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Article

Genetic diversity, population structure and demographic history of indigenous goats of Mongolia revealed by SNP genotyping

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Simple Summary: We originally performed SNP genotyping of indigenous goats of Mongolia to estimate their genetic risks which has become a subject of concern in recent times due to the recent climatic disasters and uncontrolled massive breeding, and explored demographic history of these goats. Two Mongolian breeds that showed highest estimates of genetic risks were Erchim from Darkhat Valley and Gobi Gurvan Saikhan from the same named desert. The first one is the most geographically autonomous population and the second one is subjected to artificial selection to a much greater extent than the other Mongolian goats. The third studied population, Buural, is the largest population of Mongolian goats that is often used to improve other local breeds, exhibited the shortest genetic distances within the other local breeds and showed the lowest estimates of inbreeding. Dorgon and Ulgii Red goats, both from Altai Mountains region, are the two most closely related Mongolian breeds according to our data. Given the inbreeding values, Erchim goats and Gobi Gurvan Saikhan goats are more endangered genetically than Buural goats. Various clustering methods showed close genetic relations between Mongolian and Russian, Chinese and West Asian breeds. Mongolian goats exhibited low to moderate estimates of genetic differentiation between each other with the exception of Erchim goats that probably may have originated from separate ancestral population.

Abstract: Recent climatic disasters (dzudzs) and uncontrolled massive breeding endangered valuable genetic resources of Mongolian goats labored by five thousand years of evolution in extremes of Altai Mountains and Gobi deserts. Meanwhile, Mongolian goats have never been studied on genomic data. We used Illumina Goat SNP50 to investigate phylogenic relationships and genetic risks in five local Mongolian populations: Erchim from geographically remote Darkhat Valley in the northern mountains, Ulgii Red and Dorgon from the western mountain region, Buural from the western steppe and mountain areas and Gobi Gurvan Saikhan from semi-arid steppe area in the South Gobi region. ROH analyses, estimated populations sizes and Fst values showed South Gobi and Darkhat Valley goats to be at a high risk of inbreeding that however appears to be of distinct origin (artificial selection vs geographical isolation). Indices of genetic differentiations between Mongolian goats were relatively low probably because they were not subjected to intense selection. Part of Darkhat Valley goat population was clearly differentiated from other Mongolian breeds according to various types of analyses. Principal component analysis and the neighbor-joining tree based on pairwise differences among worldwide populations showed that Mongolian goats are clustering closely to some Russian (Altai, Orenburg) and Chinese (Nanjiang and Qinggeda) breeds. Thus, present study (i) highlights demographic history of Mongolian goats and (ii) provides unified SNP-data which supports decisions in conservational genetics. Finally, our work (iii) will help to make objective choices when developing conservational programs in the near future.

Keywords: SNP genotyping; Mongolian goats; breed; conservational genetics

1. Introduction

Although the conservation of biodiversity is now recognized as one of the main focuses in genetics research in domesticated animals, the great efforts made here still cannot fix the rate of loss in local animal breeds (Bélanger & Pilling 2019). Goat breeds are mainly distributed in developing countries, providing essential support for the huge part of the population, while the global demand for goat products accelerates an intensification of goat farming and promotes an invasion of transboundary breeds in order to increase productivity. Adaptability of local goats serves as the main source of stability for small holders when faced with environmental changes (Joy *et al.* 2020), so that loss in genetic diversity puts a number of cultures and ethnic groups under the threat of extinction. For goats, biodiversity conservation is particularly challenging because the number of their breeds is huge but conservation resources are very limited. In comparison with other domesticated animals, the biodiversity of goats is the least characterized (Galal 2005; Olschewsky & Hinrichs 2021). Thus, the primary challenge today is to identify breeds that need to be conserved first. Decisions might be supported by the compilation of databases containing objective information about the genotypes of these breeds: their genetic risks, phylogenetic relationships, as well as knowledge of the socioeconomic processes that can affect the risks of these breeds (Stella *et al.* 2018; Cortellari *et al.* 2021). SNP-genotyping is widely recognized as the most appropriate tool since the availability of commercial SNP-arrays that give unified data that is generally might be compared between different studies (Pogorevc *et al.* 2021).

In Mongolia, goat breeding has been the main source of food and clothing for several thousand years. Culture of indigenous peoples reflects a great role of goats both in legends and national traditions, such as foods or local arts. Some authors believe that independent goat domestication could have happened here (Ganbold *et al.* 2020). Local goats are adapted to year-round grazing in extreme climates and altitudes of Altai Mountains, steppes and Gobi Desert. In some areas, differences between summer and winter temperatures exceed 100 degrees. In certain regions, local goats can satisfy their nutritional demands by finding plant below the snow.

Meanwhile, Mongolian goat's genetic diversity and phylogenetic relationships between each other and within the goat breeds of the rest of the world are still largely unknown. In particular, we are not aware of any studies that used SNP genotyping. There are few studies that examined haplotype diversity on Mongolian breeds by STR, mtDNA and Y-chromosome genes analysis between 2003 and 2020 years (Ganbold *et al.* 2020; Beketov *et al.* 2021; Voronkova *et al.* 2021). All of these studies concluded that local Mongolian goat breeds are weakly differentiated genetically making this assumption by comparing genetic distances with the ones that were previously revealed for goat and cattle populations.

Mongolian goats were experiencing various perturbations over the past decades. With the fall of Soviet Union, the Mongolian market became open to the rest of the world. Therein, the goat population has raised several times as a result of the increase in global demand for cashmere (Ganbold *et al.* 2020), and this can give a false impression of the industry's well-being. Meanwhile, local farmers still rely on productive transboundary breeds as a source to improve the quality of their goats, which can destabilize goat's adaptation traits. Moreover, a series of climatic disasters called "dzuds" caused repeated reductions in goat population numbers, which could have cause bottlenecks and increased inbreeding. According to the National Statistical Office of Mongolia, 11.5 million of livestock animals have perished during the winters of 1999-2002, and the harshest dzud has killed 10.3 animals during the single winter of 2009-2010. Nevertheless, the total number of animals raised 2.6 times from 25.9 to 66.5 million in a 28-year period since the end of Soviet Union from 1990 to 2018 (NSOM, 2018). There is no reliable information if these dzuds affect mainly local or invasive breeds.

Historically, goat breeding in Mongolia is nomadic, that means that goat herds are moving all the year, which implies some peculiarities, such as free crossings. Many authors, both in Mongolia and around the world, believe that the loss of the nomadic style of goat breeding can result not just in a cultural and economic crisis, but also an ecological disaster. Agricultural ecosystems of Mongolia are extremely vulnerable to anthropogenic influence, and their current load due to the increase in the number of animals is already causing depletion of natural resources. This depletion mostly occurs due to the intensification of the industry and a decrease in nomadism (Tsvegemed *et al.* 2018). Traditional nomadic animal husbandry, on the contrary, treats nature with care. Many researches argue that the preservation of nomadism is the only way to stop erosion. Obviously, it needs preservation of the local goat's biodiversity and thus saving traditions and skills of the local human population.

Using SNP genotypes, we examined demographic history and estimated genetic diversity of indigenous goats of Mongolia and explored their phylogenetic relationship with goats of the rest of the world.

2. Materials and Methods

2.1. Sample Collection and Description

Blood was sampled from 244 animals in five Mongolian goat populations located in five geographical areas of the country with different climatic conditions during a research expedition of the Vavilov Institute of general genetics in 2017, one breed per location. The geographical locations of sampled populations and brief samples description are summarized in Figure 1 and Table 1.

One of the peculiarities of Mongolian goats is the lack of deep specialization of their productivity: dairy, downy or meat one, which makes them versatile. All the breeds with the exception of the Gobi Gurvan Saikhan (Gobi GS) have been formed mostly by natural selection and adapted to round-year grazing and nomadic breeding style. Gobi GS has been developed by crossing local cashmere goats in the Gobi area with Don breed bucks up to the F2, followed by pure and selective breeding (Porter 2020). Buural goats are the most widely distributed breed in Mongolia, whereas Erchim goats of Darkhat Valley are geographically isolated local populations (Takahashi et al. 2008).

2.2. DNA Extraction and Genotyping

DNA was extracted from the whole blood samples containing EDTA as an anticoagulant using Magna Prep 200 kit (Laboratory Isogen, Moscow) to the manufacturer's instructions. Quality of the DNA was measured using the Nanodrop 8000 spectrophotometer. Genotyping was performed with Goat 50K BeadChip (Illumina Inc., USA) containing ~60 000 SNP. Quality control was performed by setting a cutoff of 0.5 for the GenCall and GenTrain scores. SNP dataset was filtered to remove poorly genotyped individuals, loci genotyped in <90% of individuals and rare alleles using PLINK 1.9 (Chang et al. 2015) with geno 0.1 --mind 0.1 --maf 0.05 plink parameters. To ensure that our analysis would not be affected by the presence of SNP in strong linkage disequilibrium we also filtered data with --indep-pairwaise 50 5 0.2 PLINK filter. 184 samples passed these filters. Among highly related pairs of animals we selected only one animal per pair for future analysis; 17 animals were excluded. A total of 167 samples were processed in future analysis.

2.3. Construction of The Working Datasets

To explore relationships between Mongolian populations and breeds from the rest of the world we added to our dataset genotype data obtained in other studies (Table S1). First, we added data from the AdaptMap project described in the paper of Colli et al. (2018) and covering goat populations from all over the world. Asia was underrepresented in this dataset: there were just a few populations from West Asia (Iran, Turkey and Pakistan), but no data from the countries located close to Mongolia. To fill this gap we added genotypes from the study of Deniskova et al. (2021) covering seven goat breeds from Russia, whereas three of them were collected close to Mongolian border (Altai Mountain (ALTM), Altai White Downy (ALTW), Soviet Mohair (SOVM)) and one near the Kazakhstan border (Orenburg (OREN)). We also added data from six populations from five Chinese regions described in Berihulay et al. (2019). Among them, Nanjiang (NJ) and Qinggeda (QG) breeds were sampled in the region next to the southwest Mongolian border and Arbas Cashmere (AC) was sampled near the southern border.

Raw datasets were combined using --merge PLINK command and filtered with --geno 0.01 --mind 0.2 --maf 0.001 parameters. --mind rate is set much more relaxed than usual one to keep relatively poorly genotyped Mongolian, Russian and Chinese goats in analysis. To ensure that analyses would not be distorted by the presence of SNPs in a strong linkage disequilibrium (LD), the --indep-pairwise 50 5 0.1 command in PLINK was used to prune the SNPs that passed the initial filtering step.

To obtain datasets with different resolution we further created four subsets, namely Worldwide, Asian, Local and Mongolian. Worldwide dataset included all available samples, Asian dataset included goats from China, Mongolia, West Asia and all Russian samples except transboundary Saanen (SAAN) breed. Local dataset included Mongolian and

Nanjiang, Qinggeda and Orenburg samples, whereas Mongolian dataset consisted exclusivelyfrom the SNP-data obtained in this research. The three additional breeds included in Local dataset were chosen because of their geographic proximity and genetic closeness revealed by principal component and phylogenetic analyses.

2.4. Genetic Diversity Estimation

To evaluate within-population genetic diversity we calculated the observed heterozygosity (Ho), unbiased expected heterozygosity (He), and inbreeding coefficient (Fis) with 95% confidence intervals (CI 95%) using the R package "diveRsity" (Keenan et al., 2013).

2.4.1. Effective Population Sizes

Trends in effective population size were estimated by LD using SNeP tool (Barbato et al. 2015) with default parameters, except the ones for the sample size correction, occurrence of mutation ($\alpha = 2.2$; Corbin et al., 2012), and recombination rate between a pair of genetic markers according to Sved and Feldman (1973).

2.4.2. Runs of Homozygosity (ROH)

ROH analysis was performed for Mongolian dataset without LD and MAF pruning. To calculate ROH we used the methodology of Meyermans et al. (2020) with settings suitable for medium-density genotype samples (PLINK commands: --homozyg-density 50 --homozyg-kb 1000 --homozyg-snp 20 --homozyg-window-het 1 --homozyg-window-snp 20). Dunn test with Benjamini-Hochberg correction (p-value cutoff=0.05) for multiple testing was used to estimate differences in ROH length and frequencies among breeds.

2.4.3. Haplotype Sharing

To estimate an impact of recent admixture events we performed an analysis of haplotype sharing. To phase our worldwide dataset we used ShapeIT software (Delaneau et al. 2012) with default parameters and then performed sharing analysis with Refined IBD (Browning & Browning 2013) with default conditions. Results were processed and visualized in R.

2.5. Genetic Relationships and Population Structure

To investigate genetic relationships among Mongolian and the other breeds, we performed both PCA and phylogenetic analysis. PCA was performed using PLINK and was further visualized in R. The individual-level phylogenetic analysis of local dataset was performed using the aboot() function from the R 'poppr' package (Kamvar et al. 2014). Dendrogram (with 1000 bootstrap-support replicates) were built using bitwise genetic distances and neighbor joining algorithm.

Genomic clustering for worldwide and local datasets was performed using fastSTRUCTURE software (Raj et al. 2014). The program runs were carried out assuming K-value to be between 2 and 15 groups in 50 repeats. The cluster membership matrices of the fastSTRUCTURE outputs were visualized using PONG software (Behr et al. 2016).

Figure 1. Map of sampled populations.

Table 1. Sampled populations and their environment.

[1] Samples that passed quality controls and were further included in statistical analysis

Breed (Code)	n[1]	Prefecture	Latitude, Longitude	Environment	Areas of benefit	Color
Erchim (EB)	28	Huvsgul;	51.42, 99.73	Mountain areas with extreme continental climate.	Milk, meat and cashmere	Black
Dorgon (DG)	34	Hovd;	45.80, 92.29	Western steppes and mountains.	Cashmere, meat and milk	White and red
Buural (ZB)	35	Zavkhan;	47.95, 93.49	Gobi-like areas of Great Lake Valleys.	Cashmere and milk	Dark brown and black
Ulgii Red (UR)	37	Uvs;	49.31, 91.99	Both mountain and steppe areas.	Cashmere, meat and milk	Red and brown
Gob Gurvan Saikhan (GGS)	33	Gurvan Saikhan.	43.80, 101.58	South Gobi, Three Beauties' mountains.	Cashmere (Kashgar)	Various. Mostly red and white.

3. Results

3.1. Dataset description

200 samples left after the DNA quality control and 15 more samples were removed because of the low gonotyping efficiency. A common set of 45665 SNP from 167 animals was used for the subsequent analyses.

Filtering of combined datasets of Mongolian, Russian, Chinese and other genotypes resulted in a set of 38276SNP from 5176 animals of 151 breed from all over the world (Table S1). Asian subset included animals of 39 breeds from Russia, Mongolia, China, Iran, Turkey and Pakistan.

3.2. Genetic Diversity and Effective Population Sizes in Mongolian Populations

The indices of genetic diversity are summarized in Table 2. According to Ho and He values, Erchim goats exhibited the minimum level of genetic diversity, and Buural goats showed the maximum one. For all Mongolian populations except Gobi GS observed heterozygosity did not differ from expected values for more than 0.005. Gobi GS showed the highest difference between Ho and He equal to 0.010 which is a possible mark of inbreeding which occurred during breed development.

Table 2. Genetic diversity and inbreeding estimates in Mongolian goats by observed (Ho), unbiased expected heterozygosity (He), their difference (dH) and estimates of the inbreeding coefficient (Fis) with the 95% confidence interval.

Breed	Ho	He	dH	Fis
Dorgon	0.396	0.395	0.001	-0.004 [-0.006;-0.002]
Buural	0.406	0.405	0.001	-0.002 [-0.004;0.000]
Erchim	0.393	0.388	0.005	-0.013 [-0.015;-0.011]
Gobi GS	0.400	0.410	-0.010	0.023 [0.021;0.025]
Ulgii Red	0.397	0.399	-0.002	0.004 [0.003;0.005]

This suggestion is supported also by relatively high inbreeding coefficient value (Fis) for this breed. Erchim goats showed an excess of heterozygotes according to negative Fis values.

Ancestral and recent effective population sizes (Ne) for five Mongolian goat populations are shown in Figure 2. Estimated Ne showed a downward trend with the increase in generations across all populations. Erchim goat breed had the lowest effective population size at all time points, decreasing from 955 to 120 animals over the last 60 generations. Recent effective numbers for other breeds were 274 for Dorgon, 373 for Buural, 433 for Gobi GS and 812 for Ulgii Red. The most dramatic decrease in the effective population size was detected in Gobi GS breed.

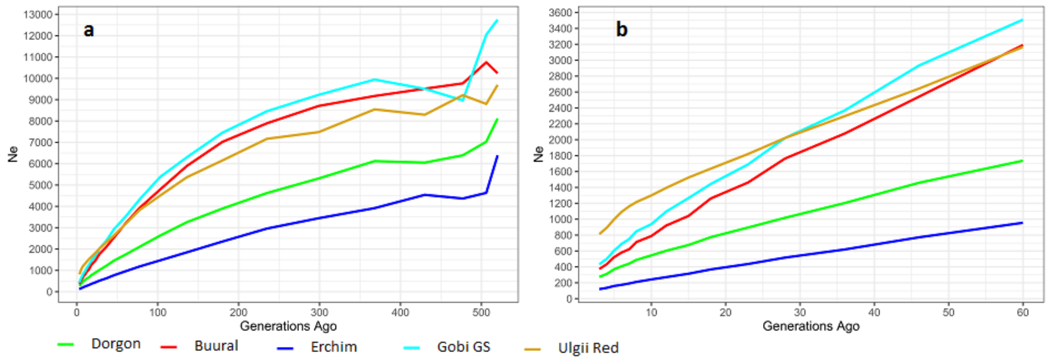

Figure 2. Long-term (a) and recent (b) trends in effective population sizes (Ne) for five Mongolian goat populations.

3.3. Runs of Homozygosity

The most variable ROH lengths were found in Gobi GS breed (Figure 3 and S1) with some outliers exhibiting a high amount of extremely long ROHs, whereas other goats were particularly poor in ROHs . Every recombination event, i.e. every next generation means ROH length reduction, so that longer ROH are resulted from inbreeding that is more recent. According to this assumption, our data suggest that some Gobi GS goats are highly inbred. Given the historical background of the breed which originated from crossbreeding of local goats with Russian Don breed, its likely to be as a result of constant artificial selection pressure.

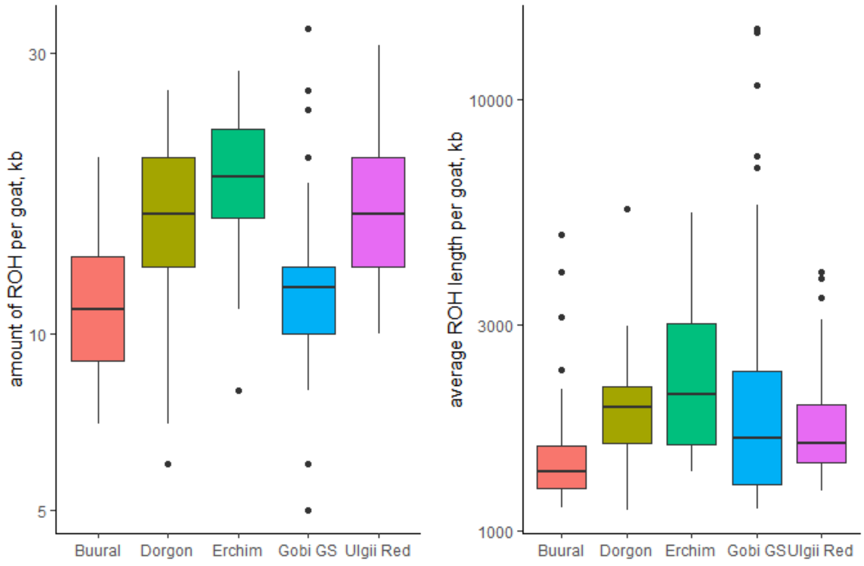

Figure 3. Distributions of ROH and their average lengths across Mongolian breeds

There were significant difference in average ROH length between Buural and other breeds with Buural goats exhibiting smallest and less frequent ROHs compared to other breeds. ROH frequency was also significantly lower in this breed comparing to Dorgon, Erchim and Ulgii Red breeds. Average ROH length in Erchim goats was significantly higher comparing to other breeds except the Buural one. Coupled with high ROH frequency this indicates relatively high inbreeding level in this population.

3.4. Ancestry of Mongolian Goat Breeds

3.4.1. Principal Components Analysis

Goat populations placed on the PCA plot in agreement with their geography and domestication history (Figures 4, S2, S3). Chinese, Mongolian, most West Asian (Iran, Pakistan, Turkey) goats and goats from Asian part of Russia form a single cluster separated from samples from other regions. On the detailed PCA graph for Asian breeds (Figure 4A, S3) only the first component (PC1) clearly separated Pakistani populations from the rest ones: Chinese, Mongolian, Russian, Turkish and Iranian breeds. Such arrangement probably resembles southern and northern goat dispersal routes in Asia (Zheng et al. 2020). After primary domestication one branch migrated through Caucasus and Siberia to China, and another one moved to Pakistan. In accordance to this scenario second component plotted Mongolian goats between two clusters consisting mainly of Russian and Chinese samples. However, more samples from Southern and Central Asia are required to fill the gap and to add more support to this scenario. Dorgon, Erchim and Ulgii Red breeds were clustered together with Chinese Nanjiang, Qinggeda and Jining Grey breeds (Figure 4A,S3), whereas Gobi GS goats tended towards Orenburg breed from Russia.

Zooming the PCA for Mongolian breeds revealed a low differentiation within Buural, Gobi GS and Ulgii Red breeds but high variability within Erchim and Dorgon breeds (Figures 4B). Gobi GS, Buural and Ulgii Red samples were plotted together in the single cluster and Erchim and Dorgon breeds were separated by the first and second principal components respectively. Both breeds formed two clusters each: one cluster was placed quite close to the other Mongolian samples whereas the second one was clearly differentiated.

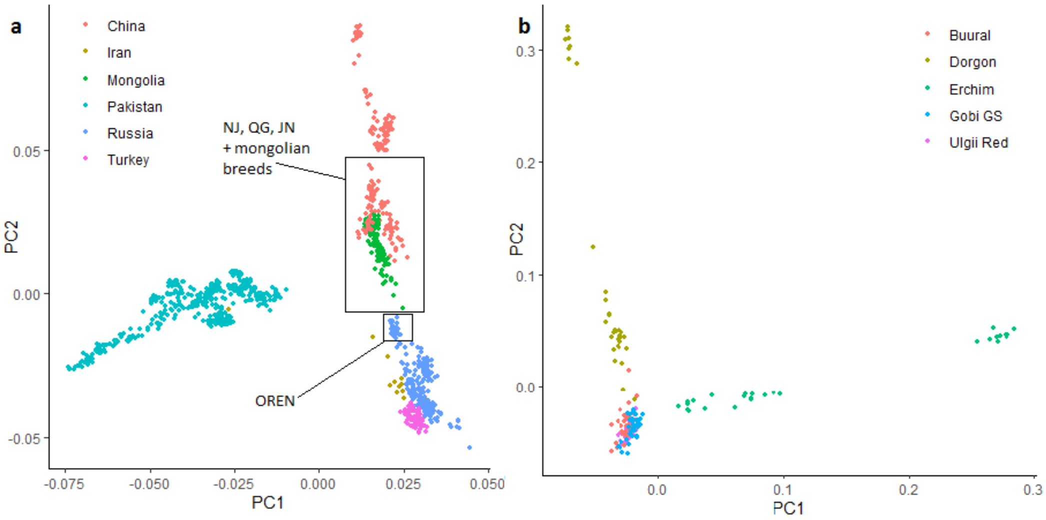

Figure 4. Principal component analysis for all goats of Asian origin (a) and Mongolian breeds (b). OREN=Orenburg, NJ= Nanjiang, QG= Qinggeda, JN=Jining Grey

3.4.2. FastSTRUCTURE Analysis

The fastSTRUCTURE analysis applied to the worldwide (Figure S4) and local datasets (Figure 5) showed data that was consistent with PCA results. Mongolian breeds displayed low differentiation among the breeds and clustered together with Chinese, most Russian and West Asian breeds (Figure 5). Small admixture with European and transborder Saanen breeds was observed as well as with Angora goats.

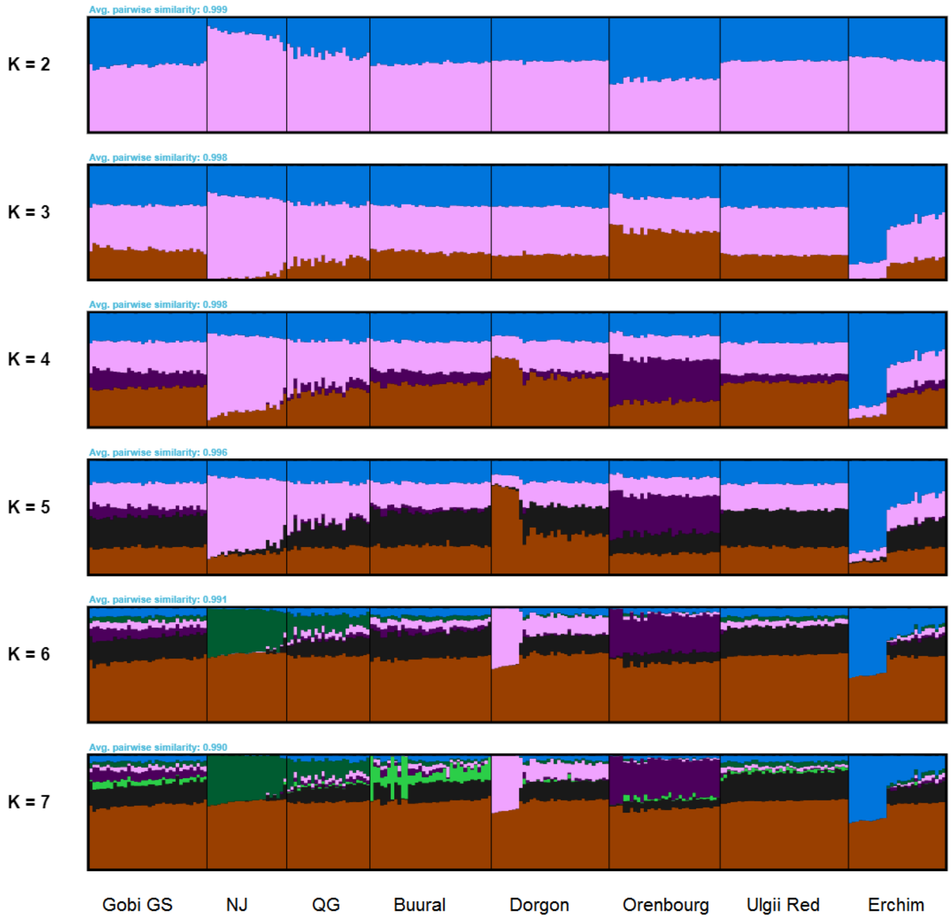

Figure 5. FastSTRUCTURE clustering for the local dataset. NJ= Nanjiang, QG= Qinggeda

Local fastSTRUCTURE revealed non-uniform structure of two goat populations, Erchim and Dorgon (Figure 5). Nearly half of the samples of these populations clearly formed their own separate clusters and showed reduced presence of other components uniformly distributed in the rest of Mongolian goats. Consistent with PCA results the genetic pool of Orenburg goats influenced the Gobi GS population. The most likely number of populations according to the maximum likelihood estimation was equal to 5.

3.4.3. Phylogenetic analysis

We constructed individual-level neighbor joining phylogenetic tree for all studied Mongolian populations of goats. As outgroups, we used two Chinese breeds (Nanjiang, and Qinggeda,) and one Russian (Orenburg) breed (Figure 6). These breeds were selected for their general similarity to Mongolian breeds revealed in PCA. Gobi GS formed a single cluster with Orenburg goats confirming fastSTRUCTURE results. Erchim goats of Darkhat valley were most closely related to Chinese breeds. Dorgon and Ulgii Red goats formed a single cluster with the last ones being closely related to 16 Buural goats. Whereas the rest 19 Buural goats were related to Gobi GS goats also confirming PCA results. Nanjiang and Qinggeda breeds positions resemble those in the original paper (Berihulay et al. 2019).

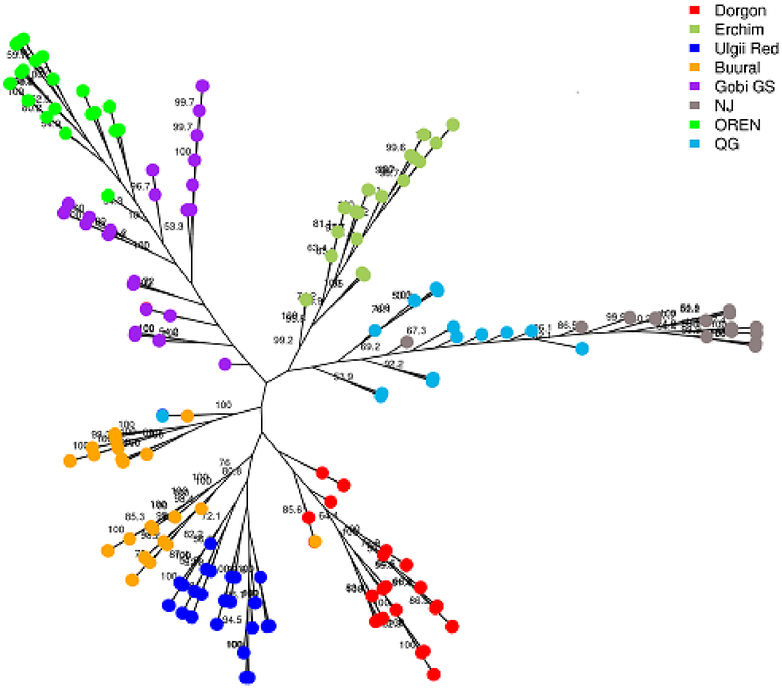

Figure 6. Neighbor joining phylogenetic tree for the local dataset (Mongolian breeds, two Chinese breeds (Nanjiang, NJ, and Qinggeda, QG) and one Russian breed (Orenburg, OREN).

3.5. Population Structure

3.5.1. Genetic Distances (Fst)

The genetic distances (*Fst*) (Table 3) and the corresponding Neighbour-Net tree (Figure 7) showed Erchim to be the most genetically autonomous breed among the Mongolian goats in our study. The closest genetic distances were found in the pairs of Buural-Gobi GS and Buural-Ulgi Red.

Table 3. The genetic distances (Fst) between Mongolian goats.

Breed	Dorgon	Buural	Erchim	Gobi GS	Ulgi Red
Dorgon	0.000				
Buural	0.015	0.000			
Erchim	0.035	0.027	0.000		
Gobi GS	0.017	0.009	0.027	0.000	
Ulgi Red	0.018	0.009	0.028	0.012	0.000

Note: All pairwise *Fst* values are significant (permuted p-values < 0.001 for all estimates).

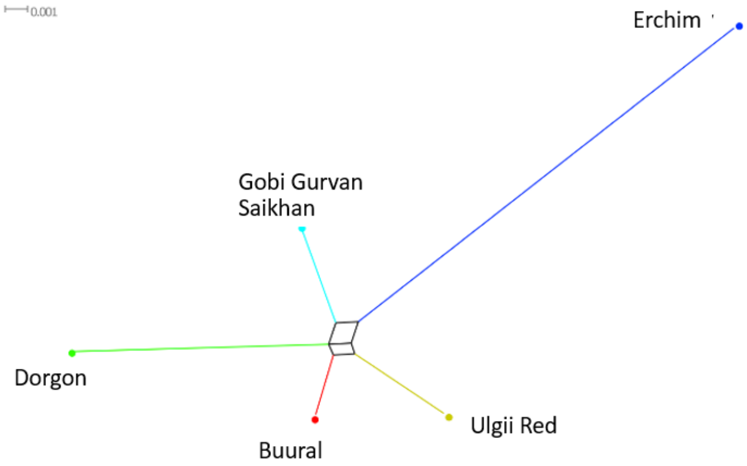

Figure 7. Fst-based Neigbour-Net tree for Mongolian goats.

3.5.2. Haplotype Sharing

To explore recent admixture events we analyzed haplotype sharing in Mongolian goat populations between each other (Figure 8) and in comparison to the top-20 related goat breeds (Figure 9).

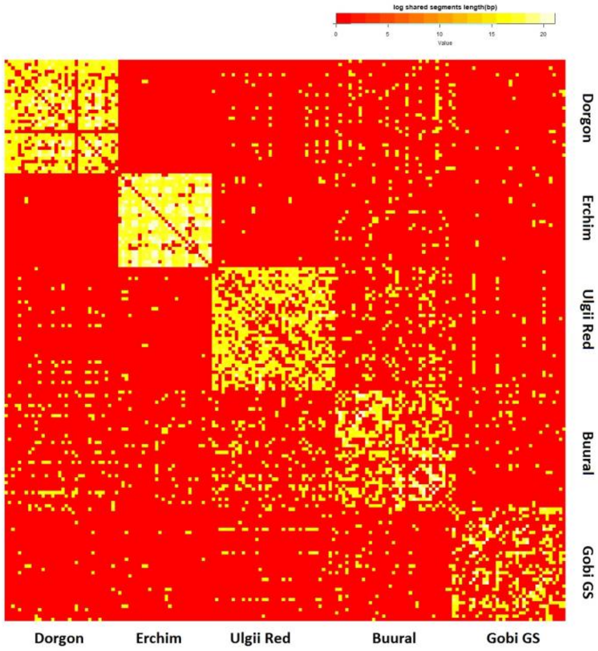

Figure 8. Heatmap: haplotype sharing (>7Mb) within Mongolian goats' populations (by individuals). Yellow indicates shared haplotypes.

According to Figure 8, the Buural breed was the most haplotype-sharing population in our study, followed by the Ulgii Red breed. These two populations had the most intensive haplotype sharing between each other, appearing almost like a single population on the heatmap. Erchim goats evidently had the lowest proportion of shared haplotypes across Mongolian populations consistent with geographic isolation of this breed.

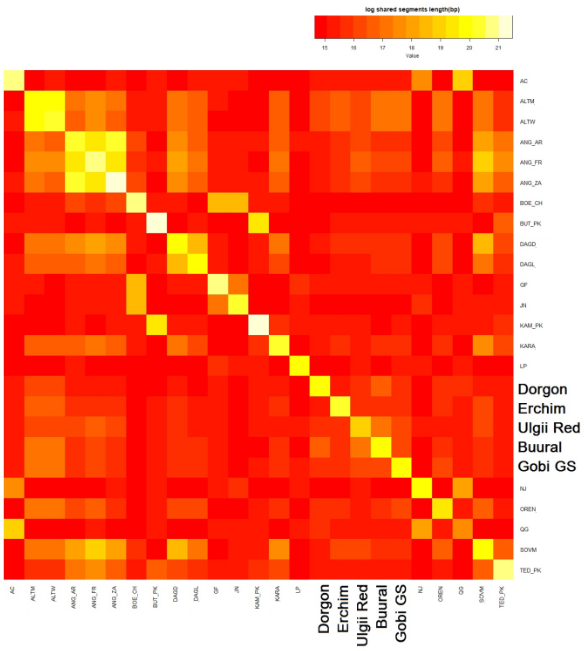

Figure 9. Heatmap: haplotype sharing within Mongolian goats and 20 most closely related breeds (samples detailed in Table S1).

When plotted within 20 most closely related breeds, all of the Mongolian goats had the highest proportion of shared haplotypes with Altai Mountain (ALTM), Altai White Downy (ATLW), Soviet Mohair (SOVM), Dagestan Downy (DAGD) and Angora (ANG_AR, ANG_FR, ANG_ ZA) goats. The Angora breed originated in Turkey and further became a transboundary breed and thus was involved in improvement of many local breeds; its impact on ALTM, SOVM and DAGD breeds is well documented (Deniskova et al. 2021). In contrast to the PCA results, Chinese Nanjiang and Qinggeda on the heatmap appeared unrelated to Mongolian goats. Dorgon goats were the only one from Mongolian populations that showed a trace of haplotype exchange with Qinggeda (but not Nanjiang) goats.

4. Discussion

Genotyping by SNP arrays is an accurate and cost-efficient tool to analyze various indicators of genetic diversity. While large efforts are dedicated towards studying commercial high-yielding breeds, there is a growing interest in genetics of local populations due to their specific traits allowing them to adapt to local environments and resist pathogens, starvation and harsh climatic conditions. There is a global trend to improve indigenous goats with transboundary breeds while trying to preserve useful local traits thereby helping these admixed goats to remain adapted, especially in such extreme regions as Mongolia. Moreover, some local breeds need to be conserved to maintain goat biodiversity and provide support to nomadic traditions and local communities which are very typical for Mongolia. Whole genome SNP analysis allows to explore genetic diversity and may as help to achieve these goals.

We provide the first whole genome SNP analysis for the five populations of Mongolian goats; our study complements the results obtained in previous works that used STR (Bolormaa et al. 2008; Beketov et al. 2021) and mtDNA (Takahashi et al. 2008; Ganbold et al. 2020; Voronkova et al. 2021) analyses. Consistent with our PCA and fastSTRUCTURE results these studies also generally assumed weak differentiation across Mongolian goats (Takahashi et al. 2008). Mongolian goats, apparently, historically were adapted to the semi-wild and nomadic way of life and therefore crossed more freely than worldwide populations. Thus, they may represent lower indices of differentiation.

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All of the five local goat populations of Mongolia showed a strong tendency in reducing effective population sizes. Overall, decrease in ancestral population size appears to be typical for local breeds (Colli et al. 2018) probably just meaning that domestication led to separation of larger populations (Islam et al. 2019). However, a rapid decline in effective population sizes in recent generations suggests that negative events in the past years resulted in the bottleneck effect. All Mongolian samples showed both long- and short-term decline in Ne with recent values ranging from 120 in Erchim to 812 in Buural goats; the most dramatic drop in Ne was observed in Gobi GS breed, which is known to be under the highest artificial selection pressure among all goat populations in this study. So that, none of the populations had Ne values decreased below the generally accepted limit of 100 or even 50 individuals to be considered as endangered one (Meuwissen 2009). However, these threshold values were mostly obtained by equational modeling (Meuwissen 2009) and are rarely verified empirically. Better modeling combined with empirical validation is expected to improve assessment of genetic risks based on Ne (Ryman et al. 2019; Green et al. 2020).

To put Mongolian goats in a broader context, we compared our results with previously reported data from the other breeds and populations of the rest of the world. PCA and fastSTRUCTURE, as well as phylogenetic analyses demonstrated extensive common ancestry shared with Asian breeds, especially with some Chinese, Altai and Orenburg populations in agreement with their geographical locations and migration history. We also detected a trace of recent admixture with Angora-like breeds but not with Chinese goats in most Mongolian populations..

Erchim. Estimated of genetic distances (*Fst*) and various clustering methods showed Erchim breed inhabiting Darkhat Valley to be the most autonomist population among the local Mongolian goats in our study. Also, Erchim goats exhibited high inbreeding level accessed by ROH and linkage disequilibrium analyses and the lowest effective population size. Origin of Erchim goats remains unclear. According to the PCA they were more closely related to Chinese goats than to the rest of Mongolian or other Asian samples. Neighbor joining and Nei-distance trees also clustered them together with Chinese Nanjiang and Qinggeda. However, analyses of shared haplotypes revealed recent admixture events from the Altai goats.

FastSTRUCTURE analysis demonstrated two separate subpopulations within this breed. One of them looks very similar to the rest of Mongolian breeds, but another one bears genetic material unique for the local population. This partition probably accounts for inconsistent ancestry results for this breed and needs future investigation.

Gobi GS. This breed was also a bit shifted on the PCA from the main pool of the Mongolian samples toward Orenburg goats. Study by Takahashi et al. (2008) showed similar results, including separation of Erchim and Gobi GS goats by PCA analysis of eight microsatellite loci in eight Mongolian goat populations. Gobi GS is the only Mongolian breed that was created by classical intense artificial selection. According to (Cerensonom 1967) selection of the breed started in 1937 by crossing “local goats from desert and semi-desert areas with imported male goats of Russian Don breed”. The last one is generally believed to be created in XIX century by small holders of the Russian Empire by crossing local goats at the Don river region with ancient Angora goats (Epstein 1965). The Don breed was officially recognized after internal Soviet Union expedition in 1934. According to FAO, animals of the breed probably produced the highest wool yield among documented goat breeds (Dmitriev & Ernst 1989). The Don goats were widely used for improvement of Orenburg and Altai Russian breeds. In turn, Angora goats originate from Ankara, the capital city of Turkey, located at the territory of ancient Anotalia, one of the regions of Fertile Crescent. This breed was also widely used for improvement of many goat breeds around the world including Australia and North America, and, more locally, for improvement of Soviet Mohair Russian goats. The fact that Gobi GS goats in our study plotted towards Orenburg breed is likely to be explained by admixture of Don goats used while creating these breeds. Thus, shared genetic variance between Gobi GS and Orenburg breeds might represent a reservoir of the Don goats gene pool, a breed that has never been characterized by SNP genotyping. The area on PCA that overlaps Gobi GS and Buural goats supposes the last ones might be Mongolian ancestor of Gobi GS breed that was documented as “local [Mongolian] goats from desert and semi-desert areas”. Indeed, Buural is the predominant breed of goats in Mongolia that was widely used in local breeding.

So, **Buural** goats appear to be the ones that were probably used in developing Gobi GS breed, showing lower genetic distances with the last ones and plotting closely on PCA. Also, Buural goats appear to exhibit lower genetic autonomy as compared with other Mongolian breeds. These goats exhibited the lowest inbreeding estimates and the widest genetic relationships both within other Mongolian breeds and within the world goat populations. These data make sense given the fact that Buural goats are the most widely distributed ones in Mongolia, at least among the studied populations (Takahashi et al. 2008).

Dorgon goats as well as Erchim also splited in two subpopulations according to PCA and fastSTRUCTURE with one subpopulation demonstrating a unique genetic material potentially of distinct origin. Same as in the case of Erchim goats this assumption needs future investigation.

Dorgon and Ulgii Red goats were the two most closely related Mongolian breeds and clustered together at the most types of analyses. Interestingly, these goats are quite distinct in their color with the first one being predominantly white and the last one mostly red according to the breed name. However, their environmental conditions and lifestyles are very similar with both of them being year-round grazing animals moving between Altai Mountains and steppe regions. Ulgii Red and Dorgon goats showed quite similar ROH pattern that also showed their genetic risks being significantly higher than for Gobi GS and Buural breeds but lower than for Erchim goats.

5. Conclusions

All the studied local goat breeds of Mongolia showed a strong tendency in reducing effective population sizes, and four of them (except Buural goats) exhibited moderate to high levels of inbreeding. Various types of analyses highlighted distinct origin and breeding history of these goats also indicating long-term preservation of specific allele combinations of ancestor’s breeds. Given together, these data suggest Mongolian goats to be a valuable reservoir of genetic resources with some of the breeds being highly endangered genetically, although in a different manner.

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