

Dynamics of the genetic structure of dairy cattle population in the Sverdlovsk region

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Abstract. By the beginning of the 21st century, the population of pedigree dairy cattle in the Sverdlovsk region was represented by the Black Pied breed, which was actively improved through the use of Holstein bulls. The resulting Holsteinization led to changes in the gene pool of the regional population, which this study aims to describe and analyze. Using GGP Bovine 150K and Bovine 50K DNA microarrays, we determined the genotypes of over 1,000 cows born between 2007 and 2022, belonging to nine agricultural enterprises in the Sverdlovsk region. Comparative groups included genotypes of Black Pied, Kholmogory, Tagil, Holstein, and Jersey breeds. Data analysis employed PCA, fastSTRUCTURE, and genetic differentiation assessment (F_{ST}). The results revealed that the vast majority of cows born in the Sverdlovsk region prior to and including 2014 exhibited genetic similarity to the Black Pied breed. Nevertheless, starting in 2015, cows born in the region showed greater genetic affinity to the Holstein breed than to the Black Pied. Genetic differentiation estimates (F_{ST}) between cows born after 2015 and Holstein bulls indicate the completion of the transition to the Holstein breed, driven by crossbreeding strategies. These findings propose a reference framework for breed identification in Black Pied versus Holstein cattle. A hypothesis linking herd gene pool characteristics to average milk yield per dairy cow was tested. Principal coordinate analysis based on the full set of genetic markers did not confirm this hypothesis. The observed differences in dairy productivity are likely attributable to environmental factors or genetic variations in specific genomic regions.

1 Introduction

The history of dairy cattle breeding in the Middle Urals dates back more than 200 years, and its main stages are shown in Figure 1. Initially, bulls of the Kholmogory and Yaroslavl breeds were used to improve unproductive native cattle, as a result of which a local breed was formed, called the Tagil breed. The final formation of the Tagil breed occurred by the beginning of the 20th century after a short period of breeding "in itself" and using Dutch bulls to improve it [1]. In the middle of the 20th century, the Ural type of Black Pied cattle appeared on the basis of the Tagil breed, through crossbreeding with East Frisian bulls. In the last 50

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years, there has been a consistent Holsteinization process by crossing breeding stock with Holstein bulls imported from abroad. During this time, a number of Holstein Black Pied cattle were formed, a patent was obtained for the Ural type of Black Pied cattle, and a significant number of breeding herds in the region were transferred to the Holstein breed [2, 3].

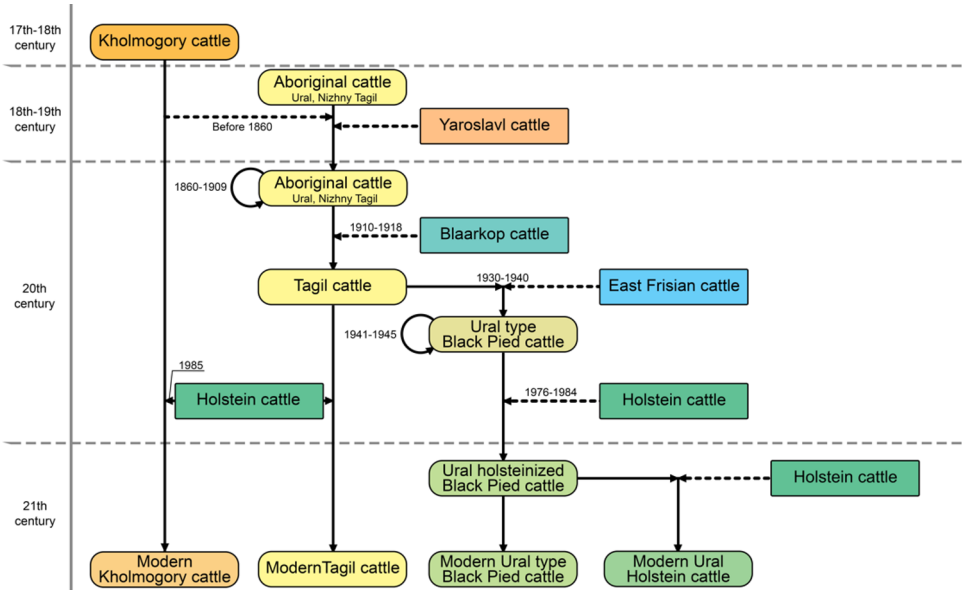


Fig. 1. The scheme of dairy cattle formation in the Sverdlovsk region. A solid line indicates a direct genealogical relationship within the breed, a dotted line indicates crossbreeding, and an arrow on the circle indicates the stages of breeding "in itself".

The current document regulating the procedure for determining the breed of livestock is the "Methodological recommendations for conducting a breed inventory of the dairy cattle breeding stock" [4]. These recommendations were prepared by a working group of the Ministry of Agriculture of the Russian Federation to harmonize with the Decision of the Board of the Eurasian Economic Commission dated 08.09.2020 No. 108. According to this document, the breed is determined by blood, i.e. by pedigree. This is a simple and affordable method, but it has limitations because it does not rely on the results of genotyping individual animals. The fulfillment of the requirements of the "Methodological Recommendations" led to a simultaneous change in the breed affiliation of a significant number of breeding cattle herds in the Sverdlovsk region. Since 2022, many animals previously classified as Black Pied have become Holsteins.

In this paper, the transition "Black Pied – Holstein breed" will be described using information about animal genotypes. Previously, a similar study was performed using microsatellite markers [5]. It showed a gradual transformation of the gene pool of cattle born in 2008-2019 towards similarity with the gene pool of bulls belonging to Uralplemcenter JSC. The main limitation in this work is the use of microsatellite loci, their small number and diversity require consideration of the gene pool of a group of livestock, but not individual animals, which is why this method has a relatively low resolution.

Today, the technology of SNP chips is widely used for genomic research, considering the species-specific single nucleotide polymorphisms (SNP) [6, 7]. SNPs are used in determining the phylogeny of a population [8, 9], establishing the origin [10], and determining the genetic diversity of a population [11-13]. When conducting population-genetic research, the use of SNP chips is a more modern and preferred method.

2 Materials and Methods

2.1 Sample collection and genotyping

Samples for the study were taken from 9 agricultural organizations in the Sverdlovsk region. For genotyping of brood stock, blood was taken from the tail vein into tubes with EDTA, and seed material was used for genotyping of Holstein breeding bulls (HOL). A total of 1,115 full-aged cattle born in 2007-2022 were selected for the study group. Data on the birth years of the studied livestock were taken from the SELEX database.

For some of the samples, DNA was isolated independently using a DNA Extran-1 kit (Syntol LLC, Russia) in accordance with the manufacturer's protocol, and some of the blood samples were sent to genotyping organizations without DNA isolation. DNA and blood were stored and transported at -20°C.

The genotypes were deciphered in two organizations, namely the Center for the Collective Use of Scientific Equipment "Bioresources and Bioengineering of Farm Animals" on the basis of the FSBSI FRC for Animal Breeding n.a. L.K. Ernst and Miratorg LLC using GGP DNA biochips Bovine 150K (Neogen, USA) – 204 samples and Bovine 50K – 396 (Illumina, USA). In the same organizations, DNA was isolated from the blood, if necessary. The genotyping data of 515 heads of cattle in the Sverdlovsk region were obtained from [14, 15]. In addition, 24 samples of Black Pied (BP), 39 of Kholmogory (KHLM) and 19 of Tagil breeds were selected from open sources [16, 17]. The Jersey (JER) samples were used as an external group [18]. The genotypes of cattle were combined using the PLINK v1.9 software (option --merge) [19].

2.2 Population structure assessment over time

In the combined database containing the genotypes of all analyzed animals, duplicate/identical twins, ancestor-descendant and first-degree relatives were identified and deleted using the KING software [20]. The data was then filtered in PLINK v1.9 with the following options --geno 0.01, --indep-pairwise 50 5 0.5, --maf 0.05, --hwe 0.000001, and --mind 0.1. As a result, 688 samples (heads) and 8057 SNPs were available for the analysis of the population structure, the total frequency of genotyping was 1. The principal component method was performed using the --pca function in PLINK v1.9, and the results were visualized in the R-project [21] using the ggplot package [22]. Clustering of samples based on PCA results was performed using the k-means method, the fviz_nbclust() function and method = 'wss' factoextra v1.0.7 package [23]. The assessment of genetic homogeneity was carried out using the fastSTRUCTURE program, in which the value of K chooseK was determined [24], and the results were visualized by pong [25]. A total of 10 calculations of genetic uniformity with specified seed values 100, 1293, 8432, 3212, 7543, 9345, 1010, 1593, 8472, and 8212 were performed. The genetic differentiation of F_{ST} was evaluated in ipADMIXTURE using the ipADMIXTURE() function and admixRatioThs=0.3 [26].

2.3 Assessment of the space-time structure

The analyzed agricultural organizations of the Sverdlovsk region were divided into groups (productivity quartiles) based on data on milk yield per feed cow in the period 2011-2023. The genotypes of Black Pied cattle and Holstein bulls were used as external controls. As a result of filtering the data according to the procedure described above, 547 samples from 8 farms and two breed groups were available for analysis, the number of SNPs was 23323, the

total frequency of genotyping was >0.97 . The PCA process and F_{ST} assessment are described above.

3 Results and Discussion

3.1 Dynamics of cattle genetic structure over time

At the first stage of the analysis, we examined the genetic similarity of cattle groups, namely five different breeds and cows of the Sverdlovsk region, considering the year of their birth (Figure 2). The results of the PCA analysis are shown in Figures 2a and 2b. The first, second, and third main components account for 7.39% of the total variance. PC1 separates the Jersey, Kholmogory, and Holstein breeds well. Jersey cattle, taken as an external comparison group, are the most distant from the Black Pied root breeds. According to PC1 and PC2, the breeds inside the Black Pied root are arranged in a row: Kholmogory – Tagil – Black Pied – Holstein. According to PC1 and PC3, Black Pied cattle and breeding stock of the Sverdlovsk region born in 2007-2014 are differentiated from Holstein cattle and cows born in 2015-2022.

The fastSTRUCTURE analysis showed that the model with $K=4$ is the most informative. The average level of pairwise matching of fastSTRUCTURE results for $K=2$ is 0.999, $K=3$ is 0.984, and $K=4$ is 0.973. The results demonstrate the separation of the Jersey, Holstein, and Kholmogory breeds into independent clusters; the remaining groups are of mixed origin (Figure 2c). At the same time, in the groups of BP and cows of the Sverdlovsk region from 2007 to 2014, a component that does not relate to other breeds prevails. The identified component decreases from generation to generation of Sverdlovsk cattle and gives way to the Holstein admixture. There was also a sharp increase in the "Holstein" component from 22% to 62% in the period 2014-2015.

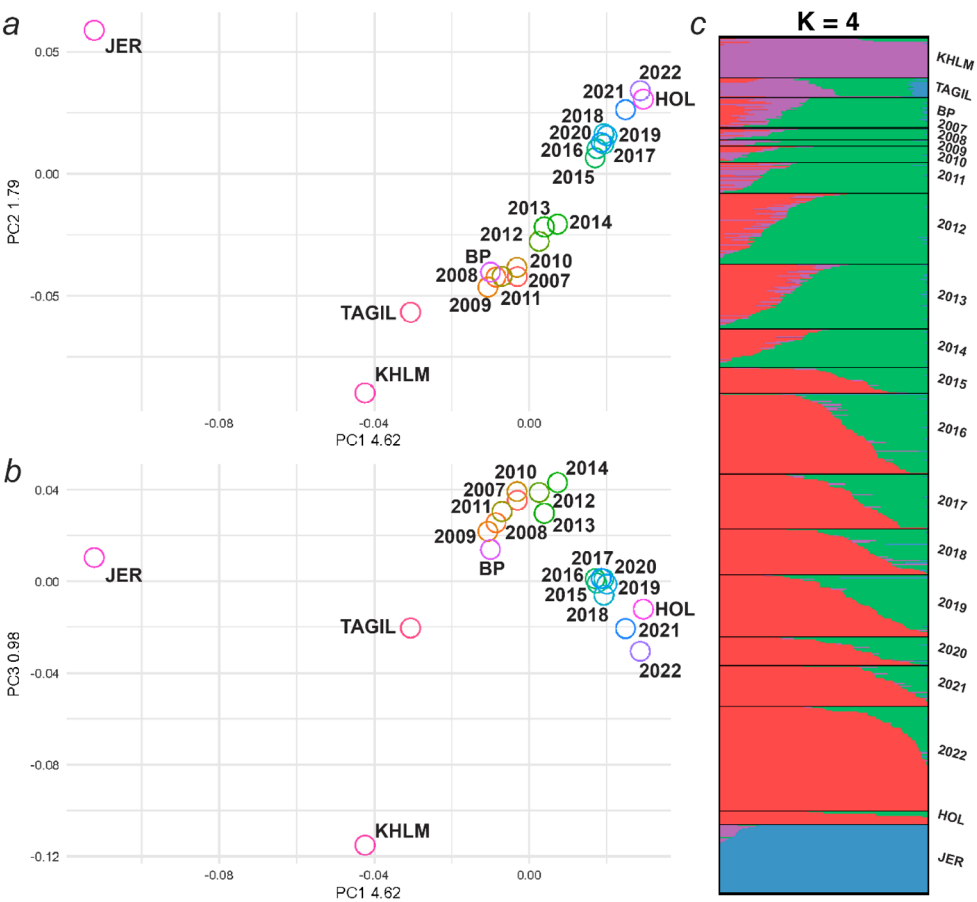


Fig. 2. Graphic representation of cattle genetic structure in the Sverdlovsk region. The results of the PCA analysis are shown on the left, each point corresponds to the average value for the group for PC1 and PC2 (a), PC1 and PC3 (b). The dots are colored depending on the breed/group. c is a genetic admixture analysis showing the proportions of ancestral populations for K=4. Each sample is represented by a separate column. KHLM – Kholmogory; TAGIL – Tagil; BP – Black Pied; HOL – Holstein; JER – Jersey; numbers from 2007 to 2022 indicate groups of breeding stock in the Sverdlovsk region of the corresponding years of birth.

At the second stage of the analysis, the genotypes of individual heads were examined, the results are shown in Table 1 and Figure 3. Based on PCA results, clustering using the k-means method was performed, the number of clusters (k=4) was determined using PC1, PC2, and PC3. According to the clustering results (Table 2), Jersey cattle and the Kholmogory breed with Tagil cattle are separated into separate clusters. An individual of one of the farms under study was assigned to the Jersey breed cluster. The samples of the local breeding stock were grouped into age groups; the starting point for the separation was the revealed increase in Holstein admixture in cows, which occurred in 2015. The majority of cows born in the period 2007–2014 are in a common cluster with Black Pied cattle, and cows born in 2015 and subsequent years with a group of Holstein cattle.

Table 1. Distribution of cattle samples by clusters based on the PCA result.

Breed/ Age group	Number of samples in cluster			
	Cluster 1	Cluster 2	Cluster 3	Cluster 4
KHLM	0	32	0	0
TAGIL	0	12	4	0
BP	0	2	22	0
2007-2011	0	2	51	0
2012-2014	0	1	126	13
2015-2017	1	0	15	114
2018-2020	0	0	7	103
2021-2022	0	0	2	115
HOL	0	0	1	10
JER	55	0	0	0

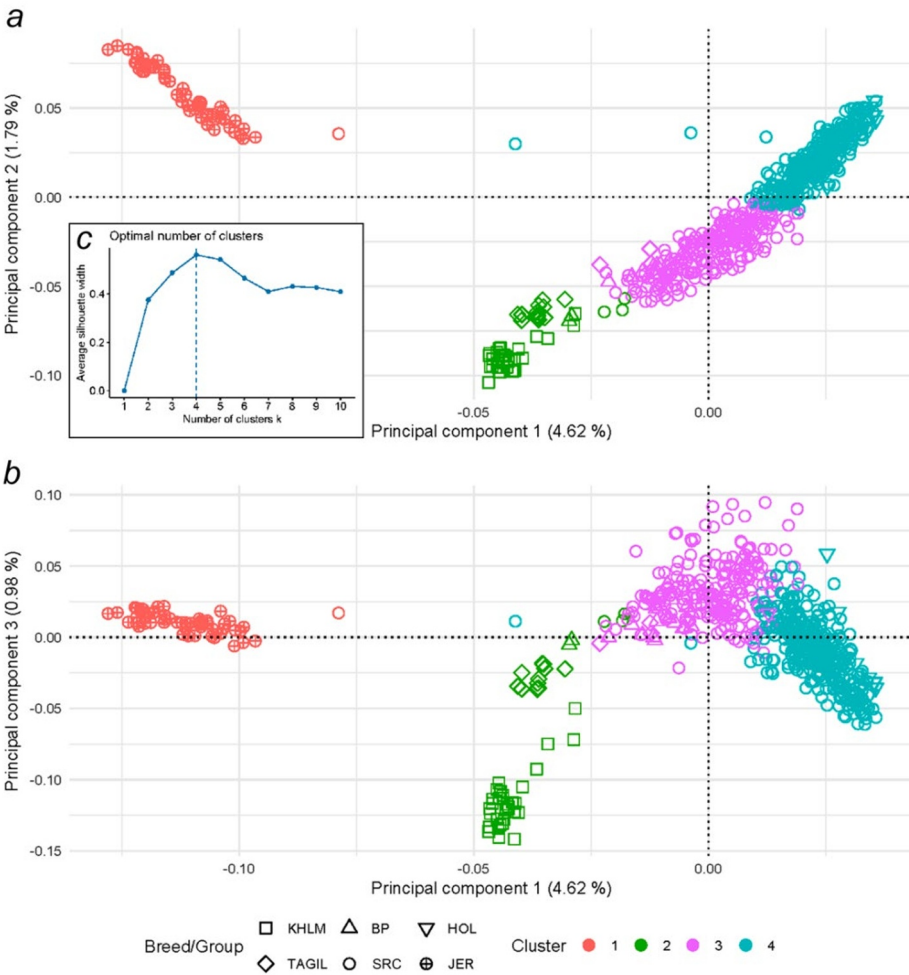


Fig. 3. Clusterization of groups of dairy cattle generations in the Sverdlovsk region, relative to breeds, using the k-means method of the PCA result. Each point represents the eigenvalues PC1 and PC2 (a), PC1 and PC3 (b) for a separate head. The corresponding color indicates the selected clusters. c is the determination of the optimal value of k by the silhouette method. KHLM – Kholmogory; TAGIL – Tagil; BP – Black Pied; HOL – Holstein; JER – Jersey; SRC – dairy cattle of the Sverdlovsk region

To assess the genetic differentiation of breeds and age groups of livestock in the Sverdlovsk region, the F_{ST} index was calculated (Figure 4). The greatest differentiation values were noted between Jersey cattle and a group of cows born in 2021-2022 ($F_{ST}=0.135$), as well as Jersey cattle and Holstein bulls ($F_{ST}=0.136$). The pairs KHLM/HOL and KHLM/2021-2022 are most distanced within the Black Pied root breeds (F_{ST} is 0.081 and 0.08, respectively). The F_{ST} value of the Black Pied breed (BP) and cows of the Sverdlovsk region increases from generation to generation from 0.012 to 0.037. In pairs of Holstein bulls and generations of Sverdlovsk cattle, on the contrary, F_{ST} decreases from 0.029 to 0.003. Between different generations of cows in the Sverdlovsk region, the lowest F_{ST} value was observed in the pair 2015-2017/2018-2020, the highest 0.029, in the pair 2007-2011/2021-2022.

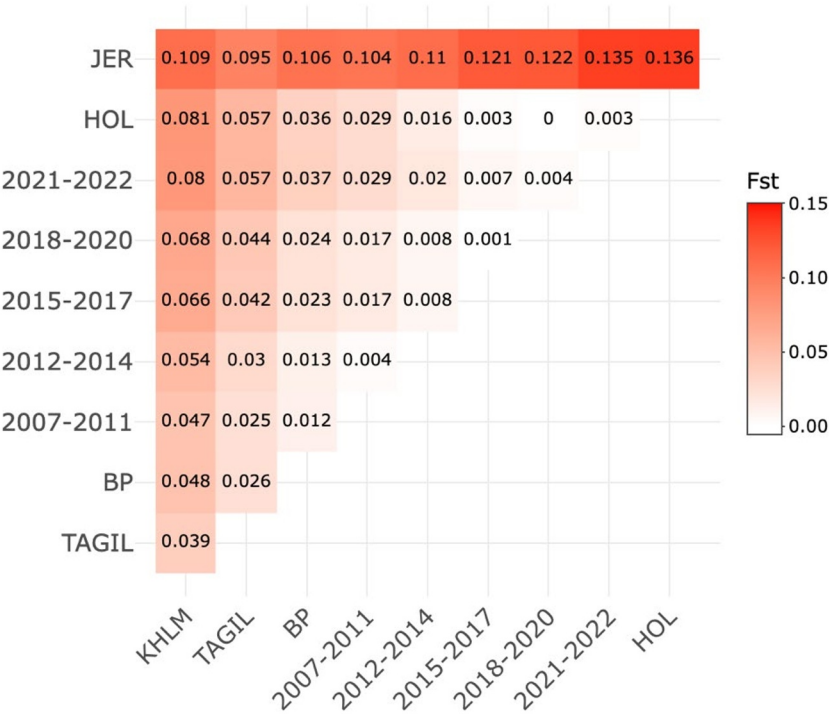


Fig. 4. Genetic differentiation of breeds and generational groups of dairy cattle. Negative F_{ST} values are replaced by 0. The color gradient from white to red reflects the F_{ST} value. The SE of the estimates varies from 0.0004 to 0.0013.

3.2 The spatial and temporal structure of the population

To assess the spatial structure, the sample was divided considering agricultural organizations and generational groups. In addition to cattle from the Sverdlovsk region, Black Pied cattle and Holstein bulls were included in the analysis. Farms were assigned quartiles of productivity according to the average milk yield per feed cow in the period from 2011 to 2023 [27]: Q1 – Farm4, Farm6, Farm9; Q2 – Farm2, Farm3; Q3 – Farm1, Farm7; Q4 – Farm5. At the same time, there are significant differences in the average milk yield per cow between the quartiles (Figure 5).

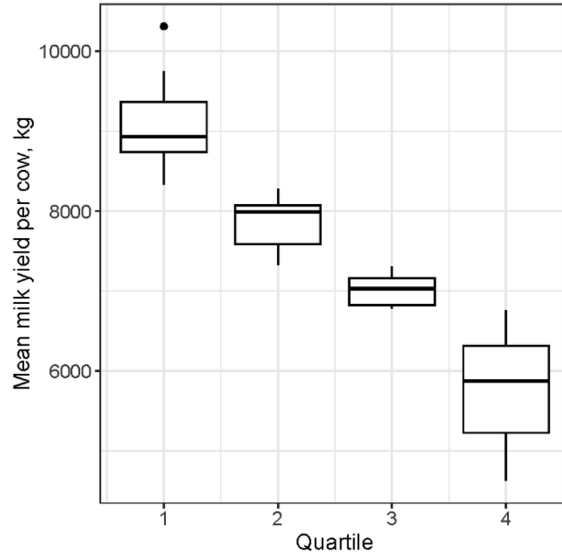


Fig. 5. Productivity quartiles of average milk yield per cow by year. Pairwise comparisons were performed using the exact Wilcoxon criterion, the $p\text{-value} < 0.05$ between quartiles, and the correction method was the Bonferroni correction.

Both in the case of the analysis of the entire livestock and in the case of sample division by farm, over the course of 15 years, the transformation of the gene pool of livestock from the Black Pied breed to the Holstein breed has been noted, Figure 6. At the same time, there are no differences in the transformation rate of the gene pool between farms or productivity quartiles.

To avoid deviations in the comparison of groups of different sizes, we used the formation of subsamples within each group of 10 samples and the F_{ST} estimate for groups of equal size in 500 repetitions, the average value and 95% confidence interval for each group are shown in Figure 7. The assessment of the genetic fixation index (Figures 8) showed a decrease in F_{ST} between farms of different quartiles of productivity from 2012 to 2020. So, the higher the quartile, the greater the F_{ST} relative to the HOL group. Interestingly, the F_{ST} scores in the latest generation are starting to rise in relation to the past in all the pairs being compared. The indices of genetic differentiation of cattle from Sverdlovsk farms for 2021-2022 and Black Pied cattle (BP) not only reach the value of $F_{ST}=0.4$ BP/HOL pairs, but exceed it. The genetic differentiation between farms is increasing, as well as between farms and Holstein bulls.

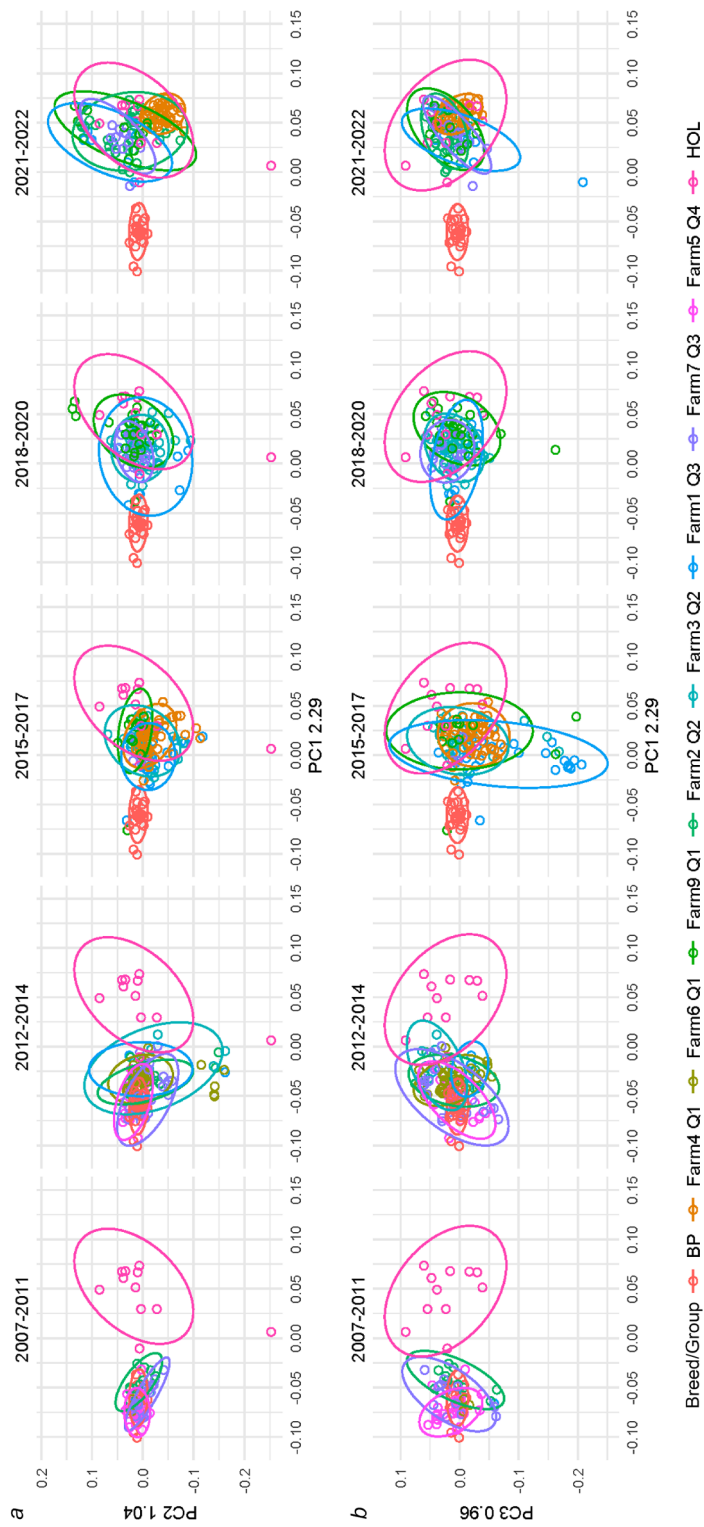


Fig. 6. The genetic structure of cattle in the Sverdlovsk region, considering farms and generations. Each point corresponds to the eigenvalues PC1 and PC2 (a), PC1 and PC3 (b). The ellipses show a 95% confidence interval calculated based on a multidimensional t-distribution. The points are colored depending on breed and farm. BP – Black Pied; HOL – Holstein; broodstock groups of the Sverdlovsk region are divided by farms and productivity quartiles.

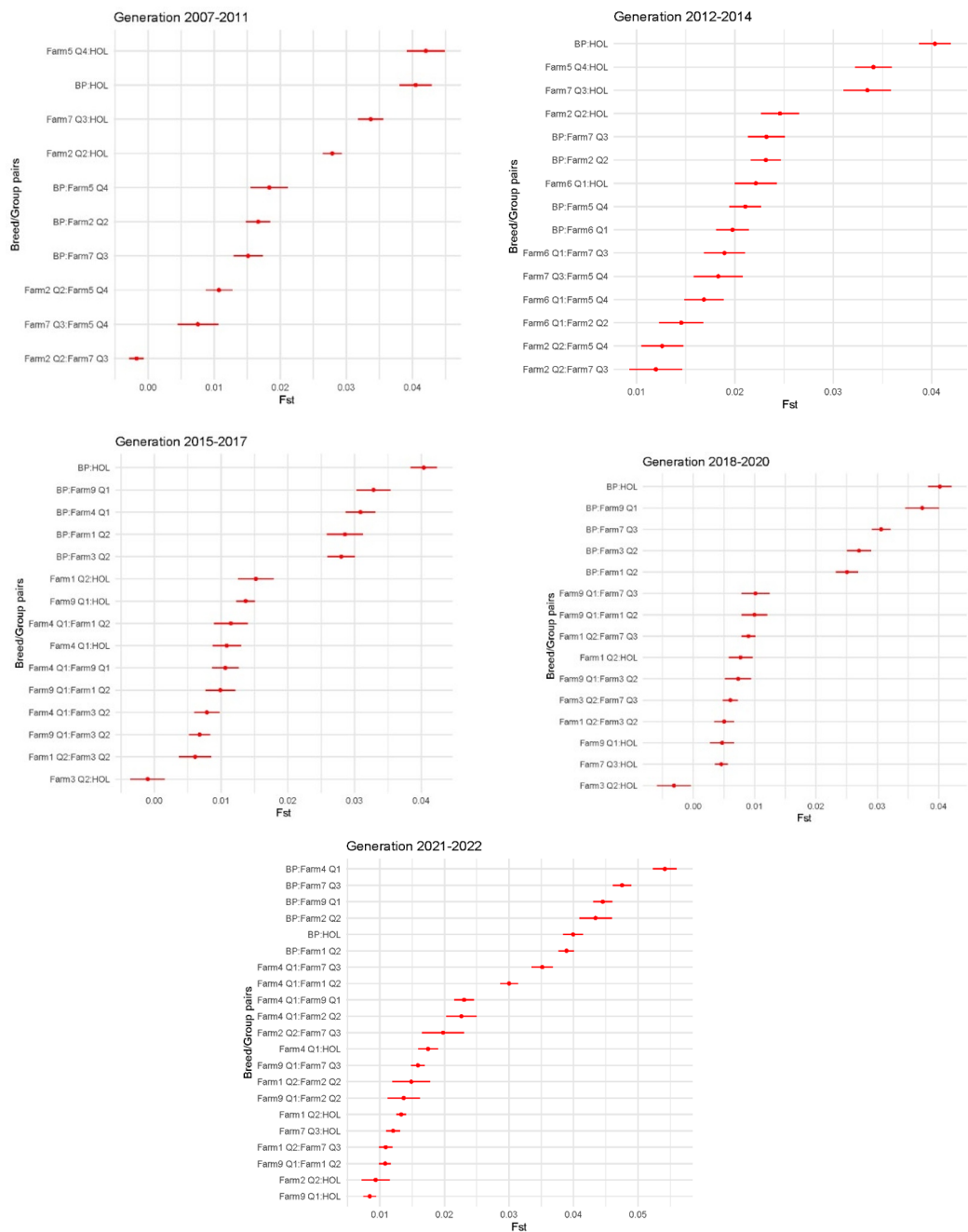


Fig. 7. Mean values (red points) and 95% confidence interval (red lines) F_{ST} . Generations are marked in the upper-left corner of each graph.

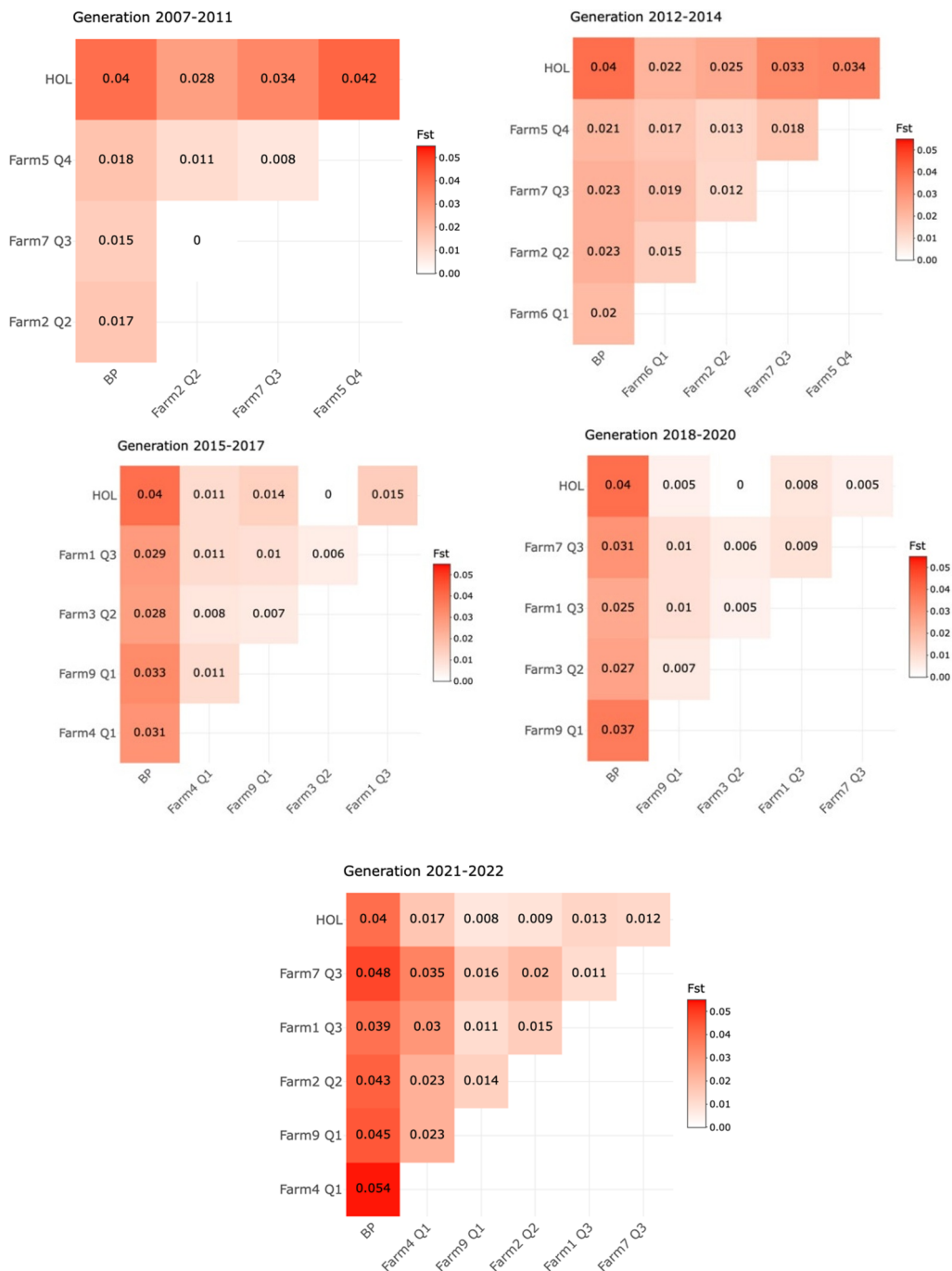


Fig. 8. Genetic differentiation of breeds and generational groups of dairy cattle from different farms. Negative F_{ST} values are replaced by 0. The color gradient from white to red reflects the F_{ST} value. The SE of the estimates varies between 0.0005–0.0011.

4 Conclusion

The data obtained indicate that in the territory of the Sverdlovsk region, the transformation of the gene pool of dairy cattle in the direction of the Black Pied breed – Holstein breed occurred in less than 15 years. At the same time, the most "dramatic" change in the gene pool took place in 2015. The reasons for this "leap" will be discussed in subsequent papers, but it can already be linked to the expansion of the range of suppliers of sperm products to the regional market. Thus, all the studied heads born up to 2014 were obtained using bull seed of European and domestic breeding from a regional supplier. Whereas, after 2014, two more organizations supplying sperm products appeared on the market, mainly distributing the seed of American-bred bulls.

The clustering of PCA coordinates by the k-means method made it possible to divide the regional livestock population into two differentiated groups, one of which is close to Black Pied cattle, and the other to Holsteins. A similar approach can be used to determine the breed of livestock, provided that reference genotypes of other breeds are used.

According to the results of the analysis of the influence of the factors "farming" and "dairy productivity of animals (productivity quartile)" on the genetic structure of livestock in the Sverdlovsk region has not been established. The increase in the values of genetic differentiation (F_{ST}) in the last analyzed generation of cows and the group of Holstein bulls may be related to the inclusion in the sample of relatively old bulls born in 2006-2015 (the average year of birth is 2012). The high value of F_{ST} in the Farm4 Q1/Farm7 Q3 pair in the 2021-2022 generation can be explained by the fact that in Farm4 the herd consists mainly of cows whose fathers are bulls of American breeding, and in Farm7 – European and domestic. Previously, the genetic difference between breeding bulls has already been shown on microsatellite data [5].

Acknowledgment

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