	0.955	0.955	0.960	1.000				O
0.927	0.941	0.949	0.925	0.960	1.000			P
0.916	0.938	0.956	0.931	0.951	0.967	1.000		Q
0.920	0.933	0.943	0.920	0.958	0.964	0.967	1.000	R

Table 5. Analysis of Molecular Variance (AMOVA) showing the partitioning of genetic diversity within and among eight populations of *Juniperus foetidissima* based on SCoT markers.

Source of variation	df	SS	MS	Est. Var.	%	p
Among population	7	222.167	31.738	2.491	13%	<0.001
Within population	40	671.667	16.792	16.792	87%	<0.001

df: Degree of freedom, SS: Sum of squares, MS: Mean squares, Est. var.: Estimate of variance, %: Percentage of total variation, P-value: Is based on 1000 permutations.

2024), *Juniperus seravschanica* (Yermagambetova *et al.*, 2024), *Prunus sibirica* (Buer *et al.*, 2022), *Acer monspessulanum* (Motahari *et al.*, 2021), and *Taxus media* (Hao *et al.*, 2018).

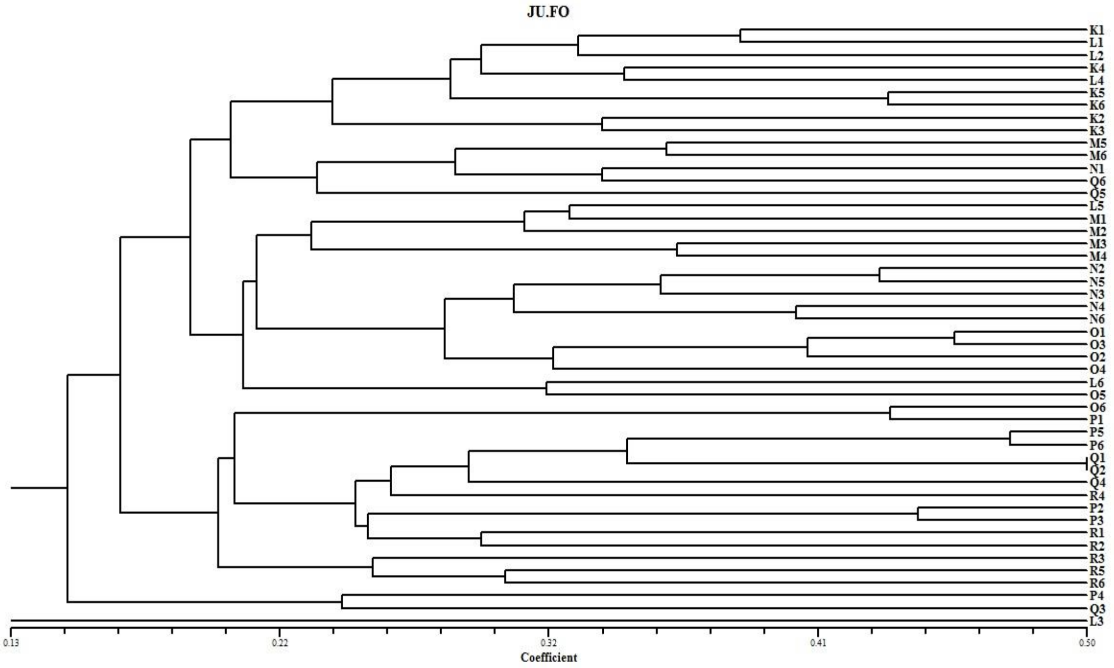

Figure 3. Dendrogram representing the genetic relationships among 48 *Juniperus foetidissima* individuals from eight populations, constructed using the UPGMA clustering method based on SCoT marker data.

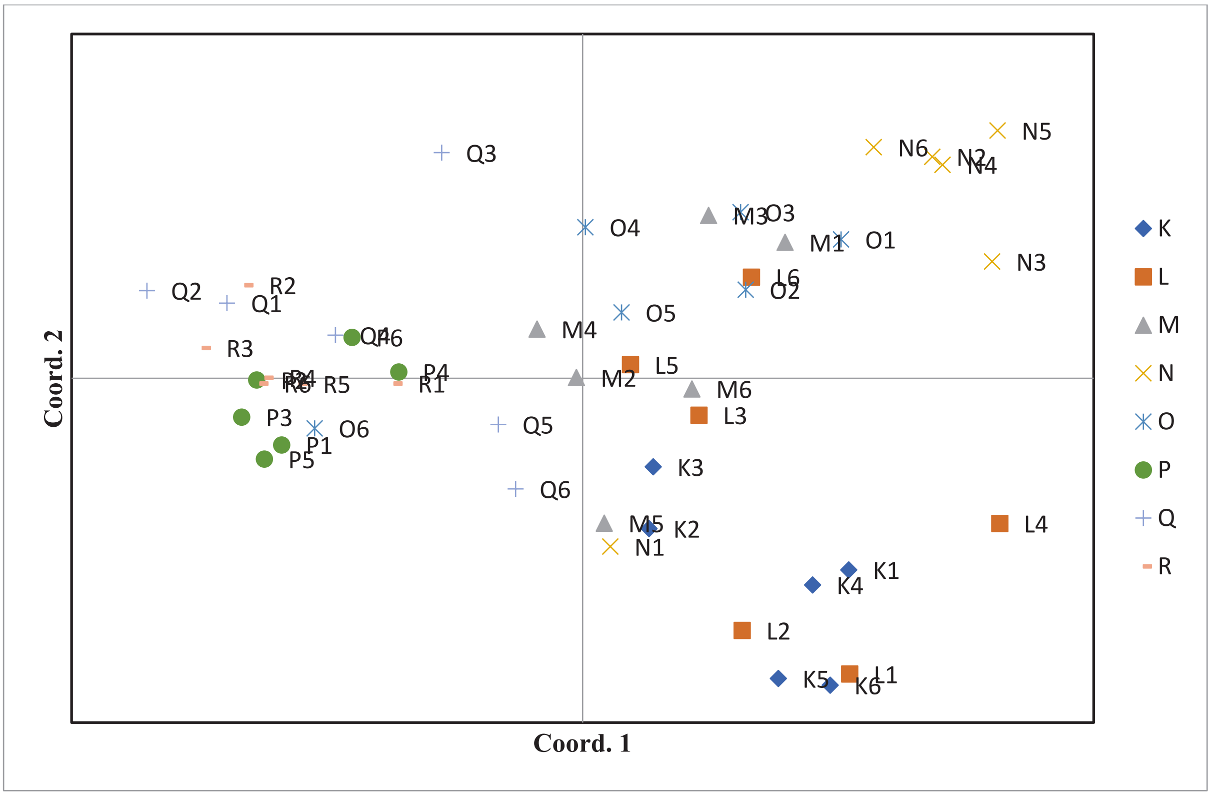

Figure 4. Two-dimensional scatter plot of Principal Coordinate Analysis (PCoA) illustrating the genetic grouping of *Juniperus foetidissima* individuals based on SCoT marker polymorphism.

In this study, we identified a high level of polymorphism (100%) using six SCoT primers. These results demonstrate that SCoT markers are highly effective in estimating genetic diversity among different plant populations. SCoT41 exhibited the greatest ability to determine genetic distance, whereas SCoT10 showed limited capacity to differentiate individuals. The Polymorphic Information Content (PIC) is influenced by both the frequency and the number of alleles present in a population. When more alleles are present at varying frequencies, the PIC value tends to be higher, indicating greater genetic diversity (Nagy *et al.*, 2012). In this study, the average PIC across all loci was 0.321. This relatively high PIC value indicates substantial polymorphism among the studied individuals. SCoT41 and SCoT8 had the highest PIC values, 0.378 and 0.330, respectively, highlighting the high efficiency of these primers in differentiating populations of *J. foetidissima*.

The genetic variability of the eight populations of *J. foetidissima* (h=0.184) was lower than that observed in other species within the same genus, including *J. seravschanica* (h=0.695; Yermagambetova *et al.*, 2023), *J. excelsa* (h=0.449; Evren and Kaya, 2021), *J. sabina* (h=0.402; Lu *et al.*, 2022), *J. squamata* (h=0.55; Ju *et al.*, 2022), *J. chinensis* (h=0.282; Kim *et al.*, 2018), *J. thurifera* (h=0.795; Teixeira *et al.*, 2014), *J. excelsa* (h=0.405; Korshikov and Nikolaeva, 2013), *J. excelsa* (h=0.584; Yücedağ and Gailing, 2013), and *J. excelsa* (h=0.456; Douaihy *et al.*, 2011). However, it was higher than the genetic variability reported for *J. phoenicea* (h=0.130; Meloni *et al.*, 2006) and *J. thurifera* (h=0.141; Terrab *et al.*, 2008).

Based on the AMOVA analysis, the genetic differentiation among the eight populations of *J. foetidissima* was 13%, which is comparable to previous studies on the same genus. Earlier research reported this parameter within a range of 9% to 18%. This value is lower than the average genetic differentiation observed in gymnosperms and allogamous plants (24% and 27%, respectively; Nybom, 2004). This reduced differentiation may result from active seed dispersal by various animals, facilitating gene flow and promoting genetic homogeneity within populations. The high levels of genetic diversity observed within *J. foetidissima* populations align with findings from other studies on coniferous species (Jimenez *et al.*, 2003; Renau-Morata *et al.*, 2005; Terrab *et al.*, 2008; Douaihy *et al.*, 2011; Dzialuk *et al.*, 2011). This diversity is likely attributable to factors such as long-distance seed dispersal, wind pollination, outcrossing, dioecy, long lifespan, and wide distribution, all of which contribute to the observed high genetic diversity within these populations (Douaihy *et al.*, 2011).

Arasbaran Forest plays a crucial ecological and biological role in northwest Iran. Among the plant species found in Arasbaran, *J. foetidissima* contributes significantly to preserving the ecosystem of this valuable forest. Therefore, obtaining genetic information about this species is essential for managing the Arasbaran Forest against the adverse effects of climate change. To gain detailed insights into the genetic diversity and structure of different *J. foetidissima* populations, additional molecular markers such as SSRs can be employed, and larger populations with more individuals should be sampled to yield more robust results.

CONCLUSION

The use of Start Codon Targeted (SCoT) markers in this study has proven effective for assessing the genetic diversity of *Juniperus foetidissima* populations in the Arasbaran forest. The high level of polymorphism observed among these populations highlights the efficacy of SCoT markers in evaluating genetic variability both within and between populations.

These findings align with previous research on woody plants, further highlighting the effectiveness of SCoT markers in assessing genetic diversity. Such insights are invaluable for guiding strategies related to the conservation, breeding, and management of *Juniperus foetidissima*.

Recognizing patterns of genetic diversity is crucial for making informed decisions in biodiversity conservation. This importance is underscored here, suggesting that further research integrating long-term monitoring and interdisciplinary approaches can deepen our understanding of genetic dynamics. Such insights can contribute to the sustainable conservation of *Juniperus foetidissima*, a species of significant ecological importance.

The current research serves as a foundational step toward a more comprehensive understanding of the genetic diversity of *Juniperus foetidissima*. It paves the way for future studies in this area and underscores the need for ongoing genetic research to effectively conserve and manage this important species. The findings emphasize the importance of continuous and dedicated efforts in genetic conservation.

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