ORIGINAL ARTICLE

Genetic diversity, population structure and origin of the native goats in Central Laos

Sang V. Le[1] | Sara de las Heras-Saldana[2] | Panoraia Alexandri[2] |
Luisa Olmo[1] | Stephen W. Walkden-Brown[1] | Julius H. J. van der Werf[1]

[1]School of Rural & Environmental Science, University of New England, Armidale, New South Wales, Australia

[2]AGBU, a Joint Venture of the NSW Department of Primary Industries and the University of New England, Armidale, New South Wales, Australia

Correspondence
Sang V. Le, School of Environmental & Rural Science, University of New England, Armidale 2351, NSW, Australia.
Email: vle4@myune.edu.au

Abstract

Maintaining genetic diversity and variation in livestock populations is critical for natural and artificial selection promoting genetic improvement while avoiding problems due to inbreeding. In Laos, there are concerns that there has been a decline in genetic diversity and a rise in inbreeding among native goats in their village-based smallholder system. In this study, we investigated the genetic diversity of Lao native goats in Phin, Songkhone and Sepon districts in Central Laos for the first time using Illumina's Goat SNP50 BeadChip. We also explored the genetic relationships between Lao goats with 163 global goat populations from 36 countries. Our results revealed a close genetic relationship between Lao native goats and Chinese, Mongolian and Pakistani goats, sharing ancestries with Guangfen, Jining Grey and Luoping Yellow breeds (China) and Teddi goats (Pakistan). The observed (Ho) and expected (He) heterozygosity were 0.292 and 0.303 (Laos), 0.288 and 0.288 (Sepon), 0.299 and 0.308 (Phin) and 0.289 and 0.305 (Songkhone), respectively. There was low to moderate genetic differentiation (F_{ST}: 0.011–0.043) and negligible inbreeding coefficients (F_{IS}: −0.001 to 0.052) between goat districts. The runs of homozygosity (ROH) had an average length of 5.92–6.85 Mb, with short ROH segments (1–5 Mb length) being the most prevalent (66.34%). Longer ROH segments (20–40 and >40 Mb length categories) were less common, comprising only 4.81% and 1.01%, respectively. Lao goats exhibit moderate genetic diversity, low-inbreeding levels and adequate effective population size. Some genetic distinctions between Lao goats may be explained by geographic and cultural features.

KEYWORDS

genetic diveristy, Lao native goats, inbreeding, runs of homozygosity, migration

1 | INTRODUCTION

Goats play a significant role in the Lao People's Democratic Republic (Laos), serving as a crucial component of the smallholder production system due to their economic, nutritional and cultural contributions. In Laos, goats are mainly raised in a semi-intensive grazing production system for export to neighbouring Vietnam, where demand for goat meat is rapidly growing (Bui et al., 2023). Only an estimated 10% is destined for domestic consumption (Gray et al., 2019). Consequently, the goat population in Laos has experienced an almost six-fold increase, rising from 128,000 in 2005 to approximately 711,200 in 2021 (FAOSTAT, 2022). Furthermore, goats provide essential socio-cultural functions and contribute to the mixed production system by supplying manure for crop cultivation (Devendra, 2013).

Goats are distributed throughout Laos, with variation in frequency across regions. Central Laos hosts 42% of the goat population, while the South and North regions accounted for <17% and 41%, respectively (Xayalath et al., 2021). Savannakhet province is a province of Central Laos with the greatest goat population (Gray et al., 2019). The goat population raised in Laos mainly consists of native breeds, with a small proportion of exotic breeds and crossbreds between indigenous breeds and Southeast Asian Mountain goats (Trach & Phiovankham, 2011; Wilson, 2007). The native breed is Kangbing-Katjang (Phengsavanh, 2006) which is kept for meat rather than milk production. This breed exhibits traits such as a small body size of on average 26 kg and a high mortality rate of 37.5% (Colvin et al., 2022; Gansberghe, 2005). Some native goats have been crossbred with the Boer goat breed, which was imported from Thailand (Wilson, 2007) and Back-Thao bucks, a Vietnamese composite breed, resulting in improved growth rates compared to indigenous goats (Trach & Phiovankham, 2011).

The majority of goats in Laos are managed by smallholder farmers according to traditional practices. Herds are small, typically comprising 2 to 12 goats (Wilson, 2007; Windsor et al., 2018), generated from random mating (Dubeuf et al., 2014). Goats are typically housed at night and range freely during the day in unsegregated groups with overlapping grazing areas between flocks and villages Windsor et al. (2018). Breeding occurs throughout the year (Olmo et al., 2022), driven by natural mating and the absence of human intervention. Bucks often reach sexual maturity before they are sold, which increases the risk of inbreeding and hampers genetic progress (Gray, 2005). However, there is a lack of research on the genetic composition and extent of inbreeding within this population. Additionally, goats are frequently kept as assets to be sold when cash is needed (Gray, 2005), leading to the inadvertent sale of superior animals due to their larger size and higher market value.

Given the importance of goats in the smallholder system, investigation of the genetic composition of goats in Laos can help inform breeding strategies to enhance goat production. Genetic diversity studies are important for understanding natural and artificial selection processes and assessing genetic relationships within and between breeds, particularly in indigenous breeds (Chokoe et al., 2022) which are better adapted to the local feed resources, environmental conditions, diseases and parasites (Brito et al., 2017). Managing and utilizing genetic diversity in these breeds is key to designing sustainable breeding programs aimed at achieving desirable phenotypes and avoiding mating close relative animals within a population.

Inbreeding coefficients derived from genomic data, such as F_{IS} and F_{ROH}, are important indicators of genetic diversity and the degree of inbreeding. F_{ROH} estimates the fraction of the total length of continuous homozygous segments, in the total length of autosomes, which is increased due to inbreeding (Purfield et al., 2012). The F_{IS} parameter estimates the average decrease in heterozygosity of individuals due to non-random mating within a population (Peripolli et al., 2017; Wright, 1965). The genetic distance can be measured with the pairwise fixation index (F_{ST}) that indicates low (0.00–0.05), moderate (0.05–0.15), high (0.15–0.25) and exceptional (>0.25) genetic relatedness between populations (Wright, 1978).

In recent years, genomic analyses, such as runs of homozygosity (ROH) have been extensively employed to study genetic diversity and indicate recent and ancient inbreeding in various livestock species (Al-Mamun et al., 2015; Makina et al., 2014; Muir et al., 2008; Munoz et al., 2019). The frequency of ROH provides insights into the demographic history and management of the population over time. ROH usually arise from the transmission of identical haplotypes from each parent to offspring (Purfield et al., 2012) and its accumulation in the genome can have significant impacts on overall biological fitness (Manunza et al., 2016).

The genetic diversity of cosmopolitan and indigenous goat breeds has been studied in Asia (Berihulay et al., 2019; Deniskova et al., 2021; Mukhina et al., 2022), Africa (Nandolo et al., 2019; Onzima et al., 2018; Tarekegn et al., 2019; Tucho & Tesfaye, 2004), Europe (Cañón et al., 2006; Lenstra et al., 2017; Oget et al., 2019) and Oceania (Brito et al., 2017). These studies have utilized genomic markers to investigate population structure, assess genetic diversity, linkage disequilibrium patterns and effective population size, together providing insight into population characteristics, demographic history and the degree of inbreeding. In a country like Laos, where pedigree and phenotype data are limited, genomic markers are valuable tools for inferring various genetic properties of its goat population based on a small

—WILEY | 533

sample of genotyped individuals and derive from that proposed informed management decisions and breeding strategies.

In this study, we aimed to describe the population structure of native goats across three districts in Central Laos, to estimate the inbreeding and genetic diversity, both within and between districts and elucidate the genetic relationship between Lao native goats and global goat breeds, providing insights into their genetic origins and potential admixture.

2 | MATERIALS AND METHODS

2.1 | Sample collection and genotyping

A total of 420 ear-notch samples were collected between February and April 2022 from three districts in the Savannakhet province of Laos (Figure 1). In Laos, there are limited genetic introductions from outside Laos and therefore, all samples in this study were considered as the same breed, Lao native goats. These samples were obtained from 140 households situated in seven villages located in Phin (184 samples), Songkhone (176 samples) and Sepon (60 samples) districts. In each household, three healthy male or female goats were collected. Field staff were instructed to avoid taking samples from full-sibs. Staff verified that the goats were not full-sibs by asking

the goat owners. These samples were stored in the Allflex Tissue Sample Units (Neogen, Australia) with preservatives and kept in a fridge in Laos before being exported to New Zealand for analysis.

DNA extraction and genotyping were conducted by GenomNZ (AgResearch Ltd., Mosgiel, New Zealand). Genotyping was performed with the goat 50 K Illumina BeadChip (Tosser-Klopp et al., 2014) containing 59,727 SNPs with 56,204 SNPs on autosomes.

2.2 | Construction of the working datasets

Three working data sets were constructed for this study. The first one, the Lao dataset, included 420 samples from three sampling districts in Laos as described above. To compare the genetic diversity of Lao goats with other goat breeds in Asia and the rest of the world, we combined the SNP profiles from the first dataset with four public reference datasets (Berihulay et al., 2019; Colli et al., 2018; Deniskova et al., 2021; Mukhina et al., 2022). The second working dataset, the Global dataset, contained 5688 goats from 165 breeds, including 69 populations from Africa, 43 from Asia, 37 from Europe, 13 from America and 2 from Oceania. The third working dataset, the Asian dataset, encompassed 1552 goats from 43 populations in Asia, including 16 populations from Pakistan, 8 from Russia, 6 from
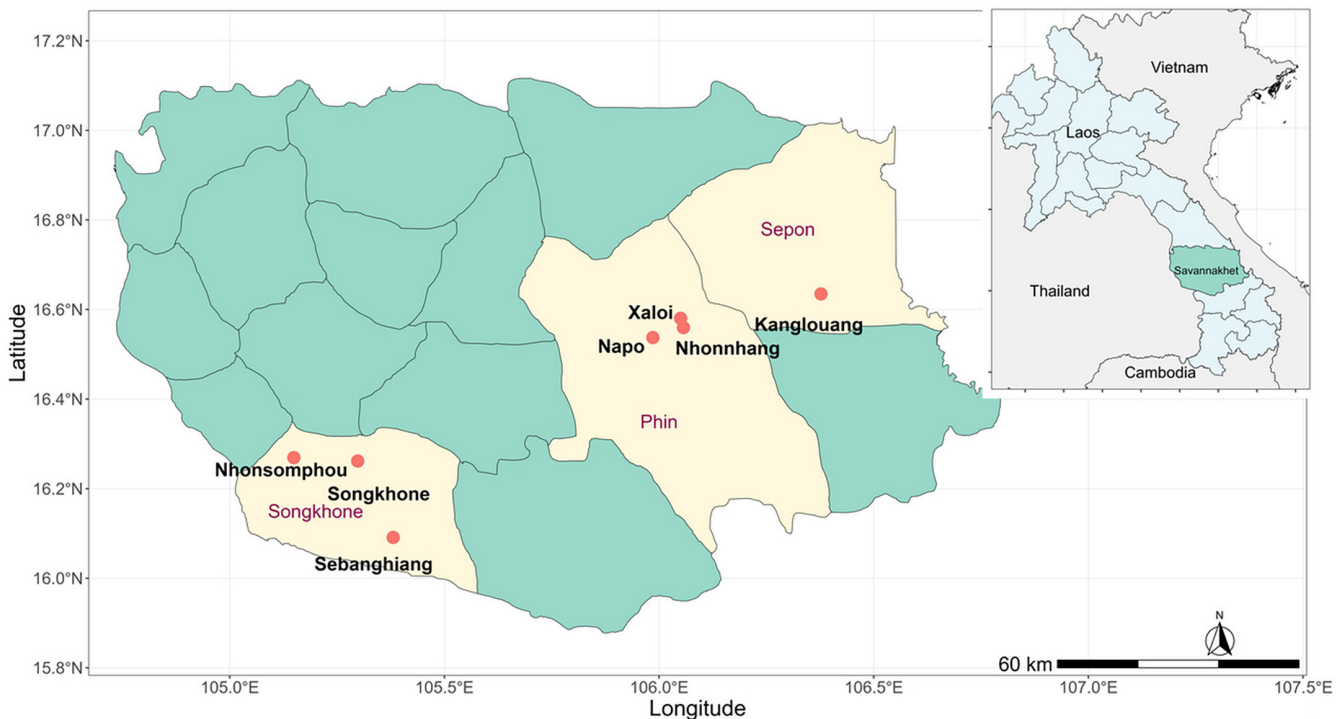

FIGURE 1 Geographical location of goat samples used in this study. The samples were collected in Savannakhet, a Central province in Laos. The red circles in the map are shown as samples collected in seven villages in Songkhone, Phin and Sepon districts. [Colour figure can be viewed at wileyonlinelibrary.com]

China, 5 from Mongolia, 3 from Turkey, 3 from Laos (from this study) and 2 from Iran. Details of full breed name and geography distribution are presented in Table S1.

Quality control was performed in PLINK v1.9 (Purcell et al., 2007) for each dataset. This process involved excluding SNPs on the sex chromosomes and unmapped locations, as well as those with a minor allele frequency (MAF) lower than 0.05, a call rate lower than 90% or a deviation from Hardy–Weinberg equilibrium (p-value $<10^{-6}$). Individuals with more than 10% missing SNPs were also excluded. After quality control, the Lao dataset consisted of 419 genotyped goats with 42,666 SNPs, the Asian dataset included 1546 goats with 43,612 SNPs and the Global dataset comprised 5574 goats with 43,886 SNPs. The MAF filter was not applied for the run of homozygosity (ROH) based analyses.

2.3 | Genetic diversity

To assess the genetic diversity for the Lao dataset, the observed (Ho) and expected (He) heterozygosity and inbreeding coefficient (F_{IS}) along with a 95% confidence interval (CI 95%) were calculated in the R package 'hierfstat' (Goudet, 2005). The PLINK files were converted to hierfstat format using the PGDSpider program (Lischer & Excoffier, 2012).

2.4 | Effective population sizes

Effective population size (Ne) is a genetic parameter that contributes to our comprehension of the population's evolutionary history and its diversity. In this study, we estimated Ne for the Lao dataset and for each district separately using the SNeP version 1.1 software (Bertolini et al., 2018), where Ne is derived based on measures of linkage disequilibrium (LD). We applied the default parameters with an exception for the sample size correction, occurrence of mutation (−alpha 2.2 as suggested by (Corbin et al., 2012)), along with a recombination rate between a pair of genetic markers determined using the Sved and Feldman (1973) method: $c = (1-d/2)$, where c is recombination rate, d is the linkage distance.

2.5 | Run of homozygosity (ROH) and genomic inbreeding (F_{ROH})

Runs of homozygosity (ROH) are the estimated length of segments of continuous homozygous genotypes inherited in an identical-by-descent manner from an animal's parents and present in its genome (Purfield et al., 2012). ROH was detected in all autosomes and examined in each

district individually. We used the "detecRUNS" package in R (Biscarini et al., 2018) with the consecutive run methods proposed by Marras et al. (2015) for the analysis of ROH.

The pattern of ROH coverage can provide insights into both recent and historical inbreeding events (Cardoso et al., 2018). For the identification of ROH, we imposed the restriction that no more than one SNP with a missing genotype could be included per window and up to one possible heterozygous genotype was allowed. The minimum ROH length was 1 Mb. To minimize the false positive results, we applied a threshold for the minimum number of SNPs (l) per sliding window, which was computed using the formula introduced by Lencz et al. (2007) and subsequently adopted by Purfield et al. (2012):

$$l = \frac{\log_e \frac{\alpha}{n_s - n_i}}{\log_e (1 - het)},$$

where n_s represents the number of genotyped SNPs per animal, n_i is the number of genotyped individuals, α corresponds to the percentage of false positive ROH (set to 0.05 in this study) and het denotes the mean heterozygosity across all SNPs. We determined that the minimum number of SNPs per sliding window for this study was 47.

The identified ROH were classified into five groups based on their length: 1–5 Mb, 5–10 Mb, 10–20 Mb, 20–40 Mb and >40 Mb, to determine the distribution of recent and ancestral inbreeding in Laos and compare the distribution of ROH length among sampling areas. The mean sum of the number of ROH within each ROH length category was calculated by averaging the total number of ROH per animal. Additionally, the percentage of SNPs involved in ROH was determined by counting the number of times a SNP appeared in an ROH in the district.

Genomic inbreeding coefficients (F_{ROH}) for individuals and districts were estimated using the ROH data. The F_{ROH} defined as the genomic autosomal proportion of ROH of an individual, was the sum of the lengths of all ROH detected in that individual divided by the total length of the autosomes covered by SNP markers (in this case, 2463.88 Mb) (McQuillan et al., 2008).

2.6 | Genomic relationship and population structure

To estimate the extent of genetic differentiation F_{ST}-values (Weir & Cockerham, 1984) were calculated between goat populations from different districts with PLINK v1.9. The matrix of pairwise F_{ST} values was visualized in a distance tree with iTOL (http://itol.embl.de) (Letunic & Bork, 2016).

A principal component analysis (PCA) was performed to provide insights into the goat population structure in

Central Laos and assess the Lao goat relationships with other breeds at the global and Asian levels. The PCA was performed in PLINK v1.9 and visualized with the R package 'ggplot2' (Wickham, 2011).

To describe common ancestry between Lao goats and other goat breeds, the ADMIXTURE v1.3.0 program (Alexander et al., 2015) was used. The optimal number of clusters (K) was determined for each dataset and multiple runs with varying K levels were performed. Specifically, for the Lao dataset, ADMIXTURE was run from $K=2$ to 20, for the Asian dataset from $K=2$–70 and for the global dataset from $K=2$–170, using a 10-fold cross-validation (CV=10). Each run was repeated 10 times to evaluate the lowest cross-validation error. The resulting admixture outputs were visualized using the R package 'BITE' (Milanesi et al., 2017).

2.7 | Linkage disequilibrium analysis

To determine different LD patterns for each Lao goat district, PLINK v1.9 was used with default parameters. The LD coefficient (r) (Alexander et al., 2015) was used as a measure of LD strength, as it is considered more reliable and unaffected by allele frequency and population size (Zhao et al., 2005). For visualizing the relationship between LD and physical distance between SNPs, the average r^2 within a 1000 kb interval was calculated and plots were created using the 'ggplot2' package in R.

2.8 | Migration analysis

Historical introgression events and past migrations between Asian goat populations were investigated with the maximum likelihood algorithm implemented in TreeMix v1.13 (Pickrell & Pritchard, 2012). The analysis involved testing a range of migration edges (m) from 1 to 20, employing the bootstrap command, excluding sample size correction and allowing for global rearrangements. The optimal number of migration events was determined using the Evanno method (Evanno et al., 2005) from the 'OptM' package (Fitak, 2021) and the results were visualized using the TreeMix function 'plot_tree' in the 'BITE' package in R.

3 | RESULTS

3.1 | Comparative analysis of genetic diversity and genetic structure: Lao goats at the global level

In the global dataset (Figure 2a, Figure S1A), the first principal component (PC1) explained 29.24% of the total

variation and separated Asian breeds from the breeds from Africa, Europe and the Americas. The PC2 accounted for 20.01% of the total variation and divided the global goat breeds into two groups, North American, European and some African goat breeds in quadrant II and most African, Oceanian and South American goat breeds in quadrant III and IV. The PC3 (Figure S1A) accounted for 9.99% of the total variation and mainly separated the Oceanian breeds. The first three PCs (Figure 2a, Figure S1A) accounted for 59.24% of total variation and divided the global goat breeds into four main clusters: one including Asian goats, a second cluster consisting of the majority of African breeds and South American breeds, a third cluster enclosing European and North America breeds and a fourth cluster enclosing Oceanian breeds along with some breeds from Asia and Africa. The result of PCA at the global level (Figure 2a) and Asian level (Figure 2b) show Lao goats are in closer proximity to Chinese breeds than other breeds in Asia.

Admixture analysis applied for global (Figure S2) and the Asian datasets (Figure 3) were similar to the PCA results. Lao goat breeds showed a high differentiation among the global goat breeds but clustered together with goats from China, Pakistan and Mongolia. At K levels 2, 4, 6 and 9 (Figure 3) the major blue-coloured cluster is displayed in Lao goats and those were also found in smaller proportions in Guangfen (CHN_GF), Jining Grey (CHN_JN) and Luoping Yellow (CHN_LP) goats in China and in Teddi goats (PAK_TED) in Pakistan (Figure 3). At $K=2$, the blue colour cluster comprised 97–99% of the genetic composition in Laos, 46% in CHN_LP, 45% in CHN_GF, 30% in CHN_JN, 25% in PAK_TED and 17% in Mongolian goats. At $K=4$, these percentages were 96–99%, 24%, 22%, 36%, 15% and below 5%, respectively. At $K=9$, the blue cluster remained dominant in Lao goats at 95–99%, while accounting for 21% in CHN_GF, 13% in CHN_JN and CHN_TED and less than 1% for CHN_LP and Mongolia goats. Across all K levels, the lowest CV error for the Asian breeds was acquired for $K=50$ (Figure S6).

The genetic distances measured as pairwise F_{ST} between 43 Asian goat breeds (Table S2) showed that the average pairwise F_{ST} values among these breeds were 0.087 and ranged from 0.003 to 0.221. This indicates a range of genetic differentiation, from low to high, across the populations. Notably, the Russian breeds ALTW and ALTM exhibited the lowest genetic differentiation in all pairwise F_{ST}, while the highest level of differentiation was observed between the breeds Luoping Yellow in China and Barbari in Pakistan.

Among all the Asian goat breeds, the Lao goat populations showed little genetic differentiation within themselves ($F_{ST} < 0.05$) while displaying moderate to
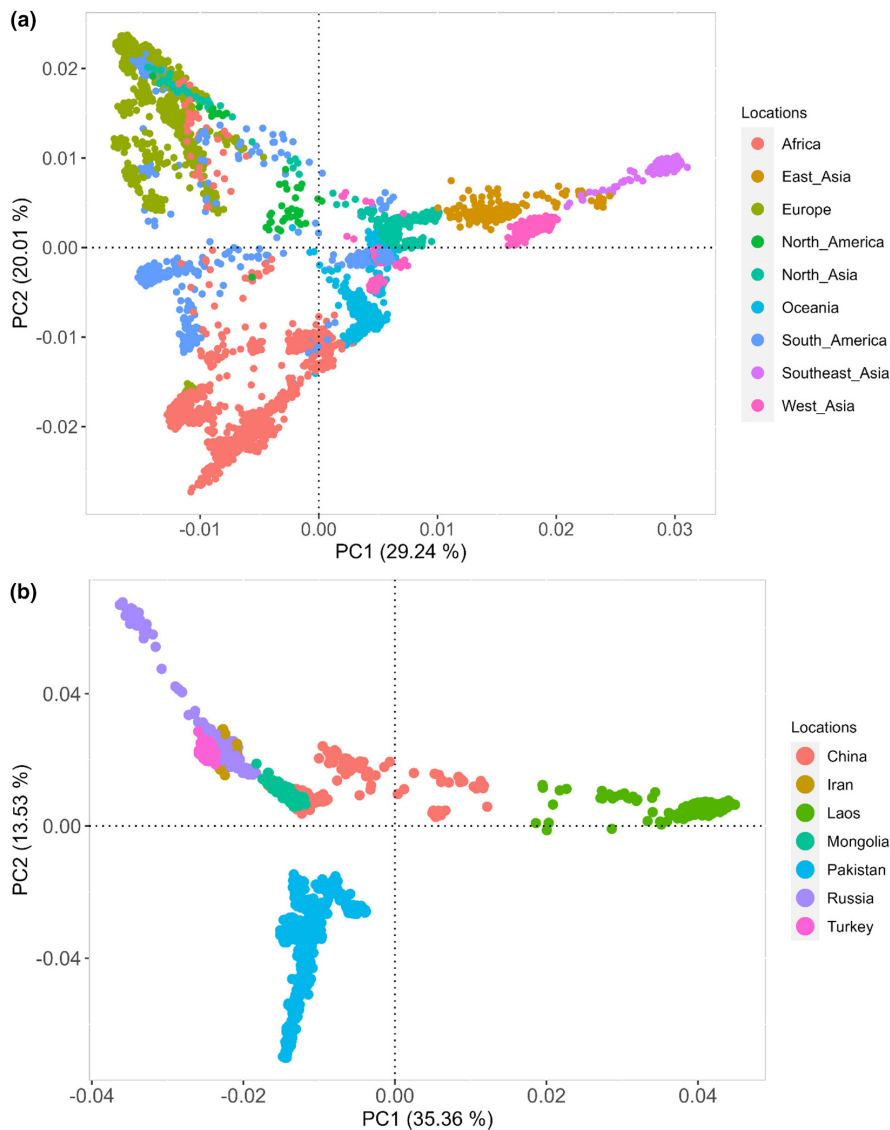
FIGURE 2 Principal component analysis at the global (a) and Asian (b) levels. One dot represented an individual and colours represented populations. [Colour figure can be viewed at wileyonlinelibrary.com]

high genetic differentiation from other Asian breeds (Table S2). However, the F_{ST} values between Sepon (LAO SEP) and Asian goat breeds (ranging from 0.056 to 0.175) were slightly higher than the F_{ST} value between Phin (LAO PHI) and Songkhone goats (LAO SON) with Asian goat breeds (F_{ST} from 0.054 to 0.165). This indicates a significant genetic disparity between Sepon and other Asian goat breeds, ranging from moderate to high differentiation. Low genetic differences were observed between Lao goats and Chinese goats ($F_{ST} = 0.0481$), as well as Mongolian goats ($F_{ST} = 0.0512$) confirming the results from PCA analysis.

The neighbour-net graph based on Weir and Cockerham F_{ST} between Lao goat breeds and Asian goat breeds is presented in Figure 4. It revealled that there are three main cluster groups, the first includes Lao, Chinese and Mongolian goat breeds, the second includes the Russian, Iranian and Turkish goat breeds and the third includes Pakistani goats. In the first genetic cluster group, Lao goat

breeds had an independent branch and goat populations in Phin (LAO PHI) and Songkhone (LAO SON) clustered together before joining with those in Sepon (LAO SEP) within the relevant genetic cluster. The Chinese Guangfen (CHN GF) and Jining Grey (CHN JN) goats clustered together with Lao goats in the next sub-cluster before other Chinese and Mongolia goat breeds were classified within the first main group cluster.

The results from migration analyses align with the PCA and admixture results. The optimal migration edge number was 6 which had the biggest delta M (an ad hoc statistic based on the rate of change in the log probability of data between clusters – Evanno method), followed by 3 and 4 migration events. In the six migration events (Figure 5), there were two possible migration events between Laos and China: one from the Guangfeng (CGF) breed in South China to Central Laos and another from the Sepon and Phin district in Central Laos to the Luoping Yellow (CLP) breed in Southwest of China, which shares a border with North
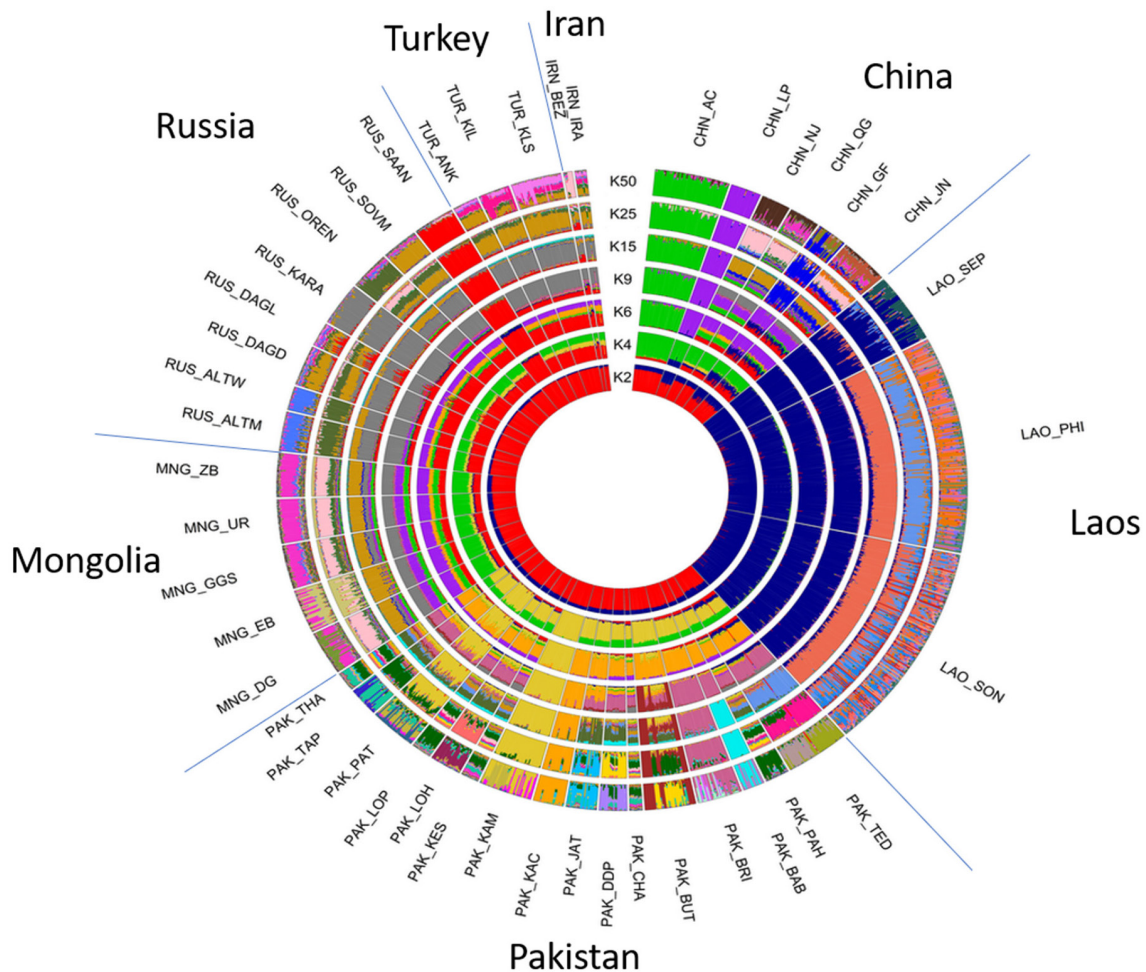
FIGURE 3 Admixture analysis of 1546 individuals from the 43 goat populations in Asian regions. Results for number of clusters $K=2$, 4, 6, 9, 15, 25 and 50 are shown from inner to outer circles. Goats are grouped by population and each individual is represented as a single vertical line. The proportion of the coloured segment in each K cluster band represents their estimated ancestry from different populations with each colour representing a different ancestry. For a description of the goat breeds, see Table S1. [Colour figure can be viewed at wileyonlinelibrary.com]

of Laos. At three and four migration events (Figures S3 and S4), there were two main events of migration: the first one between Pakistan and Central Laos and the second between Laos and the Luoping Yellow (CLP) breed in Southwest and the Jining Grey breed in Eastern of China.

3.2 | Genetic diversity, genetic structure and inbreeding level within Lao native goats

PCA indicated that genetic structure exists within the Lao goat population. Goats in Sepon were different from those in the Phin and Songkhone districts. It also revealled low differentiation between Phin and Songkhone where in PC1, PC2 and PC3, the cluster of these districts overlapped to some extent. The principle components PC1, PC2 and PC3 accounted for 12.64%, 8.75% and 7.48% of the total variation (Figure 6a,b), respectively.

Admixture results of the Lao dataset for $K=2$–9 are presented in Figure 7 and a cross-validation (CV) error is presented in Figure S5. In Lao goats, the analysis of admixture revealed a clear differentiation of goats in Sepon from other Lao goats in $K=2$, 3 and 4, which is consistent with results obtained from the PCA (Figure 6a,b).

Across all K levels, admixture was observed among goat populations in Laos but the proportion of each cluster varied depending on the common ancestral level. In Sepon, for instance, the blue colour cluster accounted for a majority of the proportion (from 80% at $K=6$ to 84% at $K=2$) in all K levels. However, this cluster showed a small proportion at $K=2$ in both Phin (18%) and Songkhone (13%) and this significantly decreased as the K level increased. At $K=6$, this cluster accounted for 4% of both Phin and Songkhone populations. In contrast, while the red colour cluster held a minor proportion in Sepon, it emerged as a significant component in
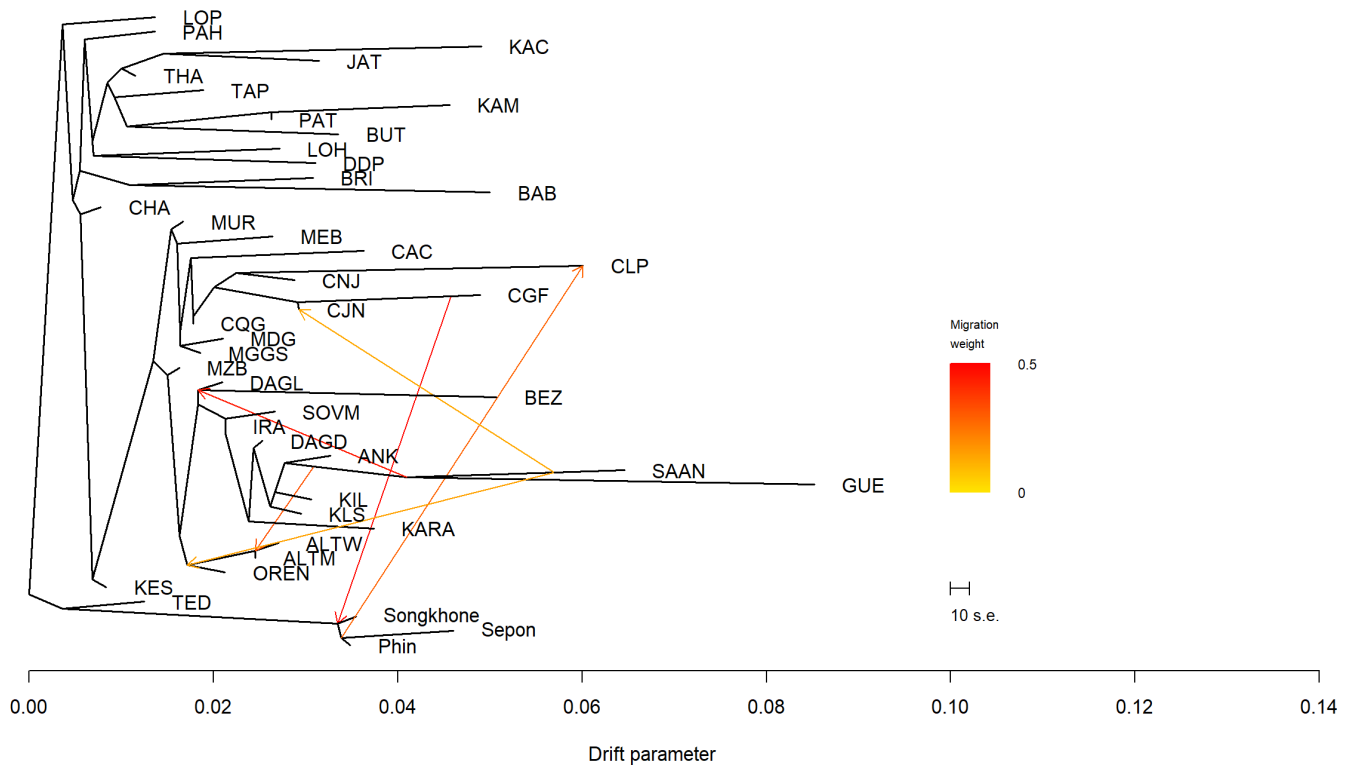
FIGURE 4 Neighbour-Net graph based on Weir and Cockerham distance for Lao goats and Asian goat breeds. For a description of the goat breeds, see Table S1. [Colour figure can be viewed at wileyonlinelibrary.com]

Songkhone and Phin. When $K = 2$, the red colour cluster represented 16% of Sepon, 82% of Phin and 87% of Songkhone. This distribution shifted at $K = 4$, where the cluster constituted 14% in Sepon, 81% in Phin and 44% in Songkhone. Additionally, from $K = 3–9$, individual goats in Phin showed less admixture compared to goats in Songkhone.

Based on the classification of F_{ST} by Wright (1965), there was overall low genetic differentiation among Lao native goats from three districts. However, a greater differentiation was found between the Sepon district and both Phin and Songkhone districts compared to the differentiation between Phin and Songkhone themselves (Table 1). These findings align with the result from PCA (Figure 6) showing that goats from Phin and Songkhone districts are more related.

To estimate genetic diversity, we computed Ho and He for goats in three Lao districts (Table 2). The average values for Ho and He were 0.292 and 0.303, respectively, with the lowest observed in Sepon and the highest in the Phin goat population. Except for the Sepon district, the Ho value was slightly greater than the He value. In Phin and

Songkhone, Ho values were, on average, 0.012 lower than He, while in Sepon, He was 0.0002 lower than Ho.

In general, the estimated inbreeding coefficient was close to zero with an average F_{IS} of 0.037, varying from negative values in Sepon (−0.001) and positive values in Phin (0.028) and Songkhone (0.052). Based on the 95% confidence intervals, F_{IS} values in Phin and Songkhone were moderately positive and significant, while the F_{IS} value in Sepon was not significantly different from zero. In addition, the mean F_{ROH} values in all Lao goat populations were generally low. However, some individual animals exhibited high inbreeding, with the highest F_{ROH} values found in Phin, Sepon and Songkhone at 0.412, 0.405 and 0.422, respectively (Table 2).

To estimate the level of inbreeding, we calculated the ROH segments for each Lao goat population, as shown in Table 3 and Figure 8. The average ROH length varied from 5.92 Mb in Phin to 6.85 Mb in Songkhone, with the average number of ROHs per goat ranging from 33.22 (Phin) to 38.69 (Songkhone). Longer ROHs are indicative of more recent inbreeding events since each recombination event reduces the length of an ROH. The Songkhone district

FIGURE 5 Maximum likelihood tree with 6 migration events between 43 goat breeds in Asian regions. Migration edges are coloured according to their migration weight (reflects the strength of inferred gene flow between populations). The scale bar indicates 10 times the average standard error of the entries in the sample covariance matrix. For a description of the goat breeds, see Table S1. [Colour figure can be viewed at wileyonlinelibrary.com]
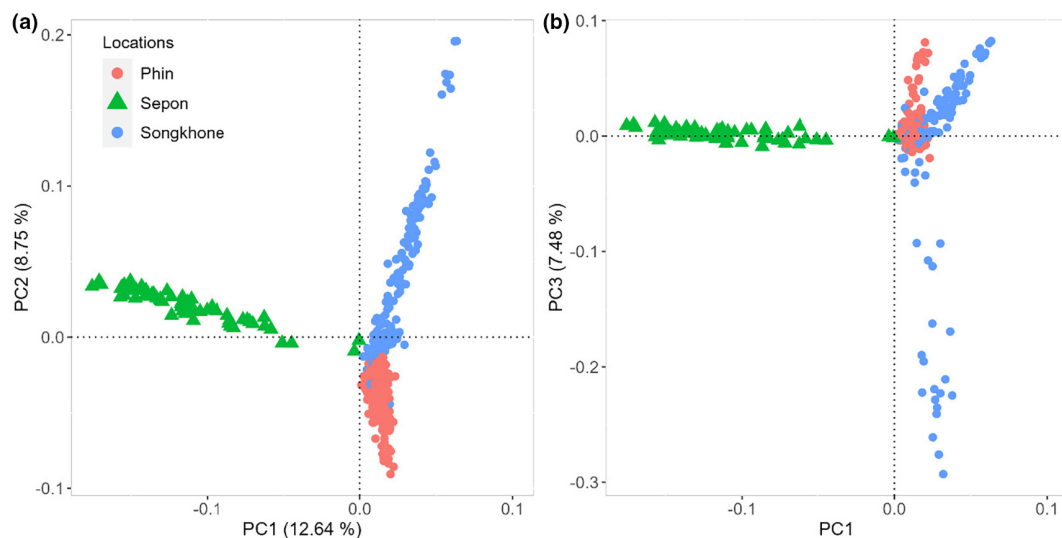

FIGURE 6 Principal component analysis for goats from three districts in Laos. The PC1 vs PC2 (a) and PC1 vs PC3 (b). A symbol represented an individual and colours represented sampling areas. [Colour figure can be viewed at wileyonlinelibrary.com]

displayed the largest variability in ROH lengths and number of ROHs per goat, while the Sepon district showed the lowest variability. Nevertheless, the majority of goats from the three districts exhibited similar patterns in the individual homozygosity, with several ROH segments of 60 and genome coverage ranging between 250 and 300 Mb (Figure 8a).

Overall, goats showed a higher frequency of ROH segments in the shorter-length categories, as represented in Figure 8b. The most common ROH length category was 1–5 Mb, accounting for 63.93% of the total ROH segments in Sepon, 64.28% in Songkhone and 70.80% in Phin. The amount of genome coverage of this class of ROH length segments was 67.74, 66.03 and 65.78 Mb in Phin, Sepon
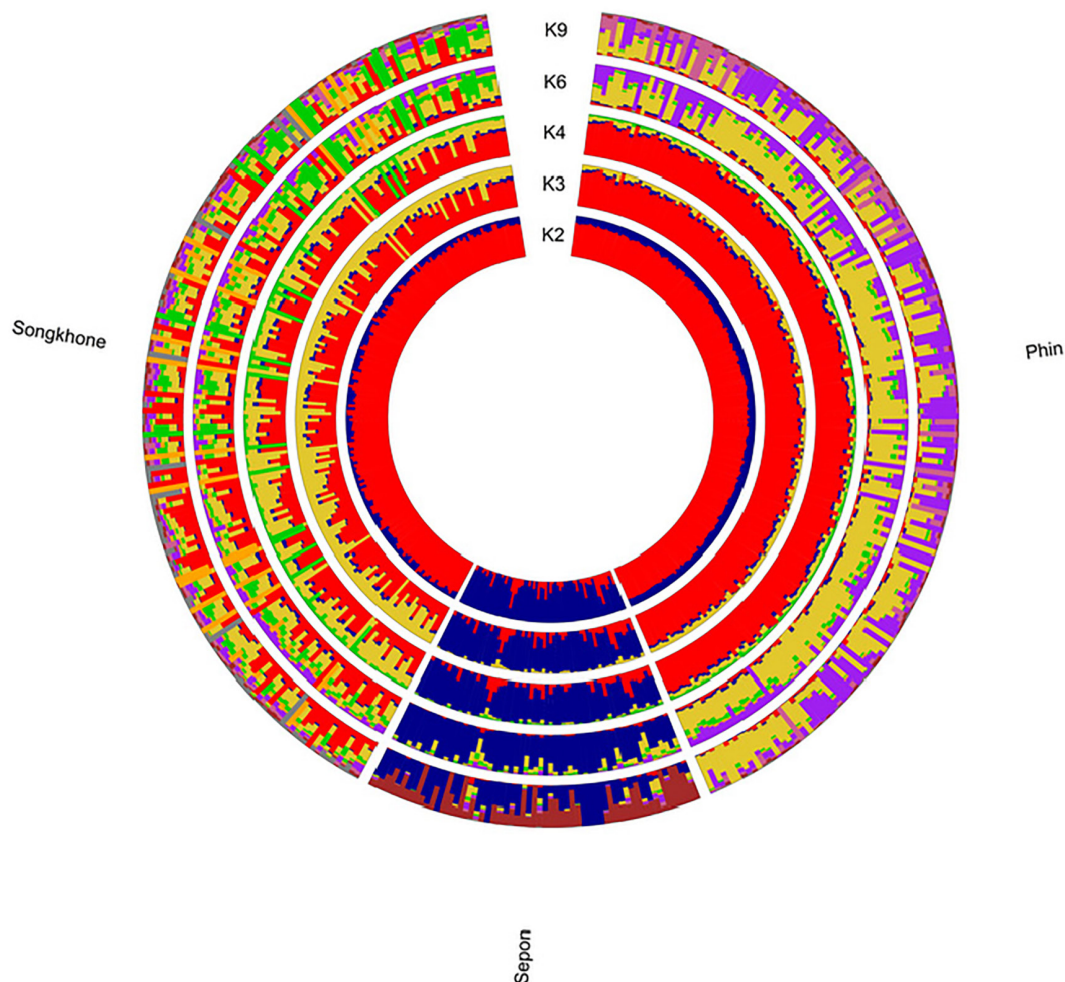
FIGURE 7 Admixture analysis of 419 goats from three districts in Central Laos. Goats are grouped by district and each individual is represented as a single vertical line. The proportion of the coloured segment in each K represents their estimated ancestry deriving from different populations. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Pairwise fixation index (F_{ST}) among three districts in Laos.

	Phin	Sepon	Songkhone
Phin	–		
Sepon	0.041	–	
Songkhone	0.011	0.043	–

and Songkhone, respectively. The second most frequent ROH length category was 5–10 Mb, with a proportion of 15.84% (Phin), 18.37% (Songkhone) and 19.62% (Sepon) with a mean genome coverage of 8.37, 13.33 and 14.80 Mb, respectively. Long ROH segments (10–20 and 20–40 Mb) accounted for 9.9% (ranging from 8.18% to 11.07%) and 4.81% (varying from 4.22% to 5.62%) of the total number of ROH segments. The frequency of the longest ROH length category (>40 Mb) ranged from the rarest in Sepon (0.79%) to low in Phin (0.97%) and Songkhone (1.26%). The average sum of the total ROH segment length per animal

for long ROH length categories (10–20, 20–40 Mb and >40 Mb) was <12 Mb.

The estimation of LD was based on r^2 values between pairs of SNPs for each of the three Lao goat districts (Figure 9). The result demonstrated a consistent trend in which the average r^2 values decrease as the genetic distance between pairwise SNPs increases, with a pronounced decline observed within the initial 0.5 Mb of genomic distance. A comparison of the average r^2 values among the three districts revealed similar results for Phin and Songkhone, both of which exhibited lower values than those observed in Sepon. The average LD of Sepon, Songkhone and Phin were 0.083, 0.032 and 0.03, respectively. The average LD up to 1000 Kb was highest in Sepon at 0.203.

The values for recent and ancestral Ne estimated for the Lao goat population are presented in Figure 10. The estimated Ne showed a stable declining trend in the most recent generations across the three districts. The Phin goat population consistently had the highest Ne,

—WILEY—

TABLE 2 Genetic diversity and inbreeding estimates in Lao goats by observed (Ho) and expected heterozygosity (He), estimates of the inbreeding coefficient (F_{IS}) with 95% confidence interval, fixation index (F_{ST}) within districts, mean, standard deviation (SD), min and max of genomic inbreeding coefficients (F_{ROH}).

Location	N	Ho	He	F_{IS} [95% CI]	F_{ROH} Mean ± SD	Min	Max
Phin	184	0.299	0.308	0.028 [0.027; 0.030]	0.080 ± 0.073	0.005	0.412
Sepon	59	0.288	0.288	−0.001 [−0.002; 0.001]	0.100 ± 0.061	0.023	0.4049
Songkhone	176	0.289	0.305	0.052 [0.051; 0.053]	0.108 ± 0.096	0.001	0.422
Laos	419	0.292	0.303	0.037 [0.036; 0.038]	0.094 ± 0.083	0.001	0.422

TABLE 3 Mean ROH length and mean ROH number in three goat populations in Laos.

Population	N	ROH length (mb) Mean ± SE	Min	Max	Number of ROH Mean ± SE	Min	Max
Phin	184	5.92 ± 0.09	0.03	80.79	33.22 ± 0.87	5	66
Sepon	59	6.42 ± 0.15	0.12	62.92	38.44 ± 1.3	18	62
Songkhone	176	6.85 ± 0.1	0.03	106.17	38.69 ± 1.13	2	84

while the Sepon goat population had the lowest Ne. The recent effective population sizes, 13 generations ago, were 92 for Sepon, 372 for Songkhone, 401 for Phin and 626 for the whole Lao datasets. The peak of the historical effective population size was found 915 generations ago, with 1487 for Sepon, 2368 for Songkhone and 2446 for Phin.

4 | DISCUSSION

4.1 | Goat migration to Southeast Asia and genetic relationships between Lao native goats and global breeds

Archaeological and genetic evidence showed that the goats were one of the first livestock species to be domesticated around 10,000 years before the present (YBP), during the Neolithic period in the Fertile Crescent (Zeder & Hesse, 2000). Following the initial domestication, the dispersal of goats across Asia occurred through two primary corridors. One migration route passed through Pakistan and India, eventually reaching Southeast Asia through overland and/or maritime routes (Devendra & Nozawa, 1976; Porter et al., 2016). These historical communication routes between Western Asia, the Indian subcontinent and Southeast Asia, provided an opportunity for the diffusion of crops and livestock (Fuller et al., 2011). The second corridor involved goats traversing through Caucasus and Siberia, eventually reaching Mongolia and China (Amills et al., 2017; Nozawa, 1991; Porter et al., 2016). Barker et al. (2001) reported that some goat

breeds in Southeast Asia shared the same cluster with Chinese goat breeds, suggesting a possible separate dispersion via China, similar to the spread of swamp buffalo through Southeast Asia (Barker et al., 1997). Furthermore, Yi et al. (2022) found that Lao goats have shared the haplogroup A and B with Chinese, Mongolian, Vietnamese, Cambodian and Pakistani goat breeds, supporting the notion of Western Asian goat influence on Southeast Asia goats.

The result in the PCA plots from 165 goat breeds (Figure 2a, Figure S1A) demonstrated that Lao goats clustered with Asian goat breeds and were more distant from goat breeds in Africa, America and Europe. The result from Asian PCA plots (Figure 2b, Figure S1B) in this study illustrated that Laos goats are closer to Chinese, Mongolian and Pakistani goats than other Asian goat breeds. Those findings are consistent with the result of admixture analysis where admixture results indicated the common genetic background between goat breeds in Laos, Mongolia, China and Pakistan, especially with three Chinese goat breeds (Guangfen, Jining Grey and Luoping Yellow) and one Pakistan goat breed (Teddi). In addition, moderate gene flows were found between Teddie (Pakistan) and Guangfeng (China) breeds and the goat population in Central Laos. Goats in Central Laos also had weak gene flow with Luoping Yellow and Jinning Grey breeds in Southwest and Eastern China, respectively. These findings are consistent with previous studies that described Guangfen and Jining Grey goats from China clustered in the same clade Berihulay et al. (2019). Later, Mukhina et al. (2022) reported those two Chinese goats in the same clade as Erchim goats
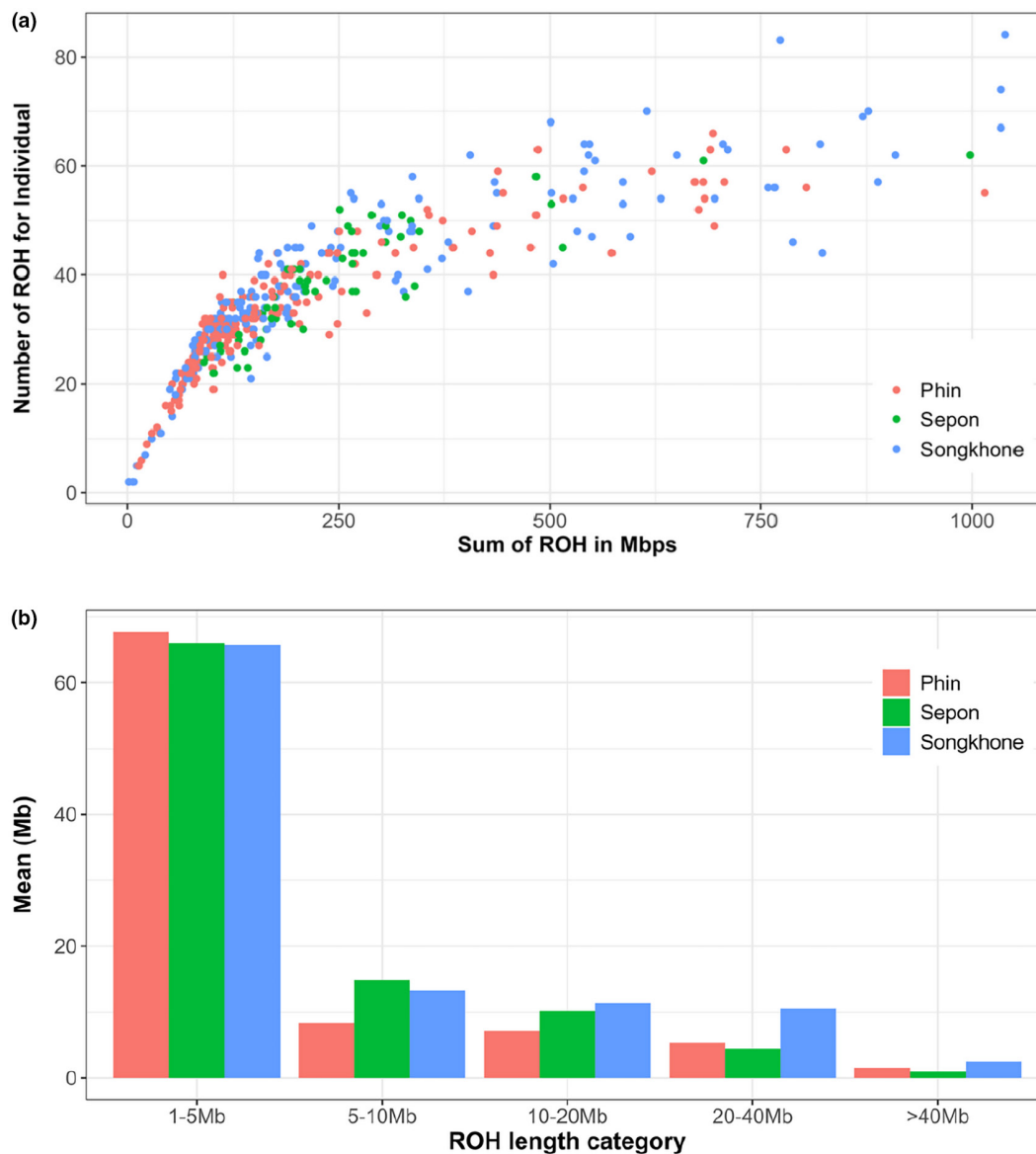
FIGURE 8 Patterns of ROH in Lao goats across districts. (a) Genomic coverage in ROH and ROH number per individual; (b) Mean sum of ROH per animal. The sum of ROH was performed per individual, measured in megabases (Mb) within each ROH length category averaged per district. [Colour figure can be viewed at wileyonlinelibrary.com]

from Mongolia and suggested that these breeds may share a common ancestry. These findings in this study supported the hypothesis that goats in Central Laos migrated from China and Pakistan.

Goats arrived in Mongolia and Northern China at approximately 4500 YBP (Colli et al., 2018; Pereira & Amorim, 2010). Goats also entered the Indian subcontinent and the broader regions of Southeast Asia. Due to the lack of archaeological evidence and genetic studies in these regions, the exact dates for their arrival are uncertain (Amills et al., 2017; Pereira & Amorim, 2010). Based on the long-term trends in effective population size in this study and an average generation interval of 4 years (Wang et al., 2021), goats would have arrived in Laos around 4000 YBP.

4.2 | Genetic diversity, structure and inbreeding patterns in Lao native goats

Since the availability of the Illumina Goat 50 K SNP BeadChip in 2014 (Tosser-Klopp et al., 2014), several studies to understand the genetic variation of local and international goat breeds using SNP datasets were conducted (Berihulay et al., 2019; Colli et al., 2018; Le et al., 2023; Tarekegn et al., 2019; Zhong et al., 2023). To our knowledge, this is the first application of a medium SNP array and genomic approaches to assess the genetic diversity and inbreeding levels of Lao native goats. The results of genetic variation showed moderate levels of diversity within Lao goat populations.

—WILEY—| 543
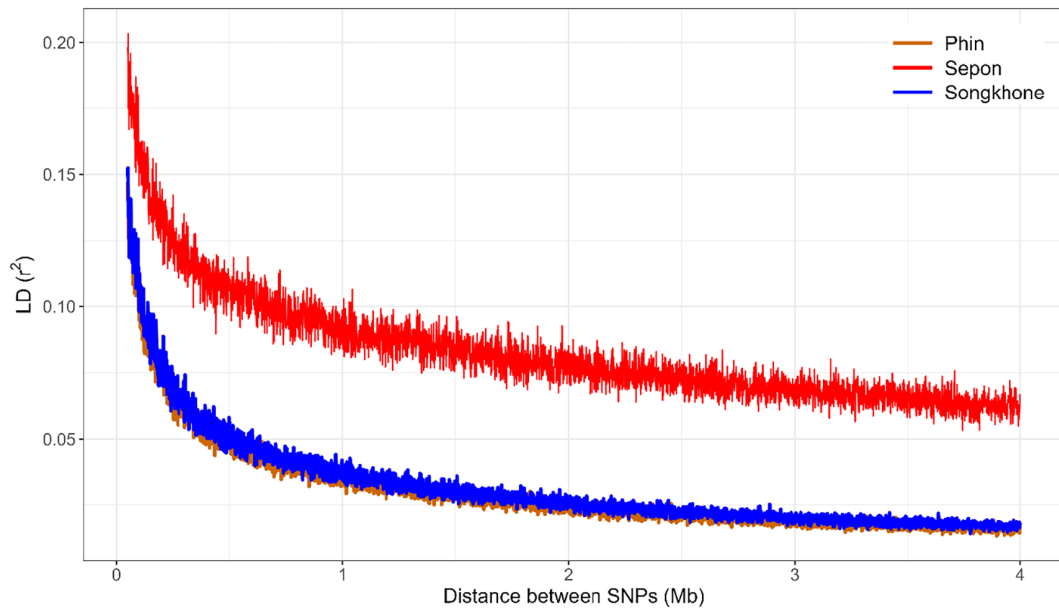
FIGURE 9 Genome-wide average LD decay estimated for each district. [Colour figure can be viewed at wileyonlinelibrary.com]
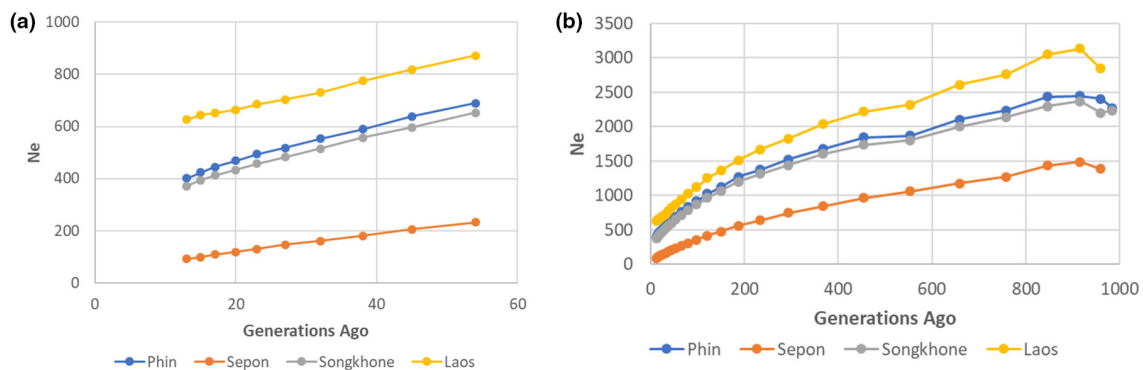

FIGURE 10 Recent (a) and long-term (b) trends in effective population size (Ne) for Lao goats in three districts and a total of Laos. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 The genetic diversity of goats in different locations.

Location	Ho	He	Genetic marker	References
Mongolia	0.393–0.406	0.388–0.410	SNP	Mukhina et al., 2022
China	0.306–0.402	0.371–0.405	SNP	Berihulay et al., 2019
Greece	0.94–0.405	0.392–0.395	SNP	Michailidou et al., 2019
West Asia	0.375	0.379	SNP	Colli et al., 2018
Pakistani	0.200–0.348	0.236–0.347	SNP	Kumar et al., 2018

The level of genetic diversity in Lao goat populations is indicated by heterozygosity levels (Ho and He). The average Ho and He for Lao breeds were 0.292 and 0.303, respectively, which were lower than the reported estimated values for goats in West Asia, China, Greece and Mongolia (Berihulay et al., 2019; Colli et al., 2018; Michailidou et al., 2019; Mukhina et al., 2022). The Ho and He of Lao goats were comparable to those of Pakistani goats (Kumar et al., 2018). One study using

65 SNPs reported Ho and He values of 0.305 and 0.342 for Laos, 0.311 and 0.340 for Vietnam, 0.292 and 0.356 for Cambodian plains goats and 0.332 and 0.324 for the Philippines (Lin et al., 2013). Table 4 depicts values of Ho and He reported by previous studies using SNP data. These findings are in alignment with the results of the present study, suggesting that Lao native goats exhibit moderate genetic diversity. Multiple factors, including inbreeding, small population size and demographic

history, could contribute to the different levels of heterozygosity observed (Cardoso et al., 2018).

The effect of population size (Ne) is a crucial parameter in population genetics due to its association with genetic variation loss, rate of inbreeding, mutation accumulation and the accuracy of genomic selection (Goddard, 2009). The Ne of Lao goats has decreased over generations, aligning with the global trend observed in goat breeds (Berihulay et al., 2019; Brito et al., 2017; Colli et al., 2018; Deniskova et al., 2021; Visser et al., 2016). The decline over time in effective population size could be due to natural and artificial selection (Monau et al., 2020). Given that goats in Laos are more likely to belong to a random mating population but with limited exchange of bucks or does between regions, the rapid change in Ne of Lao goats is possibly due to a lack of migration, rather than the consequence of domestication, selection, breed formation and breed endangerment (Shin et al., 2013). Ne values in Lao populations are not considered low in comparison with recent Ne estimates with global and indigenous goat breeds. For instance, Ne at 13 generations ago ranged from 52 for Booted goats (Burren et al., 2016), 87 for Boer (Monau et al., 2020), 96 for Eghoria (Michailidou et al., 2019) to 266 for Tswana goats (Monau et al., 2020) and 796 for Dagestan (Deniskova et al., 2021). Furthermore, the Ne at 13 generations ago in Lao native goats were higher compared to those reported for goat breeds in Australia, Canada (Brito et al., 2015) and Russia (Deniskova et al., 2021). The higher Ne of the Lao goat populations, compared to global breeds, could be attributed to the absence of artificial insemination in the breed development process and the application of less intensive management and breeding systems. This hypothesis is partially supported by the findings of Colli et al. (2018), which demonstrated that extensively managed local breeds tend to have higher Ne values compared to more intensively managed goat populations.

To ensure the preservation of genetic diversity and prevent negative effects from inbreeding, it is recommended to maintain the Ne values above 50 (Meuwissen & Goddard, 2007). The current Ne values observed in the native goat population in Laos (Ne: 626) exceed this critical threshold required for population maintenance. However, it has been proposed that a higher Ne value, exceeding 100, is necessary for the long-term viability of the livestock population (Meuwissen, 2009). The Ne value of Sepon 13 generations ago (Ne: 92) falls just below this threshold, indicating the need to increase the genetic pool in this area to achieve long-term selection and genetic response. It is advisable to consider interventions such as the exchange of breeding bucks between regions or the application of artificial insemination (Tada et al., 2013).

Wright (1978) noted that low F_{ST} values indicate a close genetic relationship between populations. Low F_{ST} values among the Lao goat population suggested minimal genetic differentiation and the presence of gene flow among those populations. Our findings showed that the global F_{ST} value within the Lao goat population was slightly higher than the global F_{ST} value in the Mongolian goats (Mukhina et al., 2022) but lower than the global F_{ST} values observed in Russian (Deniskova et al., 2021) and Chinese goat populations (Berihulay et al., 2019).

Results from F_{ST}, PCA and admixture analyses illustrate more gene flow between Songkhone and Phin districts and less between those districts and Sepon. The difference in gene flow between populations can often be explained by geographic isolation (Berihulay et al., 2019). Phin and Songkhone districts are not located far from each other, and they both have access to the main road network. Farmers in these two districts benefit from easily trading goats between each other's locations in Xathamua town which is located almost halfway between the two districts and is close to the Savannakhet province centre. On the other hand, Sepon is more culturally and geographically isolated, being a more distinct ethnic and linguistic group (Mong Kong) that speaks a different language from Lao Loum (the main ethnic group) and Phu Tai in Songkhone and Phin. These differences in ethnic and language groups may potentially result in less frequent trade with the other two districts. Additionally, Sepon is closer to the Vietnam border, making it easier for farmers to trade goats with Vietnamese dealers and previous studies using microsatellite and mitochondrial DNA have reported low genetic differentiation between Lao and Vietnamese goats (Lin et al., 2013; Nguyen et al., 2022).

The results of the LD analysis suggest that greater levels of mixing in the Phin and Songkhone populations are responsible for the faster rate of decline in the LD between SNPs and this would be consistent with the results of the admixture analysis. The disruption of the LD patterns caused by the introduction of genetic variation through mixing is likely the cause of the observed decline in LD. Sepon, on the other hand, has higher levels of LD and lower levels of mixing, indicating a breeding history with a smaller gene pool and limited exchange with other populations.

This study has disproven concerns about a high level of inbreeding in native goats, as both F_{IS} and F_{ROH} were found to be close to zero. It also implies that the small body size, slow growth rate and high mortality rate observed in Lao goats are not caused by inbreeding depression. Furthermore, the inbreeding coefficient of Lao native goats in this study was lower than that reported in Malaysian native goats (Ernie Muneerah et al., 2021) and

Lao goats Lin et al. (2013). The inbreeding coefficient values were comparable to those in other goat breeds globally, such as in Angola, Alpine, Saanen and Toggenburg (Visser et al., 2016) as well as indigenous goats in Mongolia (Mukhina et al., 2022), China (Berihulay et al., 2019) and Vietnam (Thuy et al., 2017).

In this study, the mean ROH number and mean ROH coverage (33–39 ROH and 5.92–6.85 Mb) for Lao goats were similar to those observed in Chinese (Zhong et al., 2023) and Mongolian native goats (Mukhina et al., 2022). However, the number of ROH in this study was lower than those reported for goat breeds in Russia (Deniskova et al., 2021), Turkey and Central Asia (Bertolini et al., 2018) which have been selected for specific traits. The lower relative ROH values in native breeds compared to global breeds are potentially due to an increased homozygosity pattern caused by small population size and geographic isolation (Bertolini et al., 2018). Similarly, a larger number of ROH and greater ROH coverage is commonly observed in breeds under selection compared to indigenous breeds (Bertolini et al., 2018).

Longer ROH segments indicate more recent inbreeding, while shorter ROH segments reflect more ancient inbreeding (Cardoso et al., 2018). In this study, long ROH segments in the Lao goat population accounted for a minority of all ROH segment length classes. The long ROH segments might be a consequence of artificial selection, demographic decline or recent inbreeding (Bertolini et al., 2018; Purfield et al., 2012). On the other hand, the majority of ROH segments fell in the short category. According to (Bertolini et al., 2018), short ROH segments often result from ancestral family relatedness and similar observations have been made in other global and indigenous goat populations (Deniskova et al., 2021; Michailidou et al., 2019; Onzima et al., 2018; Zhong et al., 2023). This suggests the native goat breeds in this study have historical relatedness.

This study has some limitations, primarily related to sample location and size. Due to travel restrictions during and after post COVID-19 pandemic in Laos, samples were only collected in three districts in Savannakhet province which has the largest proportion of Laos′ goat population at 26% in 2014 (Gray et al., 2019). There was also an uneven sample size among districts, with three villages in each Phin and Songkhone district, while only one village in Sepon, due to the limited access in that area. To capture the full genetic diversity across the country, it is recommended to obtain samples from different locations in Northern and Southern Laos. Furthermore, the migration analysis could not definitively explain whether goats migrated directly from China and Pakistan to Laos or through another country due to a lack of samples from other countries in Southeast Asia. This discrepancy was due to some farmers in Sepon not being willing to participate in the project. Despite these limitations, the study revealed moderate genetic diversity and low inbreeding in Lao native goats in central areas. Historical gene flow between the districts was evident, with Songkhone and Phin goats showing a closer relationship than those in Sepon.

5 | CONCLUSION

Our analysis of Lao goats revealed their close relationship with Chinese, Mongolian and Pakistani goats and shared ancestry with Chinese and Pakistani goats.

Our findings revealed that overall moderate level of genetic diversity and a low level of inbreeding in Lao native goats, with variations ranging from low to moderate across different populations. The goat population in Sepon was more differentiated compared to that in Songkhone and Phin, while the latter two populations displayed similar characteristics to each other.

Although goats in each district exhibited a strong trend of decreasing effective population sizes, none of them currently meet the criteria for being classified as endangered breeds. This indicates that efforts should be made such as increasing the number size and exchanging breeding bucks with other regions to prevent further decline in the Ne of Sepon goats.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data are owned by Project LS/2017/034 and access to the data can be negotiated by request.

ORCID

Sang V. Le https://orcid.org/0009-0000-9225-0813
Sara de las Heras-Saldana https://orcid.org/0000-0002-8665-6160
Panoraia Alexandri https://orcid.org/0000-0002-5367-3781
Luisa Olmo https://orcid.org/0000-0001-8175-8216
Stephen W. Walkden-Brown https://orcid.org/0000-0002-0638-5533
Julius H. J. van der Werf https://orcid.org/0000-0003-2512-1696

REFERENCES

Alexander, D. H., Shringarpure, S. S., Novembre, J., & Lange, K. (2015). *Admixture 1.3 software manual*. UCLA Human Genetics Software Distribution.

Al-Mamun, H. A., Clark, S., Kwan, P., & Gondro, C. (2015). Genome-wide linkage disequilibrium and genetic diversity in five populations of Australian domestic sheep. *Genetics Selection Evolution*, 47(1), 1–14. https://doi.org/10.1186/s12711-015-0169-6

Amills, M., Capote, J., & Tosser-Klopp, G. (2017). Goat domestication and breeding: A jigsaw of historical, biological and molecular data with missing pieces. *Animal Genetics*, 48(6), 631–644. https://doi.org/10.1111/age.12598

Barker, J., Tan, S., Moore, S., Mukherjee, T., Matheson, J., & Selvaraj, O. (2001). Genetic variation within and relationships among populations of Asian goats (*Capra hircus*). *Journal of Animal Breeding and Genetics*, 118(4), 213–234. https://doi.org/10.1046/j.1439-0388.2001.00296.x

Barker, J. S. F., Moore, S., Hetzel, D., Evans, D., Byrne, K., & Tan, S. (1997). Genetic diversity of Asian water buffalo (*Bubalus bubalis*): Microsatellite variation and a comparison with protein-coding loci. *Animal Genetics*, 28(2), 103–115. https://doi.org/10.1111/j.1365-2052.1997.00085.x

Berihulay, H., Li, Y., Liu, X., Gebreselassie, G., Islam, R., Liu, W., Jiang, L., & Ma, Y. (2019). Genetic diversity and population structure in multiple Chinese goat populations using a SNP panel. *Animal Genetics*, 50(3), 242–249. https://doi.org/10.1111/age.12776

Bertolini, F., Cardoso, T. F., Marras, G., Nicolazzi, E. L., Rothschild, M. F., Amills, M., & the AdaptMap c. (2018). Genome-wide patterns of homozygosity provide clues about the population history and adaptation of goats. *Genetics Selection Evolution*, 50(1), 59. https://doi.org/10.1186/s12711-018-0424-8

Biscarini, F., Cozzi, P., Gaspa, G., & Marras, G. (2018). detectRUNS: Detect runs of homozygosity and runs of heterozygosity in diploid genomes.

Brito, L. F., Jafarikia, M., Grossi, D. A., Kijas, J. W., Porto-Neto, L. R., Ventura, R. V., Salgorzaei, M., & Schenkel, F. S. (2015). Characterization of linkage disequilibrium, consistency of gametic phase and admixture in Australian and Canadian goats. *BMC Genetics*, 16(67), 67. https://doi.org/10.1186/s12863-015-0220-1

Brito, L. F., Kijas, J. W., Ventura, R. V., Sargolzaei, M., Porto-Neto, L. R., Cánovas, A., Feng, Z., Jafarikia, M., & Schenkel, F. S. (2017). Genetic diversity and signatures of selection in various goat breeds revealed by genome-wide SNP markers. *BMC Genomics*, 18(1), 229. https://doi.org/10.1186/s12864-017-3610-0

Bui, T. N., Nguyen, H. V., Nguyen, X. B., Le, V. N., Nguyen, T. M., Ngo, C. T. K., Ngo, Q. T. L., Hoang, N., Morales, L. E., Nguyen, V. D., Olmo, L., Walken-Brown, S., & Le, T. T. H. (2023). An analysis of the goat value chain from Lao PDR to Vietnam and a socio-economic sustainable development perspective. *Sustainability*, 15(18), 13781. https://doi.org/10.3390/su151813781

Burren, A., Neuditschko, M., Signer-Hasler, H., Frischknecht, M., Reber, I., Menzi, F., Drögemüller, C., & Flury, C. (2016). Genetic diversity analyses reveal first insights into breed-specific selection signatures within Swiss goat breeds. *Animal Genetics*, 47(6), 727–739. https://doi.org/10.1111/age.12476

Cañón, J., García, D., García-Atance, M. A., Obexer-Ruff, G., Lenstra, J. A., Ajmone-Marsan, P., & Dunner, S. (2006). Geographical partitioning of goat diversity in Europe and the Middle East. *Animal Genetics*, 37(4), 327–334. https://doi.org/10.1111/j.1365-2052.2006.01461.x

Cardoso, T. F., Amills, M., Bertolini, F., Rothschild, M., Marras, G., Boink, G., Jordana, J., Capote, J., Carolan, S., Hallsson, J. H., Kantanen, J., Pons, A., Lenstra, J. A., & The, A. M. C. (2018). Patterns of homozygosity in insular and continental goat breeds. *Genetics Selection Evolution*, 50(1), 56. https://doi.org/10.1186/s12711-018-0425-7

Chokoe, T. C., Hadebe, K., Muchadeyi, F. C., Nephawe, K. A., & Dzomba, E. F. (2022). Conservation status and historical relatedness of South African communal indigenous goat populations using a genome-wide single-nucleotide polymorphism marker. *Frontiers in Genetics*, 13, 909472. https://doi.org/10.3389/fgene.2022.909472

Colli, L., Milanesi, M., Talenti, A., Bertolini, F., Chen, M., Crisà, A., Daly, K. G., Del Corvo, M., Guldbrandtsen, B., & Lenstra, J. A. (2018). Genome-wide SNP profiling of worldwide goat populations reveals strong partitioning of diversity and highlights post-domestication migration routes. *Genetics Selection Evolution*, 50(58), 1–20. https://doi.org/10.1186/s12711-018-0422-x

Colvin, A., Olmo, L., Phengvilaysouk, A., Millar, J., Gray, G., Phengsavanh, P., & Walkden-Brown, S. (2022). Smallholder goat production systems in Lao PDR: Assessing production efficiency. *Animal Production. Science*, 62(10&11), lxviii. https://hdl.handle.net/1959.11/54650

Corbin, L. J., Liu, A. Y., Bishop, S. C., & Woolliams, J. A. (2012). Estimation of historical effective population size using linkage disequilibria with marker data. *Journal of Animal Breeding and Genetics*, 129(4), 257–270. https://doi.org/10.1111/j.1439-0388.2012.01003.x

Deniskova, T. E., Dotsev, A. V., Selionova, M. I., Reyer, H., Sölkner, J., Fornara, M. S., Aybazov, A.-M. M., Wimmers, K., Brem, G.,

& Zinovieva, N. A. (2021). SNP-based genotyping provides insight into the West Asian origin of Russian local goats. *Frontiers in Genetics*, *12*, 708740. https://doi.org/10.3389/fgene.2021.708740

Devendra, C. (2013). Investments on pro-poor development projects on goats: Ensuring success for improved livelihoods. *Asian-Australasian Journal of Animal Sciences*, *26*(1), 1–18. https://doi.org/10.5713/ajas.2013.r.01

Devendra, C., & Nozawa, K. (1976). Goats in South East Asia-their status and production. *Zeitschrift für Tierzüchtung und Züchtungsbiologie*, *93*(1–4), 101–120. https://doi.org/10.1111/j.1439-0388.1976.tb00891.x

Dubeuf, J.-P., Bendapudi, R., Bhandari, D., Capote, J., Carrasco-Sanchez, R., Daskiran, I., Guimaraes, V., Iniguez, L., Koluman-Darcan, N., Peacock, C., Rota, A., Richkowsky, B., & Sepe, L. (2014). Scaling up successful practices for pro-poor development projects involving goats: First outputs of a comparative study. *Small Ruminant Research*, *121*(1), 146–156. https://doi.org/10.1016/j.smallrumres.2014.02.002

Ernie Muneerah, M. A., Md Tamrin, N. A., Salisi, M. S., Zulkifly, S., Ghazali, S. S. M., Temuli, J. J., Rosali, M. H., Nazari, S., Wan Nik, W. M. K., & Mamat-Hamidi, K. (2021). Microsatellite-based genetic characterization of the indigenous Katjang goat in peninsular Malaysia. *Animals*, *11*(5), 1328. https://doi.org/10.3390/ani11051328

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, *14*(8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

FAOSTAT. (2022). *Food and agriculture data*. FAOSTAT. https://www.fao.org/faostat/en/#data/QCL

Fitak, R. R. (2021). OptM: Estimating the optimal number of migration edges on population trees using Treemix. *Biology Methods & Protocols*, *6*(1), bpab017. https://doi.org/10.1093/biomethods/bpab017

Fuller, D. Q., Boivin, N., Hoogervorst, T., & Allaby, R. (2011). Across the Indian Ocean: The prehistoric movement of plants and animals. *Antiquity*, *85*(328), 544–558. https://doi.org/10.1017/S0003598X00067934

Gansberghe, D. (2005). Smallholder Livestock Systems and Upland Development. Improving Livelihoods in the Upland of the Lao PDR 2(71-7).

Goudet, J. (2005). Hierfstat, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes*, *5*, 184–186.

Goddard, M. (2009). Genomic selection: Prediction of accuracy and maximisation of long term response. *Genetica*, *136*, 245–257.

Gray, G. D. (2005). Goat raising in northern Lao PDR. In: *Participatory livestock development project ADB PPTA no. 4287 – LAO*.

Gray, G. D., Walkden-Brown, S. W., Phengsavanh, P., Hergenhan, R., Hoang, N., Phengvilaysouk, A., Carnegie, M., Millar, J., & Hữu, V. N. (2019). Final Report: Assessing goat production and marketing systems in Laos and market linkages into Vietnam, Canberra.

Kumar, C., Song, S., Dewani, P., Kumar, M., Parkash, O., Ma, Y., Malhi, K., Yang, N., Mwacharo, J. M., & He, X. (2018). Population structure, genetic diversity and selection signatures within seven indigenous Pakistani goat populations. *Animal Genetics*, *49*(6), 592–604. https://doi.org/10.1111/age.12722

Le, S., de las Heras-Saldana, S., Alexandri, P., Olmo, L., Walkden-Brown, S., & van der Werf, J. (2023). Genetic diversity of

domestic goats from Central Laos. In *Association for the Advancement of animal breeding and genetics* (pp. 250–253). The University Club of Western Australia.

Lencz, T., Lambert, C., DeRosse, P., Burdick, K. E., Morgan, T. V., Kane, J. M., Kucherlapati, R., & Malhotra, A. K. (2007). Runs of homozygosity reveal highly penetrant recessive loci in schizophrenia. *Proceedings of the National Academy of Sciences*, *104*(50), 19942–19947. https://doi.org/10.1073/pnas.0710021104

Lenstra, J. A., Tigchelaar, J., Biebach, I., Hallsson, J. H., Kantanen, J., Nielsen, V. H., Pompanon, F., Naderi, S., Rezaei, H. R., Saether, N., Ertugrul, O., Grossen, C., Camenisch, G., Vos-Loohuis, M., van Straten, M., de Poel, E. A., Windig, J., & Oldenbroek, K. (2017). Microsatellite diversity of the Nordic type of goats in relation to breed conservation: How relevant is pure ancestry? *Journal of Animal Breeding and Genetics*, *134*(1), 78–84. https://doi.org/10.1111/jbg.12226

Letunic, I., & Bork, P. (2016). Interactive tree of life (iTOL) v3: An online tool for the display and annotation of phylogenetic and other trees. *Nucleic Acids Research*, *44*(W1), W242–W245. https://doi.org/10.1093/nar/gkw290

Lin, B. Z., Kato, T., Kaneda, M., Matsumoto, H., Sasazaki, S., & Mannen, H. (2013). Genetic diversity and structure in a sian native goat analyzed by newly developed SNP markers. *Animal Science Journal*, *84*(8), 579–584. https://doi.org/10.1111/asj.12039

Lischer, H. E., & Excoffier, L. (2012). PGDSpider: An automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, *28*(2), 298–299. https://doi.org/10.1093/bioinformatics/btr642

Makina, S. O., Muchadeyi, F. C., van Marle-Köster, E., MacNeil, M. D., & Maiwashe, A. (2014). Genetic diversity and population structure among six cattle breeds in South Africa using a whole genome SNP panel. *Frontiers in Genetics*, *5*(333), 102346. https://doi.org/10.3389/fgene.2014.00333

Manunza, A., Noce, A., Serradilla, J. M., Goyache, F., Martínez, A., Capote, J., Delgado, J. V., Jordana, J., Muñoz, E., & Molina, A. (2016). A genome-wide perspective about the diversity and demographic history of seven Spanish goat breeds. *Genetics Selection Evolution*, *48*(52), 1–9. https://doi.org/10.1186/s12711-016-0229-6

Marras, G., Gaspa, G., Sorbolini, S., Dimauro, C., Ajmone-Marsan, P., Valentini, A., Williams, J. L., & Macciotta, N. P. (2015). Analysis of runs of homozygosity and their relationship with inbreeding in five cattle breeds farmed in Italy. *Animal Genetics*, *46*(2), 110–121. https://doi.org/10.1111/age.12259

McQuillan, R., Leutenegger, A. L., Abdel-Rahman, R., Franklin, C. S., Pericic, M., Barac-Lauc, L., Smolej-Narancic, N., Janicijevic, B., Polasek, O., Tenesa, A., Macleod, A. K., Farrington, S. M., Rudan, P., Hayward, C., Vitart, V., Rudan, I., Wild, S. H., Dunlop, M. G., Wright, A. F., … Wilson, J. F. (2008). Runs of homozygosity in European populations. *American Journal of Human Genetics*, *83*(3), 359–372. https://doi.org/10.1016/j.ajhg.2008.08.007

Meuwissen, T. (2009). Genetic management of small populations: A review. *Acta Agriculturae Scand Section A*, *59*(2), 71–79. https://doi.org/10.1080/09064700903118148

Meuwissen, T. H., & Goddard, M. E. (2007). Multipoint identity-by-descent prediction using dense markers to map quantitative trait loci and estimate effective population size. *Genetics*, *176*(4), 2551–2560. https://doi.org/10.1534/genetics.107.070953

Michailidou, S., Tsangaris, G. T., Tzora, A., Skoufos, I., Banos, G., Argiriou, A., & Arsenos, G. (2019). Analysis of genome-wide DNA arrays reveals the genomic population structure and diversity in autochthonous Greek goat breeds. *PLoS One*, *14*(12), e0226179. https://doi.org/10.1371/journal.pone.0226179

Milanesi, M., Capomaccio, S., Vajana, E., Bomba, L., Garcia, J. F., Ajmone-Marsan, P., & Colli, L. (2017). BITE: An R package for biodiversity analyses. *bioRxiv*, 181610. https://doi.org/10.1101/181610

Monau, P., Visser, C., Muchadeyi, F., Okpeku, M., Nsoso, S., & Van Marle-Köster, E. (2020). Population structure of indigenous southern African goats based on the Illumina Goat50K SNP panel. *Tropical Animal Health and Production*, *52*(4), 1795–1802. https://doi.org/10.1007/s11250-019-02190-9

Muir, W. M., Wong, G. K.-S., Zhang, Y., Wang, J., Groenen, M. A., Crooijmans, R. P., Megens, H.-J., Zhang, H., Okimoto, R., & Vereijken, A. (2008). Genome-wide assessment of worldwide chicken SNP genetic diversity indicates significant absence of rare alleles in commercial breeds. *Proceedings of the National Academy of Sciences*, *105*(45), 17312–17317. https://doi.org/10.1073/pnas.0806569105

Mukhina, V., Svishcheva, G., Voronkova, V., Stolpovsky, Y., & Piskunov, A. (2022). Genetic diversity, population structure and phylogeny of indigenous goats of Mongolia revealled by SNP genotyping. *Animals*, *12*(3), 221. https://doi.org/10.3390/ani12030221

Munoz, M., Bozzi, R., Garcia-Casco, J., Nunez, Y., Ribani, A., Franci, O., Garcia, F., Škrlep, M., Schiavo, G., & Bovo, S. (2019). Genomic diversity, linkage disequilibrium and selection signatures in European local pig breeds assessed with a high density SNP chip. *Scientific Reports*, *9*(1), 13546. https://doi.org/10.1038/s41598-019-49830-6

Nandolo, W., Mészáros, G., Banda, L. J., Gondwe, T. N., Lamuno, D., Mulindwa, H. A., Nakimbugwe, H. N., Wurzinger, M., Utsunomiya, Y. T., Woodward-Greene, M. J., Liu, M., Liu, G., Van Tassell, C. P., Curik, I., Rosen, B. D., & Sölkner, J. (2019). Timing and extent of inbreeding in African goats. *Frontiers in Genetics*, *10*, 537. https://doi.org/10.3389/fgene.2019.00537

Nguyen, N., Tram, M., Pham, T., Le, T., Nguyen, T., Hoang, T., Pham, C., & Duong, N. (2022). Genetic divergence of local goats in Ninh Thuan province Vietnam. *Advances in Animal and Veterinary Sciences*, *10*(8), 1761–1768.

Nozawa, K. (1991). *Domestication and history of goats*. Elsevier.

Oget, C., Servin, B., & Palhière, I. (2019). Genetic diversity analysis of French goat populations reveals selective sweeps involved in their differentiation. *Animal Genetics*, *50*(1), 54–63. https://doi.org/10.1111/age.12752

Olmo, L., Phengvilaysouk, A., Colvin, A. F., Phengsavanh, P., Millar, J., & Walkden-Brown, S. W. (2022). Improving lao goat production when resources are limited. In R. B. E. Charmley, S. S. Chauhan, D. Innes, S. Muir, L. Watt, & C. Wilson (Eds.), *Australian Association for the Advancement of animal science* (p. cvi). Animal Production Science.

Onzima, R. B., Upadhyay, M. R., Doekes, H. P., Brito, L. F., Bosse, M., Kanis, E., Groenen, M. A. M., & Crooijmans, R. (2018). Genome-wide characterization of selection signatures and runs of homozygosity in Ugandan goat breeds. *Frontiers in Genetics*, *9*, 318. https://doi.org/10.3389/fgene.2018.00318

Pereira, F., & Amorim, A. (2010). *Origin and spread of goat pastoralism*. Encyclopedia of Life Sciences. https://doi.org/10.1002/9780470015902.a0022864

Peripolli, E., Munari, D., Silva, M., Lima, A., Irgang, R., & Baldi, F. (2017). Runs of homozygosity: Current knowledge and applications in livestock. *Animal Genetics*, *48*(3), 255–271. https://doi.org/10.1111/age.12526

Phengsavanh, P. (2006). Goat production development in Lao PDR: Potential, limitations and approaches of forage development. In: *APHCA-ILRI regional workshop on goat production systems and markets, Luang Prabang, Lao PDR*.

Pickrell, J. K., & Pritchard, J. K. (2012). Inference of population splits and mixtures from genome-wide allele frequency data. *PLoS Genetics*, *8*(11), e1002967. https://doi.org/10.1371/journal.pgen.1002967

Porter, V., Alderson, L., Hall, S. J., & Sponenberg, D. P. (2016). *Mason's world encyclopedia of livestock breeds and breeding, 2 Volume Pack*. Cabi.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A., Bender, D., Maller, J., Sklar, P., De Bakker, P. I., & Daly, M. J. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *The American Journal of Human Genetics*, *81*(3), 559–575. https://doi.org/10.1086/519795

Purfield, D. C., Berry, D. P., McParland, S., & Bradley, D. G. (2012). Runs of homozygosity and population history in cattle. *BMC Genetics*, *13*(70), 1–11. https://doi.org/10.1186/1471-2156-13-70

Shin, D. H., Cho, K. H., Park, K. D., Lee, H. J., & Kim, H. (2013). Accurate estimation of effective population size in the Korean dairy cattle based on linkage disequilibrium corrected by genomic relationship matrix. *Asian-Australasian Journal of Animal Sciences*, *26*(12), 1672–1679. https://doi.org/10.5713/ajas.2013.13320

Sved, J. A., & Feldman, M. W. (1973). Correlation and probability methods for one and two loci. *Theoretical Population Biology*, *4*(1), 129–132. https://doi.org/10.1016/0040-5809(73)90008-7

Tada, O., Muchenje, V., & Dzama, K. (2013). Effective population size and inbreeding rate of indigenous Nguni cattle under in situ conservation in the low-input communal production system. *South African Journal of Animal Science*, *43*(2), 137–142. https://doi.org/10.4314/sajas.v43i2.3

Tarekegn, G. M., Wouobeng, P., Jaures, K. S., Mrode, R., Edea, Z., Liu, B., Zhang, W., Mwai, O. A., Dessie, T., Tesfaye, K., Strandberg, E., Berglund, B., Mutai, C., Osama, S., Wolde, A. T., Birungi, J., Djikeng, A., & Meutchieye, F. (2019). Genome-wide diversity and demographic dynamics of Cameroon goats and their divergence from east African, north African and Asian conspecifics. *PLoS One*, *14*(4), e0214843. https://doi.org/10.1371/journal.pone.0214843

Thuy, L. T., Binh, D. V., Binh, N. T., Minh, L. Q., Thuy, T. T. T., Ton, N. D., Ba, N. V., Han, J.-L., & Periasamy, K. (2017). Evaluation of genetic diversity and structure of Vietnamese goat populations using multi locus microsatellite markers. *Small Ruminant Research*, *148*, 43–50. https://doi.org/10.1016/j.smallrumres.2016.12.029

Tosser-Klopp, G., Bardou, P., Bouchez, O., Cabau, C., Crooijmans, R., Dong, Y., Donnadieu-Tonon, C., Eggen, A., Heuven, H. C., & Jamli, S. (2014). Design and characterization of a 52K SNP chip for goats. *PLoS One*, *9*(1), e86227. https://doi.org/10.1371/journal.pone.0152632

Trach, N. X., & Phiovankham, B. (2011). Determination of growth functions of indigenous and crossbred goats in Laos. *Journal of Southern Agriculture*, *42*(1), 82–85.

Tucho, T. A., & Tesfaye, A. (2004). *Genetic characterization of indigenous goat populations of Ethiopia using microsatellite DNA markers*. NDRI.

Visser, C., Lashmar, S. F., Van Marle-Köster, E., Poli, M. A., & Allain, D. (2016). Genetic diversity and population structure in south African, French and Argentinian angora goats from genome-wide SNP data. *PLoS One*, *11*(5), e0154353. https://doi.org/10.1371/journal.pone.0154353

Wang, Z., Zhou, B., Zhang, T., Yan, X., Yu, Y., Li, J., Mei, B., Wang, Z., Zhang, Y., Wang, R., Lv, Q., Liu, Z., Zhao, Y., Du, C., & Su, R. (2021). Assessing genetic diversity and estimating the inbreeding effect on economic traits of Inner Mongolia white cashmere goats through pedigree analysis. *Frontiers in Veterinary Science*, *8*, 665872. https://doi.org/10.3389/fvets.2021.665872

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*(6), 1358–1370. https://doi.org/10.1111/j.1558-5646.1984.tb05657.x

Wickham, H. (2011). ggplot2. *WIREs Computational Statistics*, *3*(2), 180–185. https://doi.org/10.1002/wics.147

Wilson, R. T. (2007). Status and prospects for livestock production in the Lao People's Democratic Republic. *Tropical Animal Health and Production*, *39*(6), 443–452. https://doi.org/10.1007/s11250-007-9048-7

Windsor, P., Nampanya, S., Putthana, V., Keonam, K., Johnson, K., Bush, R., & Khounsy, S. (2018). The endoparasitism challenge in developing countries as goat raising develops from smallholder to commercial production systems: A study from Laos. *Veterinary Parasitology*, *15*(251), 95–100. https://doi.org/10.1016/j.vetpar.2017.12.025

Wright, S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution*, *19*(3), 395–420. https://doi.org/10.2307/2406450

Wright, S. (1978). Evolution and the genetics of populations. In *Vol. 4: Variability within and among natural populations*. Univ. Chicago Press.

Xayalath, S., Mujitaba, M. A., Ortega, A. D. S. V., & Rátky, J. (2021). A review on the trend of livestock breeds in Laos. *Acta Agraria Debreceniensis*, *55*(1), 227–237. https://doi.org/10.34101/actaagrar/1/9047

Yi, G., Ying, G., Yong-meng, H., Bai-gao, Y., Wei-yi, Z., Bo-er, C., Yong-fu, H., Yong-ju, Z., Dan-ping, Z., & Yue-hui, M. (2022). Investigation of mitochondrial DNA genetic diversity and phylogeny of goats worldwide. *Journal of Integrative Agriculture*, *21*(6), 1830–1837. https://doi.org/10.1016/S2095-3119(21)63882-0

Zeder, M. A., & Hesse, B. (2000). The initial domestication of goats (*Capra hircus*) in the Zagros mountains 10,000 years ago. *Science*, *287*(5461), 2254–2257. https://doi.org/10.1126/science.287.5461.2254

Zhao, H., Nettleton, D., Soller, M., & Dekkers, J. (2005). Evaluation of linkage disequilibrium measures between multi-allelic markers as predictors of linkage disequilibrium between markers and QTL. *Genetics Research*, *86*(1), 77–87. https://doi.org/10.1017/S001667230500769X

Zhong, T., Wang, X., Huang, C., Yang, L., Zhao, Q., Chen, X., Freitas-de-Melo, A., Zhan, S., Wang, L., & Dai, D. (2023). A genome-wide perspective on the diversity and selection signatures in indigenous goats using 53K single nucleotide polymorphism array. *Animal*, *17*(3), 100706. https://doi.org/10.1016/j.animal.2023.100706

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.