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Research article

Genetic diversity and within-breed variation in three indigenous Ethiopian sheep based on whole-genome analysis

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ABSTRACT

The objective of this work was to study genetic diversity by comparing whole genome sequence data of Rutana, Gumuz and Washera sheep found in Amhara and Benishanguel gumuz regional states of Ethiopia. We employed variant calling format tools version 0.1.15 to calculate some genetic diversity indices such as observed heterozygosity, expected heterozygosity, inbreeding coefficient, and nucleotide diversity. The results revealed that, observed heterozygosity ranged from 0.33 in Gumuz to 0.34 in Rutana and Washera sheep. Expected heterozygosity ranged from 0.37 in Rutana to 0.38 in Gumuz and Washera sheep. Expected heterozygosity was found to be higher than observed heterozygosity. Higher inbreeding coefficient (0.12) was recorded for Gumuz sheep compared to 0.09 of Rutana and Washera sheep. Mean nucleotide diversity values were 0.0029, 0.0030 and 0.0028 for Gumuz, Rutana and Washera sheep, respectively. Higher values of nucleotide diversity were recorded. Population structure analysis using principal component analysis revealed no clear separation between Gumuz, Rutana and Washera sheep populations with possibility of gene flow attributed to geographical location proximity. The smaller population size, closed breeding system, genetic drift and uncontrolled (non-random) mating might lead to higher rate of inbreeding in Gumuz, Rutana and Washera sheep, requiring timely intervention. This intervention helps to prevent inbreeding depression and extinction of these valuable breeds of sheep, which helps in sustaining the livelihood of sheep keepers in lowlands and highlands. Nevertheless, the whole-genome analysis revealed high within-breed variation. Uncovered areas of studies like mapping quantitative trait loci, identifying genes underpinning productivity traits such as carcass quantity and meat quality could be carried out on diversified sheep resources identified by the current study. Identifying the genomic regions and biological pathways that contribute to explaining variability in these traits is of great importance for selection purposes. Designing conservation-based within-breed sheep selective breeding programs are recommended considering economically important traits into account.

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1. Introduction

Farm animals are regarded as a major means of avoiding poverty in the developing world [1]. Sheep are an extremely important livestock species for food security due to their high reproductive capacity and low initial investment, making them ideal for resource-limited farmers such as landless youth and women [2,3]. With Ethiopia's growing human population, urbanization, economic development, and domestic and export markets, there is a huge opportunity to increase sheep production using diverse indigenous sheep [2]. The first step in conserving and exploiting these diverse sheep populations is obtaining a thorough understanding of the genetic diversity that exists [4,5]. The ability to select superior animals for breeding is enabled by the presence of genetic diversity. If there is no genetic diversity, i.e. if all animals are genetically related, selection will not result in an improvement in the next generation [6].

Among the indigenous sheep populations of Ethiopia, Washera and Gumuz were predominant in Burie and Mandura districts of Amhara regional state of Ethiopia, respectively [7]. Washera has a short fat tail, a large body size, short hair, and is predominantly brown. Both males and females are polled and are kept by Amhara and Agew communities. Washera is a good meat producer in a favorable environment [8]. Gumuz sheep are thin-tailed, somewhat dwarf, with a convex face profile and a long pendulous ear, and are polled and reared by Gumuz and Amhara communities [7]. Gumuz sheep were bred for meat and skin production in lowland and hotter areas of northwestern Ethiopia. The prolific and large-sized Rutana sheep were found in Benishanguel Gumuz regional state and the northwestern lowlands of Amhara regional state of Ethiopia, where they were primarily reared for meat and skin under arid agro-pastoral production systems [9,10].

Genetic diversity among organisms is measured as a result of changes in DNA sequences and environmental factors [11]. Basic genetic diversity analysis deals with different types of variables or parameters. Some of them are intra-population genetic diversity, inter-population genetic diversity, and diversity and differentiation at the nucleotide level. Molecular markers found to be suitable for marking such variability. A molecular marker, also known as a DNA marker, is a segment of DNA that indicates mutations or variations and can be used to detect polymorphism (base deletion, insertion, and substitution) between different genotypes or alleles of a gene in a specific population or gene pool [12,13]. Single nucleotide polymorphism (SNPs) is becoming especially important as markers. Because they are very stable, i.e. have very low mutation rates and they can be amplified with PCR for testing. SNP studies have recently been proposed in population genetics to investigate for adaptive evolution imprints. A single nucleotide polymorphism is a difference in DNA sequence caused by a nucleotide substitution at a specific site in the genome [14]. Because of their prevalence in any organism's genome (coding and non-coding regions), and capacity to uncover hidden polymorphism that is not typically identified by other genetic markers and methodologies, these types of markers are becoming increasingly appealing in molecular marker development [15]. SNPs account for more than 90% of all differences between people, making them a valuable genetic variation resource for population studies and genome mapping [16]. Other genomics technologies applied to diversified sheep populations include candidate gene approach. According to Ref. [17], the candidate gene approach investigates the association between phenotypes and known genes that may be involved in the physiological pathways that underpin the trait. In other words, this approach assumes that a gene involved in the physiology of the trait could harbor a mutation causing variation in the trait. SNPs and whole genome sequencing are among the cutting-edge molecular and genomic technologies used to study genetic variability of sheep. This broadens the options for determining breed ancestry, variability, and genetic value of specific markers and candidate genes for adaptation, genomic selection, and production enhancement [18]. Reference [19] reported that the use of 22 microsatellite data to characterize eastern Ethiopia sheep revealed significant genetic variation within ten subpopulations, which was linked to their inherent breeding practice. Genomic data of some of Ethiopian sheep groups (Gumuz and Rutana sheep not included in the study) were analyzed using medium density SNP bead chips. The genetic variation between these sheep groups was attributed to variations within and among populations [20–22]. Despite the advancement of whole-genome sequencing technology, little research has been done on diversity studies of Gumuz, Rutana and Washera sheep populations based on whole-genome sequence data. To this end, whole-genome sequencing and genotyping enable the identification of a large number of single-nucleotide polymorphisms (SNP). The large number of SNPs allows for unprecedented accuracy in describing individual and breeds relationships and has the potential to supplement or substitute pedigree data when there are no pedigree records or are insufficient [23]. Whole-genome sequence data allows us to obtain comprehensive dataset to investigate the phenotypic and genetic variability, recommending conservation priority and proposing appropriate selective breeding strategies. This study, therefore, was carried out to investigate genetic diversity of three sheep populations in Ethiopia using whole-genome analysis and use the information as an input for conservation and sustainable sheep breeding programs.

2. Materials and methods

2.1. Ethics statement

Earlier to the study, data collection formats and procedures were reviewed and agreed by the research ethics review committee of Debre Markos University, Ethiopia (Ref. number DMU 10/2019). The committee confirmed that these experiments were conducted according to established animal welfare guidelines. In addition, target group small holder farmers provided their verbal informed consent to participate in this study. Besides, the data were analyzed anonymously; ethnicity and religious issues were not asked or recorded during data collection.

2.2. Description of study area and sheep production environments

This study was conducted in three districts, Mandura, Quara and Burie of North Western Ethiopia. Gumuz, Rutana and Washera sheep (Fig. 1) were predominant indigenous sheep populations found in Mandura, Quara and Burie districts, respectively. The coordinates of each sheep population were recorded using the Global Positioning System (GPS). Burie is located at 10°12′7.8″ latitude and 37°03′58″ longitudes and at an altitude of 1600–2000 m above sea level (Table 1). The rainy season in Burie is from May to September with a monomial pattern and annual rainfall of 1386–1757 mm. The long term annual temperature of Burie ranges from 14 °C to 24 °C. Mandura is one of the 20 districts in the Benishangul-Gumuz Region of Ethiopia. Geographical coordinates of Mandura district is 10°50′6″ latitude and 35°33′36″ longitudes and it is located at an altitude of less than 1000 m above sea level. The minimum temperature of Mandura district was 28 °C and it receives 900–1400 mm annual rainfall. Similarly, geographical coordinates of Quara district is 12°37′5″ latitude and 37°28′23″ longitudes and is located at an altitude of 528–654 m above sea level. The minimum and maximum temperature of Quara district was 26–42 °C and it receives 400–1200 mm annual rainfall.

Washera is a short fat tail, large body size, short-haired sheep, predominantly brown coat color, both males and females are polled reared by Amhara and Agew communities. Washera is a good meat producer under good environment [8]. Gumuz sheep is long thin tail, somewhat dwarf, convex face profile, long pendulous ear, commonly plain brown or with patch, polled and reared by Gumuz and Amhara communities [7]. Gumuz sheep are heat-adapted and have a unique genetic make-up to thrive in lowland and hotter areas reared for meat and skin production [8]. The prevailing sheep production systems of Burie and Mandura districts were highland cereal-livestock system and lowland crop-livestock system, respectively [7]. These systems are also characterized by inadequate health care, smaller land holding often less than 2 ha and small sheep flock size. Based on these criteria [7], described the scale of sheep production system as small scale, semi intensive, low input and traditional type. Rutana sheep were found in Benishanguel Gumuz regional state and the northwestern lowlands of Amhara regional state of Ethiopia, where they were primarily reared for meat and skin products under arid agro-pastoral production systems [9,10].

2.3. Sampling

Average flock size of 310 Gumuz, 180 Rutana and 550 Washera sheep were considered for this study in three districts selected purposively. A total of 30 Ethiopian indigenous sheep from three diverse indigenous breeds were selected by purposive sampling method. Whole blood samples were collected from Gumuz and Rutana sheep distributed in moist lowlands and Washera in wet, warmer mid-highland environments of northwestern Ethiopia. Table 1 depicts the phenotypic characteristics and ecology of sheep populations under study. The samples were collected from different households with each sheep were as unrelated as possible considering the pedigree relationships information obtained from sheep owners according to the recommendations of [23]. From each sheep, 5 ml whole blood was collected from jugular vein and stored in a tube that contained 1 ml preservative and anti-coagulant ethylene diamine tetraacetic acid (EDTA k+). The sample tube was identified with a permanent marker and the sampling form was filled at the time of sampling. The collected whole blood was refrigerated at −20 °C immediately after collection until DNA isolation. DNA was extracted from blood using the Quick-start protocol QIAGEN kit user manual QIAGEN-DNeasy QIAGEN Group, 2011, according to the manufacturer's instructions. The quality and quantity of DNA were evaluated using Nano Drop spectrophotometer and agarose gel electrophoresis. A total of 30 DNA samples were selected with greater DNA integrity for sequencing.

Fig. 1. Indigenous sheep populations under study.

Table 1
Agro-ecological distribution of sheep and their phenotypic features.

Sheep populations	Agro-ecology	Geographic distribution	Phenotypic feature	Production system	Purpose of keeping sheep	Reference
Gumuz	Moist lowlands (<1000 m.a.s.l)	Benishangul-gumuz regional state; lowlands of Amhara regional state	Long thin tail; dwarf; convex face profile; commonly plain brown or with patch coat pattern	Lowland crop-livestock system	Meat; Skin, manure	Gizaw et al., 2008
Rutana	528–654 m.a.s.l	Lowlands of Metema and Quara districts of Amhara regional state	Long thin tailed; long legged	arid pastoral system	Meat; Skin, manure	Gizaw 2009; Dagnew et al., 2017
Washera	Wet, warmer mid-highlands (1600–2000 m.a.s.l)	West and East Gojam and Agew Awi zones of Amhara regional state; Dangur, madura and Alefa Takusa districts	Short fat tail; large body size; short-haired; predominantly brown	Highland cereal-livestock system	Meat; Skin, manure	Gizaw et al., 2008

2.4. SNP genotyping read mapping and variant calling

After evaluating the quality of our FASTQ data and quality filtration of the raw FASTQ files (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/), low-quality reads were trimmed using trimmomatic software version 0.36 [24]. The Burrows–Wheeler Aligner (BWA) [25] alignment tool was applied for alignment of RAW reads to the Oar_v3.1 reference genome (Ensemble AssemblyaccessionnumberGCA_000298735.1) http://www.ensembl.org/Ovis_aries_rambouillet/Info/Strains?db=core). Only paired-end reads were used in the alignment step. Picard-tools, Version 2.22.8 (http://broadinstitute.github.io/picard/) was employed for sorting the aligned reads to the Binary Alignment MAP (BAM) files. Polymerase chain reaction (PCR) duplicates are marked with a certain tag using an algorithm (Mark Duplicates) available in the Picard-tools version 2.22.8. Picard-tools, v 2.22.8 (http://broadinstitute.github.io/picard/) was also employed for indexing the BAM file and for performing Add or Replace Read Groups step to the BAM files (https://github.com/broadinstitute/picard). The sequencing machine's raw scores are prone to technical errors, resulting in over- or under-estimated base quality scores. To address this issue, base quality score recalibration (BQSR) empirically models these errors and re-adjusts the base quality scores accordingly [26]. Base quality scores were generated and readjusted by performing the recalibration table and printing the recalibrated reads using GATK-Base Recalibrator, v 4.1.7.0. We then applied the Best Practices of Genome Analysis Toolkit (GATK) v 4.1.7.0 workflow from the Broad Institute to perform variant discovery (https://software.broadinstitute.org/gatk/best-practices) using GATK- Haplotype Caller (GATK v 4.1.7.0 and comparing the aligned reads to reference genome. GATK-Genotype GVCFs, Version 4.1.7.0 was used for joint-genotyping the variants. Variant quality score recalibration (VQSR) was performed using gatk Variant Recalibrator v 4.1.7.0.

2.5. Quality control, joint – genotyping and selecting variants

Three-stage quality control strategies including quality control of the raw data using FastQC, alignment quality control involving trimming of low quality reads using trimmomatic and quality control on variant calling were performed as implemented by Ref. [27]. SNPs associated with all individuals were identified and filtered using PLINK v.1.9 [28] following the specified standards [29]. Accordingly, quality control of SNP data applied the following criteria: (1) Minor allele frequency (MAF) > 0.01 within the breeds; (2) SNPs with a call rate >0.90; (3) Missing genotyping frequency <0.02; (4) p-value for Hardy-Weinberg equilibrium >0.000001; and (5) only autosomal SNPs with known positions were used. The GATK v 4.1.7.0 Combine GVCFs and Joint-Genotype GVCFs commands were employed to combine and genotype raw variants, respectively. The command select variants were used to select SNP and INDEL in autosome using GATK v 4.1.7.0. The final dataset after QC filtering comprises of 29,103,927 autosomal SNPs and 15 animals.

2.6. Calculating mean values of genetic diversity parameters

Within breed genomic diversity including observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient, polymorphic SNP (polymorphic information content) and nucleotide diversity (π) were analyzed by employing vcftools v 0.1.15 software. For each parameter, different bioinformatics scripts or commands were used. Similarly, mean and standard deviations of the observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient and nucleotide diversity (π) were calculated using R v.4.0.3 software and bioinformatics scripts or commands. PLINK v 1.9 [28] was also employed to investigate the population differentiation between Gumuz, Rutana and Washera sheep using principal component analysis. A schematic diagram of the first two principal components (PC1 and PC2) was generated using the prcomp function in the R package [30].

3. Results

3.1. Mapping output of three sheep populations

In total, 29,103,927 SNPs (single nucleotide polymorphisms) were discovered in all individuals out of which 22,946,362 were

Table 2
Number of biallelic SNPs and INDELS.

Particulars	Sheep populations			
	Washera	Gumuz	Rutana	Combined (All samples)
Number of Biallelic SNP in the Autosomes	21,226,832	21,812,392	22,695,900	29,103,927
Number of INDELS in the Autosomes	2,949,919	3,012,770	3,095,901	3,758,552
Already Reported SNP in dbSNP	17,492,652	17,991,477	18,791,133	22,946,362
Number of Novel SNP obtained	3,734,180	3,820,915	3,904,767	6,157,565

Table 3
Mean sequencing depth of individual sheep.

Individuals	N_sites	Mean site_depth
G1	29081378	7.56
G10	29081436	7.63
G14	29081824	7.71
G4	29081714	7.48
G9	29081056	7.63
R14	29081286	7.61
R16	29082087	7.93
R4	29081827	7.66
R5	29081499	7.76
R8	29081850	7.57
W13	29081815	7.31
W14	29081467	7.23
W15	29081679	7.15
W17	29080506	6.86
W9	29081493	7.20

already reported SNPs in dbSNP (disabled single nucleotide polymorphisms) and 6,157,565 are novel SNPs obtained by this study (Table 2). The mean sequence depth was 7.48 per sample ranging from 6.86 to 7.93 (Table 3) in all individuals across the three sheep populations.

3.2. Genetic diversity

To estimate the genetic diversity across the three sheep populations (Gumuz, Rutana and Washera), we calculated polymorphic SNP, observed heterozygosity (HO), expected heterozygosity (HE), inbreeding coefficient (FiS), and nucleotide diversity using vcftools v 0.1.15. Expected heterozygosity (gene diversity) ranged from 0.37 in Rutana to 0.38 in Gumuz and Washera sheep. Mean nucleotide diversity values were 0.0029, 0.0030 and 0.0028 for Gumuz, Rutana and Washera sheep, respectively (Table 4, Fig. 2).

3.3. Population structure using principal component analysis

Principal component analysis (PCA) was used to elucidate relationships within individual sheep and among the three sheep populations (Gumuz, Rutana and Washera) with 27,600,963 SNPs passing filtering and quality control (QC). Principal component one (PC_1) and Principal Component two (PC_2) accounted for 11.16%, and 9.08% of the total variation, respectively. Individuals in the three sheep populations were not clearly clustered to separate the sheep populations although, PC1 looks better in segregating long-thin tailed Rutana sheep from the short fat-tailed Washera and thin-tailed Gumuz sheep (Fig. 3). PC_2 partitioned short fat-tailed Washera from thin-tailed Gumuz sheep although one individual from Washera found to be an outlier.

4. Discussion

The genetic diversity of an animal population is a measure of its genetic differences (i.e. genetic variation). It is vital to monitor and maintain genetic diversity in order for a conventional breeding to remain viable in the future [6]. Recently studies [20–22] were conducted to assess the relationships among Ethiopian sheep breeds using phylogeny tree, principal component analysis, and Bayesian model based population structure. According to these researches, the ancestral relationship between Ethiopian sheep populations, including the breeds under investigation, follows a distinct pattern of tail morphology, phylo-geography, and environmental adaptation (altitude or temperature). Nonetheless, genetic diversity and population structure in Gumuz, Rutana, and Washera sheep have not been adequately addressed in previous studies using whole-genome data. Stratification of the sheep populations using principal component analysis was not clear especially that explained by PC_2. However, between-breeds phenotypic variation in body weight was reported by different scholars, which was attributed to their genetic make-up. In this regard, large sized Rutana sheep weighing 43.1 kg [10] differs phenotypically with both Washera sheep weighing 32.8 kg and Gumuz sheep weighing 31.0 kg [31]. High within-breed variability is a feature of large traditional populations that have not been subjected to intense selection [32]. Meanwhile, we focused

Table 4
Mean values of genetic diversity indices.

Sheep population	Polymorphic SNP (PN)	Observed heterozygosity (HO)	Expected heterozygosity (HE)	Inbreeding coefficient (FIS)	Nucleotide diversity (π)
		Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Gumuz	0.89	0.33 ± 0.01	0.38 ± 5.34	0.12 ± 0.01	0.0029 ± 0.00
Rutana	0.90	0.34 ± 0.01	0.37 ± 3.79	0.09 ± 0.01	0.0030 ± 0.00
Washera	0.88	0.34 ± 0.01	0.38 ± 8.28	0.09 ± 0.02	0.0028 ± 0.00

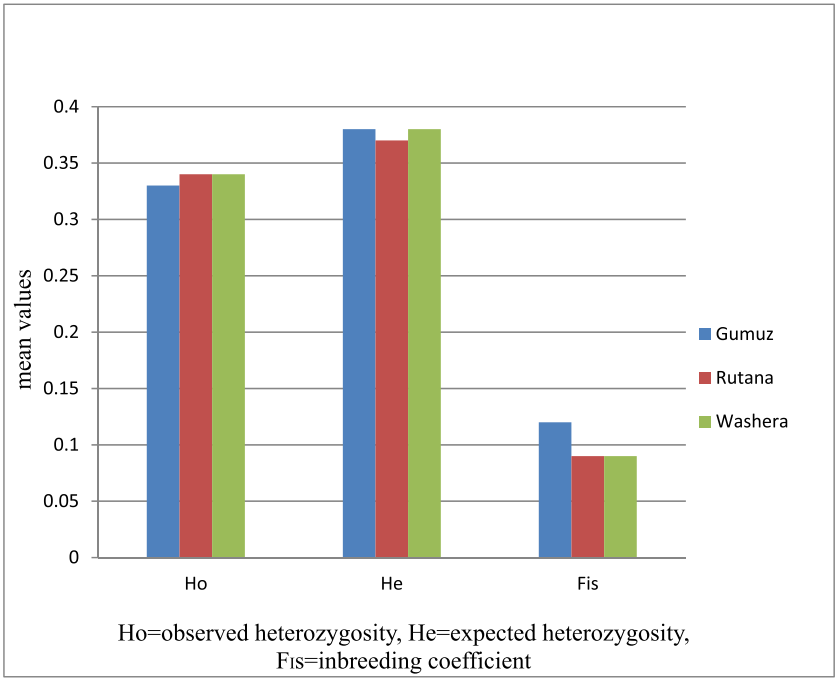

Fig. 2. Heterozygosity and rate of inbreeding estimates for the three sheep populations.

on evaluating within-breed genetic variability of Gumuz, Rutana and Washera sheep populations using genetic diversity indices such as polymorphic SNP (PN), observed heterozygosity (HO), expected heterozygosity (HE), inbreeding coefficient (FIS), and nucleotide diversity (π).

Polymorphic SNP (PN) contents of the current study were lower than Asian breeds such as 0.93 of Changthangi, 0.92 of Tibetan sheep, and 0.96 of Australian Merino, European breeds such as 0.95 of Finnsheep and 0.95 of German Texel, African breed such as 0.93 of Red Maasai but, were close to 0.91 of African Dorper, and were comparable to 0.88 of Cyprus Fat Tail sheep [29].

The average observed and expected heterozygosity values of the current study were in line with [33]. According to Ref. [33], the heterozygosity value ranges from zero to one. Values of expected heterozygosity were higher than observed heterozygosity for the three sheep populations. The genetic diversity across all loci of sheep populations under study were in accord with 0.35–0.38 [22] reported for Horro, Wollo, and Farta breeds studied using 50 kilo base (kb) SNP markers. Mean genetic diversity values of the current study were higher than 0.29–0.32 [20] reported for Adilo, Arsi-Bale, Blackhead Somali and Horro sheep studied using 60 kb SNP markers. The likelihood of sheep being heterozygous at a marker site is determined by the number of alleles and their frequency in the population. The mean heterozygosity values of Gumuz, Rutana, and Washera sheep (0.37–0.38) were less than 0.5, the value appropriate to study genetic diversity as suggested by Ref. [34]. However, these results are considered moderately heterozygous although they were on the low side. These mean heterozygosity values were far below heterozygosity values 0.65 to 0.74 [5] reported for fourteen traditional sheep populations of Ethiopia studied using 17 microsatellite markers. This difference in values of heterozygosity could be due to decreasing genetic diversity of Gumuz, Rutana and Washera sheep attributed to small base population, inbreeding, and genetic drift. Comparing these values from global point of view, mean expected heterozygosity (gene diversity) of the current study were higher than Asian breeds such as 0.35 of Changthangi, 0.34 of Tibetan sheep, 0.33 of African Dorper, and 0.32 of Red Maasai [29]. Expected heterozygosity of the current study were comparable to 0.37 of Australian Merino but, higher than 0.36 of Finnsheep, 0.35 of German Texel, and 0.31 of Cyprus Fat Tail sheep [29].

Mean inbreeding coefficient ranged from 0.09 of Rutana and Washera to 0.12 of Gumuz sheep. A high positive FIS value shows a high level of homozygosity, while a low negative value indicates a low level of inbreeding [34]. This study showed that inbreeding rates were higher than the tolerable value of 0.0625 [35] for the three sheep populations. These higher levels of inbreeding might

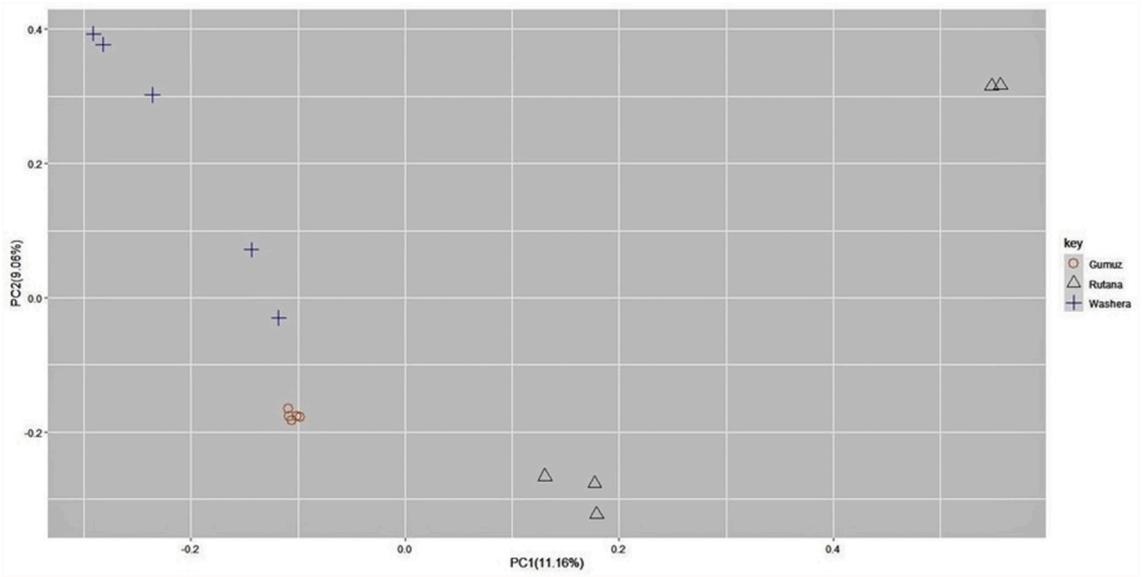

Fig. 3. Animals clustered on the basis of principal component analysis using individual genotypes.

result from non-random mating between closely related individuals. These higher levels of inbreeding might in turn cause inbreeding depression. F_{IS} values of the current study were in accord with 0.09–0.16 [36] reported for some Turkish sheep breeds but lower than 0.23 [19] reported for three sheep breeds of Ethiopia studied using 22 microsatellite markers. Higher positive F_{IS} (0.12) is recorded for Gumuz sheep. In that, an inbred Gumuz sheep is expected to have 12% more homozygous gene pairs than a non-inbred individual from the same Gumuz breed. The higher rate of inbreeding in Gumuz sheep might be because of the small population size [7], uncontrolled mating and genetic drift. In this regard, an earlier report by Ref. [5] indicated that Gumuz sheep was considered to be endangered and ranked second next to semien sheep for conservation priority. Higher nucleotide diversity estimates were recorded for Rutana sheep than its counterparts. In addition [37], reported that Rutana sheep are relatively more suitable than Gumuz and Washera sheep for production of better carcass yield. Thus, selecting individuals having higher nucleotide diversity from breeds like Rutana will lead to better yield from productivity traits such as carcass yield.

Mean nucleotide diversity (π) values ranged from 0.0028 in Washera to 0.0030 in Rutana. These sheep populations have moderate nucleotide diversity, nearly 0.3% as implemented by Ref. [38]. These values were considered to be indicators of the presence of moderate genetic diversity in Gumuz, Rutana and Washera sheep. However, the π value of Gumuz, Rutana and Washera sheep were lower than that of 0.0082, 0.0106, 0.0146 and 0.0150 [39] of Abergelle, Elle, Begait and Highland sheep, respectively studied in Tigray regional state of Ethiopia using Mitochondrial DNA.

5. Conclusion

We analyzed population structure of Gumuz, Rutana and Washera sheep populations using principal component analysis. However, individuals in Rutana and Washera sheep populations were not clearly stratified to separate the sheep populations some of the individuals being outliers. Meanwhile, we focused on evaluating within-population genetic variability of Gumuz, Rutana and Washera sheep populations using some parameters of genetic diversity such as observed heterozygosity, expected heterozygosity, rates of inbreeding, and nucleotide diversity. We found higher expected heterozygosity (gene diversity) values than the observed heterozygosity for sheep populations under investigation. In addition, we found higher values of nucleotide diversity. The smaller population size, closed breeding system, genetic drift and uncontrolled (non-random) mating might lead to higher rate of inbreeding in Gumuz, Rutana and Washera sheep, requiring timely intervention to prevent inbreeding depression and extinction of these valuable breeds of sheep, which helps in sustaining the livelihood of sheep keepers in lowlands and highlands. Nevertheless, our whole-genome analysis revealed higher within-population genetic variability. Uncovered areas of studies like mapping quantitative trait loci, identifying genes underpinning productivity traits such as carcass quantity and meat quality could be carried out on diversified sheep resource identified by the current study. Identifying the genomic regions and biological pathways that contribute to explaining variability in these traits is of great importance for selection purposes. Designing conservation-based within-breed sheep selective breeding programs are recommended considering economically important traits into account.

Author contribution statement

Sisay Asmare: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Kefyalew Alemayehu; Joram Mwacharo; Aynalem Haile; Solomon Abegaz; Abulgasim Ahbara: Contributed reagents, materials, analysis tools or data.

Data availability statement

Data associated with this study has been deposited at https://figshare.com/s/2bc42d3c7998377bd24a; DOI.10.6084/m9.figshare.14814924.

Declaration of interest's statement

The authors declare no conflict of interest.

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