Genetic diversity and population structure of the Guinea pig (Cavia porcellus, Rodentia, Caviidae) in Colombia

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Abstract

The aim was to establish the genetic diversity and population structure of three guinea pig lines, from seven production zones located in Nariño, southwest Colombia. A total of 384 individuals were genotyped with six microsatellite markers. The measurement of intrapopulation diversity revealed allelic richness ranging from 3.0 to 6.56, and observed heterozygosity (Ho) from 0.33 to 0.60, with a deficit in heterozygous individuals. Although statistically significant (p < 0.05), genetic differentiation between population pairs was found to be low. Genetic distance, as well as clustering of guinea-pig lines and populations, coincided with the historical and geographical distribution of the populations. Likewise, high genetic identity between improved and native lines was established. An analysis of group probabilistic assignment revealed that each line should not be considered as a genetically homogeneous group. The findings corroborate the absorption of native genetic material into the improved line introduced into Colombia from Peru. It is necessary to establish conservation programs for native-line individuals in Nariño, and control genealogical and production records in order to reduce the inbreeding values in the populations.

Key words: food security, microsatellite, population structure.

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Introduction

The guinea pig (Cavia porcellus, Rodentia, caviidae), is widely distributed throughout the Andean region of South America, from Venezuela to Buenos Aires Province, Argentina (Zúñiga et al., 2002). Its domestication started in the Andean region, 2500 to 3600 years ago (Chauca, 1997), when the former natives began raising captive animals as a source of meat. Nowadays, guinea-pigs play an important role in the economy, as a secure food source for Andean peasant families (Lammers et al., 2009).

In Colombia, guinea pig production is concentrated in the Nariño department (Ministerio de Agricultura y Desarrollo Rural de Colombia – MADR, 2008), where rural families breed them as a typical economic activity. There are three different levels of production, depending on the design of facilities, feeding strategies and the control of production and mating records. Three lines are used for production, native, improved and pets (Solarte et al., 2007).

Native and improved lines are used for obtaining commercial productive populations. Although the native line corresponds to small animals with low production parameters in comparison with improved lines, they are capable of transmitting adaptability and disease-resistance to succeeding litters. The pet line is inappropriate for production, due to slow growth and low reproductiveness. The main phenotypic characteristics in this kind of animal are small size and long or curly hair.

As the guinea pig has preserved a high phenotypic diversity, the development of adequate production techniques has prompted the search for highly productive animals through artificial selection (Solarte et al., 2007), such as that based on genetic merit and the crossing of highly productive lines (Solarte et al., 2002). So, in Colombia, the initial processes of genetic improvement were based on crossbreeding native animals, called “criollos”, and improved-line boars from Peru and Ecuador (Solarte et al., 2007), thus giving rise to genetic gain in certain productive features, as younger slaughtering age and more numerous litters.

The uncontrolled mating of native individuals from Nariño with improved lines has brought about a loss in indigenous genetic material (Burgos et al., 2007; Solarte et al., 2007). Given the conditions of the molecular markers used in these studies, it is possible that genetic diversity was underestimated. This led to the assumption that the loss of
genetic variability was not only between the native and improved lines, but also between other local populations.

The aim was to establish levels of genetic variability and the genetic relationship between commercial guinea pig populations in Colombia. Five microsatellite loci, reported for *C. aperea porcellus* species by Asher et al. (2008), were used for measuring data.

**Material and Methods**

**Localization**

Samples were collected in various municipalities in the Nariño department, southwest Colombia (Figure 1), between August, 2008 and January, 2009 (Table 1).

**Hair sampling and DNA extraction**

Hair samples were collected from 384 three months old specimens, weighing over 500 g. Sampling comprised the three guinea pig lines, native, pet and improved, bred in the main production centers of the zones mentioned above. Samples consisted of 100 mg of hair (about 200 to 300 single hairs) from the region where the neck connects to the body. These, first stored in paper bags at room temperature, were then transported to the Animal Genetics Laboratory at the University of Antioquia for processing. DNA extraction was performed according to the phenol-chloroform method described by Sambrook and Russell (2001), and modified for guinea pigs by Burgos et al. (2010).

**Microsatellite markers**

Six dinucleotide microsatellite markers reported for the species *Cavia aperea porcellus* by Asher et al. (2008) were evaluated. PCR amplification was carried out in a thermal cycler 1000 Bio-Rad. The final volume of the reaction was 15 μL, containing 25 ng/μL template DNA, a 1X buffer (Fermentas), a 0.2 mM dNTP mix and 0.15 U of *Taq* polymerase, (Fermentas). PCR conditions were: 95 °C for 5 min, followed by cycles of 45 s at 95 °C, 60 s of hybridization and 60 s of extension at 72 °C, and a final extension step at 72 °C for 5 min. Primer concentrations, alignment temperatures, number of cycles and corresponding information on sequences, are shown in Table 2.

PCR amplified product were electrophoretically separated in polyacrylamide gels (6%, acrylamide: bisacrylamide 19:1, urea 6 M, at 60 V for 1.5 h) and stained with silver nitrate. The allelic ladder phi724 (Promega) was used for defining the position of fragments in the gel, whereby a specific ladder was designed for each microsatellite locus with the homozygous alleles found. Allele sequencing in a 3730XL genetic analyzer (Macrogen, USA) was done to verify repetitive motifs of each locus.

**Data analysis**

Allele frequency, expected (He) and observed (Ho) heterozygosity, as well as estimated unbiased diversity for all the loci in the different lines and populations, were obtained through TFPGA software (Miller et al., 1997). Based on sample size, FSTAT software (Goudet, 2001) was used for calculating allelic richness. Polymorphic information content (PIC) (Botstein et al., 1980) was estimated with Cervus software (Marshall et al., 1998). By means of the Raymond and Rousset (1995) method, an exact test was carried out to establish deviations from Hardy-Weinberg equilibrium.

**Table 1 - Coordinates and geographical features of the guinea-pig hair-follicle sample collection sites in Nariño department.**

| Population       | Geographical Location | Elevation (m.s.n.m) | T (°C) | n(%) |
|------------------|-----------------------|--------------------|--------|------|
| Pupiales         | 0°52’15” N, 77°38’31”O | 3014               | 12     | 2    |
| Potosí           | 0°48’26” N, 77°34’20”O | 2715               | 12     | 0    |
| Obonuco          | 1°11’35” N, 77°18’16”O | 2794               | 12     | 2    |
| University of Nariño (Udenar) | 1°09’29” N, 77°16’33”O | 2820               | 13     | 82   |
| Botana           | 1°10’20” N, 77°16’36”O | 2790               | 13     | 2    |
| José M. Hernández | 0°54’20” N, 77°36’27”O | 2900               | 12     | 1    |
| Pasto            | 1°12’39” N, 77°15’09”O | 2631               | 14     | 0    |

T = average temperature, n = sample size.
The inbreeding coefficient ($F_{IS}$) and population structure ($F_{ST}$) for loci and populations were both estimated by way of the Weir and Cockerham (1984) method. Confidence intervals estimated by jacknifing sampling, and the significance of the adjusted indexes through Bonferroni adjustment (Harrys, 2001), were calculated with FSTAT (Goudet, 2001). RstCalc (Goodman, 1997) was used for estimating genetic differentiation between lines and populations, according to the stepwise mutation model ($R_{ST}$) described by Slatkin (1995).

Genetic distances DA (Nei et al., 1983) between guinea-pig lines and populations were estimated using Dispan software (Ota, 1993), whereby a Neighbor-Joining tree (Saitou and Nei, 1987), also with Dispan software, was constructed for guinea-pig lines, and a Neighbor-Net (Bryant and Moulton, 2004) with SplitsTree4 software (Huson and Bryant 2006) for guinea-pig production centers. Bootstrap values were obtained by means of 1,000 replicates. Genetic and geographical distances between population pairs were correlated, in order to establish whether genetic separation could be attributed to the isolation of populations.

According to obtained allele-frequency, individuals were grouped into a $K$-th number of populations, through Bayesian probabilistic group assignment with STRUCTURE software (Pritchard et al., 2000). $K$-Values analyzed ranged from 2 to 7, and each one was simulated five times. A mixing model with correlated allele frequencies was used for runs with 100,000 iterations following a 10,000 burn-in period. The DeltaK method described by Evanno et al. (2005) was applied for inferring optimal $K$-values.

### Results

35 alleles were identified in the 384 analyzed individuals, the number per locus ranging from 5 to 8 (Table 3). Contrary to Asher et al. (2008), the MS-II marker was, monomorphic in the populations studied. Bimodal allele frequencies in four loci of native and pet populations were observed, possibly the result of fixation in certain alleles. Within the improved population, the normal tendency in allele distribution, and alleles at high and low frequencies, was found.

The mean number of alleles per locus for the whole population was found to be $6.8 \pm 1.64$. Although the number of alleles in the native and improved lines ($6.6 \pm 1.51$ in the latter) was high, in the pet this was markedly less. Even considering the sample size of the pet line, allelic richness ($AR$) was greater in the native and improved (Table 3).

Although expected heterozygosity in the total population was higher than that observed for evaluated loci, no heterozygote deficit was noted in the pet line only in MS-IV loci. Furthermore, this line presented the highest number of loci in Hardy-Weinberg equilibrium (HWE), unlike the native and improved, where four out of five presented deviation from HWE (Table 3). The MS-V locus was in HWE throughout. $F_{IS}$ values ranged from 0.095 for the MS-V locus in the native line, to 0.660 for the MS-IV in the pet, and 0.323 for the total population. All lines showed $F_{IS}$ values higher than zero, the highest reaching 0.333 in the improved.

$F_{ST}$ values, statistically significant for all the loci ($p < 0.05$), provided the adequate information for typifying the different lines of $C. porcellus$. MS-III and MS-VI loci showed the highest $F_{ST}$ values (0.015), whereas MS-I locus presented the lowest (0.004). On the other hand, statistic $R_{ST}$, by indicating the differentiation between lines based on the stepwise mutation model, presented similar, although higher, values to those encountered when using the $F_{ST}$ infinitesimal model. The lowest $R_{ST}$ value was observed in the MS-IV locus, whereas the MS-III locus provided the highest differentiation among the evaluated lines.

### Table 2 - Amplification conditions for the microsatellite loci in guinea pig ($Cavia porcellus$).

| Locus | Repetition | Primer sequence (5’-3’) | Cycles | $T$ (°C) | $C$ (µM) | $A$ (pb) | GenBank Access |
|-------|------------|-------------------------|--------|----------|---------|--------|---------------|
| MS I  | (GA)$_{5}$AA(GA)$_{20}$ | F:ATTGGCTTCATGCTATGGAC 1 X 49 °C 1 X 51 °C 30 X 53 °C | 1 X 49 °C 1 X 51 °C 30 X 53 °C | 53 | 0.15 | 228 | AJ496558 |
| MS II | (GT)$_{23}$ | R:GGCCTGCTCTGTCTCTC 35 53 | 35 | 53 | 0.15 | 230 | AJ496559 |
| MS III| (CA)$_{35}$ | R:GGGACTTATGCCCCCACA 35 | 35 | 49 | 0.15 | 145 | AJ496560 |
| MS IV | (CT)$_{21}$ | F:CTTCCACAGCGTCAATCTC 30 49 | 30 | 49 | 0.23 | 280 | AJ496561 |
| MS V  | (GT)$_{49}$AT(GT)$_{3}$ | F:ATGGTAGGCACTTCCACTG 30 55 | 30 | 55 | 0.15 | 154 | AJ496562 |
| MS VI | (CT)$_{3}$GTTTCTGT(CT)$_{13}$ | F:GGTAACGTTTTGGGATTGAGG 35 | 35 | 53 | 0.15 | 168 | AJ496563 |

$T$ = hybridization temperature, $C$ = primer concentration, $A$ = approximate allele size.
RST values and DA genetic distances for the three evaluated lines are shown in Table 4. Genetic distances between the pet and native lines, with the notably low identity, together with coincident population structure RST statistics, revealed high mutual differentiation. The genetic structure of the individuals studied was also estimated based on geographical distribution of the production systems (Table 5).

The lowest number of alleles per locus was observed in the Obonuco population (3.40 \( \pm \) 0.54), whereas the highest number was found in the University of Nariño population (6.00 \( \pm \) 1.87). Mean allelic richness per locus was 4.11 \( \pm \) 0.45, ranging from 3.350 to 4.781. Population AR values, compared to analysis by line, were lower, possibly due to the sample-size of the Pupiales population.

He was higher than Ho in all the populations, the highest deficit in observed heterozygosity being observed in Pasto, with -0.305 deviations as regards expectation. Analysis by population revealed at least one out of five analyzed loci to be out of HWE (p < 0.05). Pasto, Obonuco and Udenar populations presented 4 loci with deviations from HWE. Worthy of note, these populations are geographically and commercially related. FIS values revealed an overall decrease in heterozygosity, pronounced and highly significant.

### Table 3 - Intrapopulation genetic diversity measures for each line and the total population of guinea pigs (*Cavia porcellus*) from Nariño.

| Locus | Na | Ho | He | PIC | FIS | AR | HWE |
|-------|----|----|----|-----|-----|----|-----|
| MS-I  | 4  | 0.543 | 0.704 | 0.644 | 0.229* | 3.997 | * |
| MS-III| 4  | 0.391 | 0.702 | 0.641 | 0.444* | 3.989 | *** |
| MS-IV | 7  | 0.337 | 0.757 | 0.716 | 0.556* | 5.485 | *** |
| MS-V  | 8  | 0.609 | 0.672 | 0.614 | 0.095NS | 6.549 | NS |
| MS-VI | 8  | 0.609 | 0.759 | 0.718 | 0.199* | 6.561 | ** |
| Mean  | 6.2 | 0.498 | 0.719 | 0.667 | 0.309* | 5.316 | |

### Table 4 - Genetic distance (below the diagonal) and population structure RST, (above the diagonal) among guinea-pig lines from Nariño.

| Line | Native | Pet | Improved |
|------|--------|-----|----------|
| RST  | 0.104** | 0.036** | 0.025** |

### Table 5 - Estimated intrapopulation genetic diversity for each guinea-pig production center.

| Population     | N  | Na | AR | Ho | He | FIS | FST | RST | AR | HWE |
|----------------|----|----|----|----|----|-----|-----|-----|----|-----|
| Pupiales       | 15 | 4.0 | 4.000 | 0.630 | 0.680 | 0.075NS | 1 |
| Potosí         | 27 | 4.4 | 4.188 | 0.563 | 0.658 | 0.147* | 2 |
| Obonuco        | 20 | 3.4 | 3.350 | 0.560 | 0.632 | 0.117NS | 4 |
| Udenar         | 141| 6.0 | 4.781 | 0.493 | 0.707 | 0.303** | 4 |
| Botana         | 73 | 5.2 | 4.424 | 0.545 | 0.698 | 0.221** | 2 |
| José M. Hernández | 25 | 4.0 | 3.838 | 0.464 | 0.673 | 0.316** | 1 |
| Pasto          | 85 | 5.0 | 4.257 | 0.329 | 0.634 | 0.482** | 4 |

N = sample size; Na = number of alleles; AR = allelic richness; He = expected heterozygosity; Ho = observed heterozygosity; HWE = number of loci with deviations from Hardy-Weinberg equilibrium; *(p < 0.05); **(p < 0.01); NS(p > 0.05).
significant (p < 0.01) in the Pasto population, and, although obvious, statistically insignificant in the Pupiales and Obonuco.

The significant contribution of each evaluated marker was revealed, when defining differentiation between populations by \( F_{ST} \) analysis. Mean \( F_{ST} \) was 0.048 ± 0.005, with MS-I and MS-III presenting the highest values (0.062 and 0.057, respectively). Estimated \( R_{ST} \) population structure and DA genetic distances, by population pairs, are presented in Table 6.

Mean \( R_{ST} \) was 0.048 ± 0.012, thus similar to \( F_{ST} \). On comparing populations it was found that, in some, differences were statistically insignificant (p > 0.05). DA genetic distances ranged from 0.0474 to 0.171. Likewise, the correlation between genetic and geographical distances was positive (p = 0.66) and highly significant (p < 0.01) throughout.

A Neighbor-Joining tree and Neighbor-Net were constructed, based on DA distances by line and population (Figure 2). Besides the relatively high bootstrap values and consistent genetic and historic relationships among the three guinea pig lines, a more recent genetic relationship between improved and native lines, and their separation from the pet line, was observed.

Several cycles were apparent in the Neighbor-Net graph, especially between the Udenar, Pasto, Botana and Obonuco populations (Figure 2b). In all the seven populations, relationship signals were conflicting, mainly due to the constant flow of individuals and non-independent populations.

On considering estimated \( \Delta K \) values, three groups of genetically homogenous individuals were identified for the different lines with STRUCTURE (Figure 3a). Nonetheless, in the absence of a pattern of homogeneity, the existence of a “mix” among the various lines was confirmed (Figure 3b), thus implying that individually each line continued to preserve a small proportion of the group component.

**Discussion**

Herein, MS-II microsatellite loci were found to be in the monomorphic state, contrary to that reported by Asher

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**Table 6** - Genetic distance (below the diagonal) and population structure \( R_{ST} \), (above the diagonal) among guinea-pig production centers in Nariño.

|                | Pupiales | Potosí  | Obonuco | Udenar | Botana | José M. Hernández | Pasto  |
|----------------|----------|---------|---------|--------|--------|-------------------|--------|
| Pupiales       |          |         |         |        |        |                   |        |
| Potosí         | 0.1272   |         | 0.0256* |        | 0.0457*| 0.0670*           | 0.1065*|
| Obonuco        | 0.1005   | 0.1718  |         | 0.0903*| 0.0268*| 0.0773*           | 0.0376*|
| Udenar         | 0.1061   | 0.1273  | 0.0956  |        | 0.0724*| 0.1158*           | 0.0160*|
| Botana         | 0.0876   | 0.1210  | 0.0711  | 0.0474 |        | 0.1043*           | 0.0506*|
| José M. Hernández | 0.1041 | 0.1544  | 0.1121  | 0.1436 | 0.1311 |                   | 0.0982*|
| Pasto          | 0.1442   | 0.1529  | 0.1266  | 0.0509 | 0.0851 |                   | 0.1512 |

*(p < 0.05); ***(p > 0.05).*
et al. (2008), when evaluating the same microsatellite loci in the species C. aperea porcellus, the wild, ancestor of the guinea pig (Künzl et al., 2003). Asher et al. (2008), besides the seven alleles for MS-II, also found an even higher number of alleles in the other loci. Loci in the monomorphic state, with a lower number of GT repeat motifs, could testify to the species selection process that took place during domestication, as well as the possible cause of allele fixation in commercial populations.

When considering allele frequency, the high frequencies of just one or two alleles per locus in the pet line could be held responsible for the low allelic diversity. Two alleles of MS-V loci reaching a frequency of 0.739, explains why this line presented the lowest number of alleles and less allelic richness. This reduction in alleles arises from such factors as selection and genetic drift caused by the limited use of boars. Pet individuals are not used for meat production due to their low yield, compared to the improved line. Furthermore, the long hair makes their reproduction difficult, thereby causing a reduction in population in the different regions of the Nariño department.

The native line presented higher allelic richness than the improved, possibly indicating preservation of vast allelic diversity by the former in spite of the small-sized population. Chauca (1997) pointed out that, in general, guinea pig populations have preserved high genetic and phenotypic variability, more so in the improved line than the native, in spite to intense selection for production features.

Nevertheless, Burgos et al. (2007) and Solarte et al. (2007) noted the low allelic variability in guinea-pig lines, particularly in the native, previously extensively bred in the Nariño department. The introduction of genetically improved animals from Peru was followed by selection and crossing, whereupon it was discovered that allele frequencies in native and improved lines are similar, with the same alleles mostly present in both populations. Hence the inference that these populations already shared genetic information derived from crossbred mating, leading to homogenization of the existing gene pool in Colombia with those from Peru and Ecuador. This shows the importance of maintaining the available native genetic material in the region.

According to Botstein et al. (1980), used markers indicated a relatively high polymorphic information content (PIC = 0.659), allowing the detection of significant differences in genetic structure of guinea pig lines. However, it is necessary looking for additional microsatellite loci to increase the number of available evaluated alleles.

Only the MS-V locus was in HWE, the others being out. This was in accordance with Burgos et al. (2007) and Solarte et al. (2007), who stated that guinea-pig populations are affected by forces that modify allele frequency, such as selection, genetic drift and especially, bottlenecks. As guinea-pig production systems are influenced by market behavior, at least twice a year, during seasons of high demand, producers sell most of the animals, keeping only the necessary few to breed a fresh population, with the consequent founder effect and bottlenecks. Prior conclusions are based on the high inbreeding values found in the lines ($F_{IS} = 0.323$), together with a decrease in observed, as against expected, heterozygosity, according to assumptions based on HWE (Table 3 and 5).

In a prior study of guinea-pig lines (Burgos et al., 2007), the low levels of expected heterozygosity were even lower, and the loss of genetic variability even greater, than the results from the present study, when using dominant markers, such as RAPDs.

$F_{ST}$ values obtained for the total population presented a significantly ($p < 0.05$) low population structure among lines. Although considered as different genetic entities, the populations presented only minor changes in allele frequency, thus insufficient to attain greater genetic structure. It is important to consider that $F_{ST}$ values could have been affected by sample size in some populations. $R_{ST}$ values were higher than $F_{ST}$, a possible indication of differences between lines arising from changes in allele frequencies, as well as differences in repeated allele units in accordance with the microsatellite mutation model (Egito et al., 2007).

Low levels of population structure and high rates of inbreeding have been found in various animal-production systems. This has been attributed to non-random mating systems, selection by features of economic importance, and the intensive use of reproductive technologies (Kumar et al., 2006; Granevitze et al., 2007; Serrano et al., 2009; Wu et al., 2009). The guinea pig is not an exception, when considering its rapid growth, high reproductive rate, and that in a traditional production system, the species is highly susceptible to inbreeding issues.

Low population genetic differentiation was also detected (Table 5). Results for $R_{ST}$ showed higher structure values between José M. Hernández and Botana populations, when compared to the remainder. Both consist of more technical and specialized production systems, with record management and mating control. In the remainder, as only some use production and reproductive records, it becomes difficult to select non-related animals, and thus control inbreeding in the target population. Our results placed in evidence the need for implementing appropriate information systems, to thus facilitate the maintenance of production and reproductive records, as a way of preserving invaluable indigenous genetic material, and increasing population genetic diversity, to so put in practice species-improvement programs.

As, according to genetic distance data, there is a separation between native and pet lines, the probability of encountering a common allele in any two populations was presumed to be greater in the native and improved lines. In fact, allele frequencies between both are similar, the estimated smaller genetic distance between the two corroborat-
ing the hypothesis of native genotype absorption into the improved line.

Correlations among the previously mentioned lines were apparent from the Neighbor-joining tree (Figure 2a). By the length of the branches, it could be inferred that the relationship between the improved and native lines is recent. Around 1975, genetic material brought to Colombia from Peru was crossed with native material (Solarte et al., 2007), thus, in accordance with tree topology. Nevertheless, according to Solarte et al. (2007), the improved population was completely separated from the others.

There is a correlation between the genetic and geographic distances of the populations. Udenar and Pasto populations showing the lowest genetic distance, the first had having been formed after the latter. Incidentally, both populations are technically advanced centers, with a high demand for stock-breeds.

Pupiales and Potosí are geographically close to one another and to the Ecuadorian border. The breeder-farms in Potosí, besides being technically advanced, still preserve individuals from the native line in the production systems. In José M. Hernández, breeder farms are technically advanced with productive and reproductive control records, thus making the local population outstanding, although not to the point of being insusceptible to the forces modifying allele frequencies and the effects of inbreeding.

As also noted by Nuwanyakpa et al., (1997), breeding-male exchange is a traditional practice among Nariño guinea-pig producers, thereby avoiding any excessive increase in inbreeding. Even so, this has given rise to the easy mutual sharing of alleles, thereby reducing the possibility of increasing genetic distance and structure. The differences observed in the assignment of genetic groups in each line are slight. Thus, it was impossible to consider each line as a single group, since the mutual genetic “mix” only permits the detection of commonly shared allelic variants.

This constitutes an initial approach in molecular genetics for evaluating the genetic structure of commercial guinea pigs, their variability and the relationship between lines and populations. In spite of its low population-size, the native line revealed high allelic variability, which could be advantageous for introducing changes in the production conditions of this important autochthonous genetic resource. Clear evidence, proving native-line absorption into the improved line from Peru and Ecuador, was found. Traditional production conditions and low genetic differentiation among geographically close populations have incited the need for establishing preservation programs for the native line, given its importance as the regional gene-pool, as well as for designing strategies for decreasing population inbreeding within the production systems.

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