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Genetic structure and diversity of the beet armyworm *Spodoptera exigua* (Hübner) (Lepidoptera, Noctuidae) in Iran

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ABSTRACT

Spodoptera exigua is a significant agricultural pest in Iran. In this research, we analysed a 700 base pair DNA fragment of *COI* to assess the genetic diversity of this harmful pest. In total, 54 specimens were sampled across six Iran's geographic areas, revealing six distinct haplotypes. The overall populations exhibited low genetic diversity (h = 0.463 ± 0.068, π = 0.00096 ± 0.00017). No distinct geographic pattern was observed in the haplotype distribution, as indicated by phylogenetic and median-joining network analyses. The median-joining network of Iranian haplotypes, combined with sequences from other global regions, demonstrated a lack of geographical clustering, with Hap.1 as the most prevalent haplotype spanning Iran, Europe, Asia, and Australia, indicative of extensive gene flow and shared evolutionary history. The *F*st values for the Iranian populations ranged from -0.12240 to 0.07189, revealing no significant differentiation among the populations. Analysis of molecular variance showed a larger proportion of the variation within rather than between them, after 1000 random permutations, the level of population differentiation was found to be non-significant. The combination of an unimodal mismatch distribution and the non-significant results of Tajima's D (D = 0.02011, P > 0.05) and Fu's Fs (Fs = 3.33384, P > 0.05) suggested the beet armyworm may have expanded recently **(~10,000–50,000 years ago)** but has returned to a state resembling neutrality without significant selection pressures acting on it. Insights from this population genetic study can aid in crafting targeted approaches for managing this extensively migratory pest.

Keywords: agricultural pest, *COI*, gene flow, haplotype distribution, population genetics.

INTRODUCTION

Spodoptera exigua (Hübner) is a polyphagous pest that feeds on over 130 plant species across more than 30 families (Robinson et al., 2010). **Originated** from South Asia, *S. exigua* has a broad

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distribution throughout the tropical and temperate regions of Europe, Africa, North America, and Asia (Wei et al., 2010). This pest's capacity for long-distance migration promotes the expansion of its populations beyond native ranges, resulting in broad dispersal (Fu et al., 2017; Ma et al., 2024). In Iran, this pest causes substantial economic losses by damaging diverse host plants (Sheikhzadeh et al., 2014). Larval feeding on leaves significantly reduces crop yields and can lead to plant death. In Iran's key beet-growing regions, encompassing approximately 160,000 hectares across 21 provinces, this pest poses a major threat to sugar beet production, especially during outbreaks. Effectively managing *S. exigua* is challenging due to the species' migratory nature and rapid insecticide resistance development (Hu et al., 2021; Huang et al., 2021).

Genetic diversity is inevitable in ecological and evolutionary contexts, as it enhances individual fitness and ecosystem functionality. In pest management, elucidating the genetic composition and population structure of pest species is critical for developing effective and sustainable control strategies. Genetic studies reveal adaptive potential, dispersal patterns, and resistance mechanisms of pest populations, thereby enabling targeted interventions that reduce economic losses and environmental impact (Cao et al., 2025; Peng et al., 2025). Moreover, elucidating population structure informs the identification of distinct genetic units, which is fundamental for monitoring gene flow and predicting the spread of resistance alleles (Greenbaum et al., 2016). Factors such as climate change, habitat variability, natural barriers, migration patterns, and anthropogenic pressures influence genetic variation and population structure, shaping evolutionary trajectories and pest success under environmental shifts **(Crispo et al., 2011; Martins et al., 2018; Song et al., 2023). Integrating genetic data into pest management frameworks enhances the precision and adaptability of control measures.** DNA markers are **widely recognized** as primary tools for evaluating genetic diversity **within and** among individuals, species **and** populations, because of their extensive polymorphism (Behura, 2006). **Various** molecular markers has been employed to deduce the geographical distribution and evolutionary background of species (Urantowka et al., 2017). **Notably**, the *cytochrome oxidase subunit I (COI)* gene is **particularly effective for phylogenetic analyses** because of its moderate **evolutionary** rate and distinct evolutionary pathway (Hebert et al., 2003; Wang et al., 2014). Studying genetic diversity and population structure is key to gaining insights into dispersal behaviors and the causes of outbreaks in pest species. Despite the **ecological and agricultural** significance of *S. exigua*, **genetic studies in Iran** is scarce particularly using ***COI* gene**

(Golikhajeh et al., 2018). This study addresses this gap by examining mtDNA *COI* variation across six Iranian *S. exigua* populations.

MATERIAL AND METHODS

Collection of Samples

The larvae of *S. exigua* were collected from sugar beet fields in six geographical regions of Iran (Table 1) between May and September of 2021-2022. The larvae were reared under optimal conditions until adulthood (Zhang et al., 2011; Jaba et al., 2020). Once the insects matured, they were preserved in 96% ethanol and stored at -20°C until DNA extraction. Ten individuals from each region were chosen for this process (Endersby et al., 2006; Anderson et al., 2016).

DNA Extraction, PCR Amplification, and Sequencing

Genomic DNA was extracted from ten randomly selected moths per population, using the Favorgen tissue genomic DNA extraction mini kit. The second and third legs of each specimen were ground in liquid nitrogen prior to extraction. The extracted DNA was stored at -20°C until PCR amplification of a *COI* mitochondrial gene fragment using primers LCO1490 and HCO2198 (Folmer et al., 1994). The PCR mixture contained 12.5 µl of PCR master mix (Amplicon), 0.5 µl from each primer set (10 pmol/µl), and 2.5 µl of template DNA. The PCR amplification was performed as follows: 94°C for 3 min; 35 cycles of 92°C for 30 s, 50°C for 40 s, and 72°C for 60 s; followed by a final extension at 72°C for 5 min. PCR products were assessed on a 1% agarose gel and subsequently sequenced by Pishgam Biotech Co.

Data Analysis

Iranian population sequences were manually modified using the BioEdit software (Hall, 1999). Bidirectional sequencing was utilized to enhance the precision of sequencing. The DNA Baser software package (version 5.15) was utilized to generate consensus sequences. The accuracy of the *COI* sequences was confirmed by verifying that they could be translated into proteins via MEGAX (Kumar et al., 2018). The alignment of nucleotide sequences was carried out using the ClustalW program implemented in MEGA X. For each population, population diversity indices including haplotype (*Hd*) and nucleotide (π) diversity as well as the number of haplotypes (*H*) Nei and Miller (1990) were computed using DnaSP v6 software presented by Rozas et al. (2017). The median-joining (MJ) network, as described by Bandelt et al. (1999), was generated utilizing the

PopART software Leigh and Bryant (2015) for Iranian sequences alone and in combination with additional sequences from GenBank, representing various countries (Table S_1). Genetic differentiation among populations was assessed using pairwise F_{ST} values. To evaluate genetic variation between population groups from diverse regions (Table 1), an analysis of molecular variance (AMOVA) was conducted. Both F_{ST} and AMOVA employed the Kimura 2-parameter model within the Arlequin software (Excoffier and Lischer, 2010). Visualization of AMOVA results was conducted using an integrated R script in Arlequin. The Mantel test (Mantel, 1967) utilizing 10,000 permutations was applied to examine the correlations between genetic distance (F_{ST} from Arlequin) and geographic distance (km) in IBD v1.52 (Bohonak, 2002). The estimation of the geographic distance between pairs of populations was done with the help of Google Maps Distance Calculator. Two neutrality tests were used to analyze the changes in demographic history for *S. exigua*, Tajima's *D* (Tajima, 1989) and Fu's F_S (Fu 1997), throughout the six geographic populations. Ultimately, Arlequin 3.0 computed the mismatch distributions between the observed and expected data (Appendix 2).

RESULTS

A 700 bp fragment of the mitochondrial *COI* gene was sequenced from 54 *S. exigua* individuals sampled across six geographic regions (Table 1). The sequences were submitted to GenBank (see Table S_1 for accession numbers) and revealed five variable sites, identifying six distinct haplotypes. The most prevalent haplotypes across all populations were $Hap._1$ and $Hap._2$, found in 38 and 12 individuals, respectively (Appendix 1). Haplotypes $Hap._3$, $Hap._4$, $Hap._5$ and $Hap._6$ were unique, each occurring only in one population (Appendix 1). Table 2 presents the genetic diversity indices including haplotype diversity (*h*) and nucleotide diversity (π). The average values for *h* and π for all populations were 0.463 and 0.00096, respectively. Haplotype and nucleotide diversities are highest in Safiabad (Pop3). This population exhibits significantly higher diversity than the others (P> 0.05) (Table 2), primarily because it contains divergent haplotypes (Appendix 1).

Median-Joining Network

A significant degree of gene flow in Iranian *S. exigua* may be inferred from the random distribution of mitochondrial DNA *COI* gene haplotypes. Furthermore, no clear geographical grouping of

haplotypes was observed in the constructed median-joining network (Figure 1). The network's shape revealed that other haplotypes were separated from Hap.$_1$ or Hap.$_2$ by a single mutation. In addition to the haplotype network, phylogenetic analysis was utilized to investigate the links among haplotypes of the beet armyworm and to uncover any groupings associated with geographic distribution. The phylogenetic tree's topology (Figure. 2) provided further confirmation of the results from the haplotype network and no clear geographic distribution pattern was observed among the haplotypes.

Using one or two representative sequences of each haplotype from Iran, we combined these sequences with additional haplotypes sourced from GenBank representing various countries to construct a MJ network (Figure. 3). The haplotype network revealed that Hap.$_1$ emerged as the most prevalent haplotype. Notably, sequences from the Iranian Hap.$_1$ were integrated within this Hap.$_1$ haplotype, along with sequences from Europe, Asia, and Australia. This widespread distribution of Hap.$_1$ suggests it may represent an ancestral or widely dispersed haplotype, potentially indicating historical migration patterns or shared evolutionary history among these geographically diverse populations. **The widespread prevalence of haplotype Hap.$_1$ likely reflects its ancestral origin and early emergence, enabling its persistence across diverse regions, as supported by Kang et al. (2023) and Ramesh et al. (2025). Furthermore, human-mediated factors, including agricultural practices and crop transport, have facilitated gene flow, promoting the dispersal of common haplotypes like Hap.$_1$, consistent with patterns observed in highly mobile pest species (McCulloch and Waters, 2023).** The second most frequent haplotype, Hap.$_4$, was exclusively composed of sequences from North American countries. This geographical clustering of Hap.$_4$ may indicate restricted gene flow between North American and other global populations, potentially due to geographical barriers or historical colonization events. **Limited gene flow critically influences population structure by reducing migration-mediated genetic homogenization, thereby increasing differentiation among populations. Over time, such isolation can enhance the effects of evolutionary processes, such as genetic drift, which drives stochastic shifts in haplotype frequencies, and local adaptation, which fosters genetic divergence in response to region-specific selective pressures.** The network topology revealed a high proportion of unique haplotypes. Notably, most haplotypes were separated by only one mutation.

153 **Genetic Distance and Genetic Diversification**

154 Pairwise genetic distances between populations, studied via the Kimura 2-parameter technique,
155 are summarized in Table 3, and average pairwise sequence variation among the populations was
156 0.1846% and varied from 0.108 to 0.279%.

157 The pairwise F_{ST} values among the populations varied from -0.00794 to 0.07189. The analysis
158 revealed that, on the whole, there was no notable differentiation among the populations (Table 3,
159 Appendix 2).

160

161 **Analysis of Population Genetic Structure**

162 Grouping populations based on geographic regions through AMOVA revealed no notable
163 differences between the groups (Table 4). No significant association was detected between genetic
164 distances (pairwise F_{ST}) and geographic distances in the Mantel's test for *COI* (r^2 =0.0017, P =
165 0.519000). **This non-significant p-value indicates that geographic distance does not explain**
166 **genetic differentiation among populations at the *COI* locus, thus supporting the null**
167 **hypothesis of no population structure related to spatial separation.** A unimodal mismatch
168 graph was observed in the mismatch distribution analysis (Figure 4), potentially pointing to a
169 recent population expansion. Nevertheless, our finding does not align with the mitochondrial DNA
170 genealogy, which did not exhibit a star-like pattern. Additionally, neither the sum-of-squares
171 deviation (SSD = 0.26357, P = 0.18486) nor Harpending's raggedness index (0.55378, P =
172 0.50367) showed significance (Figure 4), failing to indicate a population expansion. A positive
173 SSD combined with a non-significant raggedness index usually implies that while there is some
174 deviation from equilibrium (indicated by SSD), these deviations are not strong enough to indicate
175 significant demographic changes. This often points to a scenario where the population has
176 expanded recently without severe historical bottlenecks. The findings imply that the population
177 structure has remained stable over time. The evidence against population expansion was reinforced
178 by Tajima's *D* (0.02011, P = 0.56038 > 0.1) and Fu's (F_S = 3.33384, P = 0.92865 > 0.1), both of
179 which were positive and statistically non-significant.

180

181 **DISCUSSION**

182 Genetic variability underpins evolutionary processes across all organisms. Assessing intraspecific
183 genetic variation enables the identification of potential novel species and elucidates the

evolutionary histories of extant populations (McEntire et al., 2021). Our analysis of *S. exigua* populations from major sugar beet cultivation regions in Iran revealed low genetic diversity, as evidenced by limited haplotype and nucleotide diversity, with only five polymorphic sites and six haplotypes detected. This finding aligns with previously reported restricted genetic variation in *S. exigua* (Wang et al., 2020). The low genetic variation observed in *S. exigua* populations in Iran may stem from a relatively recent population expansion, limiting the accumulation of genetic diversity. Additionally, the limited sample size may influence these results. The observed low genetic variance across different geographic populations suggests **substantial gene flow and high genetic connectivity,** supporting the prevailing hypothesis that the flight capacity of *S. exigua* is adequate for dispersal. The current study's findings confirmed this assertion, indicating that Iranian haplotypes lack well-defined geographic distribution patterns. The presence of shared haplotypes across various regions of Iran implies that recent gene flow between these populations has blurred the original relationships among them. **This low level of genetic differentiation is a hallmark of frequent migration and dynamic population turnover, typical of highly mobile pests like *S. exigua*. Such extensive movement not only facilitates the rapid spread of common haplotypes but also prevents the formation of distinct genetic clusters, thereby maintaining genetic homogeneity across wide geographic areas.** Observing four unique haplotypes in pop_2, pop_3, and pop_4 might be a consequence of the small sample size. Similarly, the global haplotype network (Figure. 3) revealed a lack of clear geographical structuring among haplotypes from Asian, Australian and European populations, suggesting a high degree of genetic admixture or historical gene flow among these regions. The widespread presence of a shared haplotype across continents underscores the species' dispersal capacity. The integration of Iranian $Hap._1$ sequences within the global $Hap._1$ haplotype suggests significant genetic connectivity between Iranian *S. exigua* populations and those from other continents. This pattern aligns with observations of limited phylogeographic structure in *S. exigua*, as seen in other studies where haplotypes showed random distribution across large geographic areas (Wang et al., 2020). The observed geographical clustering of North American haplotypes suggests a potential regional differentiation or a founder effect suggesting limited gene flow between North American and other global populations. However, the close genetic proximity, differing by only a single mutational step from haplotypes elsewhere, implies a complex evolutionary scenario involving recent divergence, ongoing gene flow, or a mix of these two processes. The single-mutation difference could indicate that the

differentiation of North American populations is a relatively recent phenomenon, or that there is still some level of genetic exchange occurring, albeit at a reduced rate. This pattern underscores the importance of considering both geographical distribution and genetic distance in interpreting population structure. The haplotype network analysis reveals two key features: most haplotypes are separated by only one mutation, and there is a high proportion of unique haplotypes. The findings shed light on the population structure and evolutionary history of *S. exigua*, suggesting recent divergence or limited genetic drift among lineages. Such shallow genetic differentiation could be attributed to high gene flow between populations. Such a pattern is often observed in species with high dispersal capabilities. The abundance of unique haplotypes may be an artifact of low sample numbers. In cases of limited sampling, rare haplotypes are more likely to appear unique simply because their counterparts in the population have not been sampled.

The detection of two distinct clusters in the Bayesian phylogenetic tree, despite the absence of clear separation among the six geographic populations of *S. exigua* and the presence of mixed population membership within each cluster, suggests that gene flow among populations is high and geographic barriers to dispersal are weak or absent. This pattern is further corroborated by the random distribution of mitochondrial *COI* haplotypes and the lack of geographic structure in the haplotype network, where most haplotypes are separated by only a single mutation. Such findings are consistent with studies in other insect species, where extensive gene flow and recent demographic expansion can obscure phylogeographic structure, leading to the formation of clusters in phylogenetic trees that do not correspond to discrete geographic groupings (Kim and Sappington, 2013).

Generally, species that can actively disperse usually show minimal genetic variation across populations, and this is likely the case for migratory noctuid pests, including *S. exigua*. In this research, there were no evident statistically significant genetic distances, and the pairwise sequence differences between the populations were minor. Furthermore, the analysis revealed no significant differentiation in pairwise F_{ST} values among the populations. This result supports the findings of several earlier research, which provide strong evidence of low genetic divergence among the majority of individuals in this species (Wang et al., 2014; 2020). **The low genetic differentiation and minimal pairwise sequence differences observed in our study of *S. exigua* populations align closely with findings reported for this species on other host crops. Investigations on *S. exigua* from vegetable crops such as tomato, cotton, and pepper has**

similarly documented low genetic diversity and weak population structuring (Lee, 2017; Wang et al., 2020).

A detailed comprehension of the genetic structure of pest populations can reveal important biological information that is essential for their effective management. This knowledge improves our understanding of their occurrence patterns, migration trends across different areas, and the geographic differences within these populations (Zhang et al., 2018). Since there was no apparent habitat loss or fragmented distribution of the hosts for this pest species in the studied regions of Iran, *S. exigua* is likely to exhibit little genetic differentiation throughout the sugar-beet areas. A non-significant result indicates that while the observed Tajima's *D* is positive, it does not differ significantly from what would be anticipated according to a neutral model. This suggests that demographic factors, such as population size changes or expansions, may not have dramatically influenced genetic diversity in the studied populations. A positive non-significant Fu's *Fs* value indicates genetic stability and neutrality within the population, while also suggesting that there is insufficient evidence to conclude recent demographic changes or selective pressures affecting genetic diversity.

The combination of an unimodal mismatch distribution and non-significant positive values for Tajima's *D* and Fu's *Fs* indicates a population that most likely underwent historical expansion in size but is currently stable, with no significant evidence of ongoing evolutionary pressures affecting its genetic structure. **Previous studies on *S. exigua* populations across Asia and neighboring regions have reported similarly low genetic differentiation and high gene flow, consistent with our findings. Wang et al. (2024) demonstrated that extensive migratory behavior and continuous host availability contribute to weak population structuring in *S. exigua* populations across China. This aligns with our observation of non-significant F_{st} values and lack of distinct haplotype clustering within Iranian populations, suggesting extensive gene flow and a shared evolutionary history. Moreover, a study focusing on populations in Pakistan and adjacent areas (Wang et al., 2022) similarly reported low genetic differentiation in *S. exigua*, reinforcing the hypothesis that populations inhabiting contiguous agro-ecosystems and lacking significant geographic or ecological barriers tend to maintain genetic homogeneity. Although geographic distance can drive genetic divergence, its influence is often attenuated by the species' high dispersal capacity and the continuous availability of host plants, as reported by Wang et al. (2020). The limited sample size and**

geographic coverage may restrict the robustness of our conclusions. Consequently, there is a possibility that fine-scale genetic structure or recent demographic changes have not been fully captured in this study. Therefore, further sampling across broader spatial and temporal scales is required to fully elucidate the evolutionary dynamics and genetic structure of *S. exigua* populations in Iran.

In conclusion, while chemical treatment remains the primary method for controlling *S. exigua*, its genetic flexibility, high reproductive rate, and particularly strong selection pressure drive rapid insecticide resistance (Huang et al., 2021). Significant gene flow and long-distance migration facilitate the spread and accumulation of resistance traits across populations (Bouvier et al., 2001). Consequently, elucidating the mechanisms of resistance, population genetic structure, and gene flow is imperative to advance resistance monitoring and to inform the design of sustainable, effective pest management strategies.

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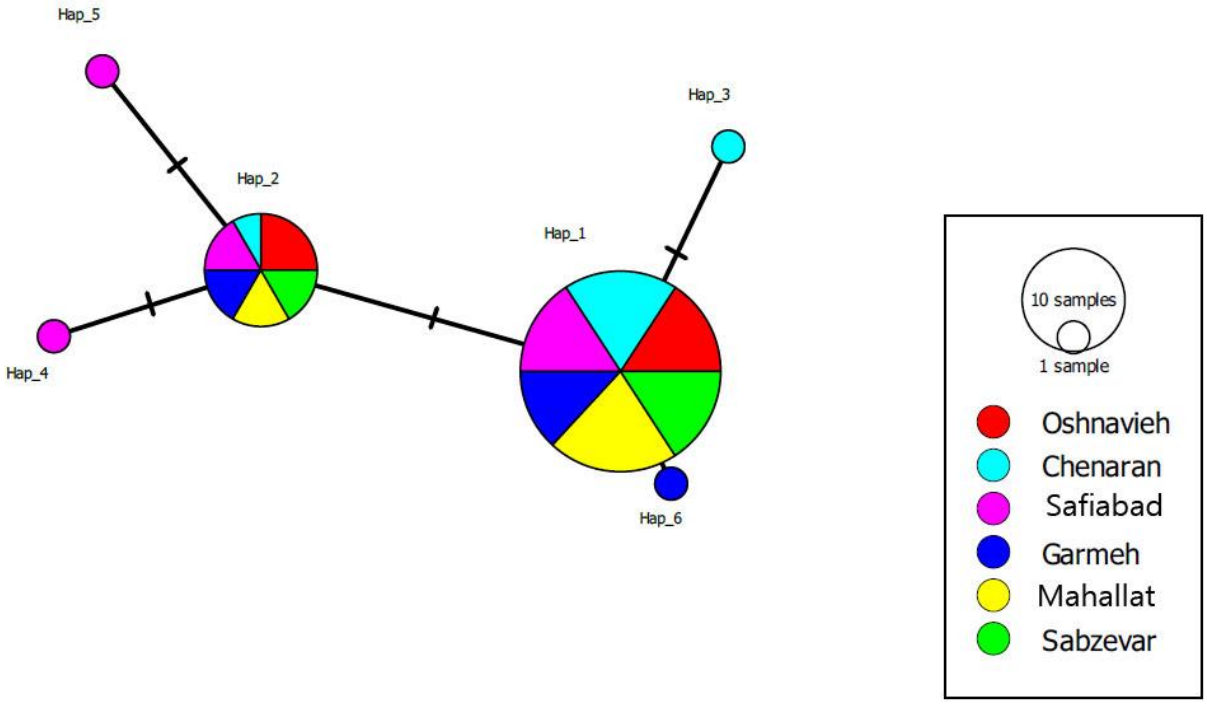


Figure 1. Haplotype network derived from partial mtDNA *COI* sequences of *Spodoptera exigua* from Iranian populations. Each circle represents a unique haplotype, identified by a number. The colours represent different populations, with the sizes of the slices and circles corresponding to the number of individuals carrying each haplotype.

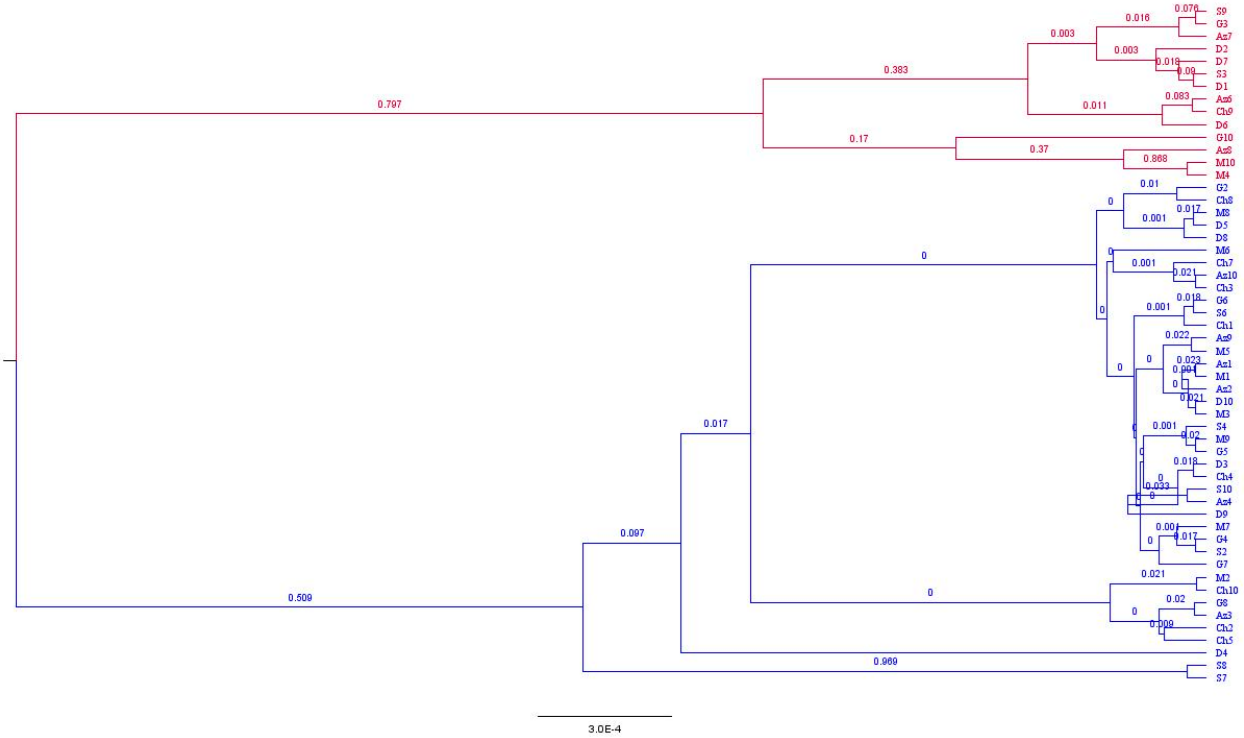
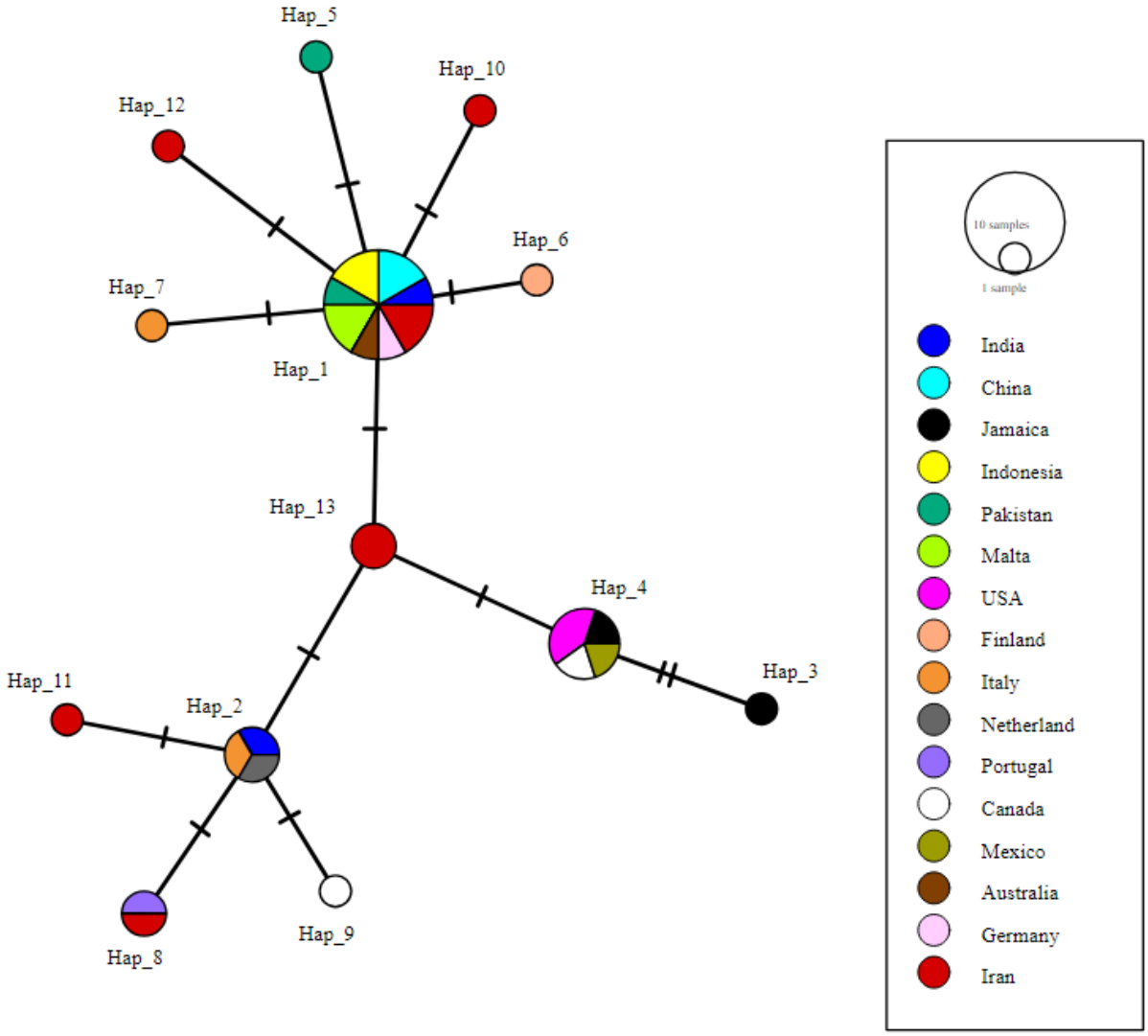


Figure 2. Phylogenetic tree based on Bayesian analysis. Numbers on nodes are posterior probabilities. Region codes are explained in Table 1.



436

437 **Figure 3.** Haplotype network created using partial mtDNA *COI* sequences of *Spodoptera exigua,*
438 encompassing both Iranian and global populations. Each circle represents a unique haplotype,
439 identified by a number. The colours represent different populations, with the sizes of the slices and
440 circles corresponding to the number of individuals carrying each haplotype.

441

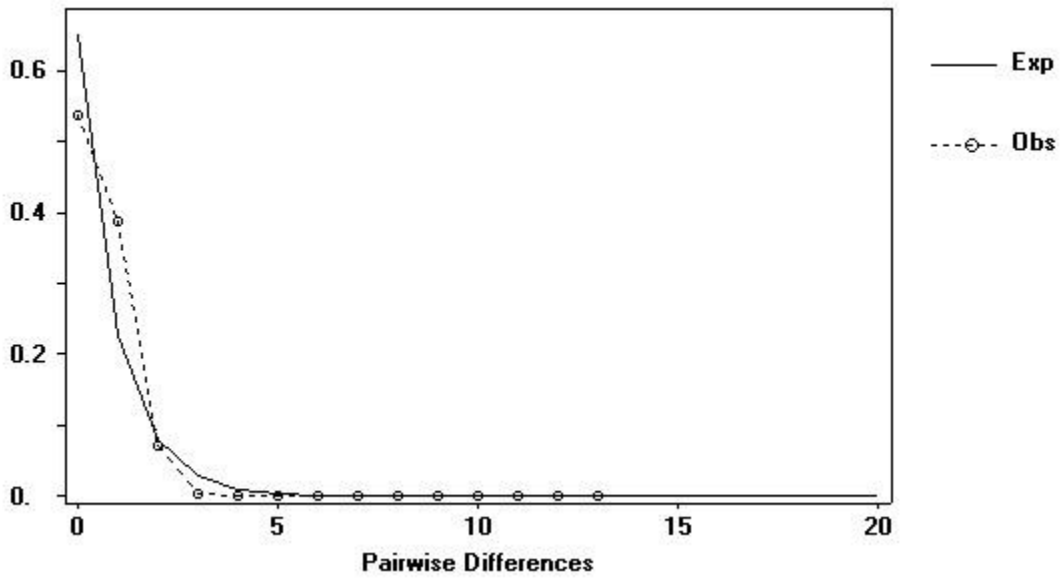


Figure 4. Mismatch distribution of the 54 *COI* sequences of *Spodoptera exigua* for Iran.

Table 1. Information on the sampling locations of *Spodoptera exigua* in Iran.

Location	Code	Geographic region	Latitude/Longitude	Collection date
West Azerbaijan, Oshnavieh (Az)	Pop1	Northwest East	37°02'14.9"N/45°08'57.5"E	Aug./18/2022
Razavi Khorasan, Chenaran (Ch)	Pop2	East	36°43'27.1"N/58°59'55.2"E	Sept./07/2022
Khuzestan, Safiabad (D)	Pop3	Southwest	32°16'48.9"N/48°26'15.8"E	Jul./07/2022
North Khorasan, Garmeh (G)	Pop4	Northeast	37°21'23.8"N/56°19'44.2"E	Sept./07/2021
Markazi, Mahallat (M)	Pop5	Center	33°52'55.9"N/50°30'01.9"E	Jul./30/2022
Razavi Khorasan, Sabzevar (S)	Pop6	East	36°37'15.6"N/57°25'17.9"E	Jul./6/2022

Table 2. Haplotype diversity (*h*) and nucleotide diversity (π) from six Iranian *Spodoptera exigua* populations.

Marker		H	Haplotype diversity (h)	Nucleotide diversity (π)
COI	Pop1 (Oshnavieh)	2	0.5000 ± 0.1283	0.001464 ± 0.001227
	Pop2 (Chenaran)	3	0.4167 ± 0.1907	0.000975 ± 0.000930
	Pop3 (Safiabad)	4	0.6444 ±0.1518	0.002152 ± 0.001603
	Pop4 (Garmeh)	3	0.6071 ± 0.1640	0.001622 ± 0.001341
	Pop5 (Mahallat)	2	0.3556 ± 0.1591	0.001041 ± 0.000960
	Pop6 (Sabzevar)	2	0.4286 ± 0.1687	0.001255 ± 0.001120

Table 3. *Fst* values for pairwise comparisons between six *Spodoptera exigua* populations in Iran.

Marker		Pop1	Pop2	Pop3	Pop4	Pop5	Pop6
COI	**Pop1**	0.00000					
	Pop2	0.02175	0.00000				
	Pop3	-0.08972	0.07189	0.00000			
	Pop4	-0.09878	-0.04368	-0.05313	0.00000		
	Pop5	-0.06790	-0.06930	-0.00794	-0.09787	0.00000	
	Pop6	-0.11504	-0.05338	-0.06173	-0.12240	-0.11863	0.00000

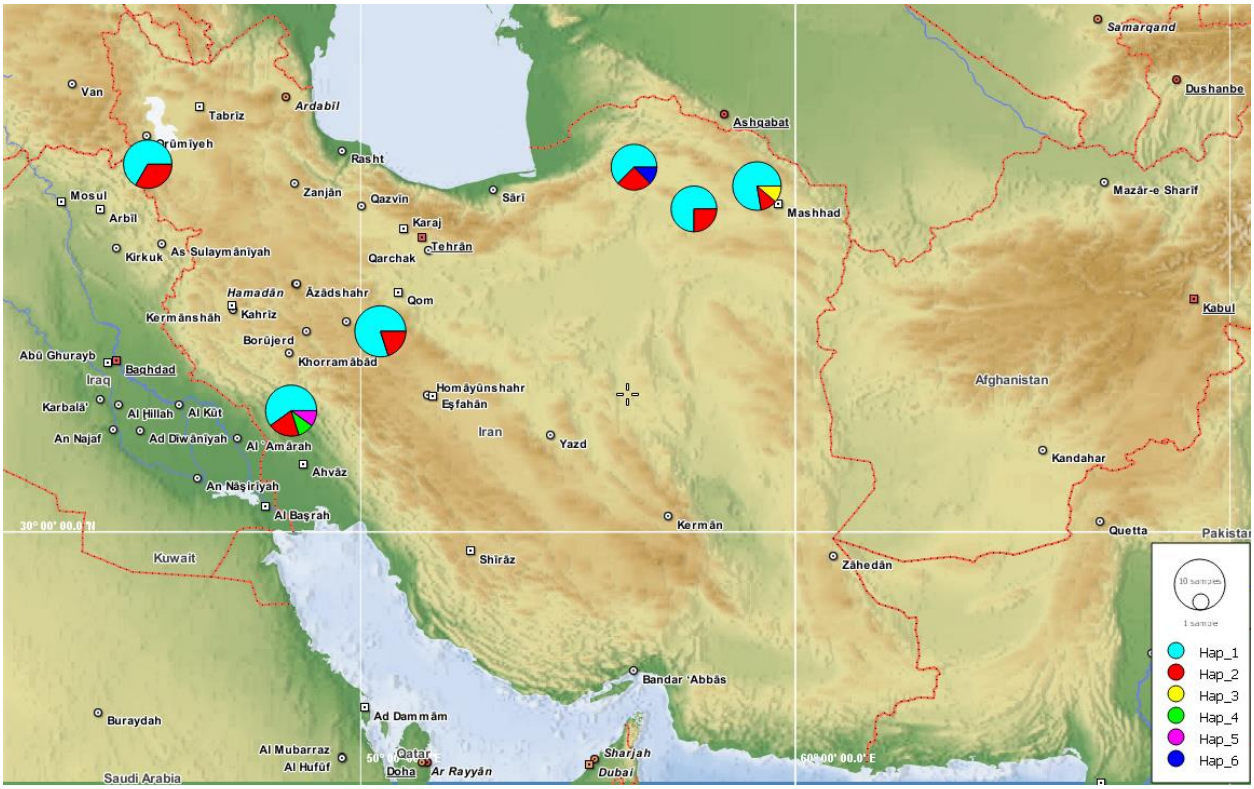
Table 4. Results of the AMOVA analysis of six Iranian *Spodoptera exigua* populations, arranged by geographic areas, P <0.05.

Marker	Source of variation	d.f.	SSD	Variance components	Percentage of variation	F-statistic
COI	Among groups	3	0.954	0.01354	2.90	0.02905
	Among populations within groups	2	0.380	-0.03591	-7.70	-0.07932
	Within populations	48	23.457	0.48869	104.80	-0.04797
	Total	53	24.791	0.46632		

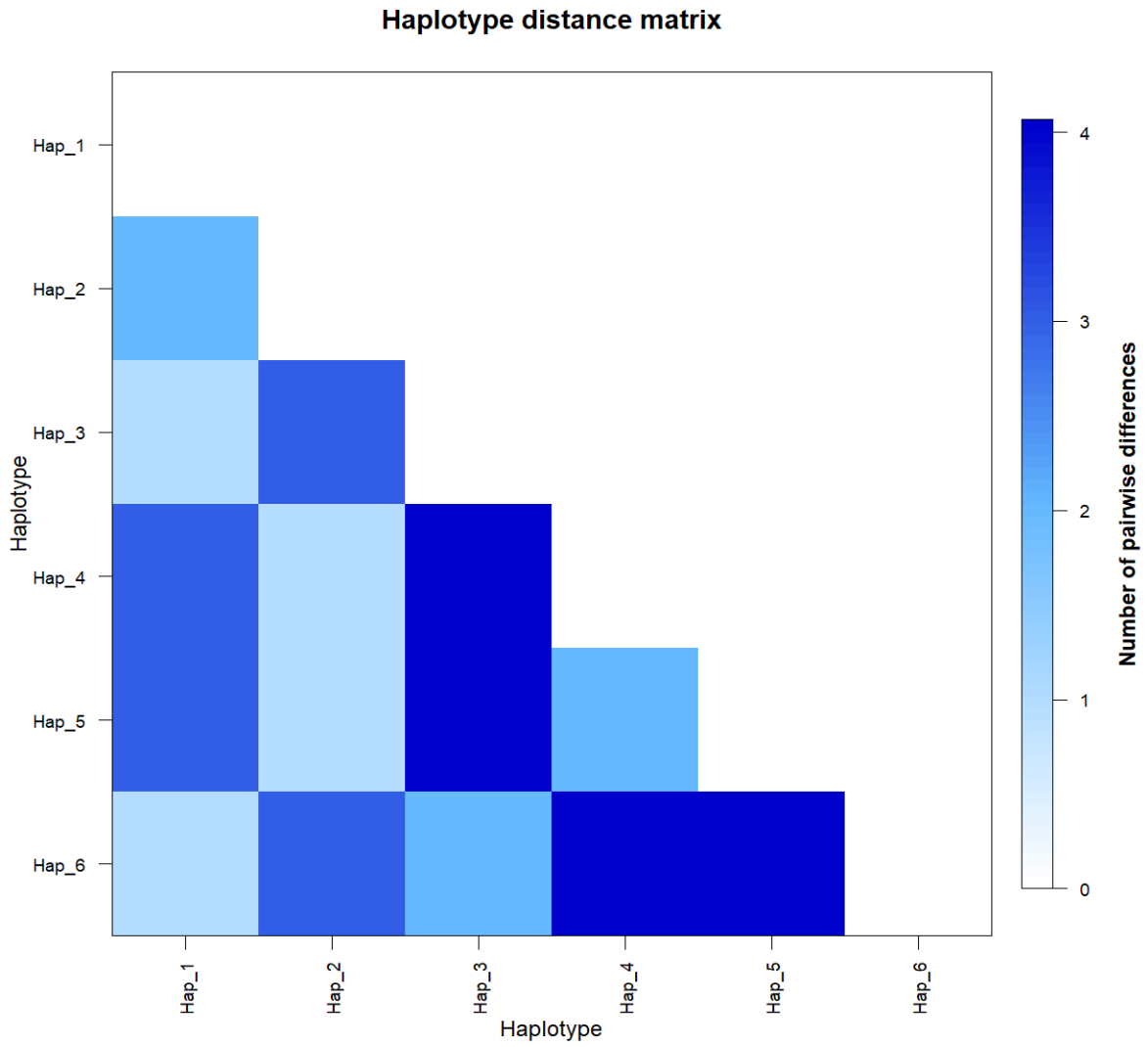
Table S1. Analysed sequences of *Spodoptera exigua* obtained from NCBI GenBank with sampling site country, accession numbers, and quantity of analysed specimens (N), including Iranian sequences from this study.

Country	N	Accession numbers
India	2	MZ297458, MZ297462
China	2	MK860943, MK860944
Jamaica	2	MT881741, MT881725
Indonesia	2	MN457694, MZ323866
Pakistan	2	HQ991336, MT449726
Malta	2	MW306009, MW306011
USA	2	MW665995, EU779856
Finland	1	JF853552
Italy	2	HQ565253, KX045943
Netherland	1	KJ634291
Portugal	1	OQ564362
Canada	2	GU687828, KX281220
Mexico	1	MK318332
Australia	1	OL539272
Germany	1	HM914242
Iran	54	PQ765817-PQ765820, PQ765822-PQ765831, PQ765833-PQ765846, PQ765848-PQ765854, PQ765856- PQ765869, PQ765871- PQ765875

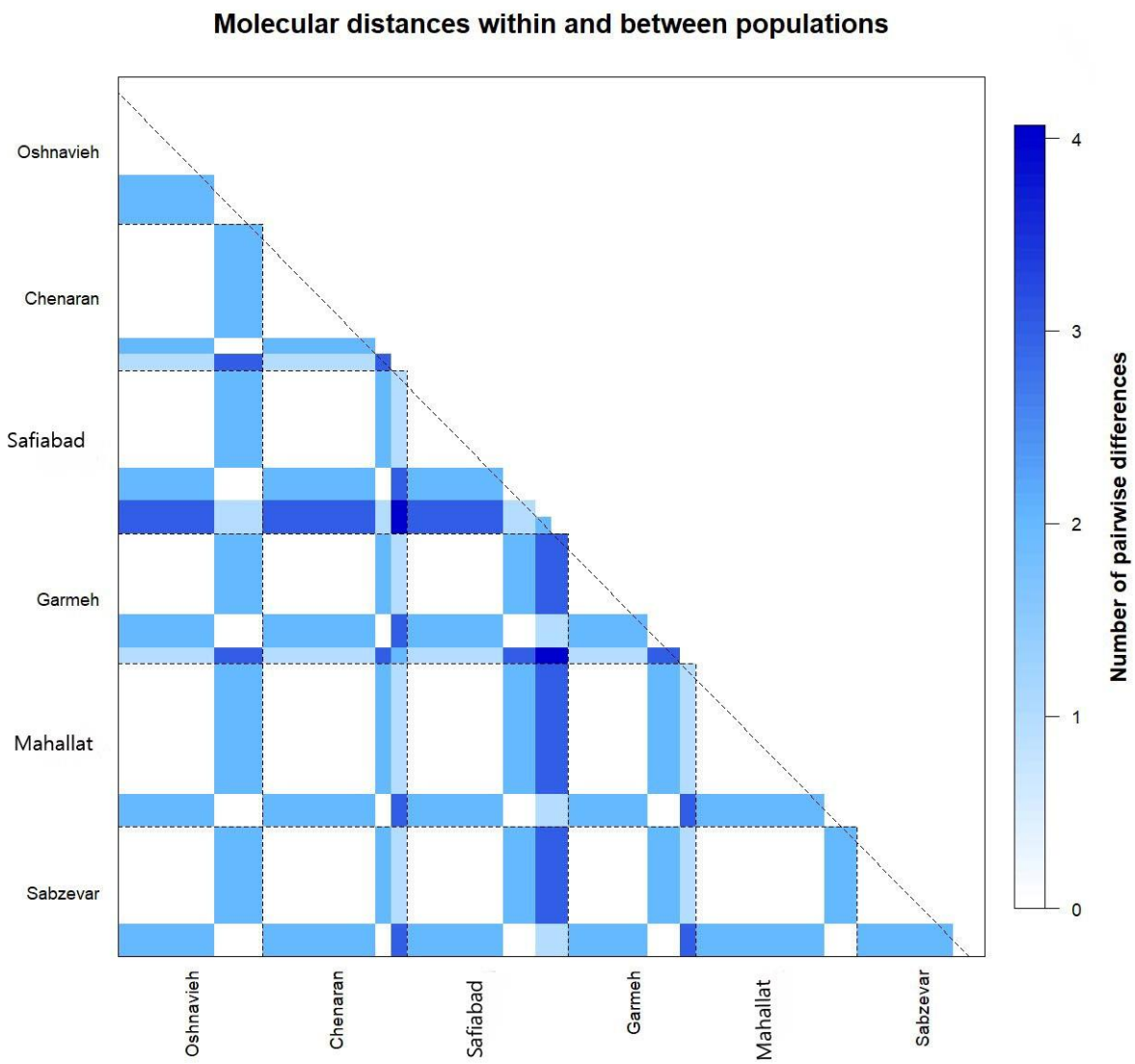
Appendix 1. Mapping haplotypes.



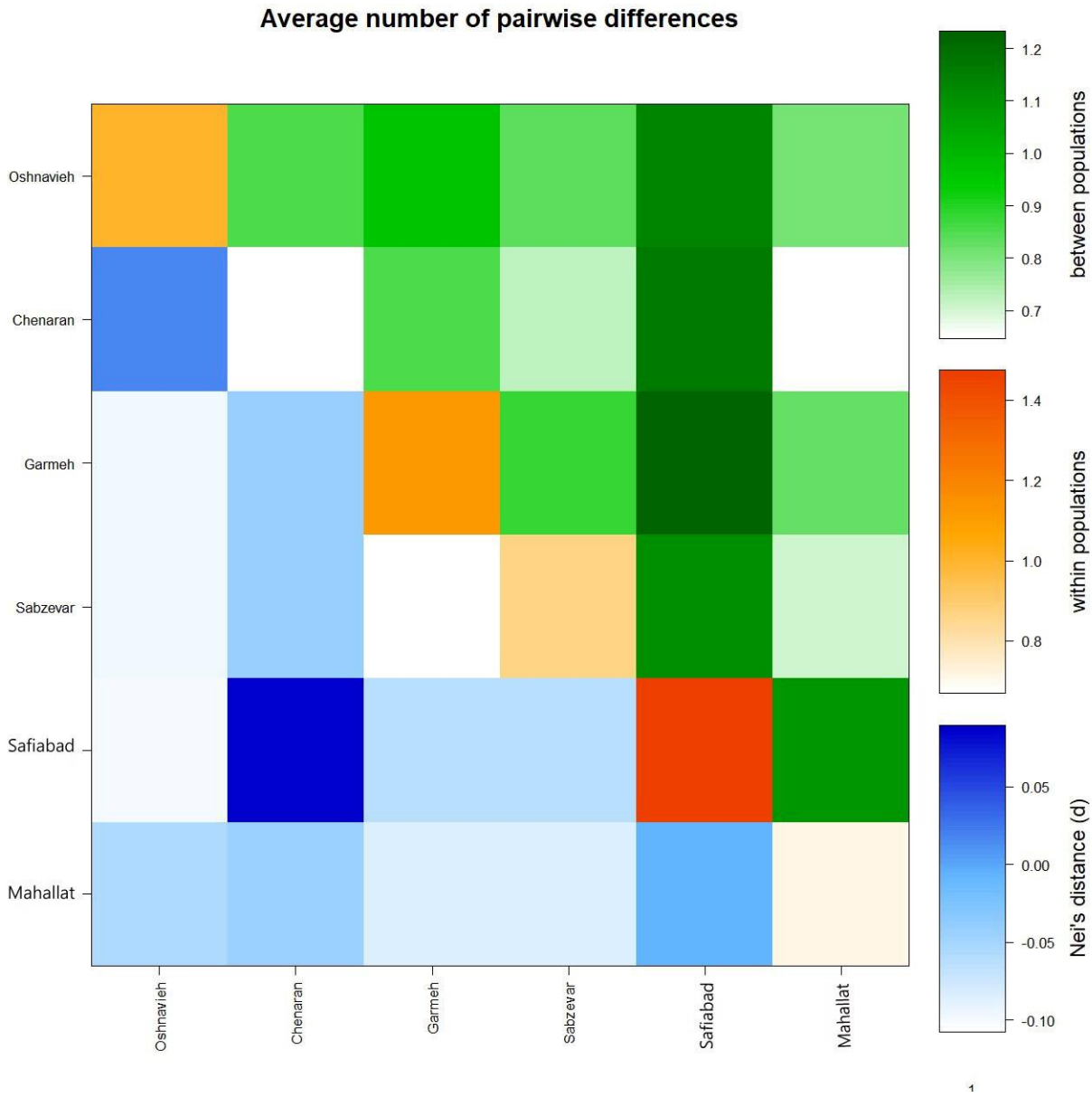
Appendix 2. AMOVA results for the *COI* gene study of *Spodoptera exigua*. (a) Haplotype distance matrix; (b) Nei`s within and between population distances; (c) number of pairwise differences between localities, and (d) comparison of F_{st} values of all populations.



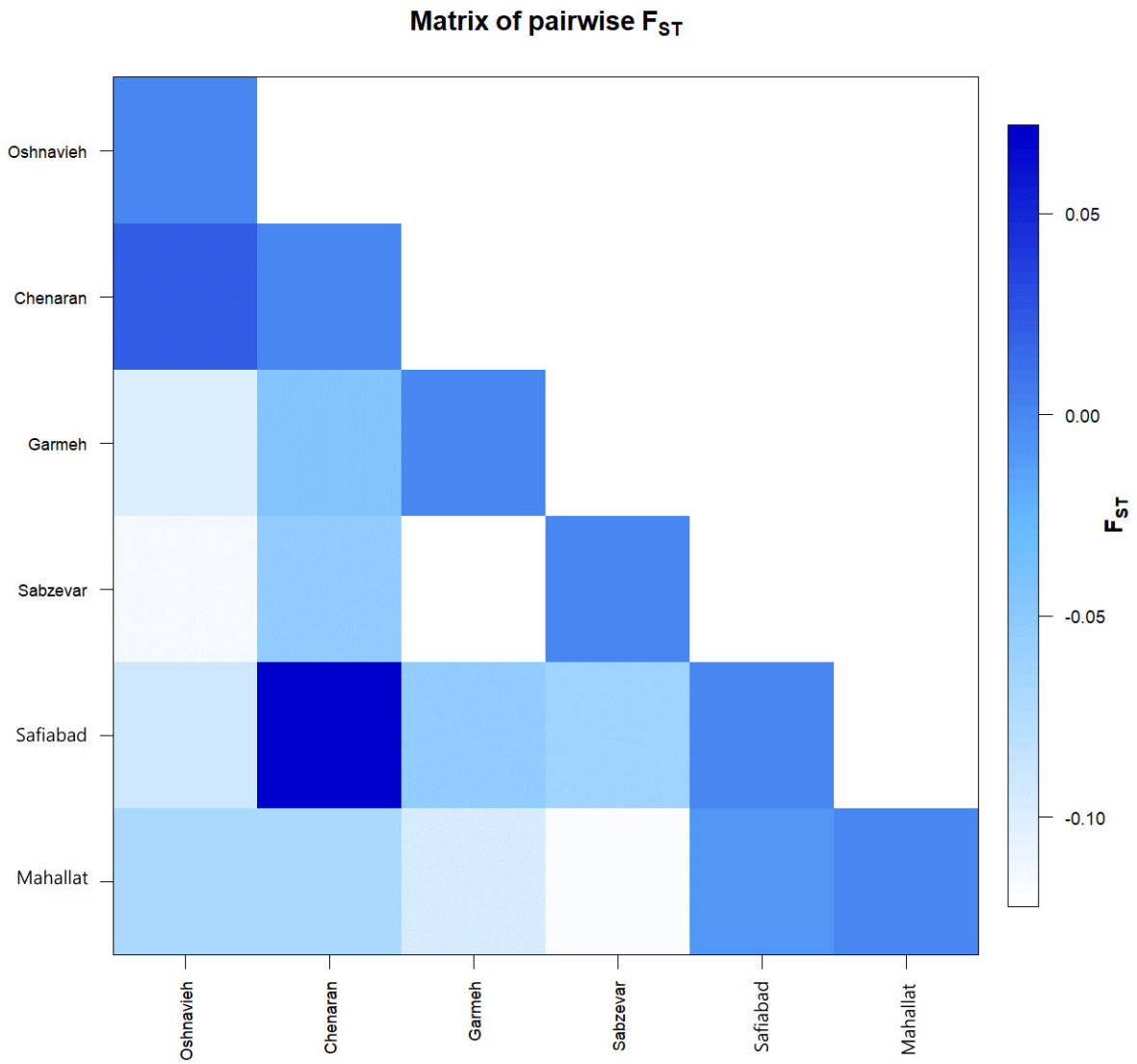
a


Molecular distances within and between populations
Oshnavieh
Chenaran
Safiabad
Garmeh
Mahallat
Sabzevar
Number of pairwise differences
0
1
2
3
4

b


Average number of pairwise differences
Oshnavieh
Chenaran
Garmeh
Sabzevar
Safiabad
Mahallat
between populations
1.2
1.1
1.0
0.9
0.8
0.7
within populations
1.4
1.2
1.0
0.8
Nei's distance (d)
0.05
0.00
-0.05
-0.10

c


Matrix of pairwise F_{ST}
Oshnavieh
Chenaran
Garmeh
Sabzevar
Safiabad
Mahallat
0.05
0.00
-0.05
-0.10
F_{ST}

513

514 d