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Whole-genome resequencing data reveal the genetic diversity of local chickens in southern Zhejiang and surrounding areas in China

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Abstract: China's local chicken breeds, especially those in the Zhejiang Province, are rich in genetic diversity owing to environmental heterogeneity and complex ecosystems. Distinctive local breeds have emerged through long-term natural selection and domestication. We investigated the genetic diversity and population structure of local chickens in southern Zhejiang and surrounding areas using whole-genome resequencing of 129 chickens from seven populations. A total of 1.8 terabytes of raw data was obtained, and 4 802 728 single nucleotide polymorphisms were detected. The Xianju chicken population exhibited the highest genetic diversity, while Yandang Partridge chickens were genetically distant from other chicken breeds. This study provides valuable information for conserving poultry genetic diversity and informs about breeding programmes of local Chinese chicken breeds.

Keywords: breeding; Chinese native chicken breeds; population structure; single nucleotide polymorphism

Following the domestication of the Red Jungle Fowl (*Gallus gallus*), domesticated chickens (*Gallus gallus domesticus*) have undergone lengthy, extensive natural and artificial selection, resulting in the development of numerous breeds (Tixier-Boichard et al. 2011; Xiang et al. 2014). Over 100 local breeds have been identified in China. Wenzhou, a city in the southeastern Zhejiang Province, has a favourable geographical position, abundant natural resources, and a unique landscape. Wenzhou's natural landscape, characterised by mountains on three sides and the sea on the fourth, supports

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a diverse array of poultry genetic resources, including the Lingkun chicken, the Yandang Partridge chicken, and the Wenzhou Red chicken (Gao et al. 2022; Wu et al. 2023).

The rapid advancement of high-throughput sequencing technology has provided novel insights for genome-level research (Goodwin et al. 2016; Xiao and Zhou 2020). High-throughput sequencing technology is now widely used to identify single nucleotide polymorphism (SNP) molecular markers in livestock and poultry. While several studies have explored the diversity and genetic structure of local chicken breeds across China, research on the local chicken breeds in Wenzhou remains incomplete (Tian et al. 2023; Tan et al. 2024). Existing studies predominantly rely on microsatellite markers, which have a low density of molecular markers (Niu et al. 2002). In addition, the number of breeds and sample size are both small (Zeng et al. 2017). In this study, we aimed to examine the genetic evolutionary relationships among local chicken breeds in Wenzhou and those from neighbouring regions using whole-genome resequencing data. The objectives were to analyse the genetic diversity and population structure among different breeds, clarify the characteristics of local chicken breeds, and provide technical support for exploring distinctive traits in high-quality chickens, conserving breed resources and facilitating their development and industrial application.

MATERIAL AND METHODS

Ethics statement

All animal experimental protocols were approved by the Animal Care and Use Committee of China Agricultural University and performed in accordance with the National Research Council's Guide for the Care and Use of Laboratory Animals (Approval No. AW80203202-1-1).

Sampling and genomic DNA extraction

We collected 134 bird samples, encompassing eight breeds: WZR, Wenzhou Red chicken (n = 20); LK, Lingkun chicken (n = 20); XJ, Xianju chicken (n = 20); XS, Xiaoshan chicken (n = 10); YD, Yandang Partridge chicken (n = 20); HT, Hetao chicken (n = 20); GJ, Gaojiao chicken (n = 19); and RJF, Red Jungle Fowl (n = 5). The geographical distribution of all Chinese local chicken breeds is shown in Figure 1, and the appearance of the Wenzhou Red chicken is presented in Electronic Supplementary Material (ESM) Figure S1. Among these 134 individuals, 110 samples (WZR, LK, XJ, XS, YD, and HT) of genomic DNA were extracted from blood and tissues using the phenol-chloroform method. The quality of the extracted DNA was assessed using 0.8% agarose gel electrophoresis and quantified using a BioDrop uLite+ spectrophotometer (Biochrom Ltd, Cambridge, UK, now part of Harvard Bioscience, USA). In addition, the sequencing data of GJ and RJF were retrieved from NCBI under the GenBank Accession Nos. PRJNA947391 and PRJNA241474, respectively (ESM Table S1).

Genome sequencing

A sequencing library was created using the NEBNext Ultra™ DNA Library Prep Kit for Illumina (New England Biolabs, San Diego, CA, USA). A mean size of 350 bp was obtained by shearing the genomic DNA. Before sequencing, the DNA fragments were subjected to end-polishing, A-tailing, and adapter addition. Polymerase chain reaction (PCR) amplification and purification were performed using the AMPure XP system (Beckman Coulter, Beverly, MA, USA). Library quality was

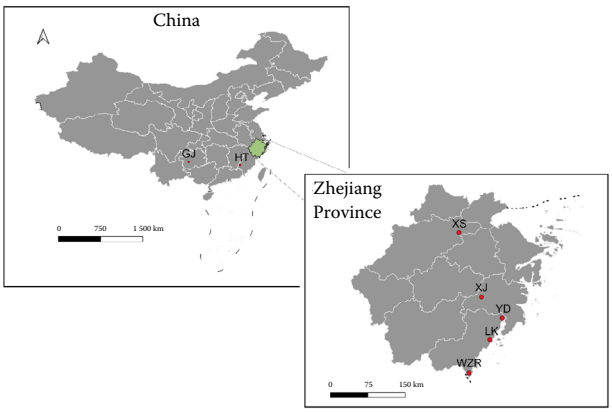

Figure 1. Geographic distribution of the sampled populations

GJ = Gaojiao chicken; HT = Hetao chicken; LK = Lingkun chicken; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

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evaluated based on insert size and DNA concentration using an Agilent 2100 Bioanalyser and a Qubit 3.0 Fluorometer (Invitrogen, Carlsbad, CA, USA). Finally, a flow cell containing the qualifying DNA nanospheres was filled, and a DNBSEQ-T7 platform was used for PE150 sequencing. The sequence data have been deposited in the NCBI Sequence Read Archive under the Bioproject No. PRJNA1178335.

Data quality control, mapping, and variant calling

Clean reads were produced by trimming the raw reads using the FASTP v0.21 software (Chen et al. 2018). The criteria for data filtering mainly include: (1) one read of a pair contained adapter contamination (> 10 nucleotides aligned to the adapter, allowing ≤ 10% mismatches); (2) more than 10% of bases were uncertain in either read; and (3) over 50% of bases in either read were of low quality (Phred score < 5). Trimmed reads were evaluated using the FastQC v0.12.1 software. The BWA-MEM (v0.7.12-r1039) programme was used to align high-quality reads to the reference genome (GRCg7b), and the alignment parameters were based on the default parameters of BWA-MEM (Li and Durbin 2010). The results were sorted, indexed, and converted to BAM files using SAMtools v1.12 software (Li et al. 2009). PCR duplicates were removed, and SNP calling was performed using a joint calling strategy with the HaplotypeCaller, CombineGVCFs, and GenotypeGVCFs functions in the Genome Analysis Toolkit (GATK) v4.2.2 (McKenna et al. 2010; Zhu et al. 2014). SNPs were filtered out using GATK according to specific standards: FisherStrand > 60.0, HaplotypeScore > 13.0, Mapping Quality (MQ) < 40.0, QualityDepth (QD) < 2.0, ReadPosRankSum < −8.0, MQRankSum < −12.5. SNPs were retained for further analysis using VCFtools v0.1.12 with a minor allele frequency (MAF) ≥ 0.01 and a missing rate ≤ 0.1.

Population genetic diversity analysis

Population genetic diversity analysis was conducted using the populations command from the Stacks R package v1.0.2. Expected heterozygosity (H_E) was estimated from the Hardy–Weinberg law. It was calculated using the following formula:

$$H_E = 1 - \sum_{i=1}^{m} (f_i)^2 \quad (1)$$

where:

m – the number of alleles;

f_i – the frequency of the i_{th} allele.

Observed heterozygosity (H_O) was the proportion of heterozygous individuals in the population. It was calculated using the formula:

$$H_o = \frac{\sum_{i=1}^{n} (1 \text{ if } a_{i1} \neq a_{i2})}{n} \quad (2)$$

where:

n – the number of samples;

a_{i1}, a_{i2} – the frequencies of the corresponding alleles.

Nucleotide diversity (*Pi*) reflects the genetic diversity within a population by measuring the degree of the average differences between samples. All these parameters were calculated using the Stacks R package. Linkage disequilibrium (LD) was calculated as the r^2 parameter between SNP pairs in VCF files using PopLDdecay (v3.4) (Zhang et al. 2019).

Population genetic structure analysis

Principal component analysis was performed using the GCTA software (v1.93.2), clustering individuals into subgroups based on their principal components (Yang et al. 2011). The maximum likelihood algorithm in the FastTree software was used to construct a phylogenetic tree based on the SNP data (Price et al. 2009). The ADMIXTURE (v1.3.0) software was used to analyse the genetic structure of the population using SNP information (Alexander et al. 2009; Pickrell and Pritchard 2012). The model was selected as a mixed model with K = 2–6 (assuming that there were 2–6 ancestral populations). All other parameters followed the default settings of the software. The optimal K value was determined to be close to the true value by minimising the cross-validation (CV) error.

Fixation index

The F_{ST}, which represents the degree of genetic differentiation among subgroups within a population, was calculated using the Stacks R package.

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RESULTS

Genetic variations

We sequenced whole genomes of 129 Chinese native chickens from seven populations, along with five Red Jungle Fowls. In total, approximately 1.81 TB of raw sequence data was generated, providing genome coverage ranging from 9.94X to 33.94X (ESM Table S1). After rigorous read alignment and genotype calling procedures, 4 802 728 SNPs were identified and used for further analysis (ESM Figure S2).

Genetic diversity

Observed and expected heterozygosities were estimated for each tested population (Table 1). XS chickens displayed the lowest H_O and H_E values among all tested populations, whereas GJ chickens displayed the highest H_O values, and XJ chickens displayed the highest H_E values. H_O values for all populations ranged from 0.265 to 0.313, whereas the H_E values ranged from 0.260 to 0.297. XJ had the highest *Pi* value (0.304), whereas XS had the lowest (0.274).

XS chickens had the highest LD levels among indigenous Chinese chickens, whereas XJ chickens displayed the lowest LD levels. In addition, the most rapid LD decay among the indigenous Chinese chickens was observed in the XJ population (Figure 2). The results of the LD analysis were consistent with the *Pi* values. Among all the tested populations, the highest F_{ST} value was observed between GJ and XS (0.0650), whereas the lowest F_{ST} value was observed between LK and XJ (0.0375) (Table 2).

Table 1. Summary of the sample and diversity parameters of the chicken populations included in this study

Populations	H_O	H_E	*Pi*
GJ	0.313	0.289	0.297
HT	0.284	0.286	0.293
LK	0.281	0.282	0.290
WZR	0.271	0.286	0.293
XJ	0.294	0.297	0.304
XS	0.265	0.260	0.274
YD	0.280	0.280	0.287

GJ = Gaojiao chicken; H_E = expected heterozygosity; H_O = observed heterozygosity; HT = Hetao chicken; LK = Lingkun chicken; *Pi* = nucleotide diversity; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

Genetic structure analysis

To understand the phylogenetic relationships and population structure of the tested populations, we used the whole-genome SNP dataset of 134 in-

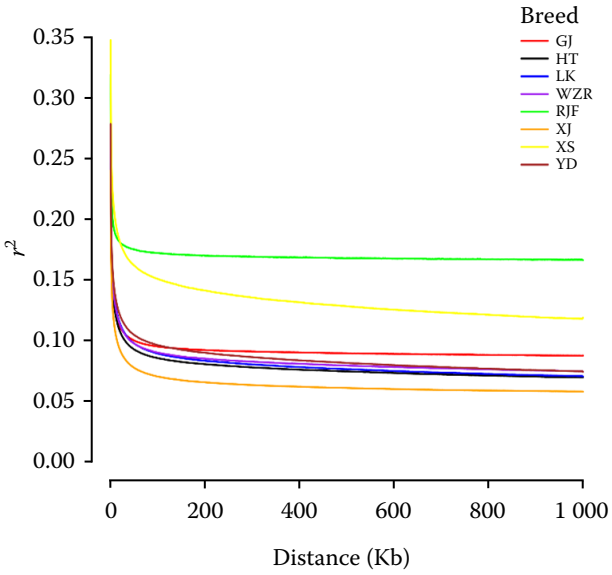

Figure 2. Linkage disequilibrium decay of all tested chicken populations

GJ = Gaojiao chicken; HT = Hetao chicken; LK = Lingkun chicken; RJF = Red Jungle Fowl; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

Table 2. Fixation index (F_{ST}) among populations

Populations	GJ	HT	LK	WZR	XJ	XS	YD
GJ	–	0.051	0.054	0.053	0.042	0.065	0.057
HT	–	–	0.050	0.050	0.039	0.063	0.054
LK	–	–	–	0.048	0.038	0.059	0.053
WZR	–	–	–	–	0.038	0.060	0.054
XJ	–	–	–	–	–	0.048	0.041
XS	–	–	–	–	–	–	0.065

GJ = Gaojiao chicken; HT = Hetao chicken; LK = Lingkun chicken; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

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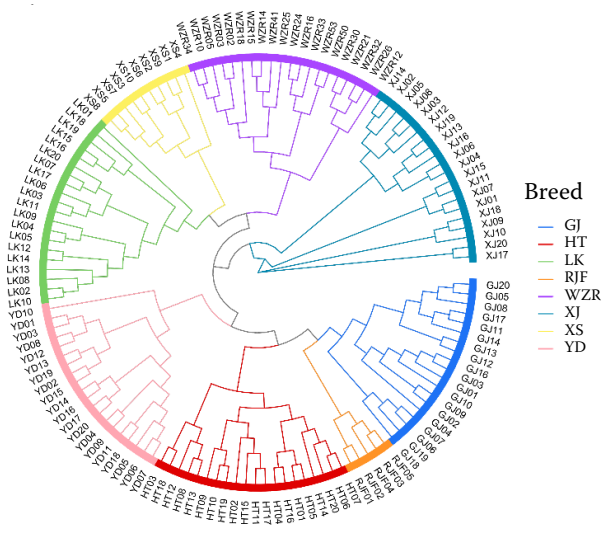

Figure 3. Phylogenetic tree of chicken populations analysed in this study

GJ = Gaojiao chicken; HT = Hetao chicken; LK = Lingkun chicken; RJF = Red Jungle Fowl; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

dividuals to construct a phylogenetic tree using RJF as an outgroup. The phylogenetic tree showed a distant relationship between GJ and the other populations (Figure 3). The results of the principal component analysis (PCA) were consistent with those of the phylogenetic tree. The PCA showed

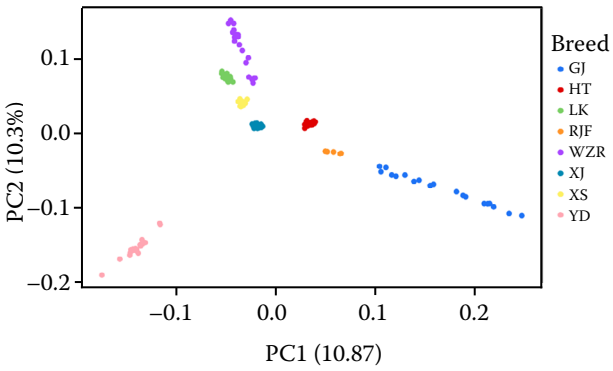

Figure 4. Plot of the first two principal components from the principal component analysis (PCA) of the chicken populations analysed in this study

GJ = Gaojiao chicken; HT = Hetao chicken; LK = Lingkun chicken; RJF = Red Jungle Fowl; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

that the contribution rates of the first two principal components to the variance in the data were 10.87% and 10.3%, respectively (Figure 4). The first PCA axis separated YD and GJ from other chickens, and both the second and the third PC separated HT from other populations (Figure 4; ESM Figures S3 and S4).

To assess possible genetic admixture, we performed the population structure analysis with a full maximum-likelihood approach using

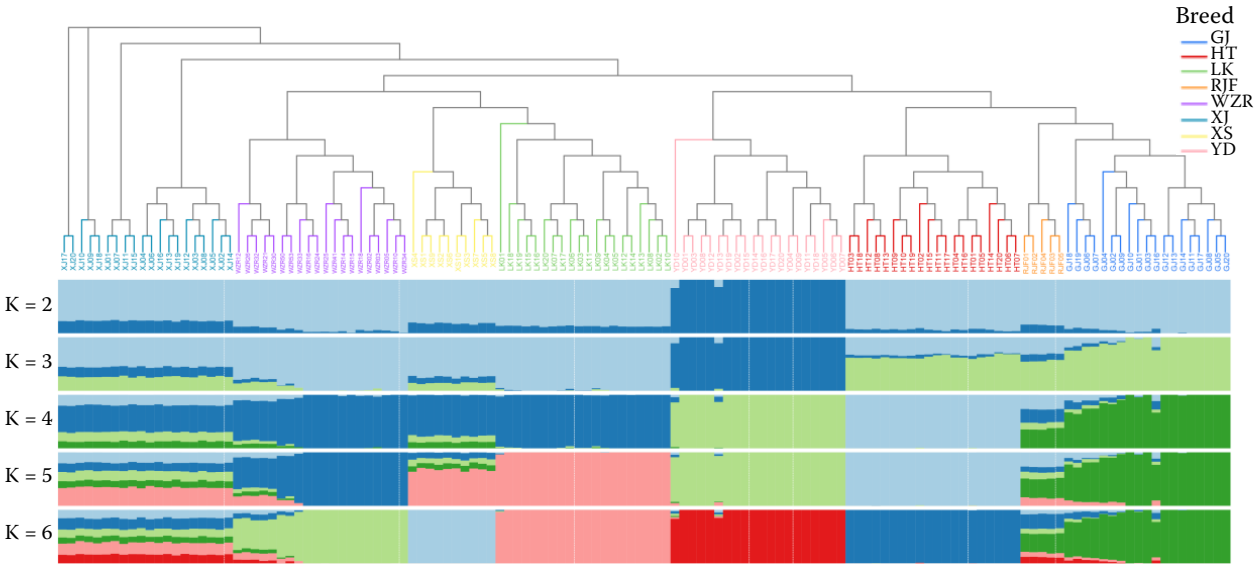

Figure 5. Analysis of the genetic population structure using ADMIXTURE

The colours in each column represent the contribution from each subcluster (K = 2–6, when K = 4 has the lowest cross-validation error)

GJ = Gaojiao chicken; HT = Hetao chicken; LK = Lingkun chicken; RJF = Red Jungle Fowl; WZR = Wenzhou Red chicken; XJ = Xianju chicken; XS = Xiaoshan chicken; YD = Yandang Partridge chicken

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ADMIXTURE. This approach estimated individual ancestry and admixture proportions, assuming K ancestral populations. At K = 2, YD was separated from the other populations. At K = 3, XJ, WZR, LK, and XS shared a similar genetic background, whereas YD had a distinct genetic background. Additionally, RJF shared the genetic background with HT and GJ. At K = 4, the best value exhibiting the lowest CV error, the results were largely consistent with the PCA results. Mutual introgression was observed among the chicken breeds (Figure 5).

DISSCUSSION

Population genetic diversity encompasses the variety and variation of genes within a specific biological population, including variation in allele frequencies and genotype diversity (Bortoluzzi et al. 2018; Lawal and Hanotte 2021). Population genetic diversity is critical for species adaptability, survival, and evolution. Scientific research and monitoring are essential for enhancing our understanding of population genetic diversity and for providing a robust scientific foundation for biodiversity conservation and resource management. Molecular markers have evolved from the first- to second-generation technologies, culminating in the third-generation approaches based on single nucleotide polymorphisms (SNPs). Compared to the second-generation microsatellite markers, SNPs exhibit advantages, such as high abundance, elevated density, strong stability, and co-dominance (Vignal et al. 2002; Zhang et al. 2010). As the most common variants at the genomic level, SNPs are frequently used in the study of population genetics and domestication. They also form the foundation for speciation and evolution (Morin et al. 2004). After filtering, a total of 4 802 728 high-quality SNPs were identified in this study. These SNPs ensure the accuracy of genetic diversity and population structure analysis.

High-throughput sequencing technology has rapidly advanced over the past decade, progressing from its nascent stage to its current state of maturity, speed, and affordability. This has become the predominant technique employed in molecular biology (Goodwin et al. 2016; Stark et al. 2019; Satam et al. 2023). In this study, whole-genome resequencing technology was used to acquire SNP information for each population, enabling the detection of genetic diversity. These findings revealed that the XJ chicken population exhibited the highest level of genetic diversity and the lowest LD, whereas XS chickens displayed the lowest polymorphism and the highest LD. Previous studies have demonstrated a higher genetic diversity in YD chickens (Tan et al. 2024). It has also been found that XS chickens had the highest contribution to the total gene diversity and the maximum gene diversity of the synthetic population in eight Chinese native chicken breeds (Gao et al. 2023). With a breeding history spanning over four centuries and renowned for their early maturation and prolific egg-laying performance, XJ chickens have earned the title of "China's First Chicken". XS chickens are characterised by their large size, and both XJ and XS represent valuable local poultry resources in the Zhejiang Province. These birds exhibit significant variation in appearance, behaviour, and adaptability to various environments. Their distinctive genetic profiles present a wealth of potential for scientific research and agricultural advancement. It is essential to preserve these indigenous chicken breeds to maintain biodiversity and guarantee the ongoing availability of a diverse range of high-quality poultry products.

Consequently, it is imperative to safeguard the genetic diversity of the populations. These results strongly emphasise the need to develop and implement improved conservation strategies aimed at mitigating inbreeding and genetic drift within populations exhibiting lower levels of genetic diversity.

We analysed three indigenous chicken breeds from Wenzhou (LK, YD, and WZR). Wenzhou Red chickens are known for their large body size, long shanks, and aggressive behaviour. All individuals clustered by breed indicated their genetic representativeness. To compare Wenzhou breeds with those from neighbouring areas, we included Xianju and Xiaoshan chickens, two well-known indigenous breeds from Zhejiang province, as well as Hetian chickens from Fujian Province, known for their aggressive behaviour. Furthermore, we included Gaojiao chickens from Guizhou province in the analysis owing to their similarity to Wenzhou Red chickens, specifically the long-shank trait. The inclusion of XJ, XS, HT, and GJ chickens provided a broader context for understanding the genetic diversity within indigenous chicken breeds in Wenzhou. The population structure analysis

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results indicated that YD exhibited substantial genetic divergence from other populations, suggesting potentially distinct origins compared to those of the two other breeds in Wenzhou, LK, and WZR. It is possible that YD chickens have undergone unique genetic adaptations or have been influenced by different selective pressures.

We primarily used whole-genome data to reveal genetic diversity and population structure in this study. In the future, we can also identify genetic variants that may be associated with particular traits or adaptations by these data, thus providing insights into the evolutionary history and adaptive potential of populations. Furthermore, this data can serve as a valuable resource in breeding conservation programs. By pinpointing regions of the genome that are under selection or experiencing reduced diversity due to artificial selection or environmental changes, ensuring that genetic resources are preserved for future generations.

CONCLUSION

In this study, we investigated the genetic diversity and population structure of seven indigenous Chinese chicken breeds using whole-genome resequencing data. Several genetic diversity parameters, such as H_O, H_E, Pi, LD, and fixation index (F_{ST}), were determined for these chickens. Multiple analyses suggested a high level of genetic diversity in XJ population and a comparatively large genetic distance between YD and other chickens.

Overall, the genetic diversity revealed in this study is important for the conservation and utilisation of genetic resources. This study provides a better understanding of the genetic mechanisms controlling Chinese indigenous chicken characteristics and a tool for preservation strategies and utilisation of indigenous chickens.

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Conflict of interest

The authors declare no conflict of interest.

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