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**ARTICLE**

# Genetic Diversity and Population Structure of Hilacha Mango (*Mangifera indica* L.) in Montería, Colombia Based on SSR Markers

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## ABSTRACT

Understanding the distribution of genetic diversity within cultivated plant populations is essential for developing effective conservation and sustainable management strategies. Hilacha mango (*Mangifera indica* L.) is one of the most important traditional landraces cultivated in the Colombian Caribbean; however, information on its genetic diversity and population structure remains limited. This study assessed the genetic diversity and population structure of five Hilacha mango populations from Montería, Córdoba, Colombia, using eight Simple Sequence Repeats (SSR) loci. A total of 47 accessions were genotyped, and genetic diversity indices, Wright's F-statistics, gene flow, analysis of molecular variance (AMOVA), Bayesian clustering, and principal coordinates analysis were performed. The SSR loci revealed substantial allelic variation, with pronounced differences in allele distribution among populations. Florida and San Anterito exhibited the highest levels of allelic richness and genetic diversity, whereas all populations showed lower observed than expected heterozygosity, indicating a generalized heterozygote deficit. Wright's statistics revealed moderate genetic differentiation, mean Fixation Index ($F_{ST}$) = 0.109 and relatively high number of migrants per generation (Nm) of 2.464, suggesting that historical germplasm exchange has contributed to maintaining genetic connectivity among populations. AMOVA further showed that most genetic variation was distributed among individuals within populations rather than among populations. These findings demonstrate that Hilacha mango populations in Montería constitute a valuable reservoir of genetic diversity

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and provide a robust molecular foundation for germplasm conservation, sustainable management, and future breeding programs aimed at preserving this traditional mango landrace.

***Keywords:*** Allelic Diversity; Gene Flow; Germplasm Conservation; Hilacha Mango; Population Structure; Simple Sequence Repeats

# 1. Introduction

Understanding the distribution of genetic diversity within cultivated populations is essential for conserving locally adapted germplasm and maintaining the evolutionary potential of perennial fruit crops. In mango (*Mangifera indica* L.), genetic variation reflects the combined effects of domestication, repeated introductions, gene flow, and long-term selection. Together, these processes generate populations in which local differentiation coexists with substantial genetic connectivity[1–3].

Hilacha mango is one of the most widely cultivated traditional landraces in the Colombian Caribbean, particularly in the department of Córdoba, where it supports local production systems and represents a distinctive component of regional agrobiodiversity. Despite its agronomic and socioeconomic importance, little is known about how genetic variation is organized within and among its populations. Molecular studies conducted in Colombia have primarily focused on germplasm collections or cultivars from other producing regions, leaving the population genetic structure of Hilacha mango largely unexplored[4–6]. As a result, the extent to which local populations retain unique genetic variation or remain connected through the exchange of planting material is still uncertain.

Microsatellite markers have become one of the most informative tools for investigating genetic diversity and population structure in mango because they combine high polymorphism, codominant inheritance, and reproducibility[7–9]. Their application has revealed contrasting patterns of diversity and differentiation across cultivated populations in Asia[10], the Middle East[11], and, more recently, Colombia, reflecting differences in domestication history, germplasm movement, and local management practices[12,13]. Comparable information is not yet available for Hilacha mango cultivated in Montería, one of the principal production areas of this landrace in northern Colombia.

Traditional orchards in Montería are characterized by the continuous exchange of propagative material among growers, a practice that may simultaneously promote genetic connectivity and preserve locally differentiated genotypes. Whether these processes have shaped the current genetic structure of Hilacha mango has not previously been investigated, despite their relevance for germplasm conservation and the long-term sustainability of local production systems.

This study therefore investigated the genetic diversity and population structure of Hilacha mango (*Mangifera indica* L.) from five localities in Montería, Córdoba, using polymorphic SSR markers. By examining the distribution of genetic variation within and among populations, this work provides the first population-level molecular assessment of this landrace in the region and establishes a scientific foundation for its conservation, management, and future genetic improvement.

# 2. Materials and Methods

## 2.1. Sampling Area

Leaf samples were collected from 47 Hilacha mango (*Mangifera indica* L.) accessions distributed across five localities in the municipality of Montería (8°45′00″ N, 75°52′59″ W), Córdoba, Colombia, namely the urban area, Kilómetro Doce, San Anterito, Florida, and Betancí (**Figure 1**). The sampling strategy was designed to maximize the representation of the local cultivated germplasm by surveying different orchards and production areas within each locality. Healthy, mature trees were selected during field surveys. One accession was collected from each individual to avoid duplicate sampling. Whenever possible, neighboring trees likely to represent vegetatively propagated individuals of the same genotype were excluded to maximize the capture of independent genotypes while preserving the geographic representation of Hilacha mango cultivation across the study area. Young leaves were carefully collected from each selected

tree, immediately placed in resealable bags containing silica gel to preserve Deoxyribonucleic Acid (DNA) integrity, and transported to the Genetics Laboratory at the Universidad de Córdoba for subsequent molecular analyses.

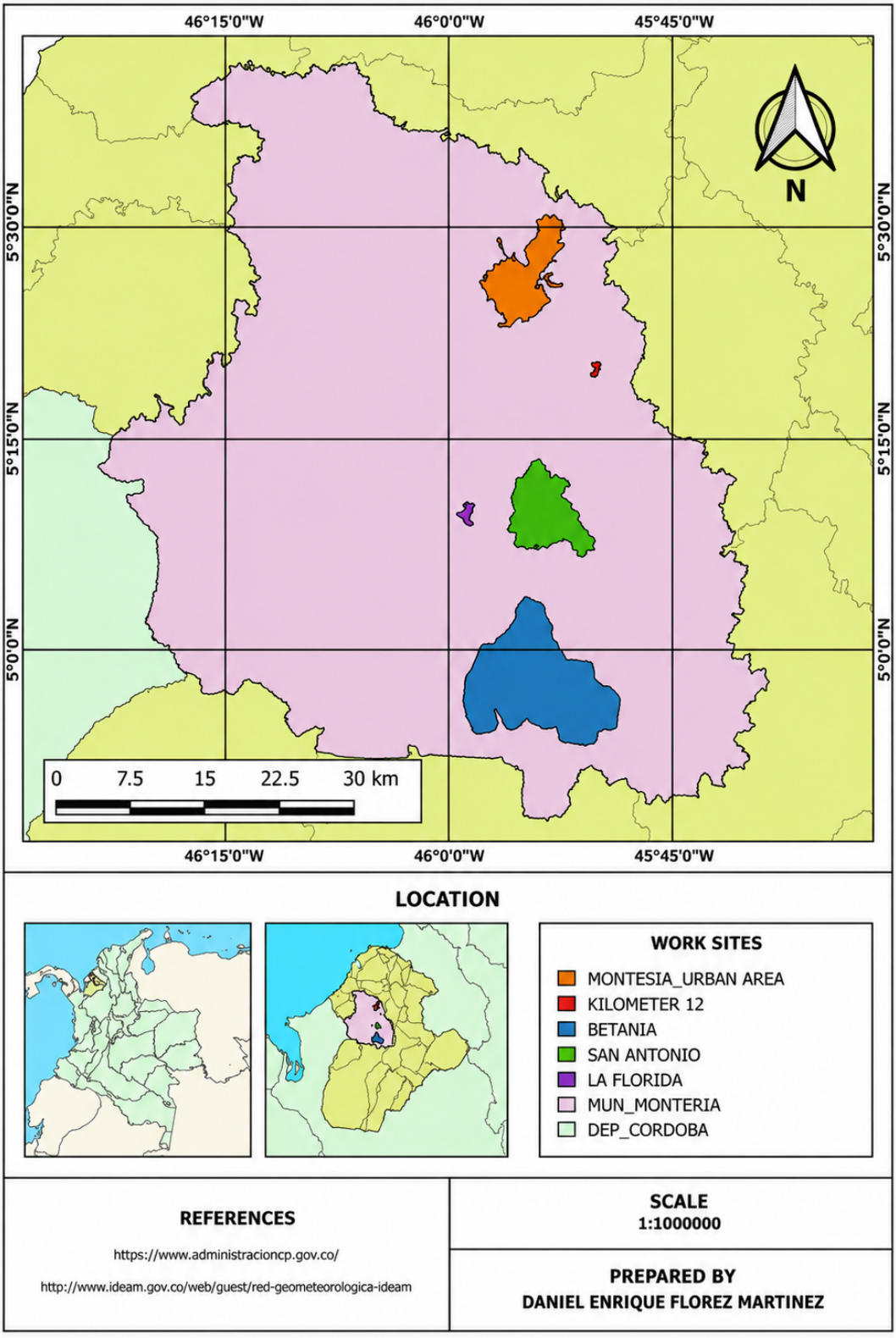


**Figure 1.** Geographic location of the localities: urban area of Montería, Kilometer twelve, Betancí San Anterito and La Florida in the municipality of Montería, Córdoba.

## 2.2. Genomic DNA Extraction

Genomic DNA was extracted from young leaf tissue previously dehydrated and ground in liquid nitrogen following the modified cetyltrimethylammonium bromide (CTAB) 2× protocol described previously [14]. Approximately 25 mg of plant tissue were incubated in preheated CTAB extraction buffer (65 °C) supplemented with 10% polyvinylpyrrolidone (PVP) and β-mercaptoethanol to facilitate the removal of phenolic compounds and secondary metabolites. Subsequently, samples were subjected to chloroform: isoamyl alcohol (24:1) extraction, followed by DNA precipitation with sodium acetate and absolute ethanol. The precipitated DNA was recovered by centrifugation, washed twice with 70% ethanol to remove residual salts and impurities, and finally resuspended in rehydration solution. DNA samples were stored at 4 °C until further analysis.

DNA concentration and purity were assessed using a NanoDrop One spectrophotometer (Thermo Scientific, Waltham, MA, USA). DNA quality was evaluated based on absorbance at 260 nm and the A260/A280 and A260/A230 absorbance ratios.

## 2.3. Microsatellite Amplification by Polymerase Chain Reaction (PCR)

Eight polymorphic microsatellite (SSR) *loci* previously developed *for Mangifera indica* [6] were evaluated (**Table 1**). Marker amplification was performed using polymerase chain reaction (PCR) in a final reaction volume of 20 µL containing 10 µL of Master Mix (Taq DNA polymerase, dNTPs, $MgCl_2$, and reaction buffer), 0.6 µL of each primer (forward and reverse), 2 µL of genomic DNA, and nuclease-free water to complete the final volume.

**Table 1.** Primers of *Mangifera indica* [6].

| Marker | Primer Forward 5' – 3' | Primer Reverse 5' – 3' | Ta (°C) |
|---|---|---|---|
| *MiIIHR10*[d] | CGATTCAAGACGGAAAGGAA | TTCAAGCACAGACGACCAAC | 55.6 |
| *MiIIHR15*[c] | TAACCATTCGGCATCCTCT | TGTGATAGAATGGCAAAAGAA | 57.4 |
| *MiIIHR03*[c] | GTCGATGCCTGGAATGAAGT | CCTCCTTACATGCCTCCTTG | 55.7 |
| *MiIIHR22*[b] | TGGCCGAACTAGCAAACTCT | TTAATTGCAGGACTGGAGCA | 55.9 |
| *MiIIHR31*[a] | TTCTGTTAGTGGCGGTGTTG | CACCTCCTCCTCCTCCTCTT | 56.1 |
| *MiIIHR34*[d] | CTGAGTTTGGCAAGGGAGAG | TTGATCCTTCACCACCATCA | 54.9 |
| *MiIIHR13*[b] | CCCAGTTCCAACATCATCAG | ATTTCCCACCATTGTCGTTG | 54.4 |
| *MiIIHR14*[b] | CCGAAACAACTCTTCCTCCA | TTCCTCTGGAAGAGGGAAGA | 57.6 |

Note: [a]: 6-FAM™; [b]: VIC®; [c]: NED™; [d]: PET®.

PCR amplifications were carried out in a T100™ Thermal Cycler (Bio-Rad, Hercules, CA, USA) under the following conditions: an initial denaturation step at 95 °C for 3 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing for 30 s at the locus-specific temperature (**Table 1**), and extension at 72 °C for 1 min, with a final extension step of 5 min at 72 °C.

PCR amplification products were verified by electrophoresis on 2% (w/v) agarose gels using a horizontal electrophoresis system (Owl Separation Systems, Portsmouth, NH, USA). Briefly, 5 µL of each PCR product were stained with GelRed™ and separated in 0.5× TBE buffer at a constant voltage of 100 V for 40 min. Subsequently, amplicons were subjected to a pseudomultiplex cleaning protocol [15] and purified using multilayer silica columns to remove impurities and improve fragment quality. Purified products were processed at the Institute of Genetics of the National University of Colombia, where fragment analysis was performed by capillary electrophoresis using an Applied Biosystems automated DNA analyzer. The resulting allele sizes were used for subsequent analyses of genetic diversity and population structure among the evaluated accessions.

Quality control and genotype validation: DNA quality was verified by NanoDrop absorbance measurements and agarose gel electrophoresis prior to PCR amplification. Fragment sizes were scored using the Applied Biosystems allele-calling software and subsequently verified by visual inspection of all electropherograms to confirm allele assignments and resolve ambiguous peaks. Only clear and reproducible amplification profiles were retained for subsequent analyses. Missing genotypes, when present, were maintained as missing values during statistical analyses and did not affect

the inclusion of loci or individuals in the final dataset.

### 2.4. Statistical Analysis

Genetic diversity parameters, including the number of alleles (Na), effective number of alleles (Ne), allele frequencies, private alleles, observed heterozygosity (Ho), expected heterozygosity (He), Shannon's diversity index (I), fixation index (F), and Hardy–Weinberg equilibrium (HWE), were estimated using GenAlEx v6.5 [16,17]. The polymorphic information content (PIC) of the SSR markers was calculated with CERVUS v3.0.7 [18]. Population genetic structure was assessed through Wright's F-statistics: inbreeding coefficient within populations ($F_{IS}$), overall inbreeding coefficient ($F_{IT}$) and genetic differentiation among populations ($F_{ST}$) and an analysis of molecular variance (AMOVA), both implemented in GenAlEx v6.5 [16,17]. Genetic differentiation and relationships among populations were evaluated using Nei's genetic distance [19]. The resulting distance matrix was used to construct an unweighted pair group method with arithmetic mean Unweighted Pair Group Method with Arithmetic Mean (UPGMA) dendrogram in MEGA X [20]. Finally, genetic clustering patterns were explored through a Principal Coordinates Analysis (PCoA) performed in PAST v4.10, based on a binary genetic distance matrix proposed by Huff et al. [21] and generated in GenAlEx v6.5 [16,17].

## 3. Results

### 3.1. Allele Frequencies and Allelic Patterns

The eight SSR loci evaluated were polymorphic and exhibited differences in allele frequency distribution among the *Mangifera indica* populations studied (**Table 2**). Overall, the populations shared several predominant alleles, although low-frequency and population-specific alleles were also detected. This pattern indicates a heterogeneous distribution of genetic variation among localities, characterized by the coexistence of widespread alleles and locally restricted variants.

**Table 2.** Allele frequencies of microsatellite loci in *Mangifera indica* populations from Montería, Córdoba, Colombia.

| *Locus* | Allele | Zona Urbana | Km 12 | Florida | Betancí | San Anterito |
|---|---|---|---|---|---|---|
| *MiIIHR31* | 217 | 0.000 | 0.000 | 0.111 | 0.000 | 0.000 |
| | 218 | 0.800 | 1.000 | 0.556 | 0.778 | 0.667 |
| | 219 | 0.200 | 0.000 | 0.333 | 0.222 | 0.333 |
| *MiIIHR15* | 135 | 0.000 | 0.000 | 0.222 | 0.000 | 0.111 |
| | 149 | 0.000 | 0.100 | 0.000 | 0.000 | 0.000 |
| | 150 | 0.450 | 0.000 | 0.333 | 0.000 | 0.278 |
| | 151 | 0.350 | 0.800 | 0.444 | 0.444 | 0.389 |
| | 154 | 0.200 | 0.100 | 0.000 | 0.556 | 0.167 |
| | 182 | 0.000 | 0.000 | 0.000 | 0.000 | 0.056 |
| *MiIIHR03* | 218 | 0.000 | 0.000 | 0.111 | 0.000 | 0.000 |
| | 225 | 0.600 | 0.500 | 0.389 | 0.722 | 0.500 |
| | 226 | 0.100 | 0.100 | 0.000 | 0.056 | 0.111 |
| | 231 | 0.300 | 0.400 | 0.500 | 0.222 | 0.389 |
| *MiIIHR22* | 210 | 0.100 | 0.000 | 0.111 | 0.000 | 0.000 |
| | 218 | 0.400 | 0.650 | 0.333 | 0.444 | 0.389 |
| | 219 | 0.100 | 0.200 | 0.333 | 0.333 | 0.222 |
| | 220 | 0.300 | 0.100 | 0.167 | 0.000 | 0.333 |
| | 223 | 0.000 | 0.050 | 0.000 | 0.000 | 0.000 |
| | 225 | 0.000 | 0.000 | 0.000 | 0.167 | 0.000 |
| | 226 | 0.000 | 0.000 | 0.000 | 0.000 | 0.056 |
| | 230 | 0.000 | 0.000 | 0.056 | 0.000 | 0.000 |
| | 233 | 0.000 | 0.000 | 0.000 | 0.056 | 0.000 |
| | 335 | 0.100 | 0.000 | 0.000 | 0.000 | 0.000 |
| *MiIIHR14* | 330 | 0.000 | 0.000 | 0.222 | 0.000 | 0.000 |
| | 331 | 0.000 | 0.000 | 0.000 | 0.056 | 0.000 |
| | 332 | 0.450 | 0.700 | 0.278 | 0.500 | 0.333 |
| | 333 | 0.350 | 0.200 | 0.278 | 0.111 | 0.611 |
| | 340 | 0.050 | 0.000 | 0.056 | 0.000 | 0.056 |
| | 344 | 0.150 | 0.100 | 0.111 | 0.333 | 0.000 |
| | 345 | 0.000 | 0.000 | 0.056 | 0.000 | 0.000 |

**Table 2.** *Cont.*

| *Locus* | Allele | Zona Urbana | Km 12 | Florida | Betancí | San Anterito |
|---|---|---|---|---|---|---|
| *MiIIHR13* | 170 | 0.000 | 0.000 | 0.000 | 0.111 | 0.000 |
| | 180 | 0.100 | 0.000 | 0.111 | 0.111 | 0.000 |
| | 181 | 0.650 | 0.900 | 0.833 | 0.778 | 0.556 |
| | 187 | 0.250 | 0.100 | 0.056 | 0.000 | 0.444 |
| *MiIIHR10* | 182 | 0.600 | 0.400 | 0.778 | 0.889 | 0.722 |
| | 183 | 0.400 | 0.600 | 0.222 | 0.111 | 0.222 |
| | 188 | 0.000 | 0.000 | 0.000 | 0.000 | 0.056 |
| *MiIIHR34* | 222 | 0.000 | 0.150 | 0.056 | 0.000 | 0.000 |
| | 223 | 0.050 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 224 | 0.050 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 225 | 0.050 | 0.050 | 0.000 | 0.056 | 0.167 |
| | 228 | 0.150 | 0.400 | 0.667 | 0.611 | 0.333 |
| | 229 | 0.650 | 0.050 | 0.111 | 0.222 | 0.056 |
| | 231 | 0.000 | 0.000 | 0.056 | 0.000 | 0.000 |
| | 234 | 0.050 | 0.300 | 0.000 | 0.056 | 0.278 |
| | 237 | 0.000 | 0.050 | 0.111 | 0.056 | 0.111 |
| | 238 | 0.000 | 0.000 | 0.000 | 0.000 | 0.056 |

At locus *MiIIHR31*, allele 218 was the most frequent across all populations, whereas allele 217 was detected exclusively in Florida. At *MiIIHR15*, allele 151 exhibited the highest frequencies, particularly in Kilómetro 12. For *MiIIHR03*, alleles 225 and 231 were the most prevalent. *MiIIHR22* was the most polymorphic locus, with ten alleles identified and allele 218 occurring at the highest frequency. At MiIIHR14, alleles 332 and 333 predominated, whereas alleles 181 and 182 were the most frequent at *MiIIHR13* and *MiIIHR10*, respectively. *MiIIHR34* also exhibited high allelic variability, with alleles 228 and 229 predominating together with several low-frequency alleles restricted to specific localities. Overall, allele frequency patterns revealed a heterogeneous distribution of genetic variation among the five populations.

Allelic patterns differed among the five Hilacha mango populations evaluated (**Table 3**). Florida exhibited the highest allelic richness (Na = 30), followed by the urban area and San Anterito (Na = 28 each), Betancí (Na = 25), and Kilómetro 12 (Na = 24). Similarly, the effective number of alleles (Ne) was highest in San Anterito (2.638) and Florida (2.604), whereas the lowest values were recorded in Kilómetro 12 (1.946) and Betancí (1.999).

Florida harbored the highest number of private alleles (6), followed by Betancí and San Anterito (4 each), the urban area (3), and Kilómetro 12 (2). Regarding allele frequency classes, only common alleles (frequency > 0.05) were detected in Florida (30), Betancí (25), and San Anterito (28), whereas the urban area and Kilómetro 12 contained five and four rare alleles (frequency ≤ 0.05), respectively.

**Table 3.** Allelic diversity patterns in *Mangifera indica* populations from Montería, Córdoba, Colombia.

| | Zona Urbana | Km 12 | Florida | Betancí | San Anterito |
|---|---|---|---|---|---|
| Number of alleles ($N_a$) | 28 | 24 | 30 | 25 | 28 |
| Effective number of alleles ($N_e$) | 2.369 | 1.946 | 2.604 | 1.999 | 2.638 |
| Private alleles | 3 | 2 | 6 | 4 | 4 |
| Common alleles (frequency > 0.05) | 23 | 20 | 30 | 25 | 28 |
| Rare alleles (frequency ≤ 0.05) | 5 | 4 | 0 | 0 | 0 |

## 3.2. Genetic Diversity Parameters

Genetic diversity parameters varied among the five Hilacha mango populations evaluated (**Table 4**). Florida and San Anterito exhibited the highest mean allelic richness (Na = 3.8 and 3.5, respectively) and effective number of alleles (Ne = 2.604 and 2.638, respectively), whereas Kilómetro 12 showed the lowest values for both parameters (Na = 3.0; Ne = 1.946).

**Table 4.** Genetic diversity estimates for five *Mangifera indica* populations from Montería, Córdoba, Colombia.

| Population | Locus | $N_a$ | $N_e$ | I | $H_o$ | $H_e$ | $uH_e$ | F | EHW |
|---|---|---|---|---|---|---|---|---|---|
| Zona urbana | *MiIIHR31* | 2 | 1.471 | 0.500 | 0.000 | 0.320 | 0.337 | 1.000 | 0.002** |
| | *MiIIHR15* | 3 | 2.740 | 1.049 | 0.200 | 0.635 | 0.668 | 0.685 | 0.029* |
| | *MiIIHR03* | 3 | 2.174 | 0.898 | 0.000 | 0.540 | 0.568 | 1.000 | 0.000*** |
| | *MiIIHR22* | 5 | 3.571 | 1.418 | 0.000 | 0.720 | 0.758 | 1.000 | 0.000*** |
| | *MiIIHR14* | 4 | 2.857 | 1.161 | 0.400 | 0.650 | 0.684 | 0.385 | 0.079$^{ns}$ |
| | *MiIIHR13* | 3 | 2.020 | 0.857 | 0.100 | 0.505 | 0.532 | 0.802 | 0.002** |
| | *MiIIHR10* | 2 | 1.923 | 0.673 | 0.000 | 0.480 | 0.505 | 1.000 | 0.002** |
| | *MiIIHR34* | 6 | 2.198 | 1.164 | 0.400 | 0.545 | 0.574 | 0.266 | 0.170$^{ns}$ |
| Mean | | 3.500 | 2.369 | 0.965 | 0.138 | 0.549 | 0.578 | 0.767 | |
| Km 12 | *MiIIHR31* | 1 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | ------ | Monomórfico |
| | *MiIIHR15* | 3 | 1.515 | 0.639 | 0.000 | 0.340 | 0.358 | 1.000 | 0.000*** |
| | *MiIIHR03* | 3 | 2.381 | 0.943 | 0.000 | 0.580 | 0.611 | 1.000 | 0.000*** |
| | *MiIIHR22* | 4 | 2.105 | 0.982 | 0.100 | 0.525 | 0.553 | 0.810 | 0.003** |
| | *MiIIHR14* | 3 | 1.852 | 0.802 | 0.200 | 0.460 | 0.484 | 0.565 | 0.017* |
| | *MiIIHR13* | 2 | 1.220 | 0.325 | 0.200 | 0.180 | 0.189 | −0.111 | 0.725$^{ns}$ |
| | *MiIIHR10* | 2 | 1.923 | 0.673 | 0.000 | 0.480 | 0.505 | 1.000 | 0.002** |
| | *MiIIHR34* | 6 | 3.571 | 1.462 | 0.700 | 0.720 | 0.758 | 0.028 | 0.683$^{ns}$ |
| Mean | | 3.000 | 1.946 | 0.728 | 0.150 | 0.411 | 0.432 | 0.613 | |
| Florida | *MiIIHR31* | 3 | 2.314 | 0.937 | 0.000 | 0.568 | 0.601 | 1.000 | 0.000*** |
| | *MiIIHR15* | 3 | 2.793 | 1.061 | 0.000 | 0.642 | 0.680 | 1.000 | 0.000*** |
| | *MiIIHR03* | 3 | 2.418 | 0.958 | 0.111 | 0.586 | 0.621 | 0.811 | 0.003** |
| | *MiIIHR22* | 5 | 3.767 | 1.436 | 0.111 | 0.735 | 0.778 | 0.849 | 0.002** |
| | *MiIIHR14* | 6 | 4.500 | 1.611 | 0.444 | 0.778 | 0.824 | 0.429 | 0.324$^{ns}$ |
| | *MiIIHR13* | 3 | 1.409 | 0.557 | 0.111 | 0.290 | 0.307 | 0.617 | 0.029* |
| | *MiIIHR10* | 2 | 1.528 | 0.530 | 0.000 | 0.346 | 0.366 | 1.000 | 0.003** |
| | *MiIIHR34* | 5 | 2.104 | 1.080 | 0.444 | 0.525 | 0.556 | 0.153 | 0.440$^{ns}$ |
| Mean | | 3.800 | 2.604 | 1.021 | 0.153 | 0.559 | 0.592 | 0.732 | |
| Betancí | *MiIIHR31* | 2 | 1.528 | 0.530 | 0.000 | 0.346 | 0.366 | 1.000 | 0.003** |
| | *MiIIHR15* | 2 | 1.976 | 0.687 | 0.000 | 0.494 | 0.523 | 1.000 | 0.003** |
| | *MiIIHR03* | 3 | 1.742 | 0.730 | 0.222 | 0.426 | 0.451 | 0.478 | 0.124$^{ns}$ |
| | *MiIIHR22* | 4 | 2.945 | 1.186 | 0.444 | 0.660 | 0.699 | 0.327 | 0.081$^{ns}$ |
| | *MiIIHR14* | 4 | 2.656 | 1.117 | 0.444 | 0.623 | 0.660 | 0.287 | 0.088$^{ns}$ |
| | *MiIIHR13* | 3 | 1.588 | 0.684 | 0.222 | 0.370 | 0.392 | 0.400 | 0.027* |
| | *MiIIHR10* | 2 | 1.246 | 0.349 | 0.000 | 0.198 | 0.209 | 1.000 | 0.003** |
| | *MiIIHR34* | 5 | 2.314 | 1.117 | 0.333 | 0.568 | 0.601 | 0.413 | 0.470$^{ns}$ |
| Mean | | 3.100 | 1.999 | 0.800 | 0.208 | 0.461 | 0.488 | 0.613 | |
| San Anterito | *MiIIHR31* | 2 | 1.800 | 0.637 | 0.000 | 0.444 | 0.471 | 1.000 | 0.003** |
| | *MiIIHR15* | 5 | 3.682 | 1.426 | 0.333 | 0.728 | 0.771 | 0.542 | 0.025* |
| | *MiIIHR03* | 3 | 2.418 | 0.958 | 0.111 | 0.586 | 0.621 | 0.811 | 0.003** |
| | *MiIIHR22* | 4 | 3.176 | 1.228 | 0.111 | 0.685 | 0.725 | 0.838 | 0.006** |
| | *MiIIHR14* | 3 | 2.051 | 0.828 | 0.111 | 0.512 | 0.542 | 0.783 | 0.028* |
| | *MiIIHR13* | 2 | 1.976 | 0.687 | 0.222 | 0.494 | 0.523 | 0.550 | 0.099$^{ns}$ |
| | *MiIIHR10* | 3 | 1.742 | 0.730 | 0.111 | 0.426 | 0.451 | 0.739 | 0.029* |
| | *MiIIHR34* | 6 | 4.263 | 1.586 | 0.778 | 0.765 | 0.810 | −0.016 | 0.011* |
| Mean | | 3.500 | 2.638 | 1.010 | 0.222 | 0.580 | 0.614 | 0.656 | |
| Overall mean | | 3.400 | 2.311 | 0.905 | 0.174 | 0.512 | 0.541 | 0.678 | |

Note: Na: number of alleles; Ne: effective number of alleles; I: Shannon's diversity index; Ho: observed heterozygosity; He: expected heterozygosity; uHe: unbiased expected heterozygosity; F: fixation index; HWE: Hardy–Weinberg equilibrium. Significance levels: (*: *p*-Valor < 0.05; **: *p*-Valor < 0.01; ***: *p*-Valor < 0.001; ns: not significant.

Shannon's diversity index was highest in Florida (I = 1.021) and San Anterito (I = 1.010). Observed heterozygosity (Ho) was lower than expected heterozygosity (He) in most loci and populations. The highest mean Ho values were recorded in San Anterito (0.222) and Betancí (0.208), whereas the urban area exhibited the lowest value (0.138). Expected heterozygosity ranged from 0.411 in Kilómetro 12 to 0.580 in San Anterito. Fixation indices were predominantly positive, with mean values ranging from 0.613 to 0.767. Most loci deviated significantly from Hardy–Weinberg equilibrium, although *MiIIHR14* and *MiIIHR34* conformed to equilibrium expectations in some populations.

## 3.3. Polymorphic Information Content

The polymorphic information content (PIC) of the SSR markers ranged from 0.314 to 0.707 (**Table 5**). The highest PIC values were observed for loci *MiIIHR34* (0.707), *MiIIHR22* (0.668), *MiIIHR15* (0.622), and *MiIIHR14* (0.620), indicating that these loci were highly informative (PIC > 0.50). In contrast, *MiIIHR31* (0.314), *MiIIHR10* (0.357), and *MiIIHR13* (0.375) exhibited moderate levels of polymorphism.

**Table 5.** Polymorphic information content of microsatellite loci in *Mangifera indica* populations from Montería, Córdoba, Colombia.

| Locus | PIC |
|---|---|
| *MiIIHR31* | 0.314 |
| *MiIIHR15* | 0.622 |
| *MiIIHR03* | 0.487 |
| *MiIIHR22* | 0.668 |
| *MiIIHR14* | 0.620 |
| *MiIIHR13* | 0.375 |
| *MiIIHR10* | 0.357 |
| *MiIIHR34* | 0.707 |

Overall, PIC values indicated differences in the informativeness of the SSR markers, with MiIIHR34 and MiIIHR22 exhibiting the highest values among the loci evaluated.

## 3.4. Population Genetic Structure

Wright's F-statistics revealed variable levels of inbreeding and genetic differentiation among the populations (**Table 6**). The inbreeding coefficient within populations ($F_{IS}$) was positive for all loci, with a mean value of 0.689. The highest $F_{IS}$ values were recorded for *MiIIHR31* (1.000), *MiIIHR10* (0.942), and *MiIIHR03* (0.837), whereas the lowest value was observed for *MiIIHR34* (0.150). Similarly, the overall inbreeding coefficient ($F_{IT}$) was positive across all *loci*, averaging 0.726 and reaching its maximum value (1.000) at *MiIIHR31*.

Genetic differentiation among populations ($F_{ST}$) ranged from 0.044 (*MiIIHR03*) to 0.156 (*MiIIHR15*), with a mean value of 0.109. The highest $F_{ST}$ values were recorded for loci *MiIIHR15*, *MiIIHR34*, and MiIIHR10, whereas *MiIIHR03* and *MiIIHR22* exhibited the lowest values. Estimated gene flow (Nm) ranged from 1.357 to 5.402 migrants per generation, with a mean value of 2.464. The highest Nm value was recorded for *MiIIHR03*, whereas the lowest was observed for *MiIIHR15*.

## 3.5. Analysis of Molecular Variance (AMOVA)

Analysis of molecular variance (AMOVA) partitioned the genetic variation into three hierarchical components (**Table 7**). Most of the total genetic variation was distributed among individuals within populations (66%), whereas 29% occurred within individuals. Only 5% of the total genetic variation was attributable to differences among populations (**Figure 2**). Genetic differentiation between populations was statistically significant ($p = 0.001$), according to the permutation test based on 999 permutations.

**Table 6.** Wright's F-statistics and gene flow estimates for SSR loci in *Mangifera indica* populations from Montería, Córdoba, Colombia.

| Locus | $F_{IS}$ | $F_{IT}$ | $F_{ST}$ | Nm |
|---|---|---|---|---|
| *MiIIHR31* | 1.000 | 1.000 | 0.104 | 2.158 |
| *MiIIHR15* | 0.812 | 0.841 | 0.156 | 1.357 |
| *MiIIHR03* | 0.837 | 0.844 | 0.044 | 5.402 |
| *MiIIHR22* | 0.769 | 0.784 | 0.064 | 3.638 |
| *MiIIHR14* | 0.471 | 0.527 | 0.107 | 2.096 |
| *MiIIHR13* | 0.535 | 0.587 | 0.111 | 1.997 |
| *MiIIHR10* | 0.942 | 0.950 | 0.130 | 1.667 |
| *MiIIHR34* | 0.150 | 0.279 | 0.152 | 1.396 |
| Mean | 0.689 | 0.726 | 0.109 | 2.464 |

Note: $F_{IS}$: inbreeding coefficient within populations; $F_{IT}$: overall inbreeding coefficient; $F_{ST}$: genetic differentiation among populations; Nm: estimated number of migrants per generation.

**Table 7.** Analysis of molecular variance (AMOVA) for *Mangifera indica* populations from Montería. Córdoba. Colombia.

| Source of Variation | Degrees of Freedom | Sum of Squares | Middle Squares | Standard Variation | Percentage of Variation | *p* Value |
|---|---|---|---|---|---|---|
| Between populations | 4 | 23.714 | 5.929 | 0.113 | 5% | 0.001 |
| Between individuals | 42 | 159.467 | 3.797 | 1.553 | 66% | |
| Within individuals | 47 | 32.500 | 0.691 | 0.691 | 29% | |
| Total | 93 | 215.681 | | 2.358 | 100% | |

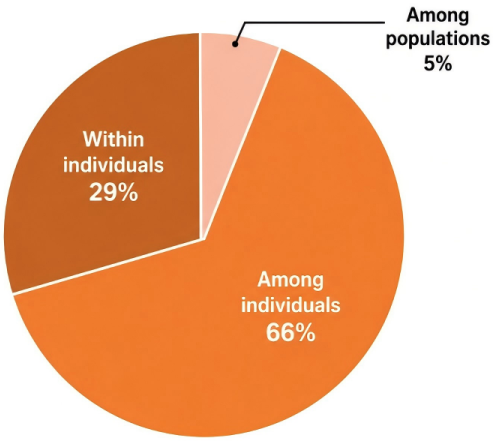


**Figure 2.** Molecular analysis of variance in the *M. indica* populations from Montería, Córdoba.

These results indicate that the genetic variation of Mangifera indica in Montería is determined primarily by differences between individuals rather than by the geographical separation between the different populations.

## 4. Discussion

The allele frequency distribution revealed that Hilacha mango populations in Montería retain substantial genetic diversity, characterized by the coexistence of widespread alleles and locality-specific variants. Such a pattern is typical of cultivated species with a long history of domestication, repeated germplasm introductions, and farmer-mediated dispersal, processes that promote the maintenance of high levels of genetic variation despite continuous human management [3,5,6]. The high polymorphism detected at loci *MiIHR22* and *MiIIHR34* further confirms the suitability of these SSR markers for assessing population diversity, in agreement with studies conducted in mango germplasm from Asia, the Middle East, and Latin America, where highly polymorphic loci provide greater power for genotype discrimination and population structure analyses [5,6,9].

The occurrence of private alleles in several localities indicates that regional genetic connectivity has not eliminated local genetic differentiation. These exclusive alleles likely reflect the combined influence of historical germplasm introductions, farmer selection, and the limited circulation of particular genotypes among production areas [10,11]. Conversely, the widespread distribution of dominant alleles across populations supports the existence of substantial gene exchange, most likely promoted by the long-term movement of planting material within the region. Together, these patterns suggest that the genetic composition of Hilacha mango has been shaped by the interaction between regional connectivity and local differentiation, preserving both shared diversity and unique genetic variants that contribute to the adaptive potential of this traditional landrace [3,9,11].

The persistence of locality-specific alleles is unlikely to result exclusively from historical introductions. Local environmental conditions, together with the continued selection of preferred trees by farmers, may have favored the maintenance of uncommon alleles over successive generations. Although *Mangifera indica* is predominantly an outcrossing species, its long lifespan and widespread vegetative propagation facilitate the persistence of locally adapted genotypes even under moderate gene flow [22,23]. This interaction between ecological processes and traditional management practices provides a plausible explanation for the retention of private alleles despite the considerable genetic connectivity observed among populations [3].

Hilacha mango populations in Montería retained substantial levels of genetic diversity, particularly in Florida and San Anterito, which exhibited the highest allelic richness, effective number of alleles, and Shannon diversity values. Similar patterns have been reported in mango populations from India, China, Oman, and Colombia, where genetically diverse populations are recognized as valuable reservoirs of germplasm for conservation and breeding [6,11,13]. The uneven distribution of diversity among localities probably reflects differences in orchard history, germplasm introductions, and long-term management practices rather than contemporary environmental conditions alone [24,25].

Despite the overall high levels of diversity, observed heterozygosity was consistently lower than expected heterozygosity, resulting in positive fixation indices across most populations. Heterozygote deficiency is a common feature of cultivated *Mangifera indica* and has been associated with vegetative propagation, recurrent selection of elite genotypes, and the preferential exchange of planting material among growers [6,10]. Significant deviations from Hardy–Weinberg equilibrium further support the influence of population subdivision and non-random mating on the genetic composition of the studied populations [3,6,10].

Another plausible explanation for the observed heterozygote deficit is the Wahlund effect, whereby the analysis

of geographically differentiated subpopulations as a single dataset reduces observed heterozygosity relative to Hardy–Weinberg expectations [7]. Together, these findings indicate that Hilacha mango populations maintain considerable genetic diversity despite a moderate deficit of heterozygotes, reflecting the combined influence of historical germplasm movement, traditional management practices, and local population structure.

The polymorphic information content (PIC) values indicate that most SSR loci employed in this study are highly informative for assessing genetic diversity in Hilacha mango. In particular, *MiIIHR34*, *MiIIHR22*, *MiIIHR15*, and *MiIIHR14* exhibited PIC values above 0.60, confirming their strong discriminatory capacity for population genetic analyses. Comparable results have been reported for mango populations from India, China, Oman, and Colombia, where highly informative SSR markers consistently provide greater resolution for detecting allelic variation and population structure [6,9,10].

From an evolutionary perspective, the high PIC values observed for *MiIIHR34* and *MiIIHR22* are consistent with their elevated allelic richness and support their suitability for characterizing the genetic diversity of Hilacha mango [5,9]. Highly polymorphic markers are particularly valuable for identifying duplicated accessions, establishing representative core collections, and selecting genetically divergent parental lines, thereby strengthening germplasm conservation and molecular breeding strategies [3].

The consistently positive $F_{IS}$ and $F_{IT}$ values indicate a generalized deficit of heterozygotes, suggesting that nonrandom mating and the recurrent propagation of selected genotypes have influenced the genetic composition of Hilacha mango populations. Similar patterns have been reported in cultivated *Mangifera indica* and are commonly associated with vegetative propagation, farmer selection, and the preferential use of elite planting material [6,7,10]. These processes, together with population subdivision, are likely to have contributed to the observed deviations from Hardy–Weinberg equilibrium and the uneven distribution of genetic diversity among localities [26].

The mean $F_{ST}$ value (0.109) indicates moderate genetic differentiation among populations according to Wright's criteria [27]. Although populations share a substantial proportion of their genetic diversity, differences in allele frequencies indicate that local evolutionary processes continue to operate. Comparable levels of differentiation have been described in mango populations from India, Oman, China, and Colombia, where historical germplasm exchange has limited population divergence without eliminating locally differentiated genetic variation [6,11,13].

The estimated gene flow (Nm = 2.464) suggests sufficient genetic connectivity to counterbalance the effects of genetic drift and maintain regional genetic cohesion [28]. The inverse relationship between $F_{ST}$ and Nm supports the hypothesis that the historical exchange of planting material has facilitated allele movement among localities while preserving moderate levels of differentiation. Rather than representing isolated or completely homogeneous populations, Hilacha mango in Montería appears to form a genetically connected system in which gene flow, local selection, and traditional management practices operate simultaneously. This balance between connectivity and differentiation is likely to enhance the evolutionary resilience of the landrace by maintaining regional genetic cohesion while preserving locally distinctive genetic variants that may contribute to future adaptation under changing environmental conditions [29–31].

The AMOVA revealed that most genetic variation in Hilacha mango was distributed among individuals within populations (66%), whereas only a small proportion (5%) was attributable to differences among localities. This pattern is characteristic of predominantly outcrossing perennial species and has been consistently reported in SSR- and SNP-based studies of *Mangifera indica* from different geographic regions [6,9,11]. The limited interpopulation differentiation indicates that historical germplasm exchange and continued movement of planting material have promoted substantial genetic connectivity, reducing divergence among localities while maintaining high levels of diversity within populations.

The predominance of intrapopulation variation highlights the importance of individual trees as repositories of genetic diversity. Such a pattern reflects the combined effects of multiple germplasm introductions, recurrent recombination, and long-term farmer-mediated selection, all of which have contributed to maintaining genetically heterogeneous populations despite their geographic proximity [3,10,11]. Similar patterns have been documented in traditional cropping systems where human management simultaneously promotes genetic connectivity and preserves substantial within-population di-

versity [27].

From a conservation perspective, these findings indicate that preserving a large number of genetically distinct individuals within each locality is likely to be more effective than focusing exclusively on the conservation of representative sites. Maintaining this intrapopulation diversity, together with the traditional exchange of planting material among localities, should help preserve the adaptive potential of Hilacha mango populations and enhance their capacity to respond to future environmental and climatic changes [32–34].

The genetically diverse populations identified in this study represent valuable biological resources for both conservation and sustainable utilization. Preserving traditional Hilacha mango landraces while maintaining their cultivation helps retain locally adapted alleles, supports ecosystem resilience, and safeguards genetic resources for future breeding under changing environmental conditions [23,31]. In particular, populations with high allelic richness and private alleles provide valuable parental material for broadening the genetic base of breeding programs and incorporating adaptive traits associated with local environments [22,25,30]. These findings reinforce the importance of integrating in situ conservation with ex situ germplasm collections to preserve the evolutionary potential and long-term sustainability of this traditional landrace.

Although this study focuses on population genetics, conserving genetically diverse germplasm also creates opportunities for applications beyond crop improvement. Plant genetic resources increasingly support environmentally sustainable technologies, including the use of plant-derived biomolecules for the green synthesis of functional nanomaterials with applications in environmental remediation [35]. In this broader context, conserving the genetic diversity of traditional landraces not only safeguards biodiversity but also preserves biological resources that may contribute to future ecological, agricultural, and biotechnological innovations.

## 5. Conclusions

This study provides the first comprehensive assessment of the genetic diversity and population structure of Hilacha mango (*Mangifera indica* L.) in Montería, Córdoba, Colombia, using SSR markers. The populations retained high levels of allelic diversity, together with moderate genetic differentiation and substantial genetic connectivity, indicating that most genetic variation is maintained within rather than among populations. The coexistence of widespread and private alleles, combined with moderate levels of gene flow, suggests that the current genetic structure has been shaped by the interaction between historical germplasm exchange, local selection, and the long-term cultivation of this traditional landrace. Florida and San Anterito exhibited the highest levels of genetic diversity and should therefore be considered priority populations for in situ conservation and as key sources of germplasm for the establishment or enrichment of ex situ collections. The presence of private alleles across all localities also indicates that conservation strategies should preserve representative individuals from each population rather than focusing on a single site, thereby maximizing the retention of regional genetic diversity. For breeding programs, the identification of genetically differentiated populations provides an opportunity to select divergent parental material, broaden the genetic base of future cultivars, and reduce the risk of genetic erosion associated with the repeated use of closely related genotypes.

## Author Contributions

Conceptualization: E.P. and T.C.; methodology: E.P., T.C., and L.C.; Investigation: E.P., L.A., and L.C.; validation: E.P., T.C., and L.A.; formal analysis: L.A., T.C., and L.C.; software: E.P., L.A., and L.C.; writing—original draft preparation: E.P. and T.C.; writing—review and editing: E.P., L.C., and L.A. All authors have read and agreed to the published version of the manuscript.

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## Data Availability Statement

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

## Conflicts of Interest

The authors declare no conflict of interest.

## AI Use Statement

During the preparation of this manuscript, the authors used artificial intelligence-assisted writing tools exclusively for language editing, refinement of the writing, and improvement of the clarity and fluency of the text. No artificial intelligence tools were used for the study design, data analysis, interpretation of the results, generation of scientific content, or formulation of the conclusions. All scientific interpretations, analyses, results, and conclusions were critically reviewed, evaluated, and approved by the authors, who assume full responsibility for the integrity, accuracy, and final content of the manuscript.

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