Ethiopian indigenous goats offer insights into past and recent demographic dynamics and local adaptation in sub-Saharan African goats

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Abstract
Knowledge on how adaptive evolution and human socio-cultural and economic interests shaped livestock genomes particularly in sub-Saharan Africa remains limited. Ethiopia is in a geographic region that has been critical in the history of African agriculture with ancient and diverse human ethnicity and bio-climatic conditions. Using 52K genome-wide data analysed in 646 individuals from 13 Ethiopian indigenous goat populations, we observed high levels of genetic variation. Although runs of homozygosity (ROH) were ubiquitous genome-wide, there were clear differences in patterns of ROH length and abundance and in effective population sizes illustrating differences in genome homozygosity, evolutionary history, and management. Phylogenetic analysis incorporating patterns of genetic differentiation and gene flow with ancestry modelling highlighted past and recent intermixing and possible two deep ancient genetic ancestries that could have been brought by humans with the first introduction of goats in Africa. We observed four strong selection signatures that were specific to Arsi-Bale and Nubian goats. These signatures overlapped genomic regions with genes associated with morphological, adaptation, reproduction
INTRODUCTION

Threats to biodiversity, and projected future food demands and climatic conditions, underscore the urgent need to characterize, monitor and maintain agricultural biodiversity. Data on molecular changes have been critical in understanding genome architecture, maintaining biodiversity and fitness and exploring impacts of genome evolution. This has been made possible through the investigation of genetic diversity and structure, demographic dynamics (Bosse et al., 2012) and assessment of autozygosity under varying degrees of reproductive isolation and inbreeding (Ceballos, Joshi, Clark, Ramsay, & Wilson, 2018; Kirin et al., 2010; Peripolli et al., 2016). As livestock dispersed from their centres of domestication, they encountered diverse environments with unique climatic, anthropological and biophysical limits. These animals responded to the niche-specific environmental pressures through behavioural and biological adjustments. The former provided short-term buffer against many of the stressors, and the latter ensured long-term survival through physiological and/or genetic adaptation.

Among domestic ungulates, goats have the longest socio-cultural and economic co-existence with humans. They were domesticated around 11,000 years ago in the Fertile Crescent of Southwest Asia and adjacent areas (Zeder & Hesse, 2000). Since their domestication, goats have been contributing to human cultural and socio-economic transformations that have shaped ancient and modern human civilizations and the goat’s genomes. Their rusticity and resilience have allowed them to cope and adapt to a wide range of environments. However, the evolutionary history of goats is complex with two contrasting hypotheses explaining their domestication and little geographic pattern in their maternal diversity. Luikart et al. (2001) observed at least six distinct mtDNA haplogroups with little geographic partitioning. They interpreted this to be the consequence of multiple domestication events and ease of translocation through commercial activities. Naderi et al. (2008) on the other hand suggested that such diversity of mtDNA haplogroups was compatible with a single domestication event, followed by a phase of human management of wild or semi-domesticated goats comprising multiple mtDNA lineages, prior to their global dispersion. Evidence from the analysis of ancient goat genomes suggests the domestication of multiple divergent wild goats in a dispersed manner resulting in distinct Neolithic populations that contributed disproportionately to modern goat genomes (Daly et al., 2018). The initial diffusion of goats to Africa is also complex. Archaeological evidence suggests at least three entry points into the continent (Gifford-Gonzalez & Hanotte, 2011). At least two mtDNA haplogroups have also been observed in Kenyan (Kibegwa, Githui, Jung’a, Badamana, & Nyamu, 2015), Ethiopian (Tarekegn et al., 2018), Sudanese (Sanhory, Gila, Ebrahim, Eldin, & Gornas, 2014) and Egyptian (Naderi et al., 2008) indigenous goats, suggesting the influence of at least two independent maternal lineages.

Palaeogenomic evidence has shown that the north-eastern and Horn of Africa region were at the centre of a vast web of maritime and terrestrial routes of ancient and modern trade and thus a major entry point of domesticates into the continent (Fuller & Boivin, 2009; Marshall, 2000). The Horn of Africa landscape exhibit considerable changes in elevation within short geographic distances due to complex volcano-tectonic activities over the past millennia (Mohr, 1971). In particular, the Ethiopian highlands, which range from 125 m below sea level in the Afar depression to altitudes exceeding 4,000 metres above sea level in the Arsi-Bale mountains, form an extensive uplifted plateau, that is delimited by pronounced escarpments (Umer et al., 2007). The altitudinal gradients result in a wide range of agro-ecoclimes and production environments. The region is also characterized by human ethnic diversity of ancient origin that has been associated with livestock husbandry. Palaeo-climatic data have also revealed periods of prolonged and severe droughts in the region with profound impacts (Verschuren, Laird, & Cumming, 2000). These factors make the region particularly attractive for investigating how the genomes of indigenous livestock might have been shaped by past and recent events. Here, we generated 52K SNP genotypes in 13 populations of Ethiopian indigenous goats. The data were used to investigate past and recent demographic dynamics through the analysis of genome-wide diversity and admixture, autozygosity and evidence for selection.

MATERIALS AND METHODS

Animals and genotypes

The animals used in this study were provided by farmers and pastoralists who participated in the study by agreeing to have their...
TABLE 1  Genetic diversity and variation statistics for 13 Ethiopian indigenous goat populations (mean ± SD)

| Population                  | Abbreviation | Regions         | N   | \(H_0\)        | \(H_E\)        | \(P_N\)        | \(D_{ST}\)     | \(F_{HOM}\)    | \(F_{ROH}\)    |
|-----------------------------|--------------|-----------------|-----|----------------|----------------|----------------|----------------|----------------|----------------|
| Abergelle                   | Abe          | Lowland         | 52  | 0.369 ± 0.131  | 0.373 ± 0.119  | 0.982          | 0.295 ± 0.008  | 0.010 ± 0.045  | 0.023 ± 0.039  |
| Gondar                      | Gon          | Central highland| 54  | 0.376 ± 0.131  | 0.373 ± 0.118  | 0.984          | 0.292 ± 0.011  | -0.007 ± 0.019 | 0.006 ± 0.014  |
| Ambo                        | Amb          | Central highland| 71  | 0.370 ± 0.125  | 0.371 ± 0.117  | 0.988          | 0.296 ± 0.014  | 0.011 ± 0.050  | 0.029 ± 0.044  |
| Western Highland/Agew       | WeH          | Highland        | 45  | 0.371 ± 0.134  | 0.372 ± 0.120  | 0.988          | 0.292 ± 0.008  | 0.001 ± 0.027  | 0.019 ± 0.022  |
| Western Lowland/Gumez       | WeL          | Lowland         | 41  | 0.370 ± 0.138  | 0.370 ± 0.122  | 0.987          | 0.291 ± 0.019  | 0.000 ± 0.062  | 0.021 ± 0.044  |
| Keffa                       | Kaf          | Middle land     | 36  | 0.348 ± 0.143  | 0.361 ± 0.130  | 0.978          | 0.289 ± 0.018  | 0.035 ± 0.105  | 0.057 ± 0.099  |
| Woyto-Guji                  | WoG          | Lowland         | 51  | 0.375 ± 0.129  | 0.375 ± 0.117  | 0.985          | 0.295 ± 0.009  | 0.002 ± 0.028  | 0.011 ± 0.015  |
| Arsi-Bale                   | ArB          | Highland        | 46  | 0.365 ± 0.130  | 0.374 ± 0.118  | 0.991          | 0.297 ± 0.009  | 0.022 ± 0.066  | 0.044 ± 0.051  |
| Afar                        | Afa          | Lowland         | 49  | 0.382 ± 0.124  | 0.386 ± 0.110  | 0.996          | 0.304 ± 0.009  | 0.009 ± 0.061  | 0.028 ± 0.070  |
| Hararghe Highland           | HaH          | Highland        | 44  | 0.379 ± 0.124  | 0.385 ± 0.109  | 0.997          | 0.304 ± 0.015  | 0.014 ± 0.062  | 0.043 ± 0.072  |
| Short-Eared-Somali          | SeS          | Lowland         | 41  | 0.379 ± 0.127  | 0.381 ± 0.111  | 0.995          | 0.300 ± 0.007  | 0.006 ± 0.045  | 0.028 ± 0.051  |
| Long-Eared-Somali           | LeS          | Lowland         | 47  | 0.375 ± 0.132  | 0.374 ± 0.118  | 0.992          | 0.294 ± 0.012  | -0.002 ± 0.030 | 0.016 ± 0.024  |
| Nubian                      | Nub          | Lowland         | 51  | 0.369 ± 0.115  | 0.391 ± 0.106  | 0.994          | 0.315 ± 0.019  | 0.054 ± 0.118  | 0.087 ± 0.116  |

Note: N, \(H_0\), \(H_E\), \(P_N\) and \(D_{ST}\), \(F_{HOM}\) and \(F_{ROH}\) refer to sample size, observed and expected heterozygosity, proportion of polymorphic SNPs, average pairwise genetic distance, inbreeding coefficients based on excess of homozygosity and runs of homozygosity, respectively.

2.2 | Data analysis

To estimate genetic diversity, observed \(H_0\) and expected \(H_E\), heterozygosity, proportion of polymorphic SNPs \(P_N\), and average pairwise genetic distance were calculated with PLINK v1.9. Higher values indicate elevated genetic distances between individuals within a population. The average proportion of alleles shared between two individuals was calculated as \(D_{ST}\) using PLINK v1.9 with the "--geno" command line.

67,644 SNPs and 628 goats for analysis. A subset of these samples had been analysed for mtDNA D-loop variation (Tarekegn et al., 2018).
computed with R (https://www.r-project.org/). The ROH was classified into four length categories: 2, 4, 8 and 16 Mb.

For each population, runs of homozygosity ($F_{ROH}$; Kim et al., 2013) and excess of homozygosity ($F_{EHOM}$; Wright, 1922) statistics were calculated as estimators of genomic inbreeding. $F_{ROH}$ was derived for each individual following McQuillan et al. (2008):

$$F_{ROH} = \frac{\sum_i \left(\text{Length(ROH}_i)\right)}{L}$$

where the numerator represents the sum of ROH per animal above a certain criteria length and the denominator (L) is the total length of the genome covered by autosomal markers (McQuillan et al., 2008). The $F_{HOM}$ statistic was derived using the formulae:

$$F_{HOM} = \frac{O_{HOM} - E_{HOM}}{1 - E_{HOM}}$$

$O_{HOM}$ and $E_{HOM}$ represent the observed and expected homozygosity for each population, respectively.

To determine the extent of linkage disequilibrium (LD) between adjacent SNPs, the $r^2$ statistic was calculated for each pair of loci using the formulae:

$$r^2 (fA, fB, fAB) = \left[\frac{f(AB) - f(A)f(B)}{fA(1-fA)fB(1-fB)}\right]^2$$

where $f(AB)$ is the frequency of haplotypes having allele A at locus 1 and allele B at locus 2 and $f(A)$ and $f(B)$ are the observed allele frequencies at each locus (Hill & Robertson, 1968). For the calculation, we used the “--ld-window 9,999 --ld-window-kb 1,000 --ld-window-r2 0” command line in PLINK v1.9. These settings allowed the analysis of adjacent SNPs, the for each population, respectively.

To reveal fine-scale population stratification independent of a priori ancestry information, network analysis was carried out using the NetView v.0.4.2.5 (Neuditschko, Khatchark, & Raadsma, 2012; Steinig et al., 2016). NetView explores network topologies using a single user-defined threshold parameter, the number of mutual nearest neighbours (k). Fewer individuals are considered nearest neighbours at small values of k, leading to only genetically more similar individuals being connected and highlighting fine-scale structure in the data set. We generated a population network based on shared allele distance matrix (1-identity by state (IBS)) generated with PLINK v1.9. The network was constructed with the super-paramagnetic clustering (SPC) algorithm and Sorting Points Into Neighbourhoods (SPIN) software, which computes the maximum number of nearest neighbours for a given individual (Neuditschko et al., 2012; Steinig et al., 2016). The network was visualized and edited in the Cytoscape v.2.8.3 network construction package (Smoot, Ono, Ruscheinski, Wang, & Ideker, 2011). SPC and CYTOSCAPE are implemented in NetView. NetView requires a specification of the maximum number of nearest neighbours (k-NN) that an individual can have. In this study, the number of k-NN values tested was between 5 and 120.

The software hapFLK v.1.2 (Fariello, Boitard, Naya, SanCristobal, & Servin, 2013) was used to implement the hapFLK algorithm, which can be applied to un-phased genotypic data, to detect signatures of selection while accounting for haplotype structure and varying $N_e$. The implementation required the construction of a neighbour-joining (NJ) tree using a kinship matrix. Pairwise Reynolds genetic distances (Reynolds, Weir, & Cockerham, 1983) were calculated and converted to a kinship
3 | RESULTS

Genetic diversity indices (mean ± standard deviation (SD); Table 1) that were calculated for each population show that Keffa had the lowest values of $H_D$ (0.348 ± 0.143), $H_E$ (0.361 ± 0.130), $P_N$ (0.978) and $D_{ST}$ (0.269 ± 0.018). The highest values were observed in Afar ($H_D$ = 0.382 ± 0.124), Nubian ($H_E$ = 0.391 ± 0.016; $D_{ST}$ = 0.315 ± 0.019) and Hararghe Highland ($P_N$ = 0.997). The lowest values of inbreeding were observed in Long-eared Somali ($F_{ROH} =$ −0.002 ± 0.03) and Gondar ($F_{ROH} = 0.006 ± 0.014$), respectively. Overall, Nubian had the highest values of $F_{ROH}$ (0.054 ± 0.118) and $F_{ROH}$ (0.087 ± 0.116). $F_{ROH}$ showed a strong positive correlation ($r = .978$) with $F_{ROH}$.

The highest and lowest proportion of SNPs with low and high MAF, respectively, were observed in Keffa (Figure 1a). Woyo-Guji and Western lowland/Gumez had the lowest variation in MAF. Figure 1b shows the proportion of ROH for the four genome length categories (2, 4, 8 and 16 Mb). Gondar had the highest proportion of short ROH (2 Mb), followed by Western highland/Agew, Western lowland/Gumez, Woyo-Guji, Keffa and Long-eared Somali, respectively. Populations with the highest proportion of long ROH (16 Mb) were Small-eared Somali, Hararghe Highland and Nubian. Abergelle, Ambo, Afar and Arsi-Bale had a high proportion of ROH segments of intermediate length.

The average number of ROH segments (mean ± SD) per animal ranged from 2.46 ± 2.99 (Gondar) to 16.85 ± 19.84 (Nubian) (Table 2). Woyo-Guji had the next lowest mean number (3.51 ± 2.99), and Keffa presented the next highest mean number (12.13 ± 12.67). The maximum number of ROH segments ranged from 14 (Woyo-Guji) to 70 (Nubian). Keffa presented the next highest maximum number (44) of ROH segments. The average length of the genome comprising of ROH segments ranged from 4,554.92 ± 2,240.02 Kb (Gondar) to 10,072.83 ± 8,267.14 Kb (Short-eared Somali). The shortest and longest lengths of the genome comprising of ROH segments were observed in Hararghe Highland (2,236.95) and Short-eared Somali (40,669.67), respectively. The average number of SNPs within an ROH segment was lowest in Gondar (84.61 ± 40.18) and highest in Short-eared Somali (187.53 ± 151.62). This presented the minimum and maximum values of 40 SNPs in Afar and 749 SNPs in Short-eared Somali, respectively. The average SNP density (SNPs per Kb) was similar across the 13 populations (53–54 SNPs/Kb), although the range was large. The proportion of homozygous sites averaged 99% across all populations (Table 2).

The average $r^2$ value (Table 3) ranged from .028 (Woyo-Guji) to .051 (Keffa). The trends in LD decay over genomic distances reveal high LD over short distances, which decays rapidly with distance (Figure 2a). LD decays more rapidly in Woyo-Guji but slower in Keffa, Western highland/Agew and Western lowland/Gumez.

One thousand (1,000) generations ago, Nubian and Keffa had the highest and lowest $N_e$, respectively (Table 3). Thirteen (13) generations ago, the lowest $N_e$ was observed in Gumez and highest in Hararghe Highland. The overall composite trend over the past 1,000 generations (Figure 2b) reveals a gradual increase in $N_e$ to about...
600 generations followed by a rapid increase to about 150 generations, and then a sharp decline to present time. Each population, however, showed contrasting trends (Figure S1). A trend similar to the composite characterizes Woyto-Guji, Short-eared Somali and Hararghe Highland. A continuous and gradual decline characterizes Arsi-Bale, Keffa, Western lowland/Gumez, Western highland/Agew and Nubian. The $N_e$ for Abergelle, Gondar, Ambo and Long-eared Somali increases gradually to 200–300 generations ago after which it declines rapidly to present time. The $N_e$ of the Afar population increases gradually to about 300 generations ago, stabilizes to 150 generations and then declines rapidly to present time.

PCA projected seven genetic clusters (Figure 3a). Cluster 1 comprised Abergelle, Ambo, Gondar, Western highland/Agew and Western lowland/Gumez. Cluster 2 comprised Hararghe Highland, and Long- and Short-eared Somali. Clusters 3, 4, 5, 6 and 7 comprised, respectively, Afar, Arsi-Bale, Keffa, Nubian and Woyto-Guji, which were depicted as distinct genetic entities. In agreement with the high $D_{ST}$ value, Nubian individuals spread out across the fourth quadrant of the PCA suggesting high intra-population variation. TreeMix (Figure 3b) replicated the PCA clusters and showed two gene flow events, from Long-eared Somali to Woyto-Guji and from Woyto-Guji to Keffa.

The optimal value of K following ADMIXTURE analysis could not be determined with certainty. At the first instance, the CV error was lowest at $4 \leq K \leq 5$. It then increased slightly at $K = 6$ before declining to the same lowest value observed at $4 \leq K \leq 5$, at $K = 7, 8, 9$ and 10 (Figure 3c inset). If the increase in CV error at $K = 6$ reflects lack of stability in allocating the genetic backgrounds, then the values of
### TABLE 2

| No of ROH segments | Mean ± SD | Max | Range | Prop. of homozygous homozygous | SNP Density (SNP/Kb) | Mean ± SD | Range | Mean ± SD |
|--------------------|----------|-----|-------|-------------------------------|----------------------|----------|-------|----------|
| No of SNP          |          |     |       |                               |                      |          |       |          |

#### TABLE 3

Average linkage disequilibrium ($r^2$), effective population size at 1,000 and 13 generations

| Goat populations | $r^2$ | $N_e$ (1,000 generations ago) | $N_e$ (13 generations ago) |
|------------------|-------|-------------------------------|-------------------------------|
| Abergelle        | .032  | 7,317                         | 2,778                         |
| Gondar           | .031  | 6,274                         | 2,899                         |
| Ambo             | .029  | 6,698                         | 1,223                         |
| WH/Agew          | .039  | 7,398                         | 1644                         |
| WL/Gumez         | .045  | 6,233                         | 719                           |
| Keffa            | .051  | 5,408                         | 1,029                         |
| Woyo-Guji        | .028  | 6,994                         | 5,390                         |
| Arsi-Bale        | .038  | 6,342                         | 1,355                         |
| Afar             | .031  | 7,302                         | 3,296                         |
| Hararge Highland | .031  | 7,274                         | 5,401                         |
| Short-eared Somali | .033 | 7,229                         | 3,988                         |
| Long-eared Somali | .035 | 6,795                         | 1,491                         |
| Nubian           | .036  | 7,408                         | 743                           |

**Abbreviations:** WH, Western highland; WL, Western lowland.

K at 7, 8, 9 and 10 may explain the variation in the data set. Taking $K = 7$ as the most optimal, it supports the PCA and TreeMix but with higher resolution. At this K-value, Keffa is the only population with one uniform genetic background which is shared with Woyo-Guji. The other major genetic backgrounds are observed in Abergelle, Ambo, Long-eared Somali, Nubian and Gumez. The seventh genetic background is unique to a few individuals of Nubian. Other than these individuals of Nubian and Kezza, the other populations exhibit variable proportions of genome admixture of at least two genetic backgrounds. Although this admixture pattern is repeated at $8 \leq K \leq 10$, the genomes of Afar and Woyo-Guji show gradual reduction in admixture while the opposite is observed for Arsi-Bale and Nubian. By revealing a common genome background between Long-eared Somali and Woyo-Guji and between Woyo-Guji and Kezza at $7 \leq K \leq 10$, ADMIXTURE corroborates TreeMix that showed migration events between these populations.

**NetView (Figure S2)** showed that from $75 \leq k$-NN $\leq 120$, only four individuals, two each of Kezza and Long-eared Somali, remained unassigned. The major clusters became evident, at the first instance, from k-NN = 55, when the 13 populations appeared to separate into two broad groups, hereby designated as G1 and G2 (Figure 4a). G1 comprised Abergelle, Ambo, Gondar, Western highland/Agew and Western lowland/Gumez. G2 comprised Afar, Arsi-Bale, Hararge Highland, Kezza, Long-eared Somali, Nubian, Short-eared Somali and Woyo-Guji. These two groups are consistently retained up to k-NN = 120. This prompted us to look at the results of ADMIXTURE at $K = 2$ (Figure 4b,c). As expected, it revealed two genome backgrounds, hereby named GB1 and GB2. GB1 occurs at a frequency of >70% in Abergelle, Ambo, Western highland/Agew, Western lowland/Gumez, and Short- and Long-eared Somali. Abergelle, Ambo,
Western highland/Agew and Western lowland/Gumez comprise G1 of NetView. GB2 is found at a frequency of >70% in Arsi-Bale, Afar, Gondar, Hararghe Highland and Nubian, all the populations found in G2 of NetView except Gondar. Long- and Short-eared Somali occur in G2 of NetView but in GB1 of ADMIXTURE. Although Keffa and Woyto-Guji occur in G2, in ADMIXTURE they show almost an equal proportion of GB1 and GB2 in their genomes. The minor discordance between NetView and ADMIXTURE could be due to differences in the way they are structured to allocate populations into clusters. Despite this minor difference, the NetView results led us to hypothesize that the analysis is revealing, possibly two ancestral genomes that could have arrived with the initial introduction of goats in the Horn of Africa.

Seventy-eight pairwise comparisons were performed with hapFLK v1.2 software and XP-EHH test, assuming that each population
was adapted to specific circumstances in its home range. Although the two approaches identified multiple regions under selection (Figures S3 and S4), here we focused only on the regions that overlapped between the two approaches. The regions revealed by XP-EHH fell within the boundaries of the ones identified by hapFLK. The most significant and consistent signals were revealed in pairwise comparisons involving Arsi-Bale and Nubian with the other 11 populations (Figures S3 and S4). The ones involving Arsi-Bale were on chromosome (CHI) 6 (8,533,828–7,357,213 bp; average size: 3,621,429 ± 2,264,393 bp) and CHI12 (53,982,423–62,977,761 bp; average size: 6,978,324 ± 952,467.8 bp). The ones involving Nubian were on CHI8 (54,717,960–63,857,851 bp; average size: 4,912,265 ± 1,773,863 bp) and CHI13 (49,975,695–67,760,577 bp; average size: 10,147,644 ± 2,916,617 bp). Comparative analysis between Arsi-Bale and Nubian revealed the four putative signatures (Figure 5a,b), suggesting they are specific to these two populations. Arsi-Bale goats carry dense hairy coats and reside at an altitude of ≥4,000 m above sea level (www.dagris.info/). Nubian goats have long-haired coats and reside at low-altitude drylands in north-western Ethiopia, northern Sudan and western Eritrea (www.dagris.info/). High altitudes present a hypoxic cold environment. Low-altitude drylands present an environment characterized by grazing stress. Grazing stress encompasses complex interacting biophysical stressors including heat, physical exhaustion, direct solar radiation and unavailability of feed (quality and quantity) and water. The selection signatures observed in Arsi-Bale and Nubian led us to hypothesize that putative selection may have resulted in adaptive and phenotypic divergence in the two populations.

We annotated the four candidate regions based on the ARS1 release 102 goat reference genome assembly. We found a total of 123 (Arsi-Bale = 29; Nubian = 94) unannotated genes, that is prefixed with "LOC/ENSCHIG" in the candidate regions. Although potentially under selection, these unannotated genes were not included in the functional enrichment and ontology analysis. In total, 20 (CHI6) and 45 (CHI12) genes were present in the Arsi-Bale regions, while 62 (CHI8) and 244 (CHI13) were observed in the Nubian regions (Table S1). Functional enrichment and GO analysis were performed separately for each population-specific gene sets using Panther and STRING. The 65 Arsi-Bale and 306 Nubian candidate genes showed greater enrichment in biological processes relating to cellular processes (GO: 0009987), metabolic processes (GO: 0008152) and biological regulation (GO: 0065007). Text mining was performed with STRING to determine gene functions from published literature. It identified that several of the candidate genes are linked with traits of adaptive, economic and functional significance. Some genes such as CDX2, NBEA and PITX (Arsi-Bale) and PROCR, CTCFL, NNAT and PDYN (Nubian) are involved in multiple functions.

4 | DISCUSSION

4.1 | Genetic variation and marker polymorphisms

We present findings from an analysis of genome diversity, structure and dynamics of indigenous goats in Ethiopia, at the route of one of the most ancient gateways of domesticates into Africa. Ethiopia is characterized by ancient and modern human ethnic diversity that

![Figure 4](image-url) Figure 4 (a) NetView P plot for K-NN = 75 showing clustering of the 13 populations into two groups. (b) Geographic sampling regions in Ethiopia together with pie charts showing ancestry proportions for K = 2 generated in ADMIXTURE. (c) ADMIXTURE bar plot showing proportion of ancestries for K = 2.
has long been associated with livestock husbandry and diverse agro-eco-climates, which may have influenced the genome architecture of indigenous livestock. The 13 study populations retained high levels of genome diversity (mean $H_0$ and $H_E$ above 0.348) and within population genetic variation ($D_{ST} > 0.289$). Although these values are high, they are close to those reported in other indigenous goats (Berihulay et al., 2019; Kim et al., 2016; Manunza et al., 2016; Mdladla, Dzomba, Huson, & Muchadeyi, 2016; Nicoloso et al., 2015; Onzima et al., 2018). Keffa was the least and Nubian was the most diverse, population. Extensive genome admixture incorporating at least two genetic backgrounds at $7 \leq K \leq 10$ was observed in all but Keffa. This admixture could explain the high diversity and genome variability in the Ethiopian indigenous goats. It is the result of past and modern-day socio-economic and cultural exchanges and natural selection which retains genetic variation.

### 4.2 | ROH and inbreeding

Genomic inbreeding coefficients, such as $F_{ROH}$ and $F_{HOM}$, are more accurate at estimating autozygosity and detecting past and recent inbreeding compared to estimates derived from pedigree data (Curik, Ferenéakoviæ, & Sölkner, 2014; Ferenčaković et al., 2013; Knief, Kempenaers, & Forstmeier, 2017). Furthermore, in the absence of genealogical information, molecular data can be used to infer population history and inbreeding (Kim, Sonstegard, Van Tassell, Wiggans, & Rothschild, 2015; Zavarez et al., 2015). The latter is important especially for African indigenous livestock that most often lack written pedigree records. The strong and positive correlation ($r = .978$) between $F_{ROH}$ and $F_{HOM}$ observed in our study corroborates previous findings in pigs (Zhang et al., 2014) and cattle (Mastrangelo et al., 2016). It confirms that the extent of a genome under ROH can be used to predict the proportion of the genome that is identical by descent (IBD). A high and positive correlation between $F_{ROH}$ and conventional pedigree-based estimates of inbreeding ($F_{PED}$) has been reported (Ferenčaković et al., 2013; Martikainen, Tyrisevä, Matilainen, Pösö, & Uimari, 2017; Purfield, Berry, McParland, & Bradley, 2012) confirming $F_{ROH}$ as an appropriate estimator of IBD alleles. The importance of understanding and quantifying genome-wide autozygosity has also been highlighted through correlations of $F_{ROH}$ with inbreeding depression for a range of production (Bjelland, Weigel, Vukasinnovic, & Nkrumah, 2013; Kim et al., 2015; Pryce, Haile-Mariam, Goddard, & Hayes, 2014) and fertility (Kim et al., 2015; Martikainen et al., 2017) traits. In this study, $F_{ROH}$ and $F_{HOM}$ revealed low levels of genomic inbreeding in Ethiopian indigenous goats, results that are consistent with findings on Egyptian Barki (Kim et al., 2016) and Ugandan goats (Onzima et al., 2018). Colli et al. (2018) suggested that significant introgression of other breeds in African goats explains their low inbreeding. We however suggest that low inbreeding in African goats is the result of extensive outcrossing within and between diverse populations and individuals considering that these flocks are communally grazed and watered, and mating is mostly uncontrolled.

### 4.3 | Demographic history and dynamics

Genome-wide ROH, LD and $N_e$ are valuable sources of information on how population structure, demography and management evolve over time (Ceballos et al., 2018; Kirin et al., 2010). Generally,
short ROH is most likely correlated with ancestral inheritance, ancient bottlenecks or consanguinity, whereas long ROH is associated with recent inbreeding (Browning & Browning, 2013; Purfield et al., 2012). The distribution of ROH can also provide information on specific selection events. The distribution of the sizes of ROH segments varied across the 13 study populations, with six reporting high proportion of short (<2 Mb) ROH segments, three with a high proportion of long (≥8–16 Mb) ROH segments and four with intermediate (4 Mb) ROH segments. The variable distribution of ROH lengths with frequent short and intermediate length ROH segments has been observed in other goats (Brito et al., 2017; Kim et al., 2016; Onzima et al., 2018), sheep (Purfield, McParland, Wall, & Berry, 2017), cattle (Mastrangelo et al., 2016) and pigs (Bosse et al., 2012). The high proportion of short ROH observed in Gondar, Western highland/Agew, Western lowland/Gumez, Woyto-Guji, Keffa and Long-eared Somali may indicate more ancient inbreeding and/or bottleneck. The high number of long ROH in the Small-eared Somali, Hararghe Highland and Nubian suggests a large effect of historical demographic dynamics of the indigenous goats may have been more complex than is reflected by the composite trend thus suggesting further investigation possibly using the PSMC algorithm (Nadachowska-Brzyska, Burri, Smeds, & Ellegren, 2016) and full genome sequences. The PSMC capitalizes on the combined pattern of the distributions of the time to the most recent common ancestor (TMRCA) between two alleles in an individual at large number of loci spread across the genome. It therefore gives more detailed information on historical-ancient N_e dynamics. Full genome sequences offer the advantage of sampling large numbers of unlinked loci across the genome. This may be necessary to accurately estimate population genetic parameters and determine the timing of demographic events.

4.4 | Past and recent population genetic structure

The use of several methods to investigate population structure allowed us to reveal and describe past and recent population genetic structure in indigenous goats in Ethiopia and by extension sub-Saharan Africa. NetView revealed two broad genetic groups lacking a clear phylogeographic structure that corresponded slightly to the genetic backgrounds revealed by ADMIXTURE at K = 2. These two genetic groups may possibly represent two deep ancient ancestries that arrived with the first introduction of goats in eastern Africa. It mirrors findings of mitochondrial DNA which identified two haplogroups that also lacked a clear phylogeographic structure in Ethiopian (Tarekegn et al., 2018), Kenyan (Kibegwa et al., 2015), Sudanese (Sanhory et al., 2014) and Egyptian (Naderi et al., 2008) indigenous goats. With the current data set, we nevertheless cannot determine the origin and route of entry and dispersal of the two deep ancestries and whether they arrived together or independently. However, their occurrence in all the 13 populations, albeit at different frequencies, points to a relatively early dispersal in the region, most likely facilitated by human socio-cultural and trade interactions as inferred from anthropologic, linguistic and human genetic studies (Pagani et al., 2012).

Cryptic population genetic structure, represented by seven genetic groups, was revealed by PCA and TreeMix. These results were supported by the output of ADMIXTURE: the optimal number of clusters was K = 7. Except Keffa, the genomes of the other populations are a mosaic of at least two genetic backgrounds. This pattern was repeated at K ≥ 7 except for Abergelle, Woyto-Guji and Afar which showed one predominant genetic background. How these seven backgrounds evolved from the two ancestries remains a subject of speculation. Geo-specific local founder events accentuated by genetic drift arising from past reproductive isolation could be a possible source of the observed evolutionary hepta-groupings. With extensive human migrations across Ethiopia dating back to the 16th century (Habitam, 2014; Yeima, 1966), it is possible that human cultural and socio-economic interactions dispersed the seven backgrounds across the country resulting in admixed genomes. These results are similar to the observation of similar levels of genome admixture in Ethiopian cattle (Dadi et al., 2008), sheep (Edea, Dessie, Dadi, Do, & Kim, 2017) and humans (Pagani et al., 2012; Plaster, 2011) and in other African livestock (Benjelloun et al., 2015; Mbole-Kariuki et al., 2014; Mwacharo et al., 2017), and are explained...
by the fact that the three livestock species were and still are often kept together.

The unique genetic background in Keffa goats at K ≥ 7 is noteworthy. This population is found exclusively in the Keffa region of south-western Ethiopia, which is also the home tract of Sheko cattle. Among Ethiopian cattle, Dadi et al. (2008) observed a homogeneous and unique genetic background in the Sheko. The Keffa region is tsetse-infested, and trypanosomosis, a potential driver of selection in African cattle (Smetko et al., 2015), is endemic. Sheko cattle are reported to have some degree of trypanotolerance (Lemecha et al., 2006; Mekonnen, Gültas, Effa, Hanotte, & Schmitt, 2019). During informal conversations with Keffa goat owners, they indicated that their goats also exhibit a degree of trypanotolerance. If confirmed, it would explain the genome uniformity in the two species, the result of natural selection for trypanotolerance. Trypanosomosis acts as a natural barrier for the dispersal of other goat and cattle populations in the Keffa region, and until recently when control measures against the disease have been enhanced and the ecology drastically modified for human activities and increased settlements, reproductively isolated the Keffa goats and Sheko cattle. The correlation between the uniform genetic background and reduced susceptibility to trypanosomosis in the two species needs to be confirmed.

4.5 | Genome-wide signatures of selection

Four strong selection signatures were identified, two each in Arsi-Bale and Nubian goats. Despite the observation of a unique genetic background in Keffa that we suggest could be the outcome of trypanotolerance, no selection signatures were observed in this population. This was rather surprising and difficult to explain but may suggest that reproductive isolation and the resulting genome autozygosity could be the cause. We attribute the four strong selection signatures to differential adaptation to contrasting environments namely high altitude and the associated low temperatures experienced by the Arsi-Bale population, and low dry altitude and high temperatures experienced by the Nubian population. One Arsi-Bale candidate region spanned ALOX5AP a gene that was identified in sheep as a potential candidate for climate-mediated adaptation (Lv et al., 2014). In humans, a mutation in ALOX5AP was associated with lung function (Ro et al., 2012). Given the high altitude and restricted oxygen concentration in the Arsi-Bale mountains, ALOX5AP may play a role in adaptation to high altitude, especially in so far as respiration is concerned. Several candidate genes with critical roles in maintaining genome integrity through DNA repair processes (BRCA2, PDS5B, RAD51) (Couturier et al., 2016; Prakash, Zhang, Feng, & Jasin, 2015) overlapped with the Arsi-Bale candidate genomic regions. In the tropics, high-altitude regions receive much higher annual levels of UV radiation. Therefore, maintaining genome integrity against possible DNA damage induced by ionizing radiation is essential. Other candidate genes found in selective sweeps included KATNA1, FRY and RXFP2. KATNA1 has been associated with variation in fibre diameter in domestic sheep breeds (Seroussi, Rosov, Shirak, Lam, & Gootwin, 2017; Zhang et al., 2013). The FRY has been linked with variations in coat pigmentation in many sheep breeds (Garcia-Gamez et al., 2011; Seroussi et al., 2017; Wei et al., 2015; Zhang et al., 2013) and is also involved in growing wing hairs and bristles in Drosophila (Cong et al., 2001; Fang, Lu, Emoto, & Adler, 2010; He, Fang, Emoto, Jan, & Adler, 2005). Mutations in RXFP2 were linked to horn type and development in sheep (Johnston et al., 2011; Wang, Zhou, Li, Zhao, & Chen, 2014), reproductive success and survival in Soay sheep (Johnston et al., 2013), and the genomic region spanning RXFP2 was also identified to be under selection in Creole (Gautier & Naves, 2011) and West African Borgou cattle (Flori et al., 2014). We also observed genes (STARD13/CCNA1, FLT1, DCLK1, NBEA) that are reported to be associated with female reproduction in bovines (Kfir et al., 2018) and chicken (Shen et al., 2017; Sun et al., 2015). The PITX2 and CDX2 have been associated with puberty in cattle (Cánovas et al., 2014) and embryogenesis in the mouse (Lu et al., 2018). Evidence drawn from animal experiments suggests that conditions in high-altitude environments and prolonged exposure to altitude-initiated stress, including cold and hypoxia, can have direct negative effects on reproductive function (Heath & Williams, 1989). The exposure can have significant negative effects on female reproduction through reduction in fertility, increasing foetal loss and/or reducing fecundability (Adekilekun, Aboua, Ouyeypio, & Oguntibeju, 2019).

The Nubian is a goat breed that is adapted to arid environments. It is therefore not surprising that hapFLK and XP-EHH identified selective sweeps overlying regions that spanned genes associated with adaptation to environmental stress (PKC1, CTCFL, SPO11, BMP7), oxidative stress (PLAGL2, SRXN1), adaptation to different ecological environments (ZBTB46, ARFRP1, STMN3, GMEB2), and mitochondrial homeostasis (TDRD7) including classical innate immunity and fever induction (HCK, PROCR, CTSZ) (Table S2). Coat and skin colour are an integral part of adaptation. The coat of Nubian goats is light coloured and most often white. In one of the candidate regions, there were two genes that have been associated with colouration (GNE, EDN3). Surprisingly, we observed genes that have been associated with dairy (PROCR, AURKA, FOXS1, CD72, AVP, PXMP4, PIGU, ZNF341, NCOA6, ACSS2, E2F1), beef (MYLK2, MYL9, MYH7B, TNRFSF6B, PROCR, ERGK3), and reproduction (CTCFL, SPO11, RBM38, PMEPA1, CTNNBL1, NNAT, BLCAP, CPNE1, SPAG4, CTCFL, TGFBR1) traits (Table S2). With candidate regions overlapping these genes our results demonstrate the potential of the Nubian to be used in breeding programmes to increase production to meet future demand for proteins of animal origin under unpredictable climatic conditions.

5 | CONCLUSION

The genetic history of African indigenous goats is complex. It has obviously been closely intertwined with the history of local human communities. The need to adapt to diverse African environments
may also have shaped present-day African goat genomes. Here, we have provided insights that improve our understanding of the genomic landscape and demographic history of sub-Saharan African indigenous goats in Ethiopia. Our results provide a foundation to formulate and test biological hypotheses relating to population demographic profiles and genome dynamics in African livestock. Further studies are needed to refine and confirm our interpretations and the proposed hypotheses. These include among others, the association between the uniform genetic background in Keffa and reduced susceptibility to trypanosomosis, the origin and route of entry and dispersal of the two deep ancestries into the region, and the suggestion that the historical demographic dynamics of the indigenous goats may be more complex than is reflected by the composite trend.

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CONFLICT OF INTEREST
The authors declare no conflict of interest regarding this manuscript.

DATA AVAILABILITY STATEMENT
The data used here will be made available upon request.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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