

Whole-genome sequencing revealed the population structure of Fujian chicken breeds

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Abstract: Indigenous chicken breeds from Fujian Province, China, exhibit unique and distinctive phenotypic characteristics, including morphology, behaviour, integumentary pigmentation, feather colouration, and production performance. However, the underlying genetic basis governing these specific traits remains unclear. This study aimed to elucidate the population structure of six Fujian local chicken breeds [Bairong chickens (BRCs), Jinhua chickens (JHCs), Mingqing chickens (MQCs), Dehua chickens (DHCs), Xiangdong chickens (XDCs), and Hetian chickens (HTCs)] in terms of their genetic resources within the province. The whole-genome resequencing revealed 8 678 612 single nucleotide polymorphisms (SNPs) in a cohort of 36 chickens. The results revealed a partial mismatch between the clustering patterns and geographic distributions of the six populations, with BRC displaying a noticeable genetic divergence from other chickens. Moreover, the genetic distance between XDC and HTC in Longyan County was relatively close and converged with JHC, MQC, and DHC into a subgroup. These findings provide a comprehensive understanding of the intrinsic characteristics and utilisation prospects of chicken germplasm resources in Fujian Province.

Keywords: indigenous chicken; genetic structure; genomic resequencing; germplasm resource

The chicken is one of the earliest domesticated poultry species, with a history dating back ten thousand years (Xiang et al. 2014). Owing to their short growth cycle, ease of breeding, nutritional richness, and other advantageous traits, chickens are widely distributed in breeding centres worldwide (Gongora et al. 2008; Mwacharo et al. 2013). Chickens serve as a valuable source of high-quality

protein for human consumption and hold significant cultural significance. Throughout history, they have been utilised for religious rituals, entertainment, and ornamental purposes (Miao et al. 2013). Owing to its rich ecological and cultural diversity and distribution, China is recognised as one of the countries that possesses abundant chicken genetic resources (Wang et al. 2020). As reported

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in the 2021 release of the National Livestock and Poultry Genetic Resources, there are currently 115 indigenous chicken breeds. Unlike commercially bred chickens, which are subject to rapid and intensive artificial breeding processes, local chicken breeds have developed gradually over time through both natural and selective breeding. This slow evolution has resulted in a rich genetic diversity that enhances their ability to adapt to environmental changes (Hua et al. 2021). Furthermore, these breeds display distinct genetic variations that influence the characteristics such as the feather colour and comb shape (Dorshorst et al. 2015; Hua et al. 2021). Therefore, it is essential to protect these local chicken populations to meet future reproductive and production demands while preserving their socioeconomic, cultural, and ecological importance (Chen et al. 2019).

Located on the southeast coast of China, Fujian Province is characterised by mountains descending towards the sea, lush vegetation, and a subtropical climate that fosters ample rainfall, creating a distinctive natural environment conducive to the development of diverse livestock and poultry resources. Bairong chickens (BRCs), commonly referred to as silkies, are primarily distributed in Quanzhou, Xiamen, and the coastal regions of southern Fujian. Owing to the high concentration of melanin, the skin, bones, meat, and viscera of BRCs are black, rendering it a valuable breed with nourishing and unique medicinal properties and making it highly regarded in China as a medicinal chicken with substantial economic value (Zhang et al. 2018). With Jinhu chickens (JHCs), the hens have a cluster of black or jute crown feathers on top of their head, which is the same germplasm resource of high-quality black bone chickens in Fujian Province, such as Dehua chickens (DHCs). Hetian chickens (HTCs), known for their very palatable meat, thin skin, and fine bones, are a renowned local broiler breed that originated in Changting County, Longyan city. Minqing chickens (MQCs) are a large breed characterised by shanks covered with blue-black or jute feathers. Xiangdong chickens (XDCs) are a local breed of Sanhuang chicken with a long-standing heritage. XDCs feature a round and plump physique, and the meat is known for its tenderness and exquisite flavour, whose capon is frequently utilised in the preparation of “white-cut chicken”, which is a famous Chinese dish.

Currently, there is limited research on the local chicken population in Fujian Province, and its structure remains unclear. Zheng et al. (2008) conducted a study in which six microsatellite markers were used to assess the genetic distance between local chicken populations in Fujian and Jiangxi Provinces. However, the use of microsatellite markers for developing microsatellite loci in new breeds is arbitrary, and the detection of polymorphisms *via* these markers is a time-consuming process, presenting certain limitations (Wenne 2023). In recent years, significant advancements in genotyping chip and genomic resequencing technologies have enabled the rapid, accurate, and comprehensive acquisition of chicken genome information (Malomane et al. 2019). Furthermore, the whole-genome resequencing technology has been demonstrated to be a valuable tool for the genetic evaluation and exploration of genetic relationships in various chicken breeds (Wang et al. 2015, 2020). Wang et al. (2015) conducted a comprehensive genome analysis of Tibetan chickens inhabiting high-altitude regions. The results of their population structure analysis revealed the existence of two distinct populations of Tibetan chickens with no gene flow. Notably, one of these populations exhibited mixed ancestry with commercial chickens, suggesting that Tibetan chickens on the Qinghai-Tibet Plateau originated from two independent sources.

In the 1980s, owing to the opening of China's economy to foreign markets and the subsequent introduction of foreign chicken breeds, crossbreeding between local Chinese chicken breeds and the newly introduced breeds became widespread. This led to a significant mixing of genetic material among these populations. According to records, MQCs have been subjected to crossbreeding with foreign breeds, leading to a mixture of lineages. However, since 2007, the Chinese government has implemented various protective measures, leading to the gradual recovery of the population characteristics and production performance of the MQCs. However, the genetic relationships among local chicken populations in Fujian remain unclear, hindering the complete exploitation of their genetic potential. Accordingly, this study employed whole-genome resequencing data to analyse the population structure of six local chicken breeds in Fujian. The aim was to comprehensively grasp the population structure of the local chicken breeds in Fujian and establish a theoretical foundation for the future exploitation of local resources.

MATERIAL AND METHODS

Experimental animals

The protocol of this experiment was approved by the Animal Ethics Supervisory Committee of the Institute of Animal Husbandry and Veterinary Medicine, Fujian Academy of Agricultural Sciences, and was performed in accordance with the Animal Welfare China guidelines.

For this study, we selected a total of 36 chickens, with six individuals from each of the following local breeds in Fujian Province: BRC, DHC, HTC, JHC, MQC, and XDC. Each breed was sourced from a conservation farm (Figure 1). The selected individuals were all unrelated within three generations, ensuring genetic diversity. Each of these six breeds is listed on the National List of Livestock and Poultry Genetic Resources, highlighting their importance and preservation status. Blood samples were collected from the 36 chickens *via* standard sub-wing venepuncture techniques for the subsequent DNA extraction.

DNA extraction and whole-genome sequencing

Genomic DNA was extracted from the fresh blood samples *via* a modified phenol-chloroform

method (Yu et al. 2018). The DNA sample concentration and quality were assessed *via* a NanoDrop 2000 Spectrophotometer (Thermo Fisher Scientific, Waltham, USA) and 1% agarose gel electrophoresis. In this study, standard procedures were employed to construct a double-terminal library *via* a Nextera DNA Sample Preparation Kit (Illumina, San Diego, USA), with an average read length of 150 bp, for 36 samples. The whole-genome sequencing was conducted *via* the Illumina NovaSeq 6000 platform at Novogene (Beijing, China). After sequencing, Trimmomatic (v0.39, Usadel Lab, Aachen, Germany) (Bolger et al. 2014) was used to filter the raw data, eliminating connectors and low-quality bases to yield clean genome data for Fujian local chickens with an average coverage depth of 10.65 times (Table 1).

Variants calling and quality control

To obtain high-quality single nucleotide polymorphism (SNP) datasets, the clean reads were compared to the CH016699485.2_GRCg7b genome *via* the BWA-MEM algorithm (Li and Durbin 2009). The comparison results were then converted to the BAM format and sequenced *via* SAMtools (Li et al. 2009). After sequence alignment, we processed the data by sorting the sequences, deduplicating,

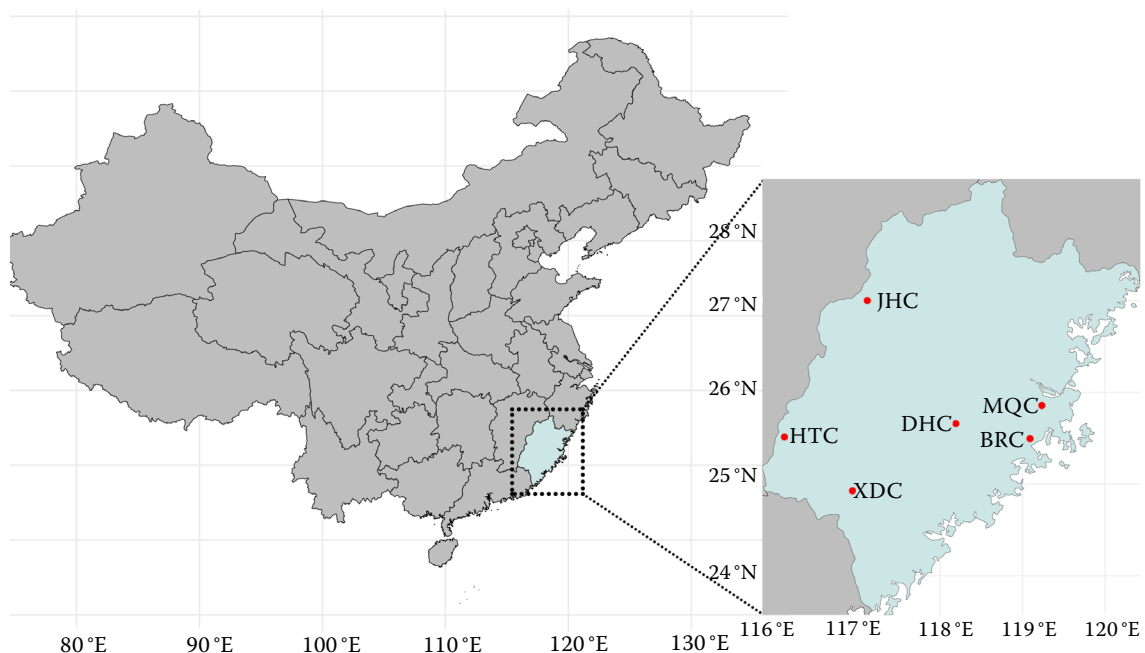


Figure 1. The distribution of six Fujian chicken breeds

BRCs = Bairong chickens; DHCs = Dehua chickens; HTCs = Hetian chickens; JHCs = Jinhu chickens; MQCs = Minqing chickens; XDCs = Xiangdong chickens

Table 1. Sequencing depth for each individual

Breed	Abbreviation	Nsnp	ID	Depth (×)
Bairong chicken	BRC	4 230 176	BRC1	9.33
			BRC4	10.84
			BRC7	9.55
			BRC43	11.44
			BRC56	10.41
			BRC59	10.00
Hetian chicken	HTC	4 782 363	HTC11	10.02
			HTC12	10.96
			HTC37	11.45
			HTC38	11.06
			HTC39	11.25
			HTC40	11.08
Jinhu chicken	JHC	4 525 969	JHC1	10.35
			JHC10	9.50
			JHC20	9.46
			JHC32	10.96
			JHC37	10.80
			JHC42	11.47
Minqing chicken	MQC	4 806 723	MQC1	10.79
			MQC7	10.98
			MQC13	11.04
			MQC34	10.88
			MQC40	10.78
			MQC45	10.62
Dehua chicken	DHC	4 733 572	DHC1	11.27
			DHC6	10.63
			DHC12	10.86
			DHC37	10.28
			DHC42	10.24
			DHC50	10.48
Xiang-dong chicken	XDC	4 521 345	XDC1	11.45
			XDC6	11.87
			XDC37	10.83
			XDC42	10.85
			XDC52	10.71
			XDC84	8.74

Nsnp = number of SNPs in the breeds; snp = single nucleotide polymorphism

and reindexing them *via* the LocusCollector and Realigner commands in Sentieon (Aldana and Freed 2022). To ensure the selection of high-quality variants, we applied the VariantFiltration command in GATK (v4.1.9, Broad Institute, USA, <https://github.com/broadinstitute/gatk>), which performs

the hard filtering of the data. This step was crucial in refining our dataset to only include the most reliable SNPs. Further refinement was achieved by applying filters *via* PLINK (v2.0, Broad Institute, USA, <https://www.cog-genomics.org/plink/2.0/>) for a minor allele frequency (MAF) greater than 1% and a call rate exceeding 95%. These stringent criteria led to the identification of 8 678 612 SNPs, which were used for the subsequent analyses.

Population structure analysis

To infer the population structure of six local chicken breeds in Fujian Province, PLINK (v1.90, USA) (Purcell et al. 2007) was used to construct an identity-by-state (IBS) matrix to quantify the similarity between the individuals. The command “neighbour” in PHYLIP (v3.65, USA) (Felsenstein 1993) was used to construct a neighbour-joining phylogenetic tree (NJ tree), and the online software iTOL (Letunic and Bork 2016) was used for visualisation. Moreover, the “--grm” parameter in GCTA (v1.93.2, Australia) (Mckenna et al. 2010) was used for the principal component analysis (PCA). To assess the level of the population admixture, ADMIXTURE, v1.3.0, USA) (Peter 2016) was employed, utilising the default settings and varying the assumed *K* (the number of ancestral leanages) from 2 to 6. To minimise the influence of linkage imbalance between the SNP sites, the parameter “-- indep-pairwise 50 10 0.2” in PLINK (Purcell et al. 2007) was used to carry out linkage disequilibrium (LD) construction, and finally, the R language tool was used for the visualisation.

RESULTS

To investigate the population structure and genetic relationships of local chicken breeds in Fujian Province (Figure 1), phylogenetic trees and PCA were constructed *via* the whole-genome resequencing data from 36 chickens. The individuals of each breed formed distinct clusters, indicating consistent genetic relationships. These findings suggest that these breeds may have experienced distinct evolutionary trajectories due to the regional adaptation selection or genetic drift following domestication. The phylogenetic analysis revealed a strong genetic relationship between JHC, MQC, DHC, XDC, and

HTC, as these five breeds formed a distinct clade in the NJ tree (Figure 2A). Within this clade, all six HTC individuals are closely grouped into a single lineage, which is consistent with the sampling records. In contrast, BRC displays a distinct genetic profile, forming a separate branch in the NJ tree that distinguishes it from the remaining breeds.

In addition, the results of the PCA provided additional support for the distinct clustering of BRC, which was separate from the other five breeds and presented a greater number of unique SNPs (Figure 2B). Principal component (PC1) (12.71% total variance explained) differentiated HTC from the remaining population, whereas PC2 (6.93% total variance explained) demonstrated genetic differentiation of BRC from the other four breeds, appearing as an isolated component. This may be attributed to the fact that the samples originated from closely related individuals within the same lineage, resulting in high genetic purity. A comparable pattern is evident in the admixture results (Figure 3).

An admixture analysis was conducted to explore the evolutionary origins and historical patterns of the genetic mixing across all the tested breeds. The analysis varied the K values from 2–6 to better understand the population structure (Figure 3A). At $K = 2$, the analysis revealed a clear division into

two distinct subpopulations characterised by significant genetic differences between the HTC population and the other populations, with JHC, DHC, MQC, and XDC showing only a minor proportion of HTC genetic influence. At $K = 3$, the patterns aligned with the PCA results (Figure 2B), where BRC formed an independent genetic lineage. At $K = 4$, the JHC also formed its own distinct lineage. By $K = 5$, XDC exhibited a complex pattern of multiple ancestries. The cross-validation error plot indicates that the lowest error occurs at $K = 6$, suggesting that this level of genetic resolution provides the most robust clustering in terms of the genetic differentiation among the studied breeds (Figure 3B). At this stage, all six breeds form distinct genetic lineages, with XDC demonstrating mixed genetic relationships.

DISCUSSION

Chicken breeds from Fujian Province typically exhibit favourable characteristics, such as high meat and egg quality, robust stress resistance, high genetic diversity, and remarkable environmental adaptability. These local breeds represent invaluable genetic resources that can be utilised to enhance desirable

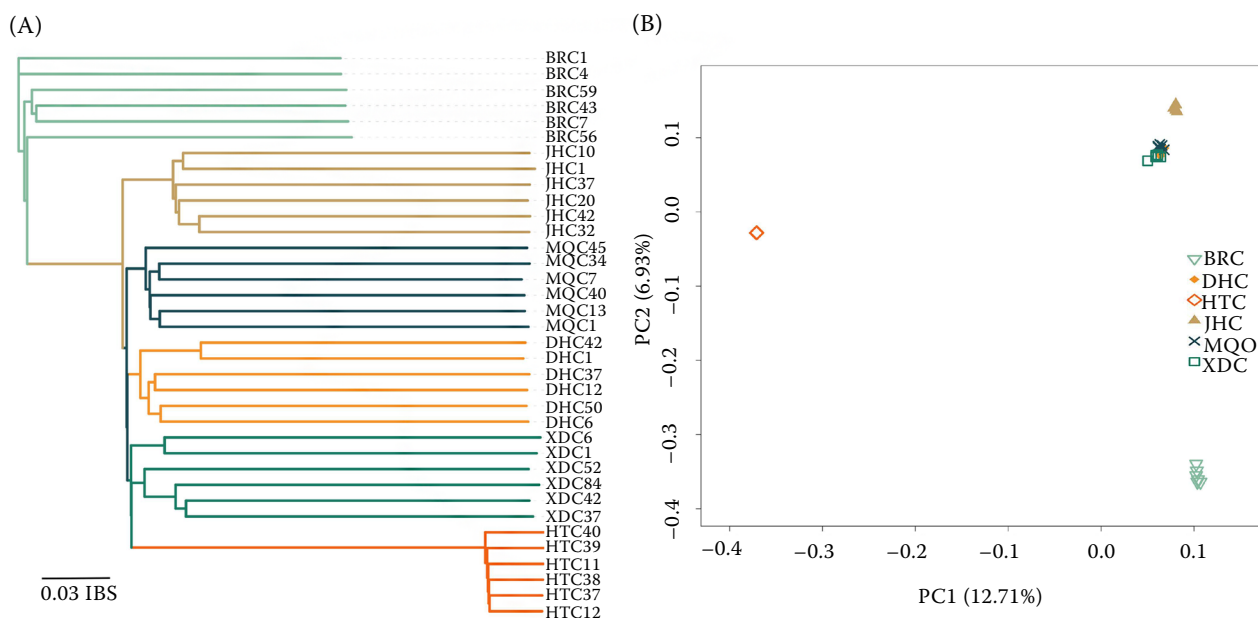


Figure 2. Population structure of six Fujian chicken breeds

(A) Neighbour-joining (NJ) tree constructed with an identity-by-state matrix among the 36 samples; each colour represents one breed; (B) Scatter plot of six Fujian chicken breeds between PC1 and PC2

BRC = Bairong chicken; DHC = Dehua chicken; HTC = Hetian chicken; IBS = identity-by-state score; JHC = Jinhu chicken; MQC = Minqing chicken; PC = principal component; XDC = Xiangdong chicken

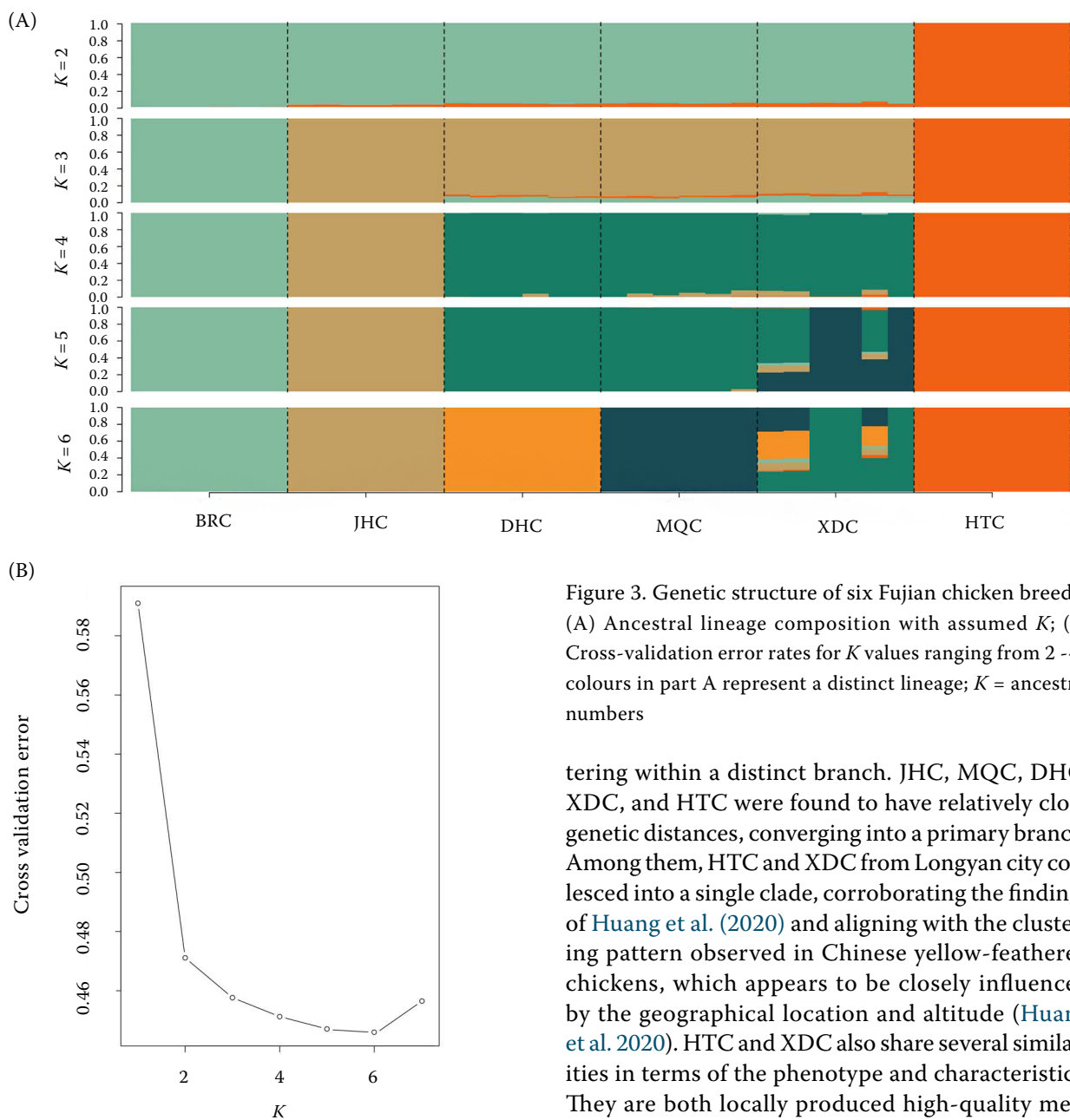


Figure 3. Genetic structure of six Fujian chicken breeds (A) Ancestral lineage composition with assumed K ; (B) Cross-validation error rates for K values ranging from 2 -- 6 colours in part A represent a distinct lineage; K = ancestral numbers

traits and facilitate the development of new breeds. The safeguarding and effective utilisation of genetic resources hold paramount importance for ensuring the sustainable development of the poultry industry. This study investigated the population structure of six local chicken breeds in Fujian Province *via* whole-genome resequencing data. An analysis of the population structure aids in advancing the understanding of breed formation processes. The results of the NJ tree analysis clearly divided these breeds into two distinct subgroups. Furthermore, BRC exhibited considerable genetic distance from the other five breeds, resulting in its separate clus-

tering within a distinct branch. JHC, MQC, DHC, XDC, and HTC were found to have relatively close genetic distances, converging into a primary branch. Among them, HTC and XDC from Longyan city coalesced into a single clade, corroborating the findings of Huang et al. (2020) and aligning with the clustering pattern observed in Chinese yellow-feathered chickens, which appears to be closely influenced by the geographical location and altitude (Huang et al. 2020). HTC and XDC also share several similarities in terms of the phenotype and characteristics. They are both locally produced high-quality meat products known for their palatable meat, thin skin, and fine bones. Furthermore, they exhibit unique flavours and are distinguished by brown or yellow feather colouration.

BRC, known for its white velvet-like feathers, holds a prominent position as an ornamental chicken worldwide. In different regions of China, various names, such as Taihe and Zhushi chickens, are used. The results of the NJ tree and the PCA indicate substantial genetic distance between the BRC and JHC, as well as between the BRC and DHC. This finding contradicts previous studies on population relationships using microsatellites (Zheng et al. 2008). The primary factor contributing to the disparity

in such results may stem from previous studies relying solely on a limited number of dispersed micro-satellite markers, thereby failing to obtain sufficient genetic information. In contrast, this study employed the whole-genome resequencing technology to comprehensively analyse the population genetic structure, enabling a thorough and precise examination of the genetic relationships among the chicken breeds. In addition, substantial genetic differences were observed between the DHC and BRC populations, which are located in Dehua County, Quanzhou city. Despite being in close geographical proximity, Dehua County, situated in the Daiyun Mountain area on the central ridge of Fujian Province, possesses complex terrain and ambiguous population characteristics. These factors may restrict gene flow and hinder gene exchange with BRCs.

The population structure analysis revealed that a predominantly pure lineage relationship existed between the BRC and HTC, although a minor admixture of the HTC lineage was observed in the other four breeds. This finding could be attributed to the germplasm characteristics and breeding history of the respective breeds. The HTC originates from Hetian town, Changting County, an area known for its complex terrain, numerous rivers, and sunny climate. The unique meat quality of HTC further distinguishes it from other breeds. Additionally, the challenging transportation conditions in mountainous areas limit the interaction of breeding chickens with other regions. In 2017, the population of HTC reached 6.77 million (Gao et al. 2018), underscoring its significant economic value compared with that of BRC. Consequently, owing to the importance of maintaining breed purity and preserving the value of the breeds, only a limited number of individuals can engage in crossbreeding between the two breeds. BRC is found in the coastal areas of Quanzhou, Xiamen, and other regions with convenient transportation, potentially contributing to the development of additional chicken germplasm resources.

In parallel with our own research findings, the lineage of BRC in Fujian was found to be distinctly separate from those of other chicken breeds in the same region. Notably, a significant proportion of the genetic lineage from DHC and MQC was present in the XDC population, despite notable differences in their physical appearance and breed characteristics. XDC, being a broiler chicken, exhibits desirable tenderness and palatability; how-

ever, it is characterised by a smaller physical stature and a suboptimal slaughter rate. Breeders may have facilitated the gene flow between XDC, DHC, and MQC to increase the meat yield of XDC.

CONCLUSION

This study offers a comprehensive genome-wide analysis of the genetic structure of six local chicken breeds in Fujian Province. The results revealed significant genetic differentiation between the BRCs and the other five breeds. However, JHC, MQC, DHC, XDC, and HTC clustered together as a distinct group, displaying a genetic structure that does not entirely align with their geographical distribution. These findings contribute to a deeper understanding of the germplasm characteristics and utilisation prospects of local chicken breeds in Fujian Province.

Conflict of interest

The authors declare no conflict of interest.

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