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Population genetics reveal potential threats from low maternal genetic diversity in wild Asian elephants in China

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ABSTRACT

In China, wild Asian elephants (*Elephas maximus*) are primarily distributed in three prefectures in Southwest Yunnan, along the border with Laos and Myanmar. These elephants occur in small, fragmented populations and face significant threats from habitat loss and fragmentation. Here, we successfully retrieved 48 mitochondrial genomes, including those from 35 wild Asian elephants in China and those from 13 captive Asian elephants, based on whole genome sequencing data to analyze their maternal population structure and genetic diversity. In addition, we extracted approximately 600 kb of non-coding genomic regions for a comparative analysis of the genetic structure between the nuclear and mitochondrial DNA. Wild Asian elephants in China exhibited extremely low genetic diversity compared to global populations, with only two haplotypes detected in the Chinese population. Despite limited mitochondrial haplotypes, the Xishuangbanna population maintains gene flow with external populations. In contrast, the genetic diversity in the Cangyuan population was even more severely limited, with no evidence of gene flow with the nearest populations in Myanmar. Given the close genetic relationship between the Cangyuan population and populations in other countries, the most promising strategy for introducing genetic diversity to rescue the Cangyuan population may involve translocating Asian elephants from other countries. This study provides a deeper understanding of the genetic status of wild Asian elephants in China and offers important insights for future conservation efforts in China and elsewhere.

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1. Introduction

The Asian elephant (*Elephas maximus*) is one of the three living Proboscidea species and was historically distributed across a vast range throughout Eurasia (Elvin, 2004; Olivier, 1978). However, today, the Asian elephant is confined to South Asia, Southeast Asia, and parts of Southwestern China (Sukumar, 2006). Habitat loss, associated with illegal hunting and, particularly, human-elephant conflict (Dai, 2022), has resulted in a dramatic decline in the global wild population of Asian elephants, from ~100,000 individuals one century ago to an estimated 45,522–48,671 individuals today (Sukumar, 2006; Tang et al., 2023). The species is currently listed as "Endangered" in the International Union for Conservation of Nature (IUCN) Red List. Given its ecological significance, urgent conservation efforts are needed, and all countries with wild Asian elephants have prioritized the protection of this iconic species.

Understanding the population structure and genetic diversity is a prerequisite for developing effective conservation plans for endangered species (Barrett and Schluter, 2008; Buckland et al., 2014; Frankham et al., 2011; Saremi et al., 2019). Over the past two decades, the genetic structure and diversity of Asian elephant populations have been extensively studied (Chen et al., 2023; Fernando et al., 2000; Karuppannan et al., 2019; Kriangwanich et al., 2018; Kusza et al., 2018; Suter et al., 2014; Vidya et al., 2005b; Vidya et al., 2007). Using a 600 bp sequence spanning over the cytochrome b gene (*CYTB*) and the mitochondrial control region (D-loop), researchers identified two major evolutionary branches: the α clade (Indochina-Laos population) and the β clade (Indo-Myanmar population; Vidya et al., 2005a, 2005b; Vidya and Sukumar, 2005). India, home to the largest Asian elephant population (~ 30,000), has experienced significant north-south population differentiation due to both geographical and human-induced isolation (Parida et al., 2022; Vidya et al., 2005a, 2005b). Despite its large population size, the genetic diversity of India's Asian elephants appears to be lower compared to much smaller populations in Vietnam, Myanmar, Laos, Thailand, and the Malay Peninsula, as well as captive or semi-captive populations (Maurer et al., 2024). These other populations exhibit relatively high genetic diversity and low genetic differentiation within populations, although some of them are facing a significant extinction risk (Fernando et al., 2000; Karuppannan et al., 2019; Kriangwanich et al., 2018; Kusza et al., 2018; Lei et al., 2012; Mohd-Radzi et al., 2022; Suter et al., 2014; Vidya et al., 2007).

The wild Asian elephant population in China constitutes less than 1 % of the global total and is primarily distributed in three prefectures in Southwest Yunnan – Lincang, Pu'er, and Xishuangbanna (Zhang et al., 2015; Zhang and Wang, 2003). With the continuous conservation efforts from the Chinese government, the population has grown from an estimated 150 individuals in 1976 to approximately 300 individuals today (Bai et al., 2022; Zhang, 2018; Zhao and Jin, 2018). Notably, the range expansion of Asian elephants in China has attracted global attention, particularly due to the northward movement of a group of Asian elephants in 2021 (Campos-Arceiz et al., 2021). Both α and β evolutionary branches have been identified in the Chinese populations, with the β clade found in Nangunhe (Cangyuan), and the α clade being more widespread (Chen et al., 2023). The rapid increase in research on Asian elephants in China has also facilitated the development of evidence-based strategies for their conservation (Chen et al., 2021). However, previous studies, using either mitochondrial DNA fragments or microsatellite markers, have revealed low genetic diversity and population differentiation in the Chinese populations, suggesting potential genetic risk, particularly for the very small and fully isolated Nangunhe population in Cangyuan.

With the continuous development of sequencing technology, the population genetic backgrounds (e.g. genetic structure, inbreeding, mutational load) of many endangered animals are becoming increasingly clear (Dussex et al., 2021; Khan et al., 2021; Lan et al., 2024). However, obtaining high-quality samples through non-invasive sampling of wild animals remains a significant challenge (Ahlering et al., 2011; Cui et al., 2024). To date, only one study has used whole-genome sequencing data to explore the genetic background of India's Asian elephants, but it relied on blood samples (Khan et al., 2024). Fortunately, the characteristics of mitochondrial DNA – specifically its multiple copies allow for the quick and cost-effective acquisition of mitochondrial sequences from non-invasive samples, such as feces (Camus et al., 2022). Using the entire mitochondrial genome, rather than single gene fragments, can increase the available genetic variation and enhance the resolution of population structure analyses, making it an increasingly preferred strategy for mitochondrial-based population genetic research (Broquet et al., 2007; Dabney et al., 2013). Whole mitochondrial genomes have been successfully used in preliminary assessments of population structure and in defining conservation units to support conservation efforts for endangered populations (Jang et al., 2017; Johri et al., 2020; Palsbøll et al., 2007).

In this study, we performed high-throughput sequencing and assembled mitochondrial genomes for 48 Asian elephant individuals (Table S1). In addition, we also retrieved 600 kb of non-coding regions from the nuclear genome to compare mitochondrial and nuclear sequences in phylogenetic analysis. Finally, we collected mitochondrial sequences from all Asian elephant distribution countries to make comprehensive comparisons between populations worldwide. By doing so, we aim to 1) investigate the population structure and genetic diversity of wild Asian elephant populations in China; (2) reveal genetic relationships and compare the genetic diversity among Asian elephant populations all over the world; and (3) explore possible resource populations for genetic rescue of wild Asian elephants in China. Findings in this study provide new insights and contribute genetic resources to global conservation efforts of Asian elephants.

2. Material and methods

2.1. Sample collection, DNA extraction and sequencing

Between 2021 and 2024, we collected a total of 175 fecal samples from the habitats of wild Asian elephants in Yunnan, China, as well as from captive Asian elephants. During the sampling process, the surface of fresh feces was collected using sterile cotton swabs or

disposable PE gloves, placed in sterile plastic bags or 50 ml centrifuge tubes, and then transferred to the laboratory on dry ice for DNA extraction. The fecal samples were first treated based on the simple SDS-based host cell selective lysis protocol described by Cui et al. (2024). Total DNA was then extracted using the AxyPrep™ Multisource Genomic DNA Miniprep Kit (Axygen, USA) according to the manufacturer's instructions. DNA quantity and quality were detected by Qubit 3.0 (Life Technologies, USA) and agarose gel electrophoresis. After individualization analysis based on 18 dinucleotide microsatellite loci (Kongrit et al., 2008), we obtained samples of 68 different individuals. After removing 28 samples with poor DNA quality that did not meet the requirements of constructing sequencing libraries, we finally retained 40 samples (captive: 5; wild: 35) for downstream experiments and analysis. Following the manufacturer's standard double-stranded library construction protocol for tissue samples, DNA libraries with insert sizes of 300–500 bp were constructed for all the above-mentioned samples, and then subjected to the DNBSEQ-T1 sequencer (MGI, Shenzhen, China) for pair-end sequencing (100 bp). In addition, we downloaded resequencing data of eight Asian elephants from public databases (Table S1) (Li et al., 2023; Tollis et al., 2021). Therefore, we finally assembled mitochondrial genomes from 48 individuals (wild--origin: 35; captive-origin: 5; public database: 8). Sample collection, follow-up experiments, and research design in this study were all approved by the Laboratory Animal Management and Ethics Committee of Northeast Forestry University.

2.2. Assembly of mitochondrial genomes

Raw sequencing reads were firstly filtered for adapters and low-quality sequencing data using Trimmomatic (v0.39) (Bolger et al., 2014), with parameters of "-phred33 ILLUMINACLIP: adapter.fa:2:30:10 SLIDINGWINDOW:5:15 MINLEN:50". Then, the filtered whole genome sequencing data was mapped to the reference genome of the Asian elephant (GCA_033060105.1) (Shi et al., 2024) using the BWA *mem* algorithm (v0.7.17) (Li and Durbin, 2010), with default parameters. Only reads mapped on the Asian elephant genome were retrieved for the subsequent analysis. Then, we used the mitochondrial *COX1* gene (NC_005129.2) as a seed to assemble the mitochondrial genomes in this study by NOVOPlasty (v.4.3.1) software (Dierckxsens et al., 2016), and all 48 individuals were successfully assembled (Table S1). Using the reference genome as a template (Rogaev et al., 2006), MEGA 11 (Koichiro et al., 2021) was used to intercept 13 mitochondrial genes and control regions (D-loop) for subsequent analysis. To compare the population structure with published works (Fernando et al., 2000; Vidya et al., 2005a, 2005b; Vidya and Sukumar, 2005), we also used the same method to extract a 600 bp mitochondrial DNA sequence including the 3′ end of *CYTB*, tRNA-Thr, tRNA-Pro, and the 358 bp control region. In addition, we downloaded whole genome sequencing data or complete mitochondrial genome sequences of 12 endangered mammals from public databases (Pečnerová et al., 2021; Wang et al., 2025; Zhang et al., 2023; Zhao et al., 2013). The same method was used to assemble mitochondrial genomes and obtain coding genes. (Table S6).

2.3. Assembly of a ~600 kb non-coding nuclear genome sequence

We assembled nuclear non-coding genome regions with a total length of ~600 kb for comparison with the mitochondrial genome to explore the possible nuclear-cytoplasmic incompatibility. Steps for this assembly were as follows: 1) we first screened all non-coding regions in the reference genome of the Asian elephant with a window of 10 kb; 2) we then randomly selected genome sequences in these non-coding regions as seeds to retrive noncoding sequences by using the NOVOPlasty (v.4.3.1) (Dierckxsens et al., 2016) with the same parameters of mitochondrial genome assembly; 3) Finally, we selected 10 non-coding regions (could be successfully assembled in most of the samples) with a total length of ~600 kb for analysis (39 individuals in total, Table S5).

2.4. Population structure and genetic diversity

Haplotype analysis was performed based on 13 mitochondrial genes of Asian elephants by using the "*Generate*" module of DnaSP (v6.0) (Julio et al., 2017), and the "*Overview*" module was used to calculate parameters of nucleotide diversity (π) and haplotype diversity (Hd). By using the same method, the same genetic parameters were calculated for other endangered species.

PopART (v1.7) (Leigh and Bryant, 2015) was used for constructing Median-joining haplotype network diagrams with the above-mentioned 600 bp sequences of 80 individuals (48 in this study and 32 published sequences) and the concatenated sequences of 13 mitochondrial genes of 48 individuals in this study. The phylogenetic tree was constructed by using the maximum-likelihood (ML) method in IQTREE(v1.6.12) (Lam-Tung et al., 2015) to elucidate the evolutionary relationships among the sequences. The best nucleotide substitution model was selected by using the jModelTest (v2.1.10) (Darriba et al., 2012) according to the comparison of the Bayesian Information Criterion (BIC) scores (Posada and Buckley, 2004), and we finally selected the HKY+F model for the 11,385 bp sequence consisting of 13 mitochondrial genes. For the 10 randomly selected non-coding regions, each region was analyzed separately using its best-fit model to generate a distance matrix (Table S5). These distance matrices were then combined to construct the phylogenetic tree. Node support was estimated by bootstrap analysis with 1000 replicates and visualized in iTOL (https://itol.embl.de/).

To compare and explore population structure in Asian elephants all around the world, we obtained all mitochondrial D-loop sequences of varying lengths from the NCBI database (https://www.ncbi.nlm.nih.gov/). These sequences, combined with those assembled in this study, were trimmed to a common region of 297 bp. The geographical origin of each sequence was marked and all distinct haplotypes from the different countries were retained, resulting in a total of 108 haplotypes. The haplotype network was constructed using the same method as described above, and the nucleotide diversity of the haplotypes in each country was calculated using DnaSP (v6.0) (Julio et al., 2017).

3. Results

3.1. Samples and mitochondrial genome assembly

In total, we obtained complete mitochondrial genomes from 48 Asian elephant individuals. 35 samples were collected from the

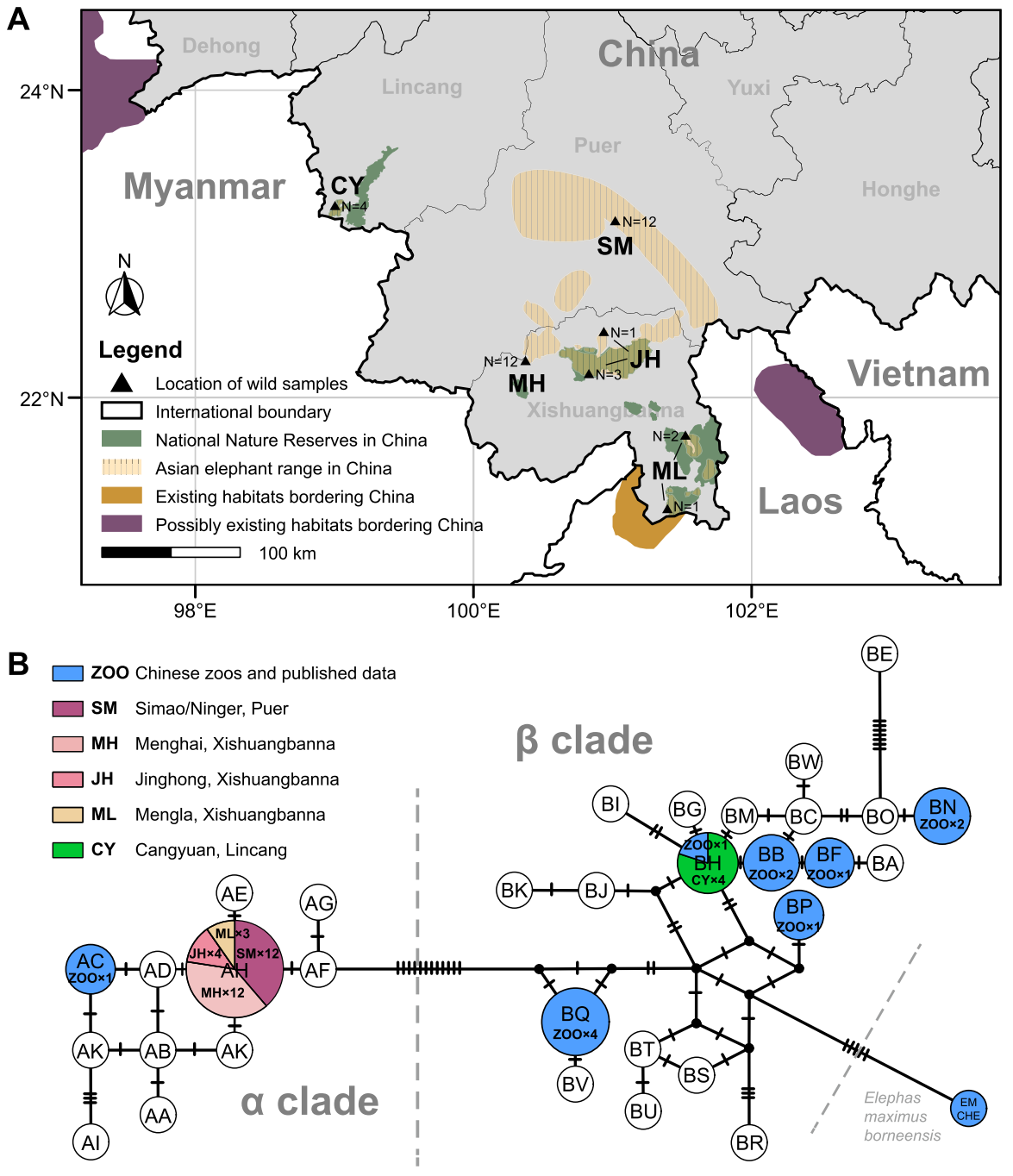

Fig. 1. The geographical distribution of samples and haplotype network analysis in this study. A. The sampling area of 35 wild Asian elephants in China (Cangyuan: N = 4, Simao: N = 12, Menghai: N = 12, Jinghong: N = 4, and Mengla: N = 3). Notes: map lines delineate study areas and do not necessarily depict accepted national boundaries. B. The haplotype network was constructed based on a 600 bp mitochondrial sequence. The 32 published haplotypes (Vidya et al., 2005a, 2005b; Vidya and Sukumar, 2005) are used as background circles to distinguish α/β clade, and the color-coded ones are the 48 samples in this study.

wild, representing all the wild Asian elephant ranges in China: 4 from Cangyuan, 12 from Simao, 12 from Menghai, 4 from Jinghong, and 3 from Mengla (Table S1, Fig. 1A). The remaining 13 individuals were from zoos. Five of these samples were obtained from captive elephants in Chinese zoos, all of which had been introduced from Myanmar; and the remaining 8 samples were obtained from published databases, representing the following geographical origins: 1 from Borneo, 2 from Myanmar, 4 from India, and 1 from China (with an unknown geographical origin). The average length of the 48 assembled mitochondrial genomes was 16838 ± 93 bp, with the mitochondrial D-loop region showing the most variation in length (Table S1).

We then retrieved 13 mitochondrial coding genes from all individuals and concatenated them into a "super gene sequence" to evaluate the maternal genetic diversity and population structure. These genes included cytochrome b (*CYTB*), two ATP synthase (*ATP6*, *ATP8*), three cytochrome c oxidase (*COX1*, *COX2*, *COX3*), and seven NADH dehydrogenase (*ND1*, *ND2*, *ND3*, *ND4*, *ND4L*, *ND5*, *ND6*) (Table S2). The total length of the "super gene sequence" concatenated from the 13 coding genes is 11385 bp, accounting for 67.36 % of the published Asian elephant mitochondrial reference genome (NC_005129.2, 16902 bp). In the three positions of the codon, the "A+T" content was higher than the "G+C" content, and the average base composition of the coding gene sequence was biased against G (11.88 ± 0.01 %) (Table S3), which was also discovered in mitochondrial genomes of other mammalian species (Broughton et al., 2001).

3.2. *Population structure analysis based on the mitochondrial genome*

It has been described that Asian elephants have diverged into α and β clades, and the divergence time between the two clades has been estimated to be approximately 1.1–1.2 million years ago (Fernando et al., 2000; Fleischer et al., 2001; Georgiadis et al., 1994). To compare with published work (Vidya et al., 2005a, 2005b; Vidya and Sukumar, 2005), we first extracted a 600 bp mitochondrial DNA sequence including the 3′ end of *CYTB*, the tRNA-Thr and tRNA-Pro, and the 358 bp control region, to verify the evolutionary branches of Asian elephants in China (Fig. 1B, Table S4). All samples from Cangyuan (the Nangunhe Nature Reserve) belong to the β clade and are concentrated in a single haplotype (BH), while all other wild samples (Simao, Menghai, Jinghong, Mengla) belong to the α clade and are also concentrated in a single haplotype (AH). However, the haplotypes identified from individuals in the zoo were found to be distributed in both α and β clades (Fig. 1B). Besides, the haplotype of the Borneo individual (EM-CHE, SRA accession: ERR2260499) was very independent and distinct from all the 32 haplotypes. Due to the difficulty of conducting in-depth research with only one individual, the Borneo individual was excluded from subsequent genetic diversity analyses.

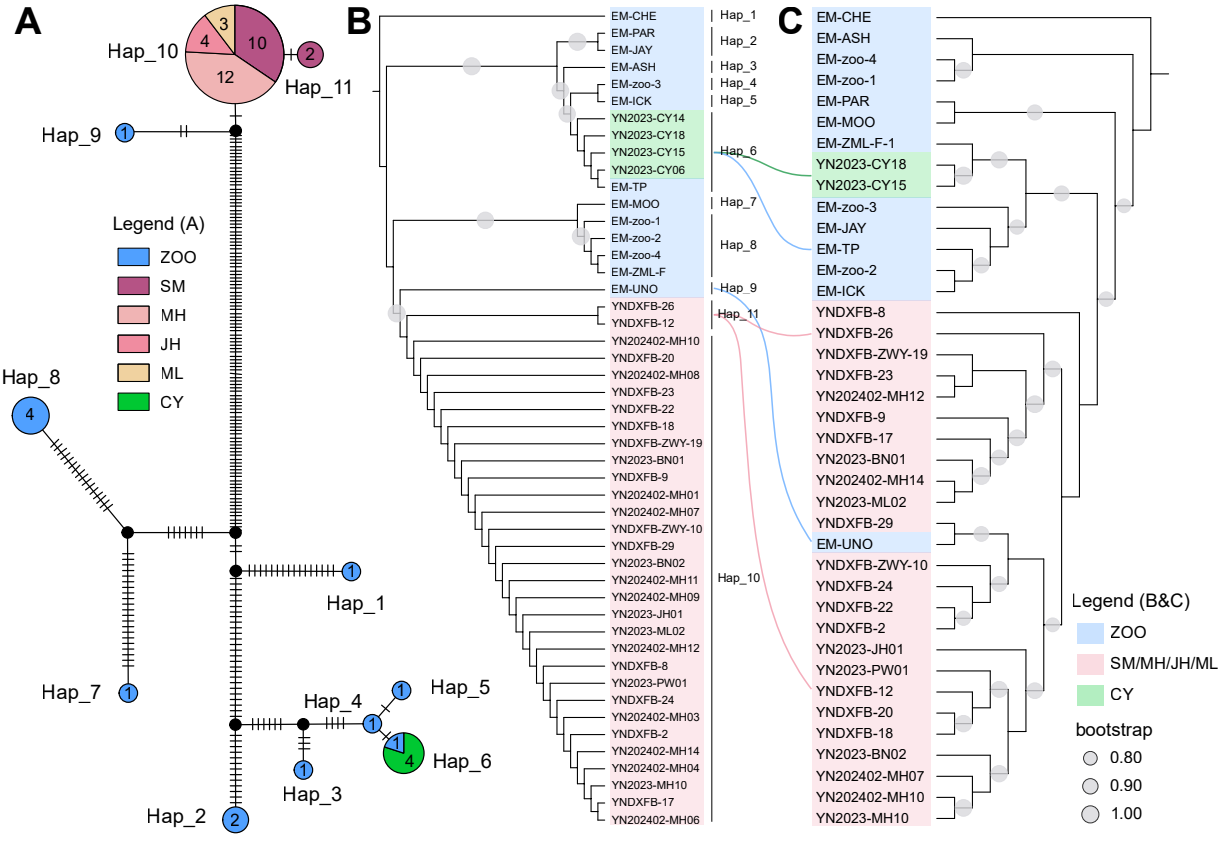

Fig. 2. Population structure of wild Asian elephants in China. A. Haplotype network of 13 mitochondrial genes for the 48 samples in this study. B. Phylogenetic tree constructed using 13 mitochondrial genes. C. Phylogenetic tree constructed using the 600 kb non-coding nuclear genomic regions.

We then used the "super gene sequence" composed of 13 mitochondrial protein-coding genes to further construct a haplotype network diagram for the 48 individuals in this study. We still found two main clusters, which corresponded to the α and β clades, with three haplotypes in the α clade and 8 haplotypes in the β clade. However, individuals forming the AH haplotype in Fig. 1B were divided into two haplotypes, which showed a higher resolution for genetic structure analysis benefiting from more variants of longer DNA sequences, while the BH haplotype in the β clade remained as a single independent haplotype (Fig. 2A, Table S4). Surprisingly, we found a large number of mutation steps between the α and β clades, and within the β clades, indicating an old separation between the two main clades and a deeper differentiation in the β clades than in the α clade. To rule out the sequencing error for these mutations, we checked the mapping reads covering all these variants and confirmed that all variant sites are correctly called (Figure S1). The genetic structure reflected by the phylogenetic tree constructed by the 13 coding genes was highly consistent with the haplotype network (Fig. 2B).

3.3. Nuclear and cytoplasmic inconsistency in the phylogenetic tree

Although Asian elephants exhibit a matriarchal social structure, it is crucial to consider nuclear genome information to fully characterize the genetic diversity of Asian elephants (Kuntner et al., 2011). Based on ~600 kb nuclear non-coding sequences, we explored the differences between the phylogenetic tree inferred by nuclear DNA and mitochondrial DNA in Asian elephants (Table S5). Phylogenetic trees of the mitochondrial genome and nuclear genome sequence showed roughly the same topology, with the α and β clades distinctly separated. However, we still found nuclear and cytoplasmic inconsistency within either the α or β clade (Fig. 2B, C). In the haplotype network of the 600 bp mitochondrial DNA, the EM-UNO individual from Assam, India (Tollis et al., 2021) was classified into the AC haplotype, which differed at two loci from the AH haplotypes (Fig. 1B). The haplotype network of 13 mitochondrial genes also supported this differentiation (Fig. 2A). However, in the nuclear phylogenetic tree, the EM-UNO formed a small branch with YNDXFB-29 from Simao (Fig. 2C). Additionally, the sample EM-TP, from a captive individual in the Wild Elephant Valley in Xishuangbanna (Li et al., 2023), was clustered with four individuals from Cangyuan in the mitochondrial tree but was placed into a different branch in the nuclear tree (Fig. 2C). This suggested that the EM-TP individual indeed belongs to the β clade, but may be originated from Myanmar, Laos, or Thailand.

3.4. Genetic diversity of worldwide Asian elephant populations

To understand the mitochondrial level genetic diversity, we calculated the nucleotide diversity (π) based on 13 protein-coding genes for the 48 Asian elephants. The overall π and Hd for these elephants were 0.00598 ± 0.00077 and 0.608 ± 0.079, respectively (Table 1). The α clade exhibited a relatively lower diversity ($\pi = 0.00003 \pm 0.00002$, $Hd = 0.179 \pm 0.088$) compared to the β clade ($\pi = 0.00317 \pm 0.00049$, $Hd = 0.838 \pm 0.068$), which was consistent with previous studies (Zhang et al., 2015). To compare the overall genetic diversity of Asian elephants to other species, we downloaded the mitochondrial genome sequences of the other 12 endangered mammal species from NCBI and calculated the nucleotide diversity based on 13 protein-coding genes with 15 individuals for each species (Fig. 3, Table S6). The results showed that the α clade Asian elephants presented the lowest genetic diversity among the 13 endangered mammals, indicating the potential genetic risk for Asian elephants in China. In contrast, the β clade Asian elephants exhibited medium-level genetic diversity, which was advantageous when compared to the giant panda, snow leopard, and Siberian tiger. However, this does not necessarily mean that all β clade Asian elephant populations are genetically safe. In this study, China's Cangyuan population has only one haplotype (BH, Table 1), facing potential threats of extinction.

The genetic status of Asian elephants may differ significantly among populations in different countries, due to different management and conservation efforts, as well as different breeding practices in different countries. In this study, we prepared 108 mitochondrial haplotypes (the 297 bp mitochondrial sequence) from public databases with geographical origins of 10 different countries, including China (N = 2), India (N = 16), Myanmar (N = 20), Thailand (N = 25), Bhutan (N = 3), Laos (N = 13), Vietnam (N = 5), Malaysia (N = 2), Indonesia (N = 4), Sri Lanka (N = 9), and captive Asian elephants in North America (N = 9) (Table S7), to make a comprehensive comparison of genetic diversity of Asian elephants across the world. Similar to previous studies (Chen et al., 2023), Asian elephants in India, Myanmar, and Thailand harbored many more haplotypes than elephants in other countries, with 26.67 %, 33.33 %, and 41.67 % haplotypes detected in elephants from these three countries, respectively, including both shared and unique haplotypes (Fig. 4A). The nine haplotypes of captive individuals in North America shared haplotypes with other countries and were evenly distributed across the haplotype network, indicating the diverse progenitor populations (Fig. 4A). Notably, the four

Table 1
Statistics of mitochondrial genetic diversity in Asian elephants based on 13 mitochondrial coding genes.

Parameter	All	α clade	β clade	β clade (Hap_BH)
Ni	47	32	15	5
Ns	11385	11385	11385	11385
Nv	212	4	100	0
π	0.00598 ± 0.00077	0.00003 ± 0.00002	0.00317 ± 0.00049	0.00000
Nh	10	3	7	/
Hd	0.608 ± 0.079	0.179 ± 0.088	0.838 ± 0.068	/

Ni: number of samples, Ns: number of sites, Nv: number of variable sites, π: nucleotide diversity, Nh: number of haplotypes, Hd: haplotype diversity.

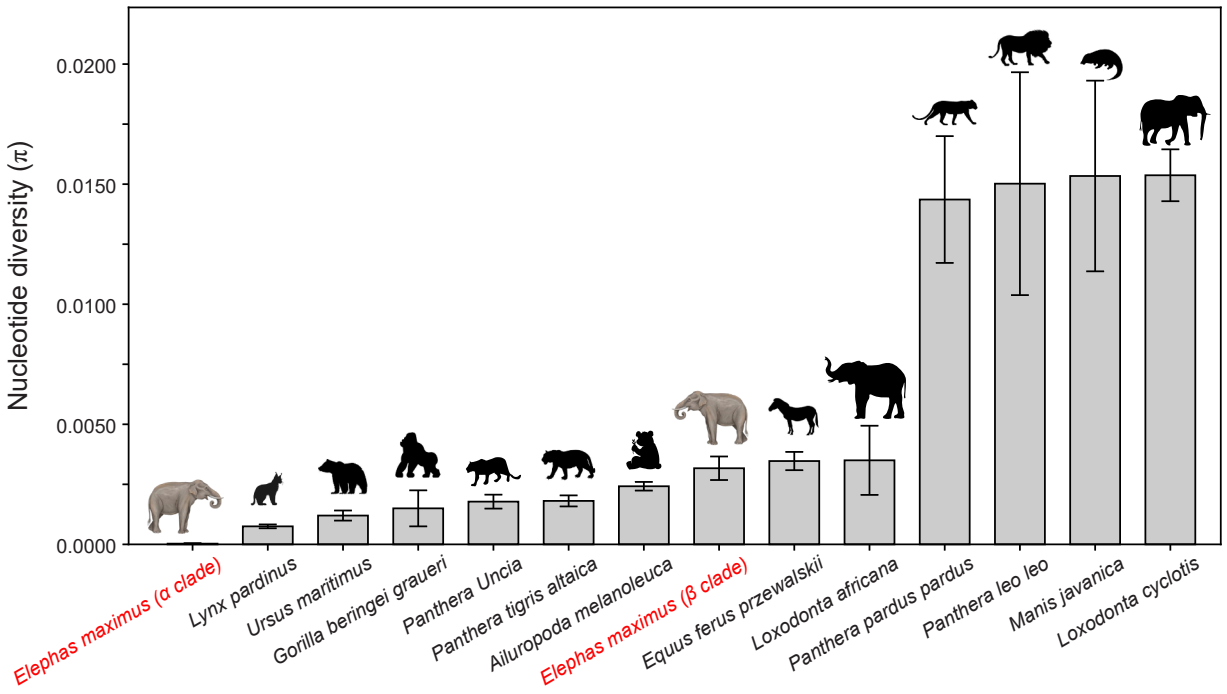

Fig. 3. Nucleotide diversity calculated based on 13 mitochondrial genes of Asian elephant populations and other 12 endangered mammals.

haplotypes in Indonesia are not shared with other countries, which may have resulted from the long-term geographical isolation facilitated by insularity (Fig. 4A) (Azmi and Gunaryadi, 2011). The only two haplotypes in the Chinese population are both shared with other countries. The BH haplotype (Hap_1, Fig. 4A), distributed in Cangyuan, was widely shared with Sri Lanka, India, Bhutan, Myanmar, and Thailand. The AH haplotype (Hap_19, Fig. 4A), found in Simao, Jinhong, Mengyang, and Mengla, was also shared with India, Bhutan, Myanmar, Laos, and Thailand. The haplotypes of Asian elephants in Laos are primarily distributed in the α clade and are close to the AH haplotype.

In terms of nucleotide diversity, Asian elephants in India have the richest genetic diversity for both the α clade and β clade. Although the overall nucleotide diversity in the Chinese population seemed to be significantly higher than populations in other countries, the fact is that only two haplotypes existed in Chinese populations, with each haplotype belonging to a different clade (Fig. 4B). Therefore, the Chinese population may represent the lowest genetic diversity among all Asian elephant populations all over the species range. Besides, the α clade exhibits lower diversity than the β clade for most of the Asian elephant populations (Fig. 4), which may be attributed to the more ancestral origins of the β clade.

4. Discussion

4.1. Potential threats from low maternal genetic diversity in Chinese populations

For wild Asian elephants in China, we identified two distinct clusters—Nangunhe and Xishuangbanna—corresponding to the α and β clades, respectively, consistent with previous research (Chen et al., 2023). While the overall nucleotide diversity of Chinese Asian elephants appears high (Fig. 4B), this diversity is primarily driven by the large genetic differences between the α clade (Simao, Menghai, Jinhong, Mengla) and the β clade (Cangyuan). However, the overall nucleotide diversity in China does not accurately reflect the low intra-population genetic diversity within the Xishuangbanna and Cangyuan populations. Specifically, we found only two α haplotypes in Xishuangbanna and one β haplotype in Cangyuan, even when considering the entire mitochondrial genome. Consequently, Asian elephants in China face extremely low maternal genetic diversity.

Although the Asian elephant population in China has experienced rapid expansion in recent decades (Bai et al., 2022; Campos-Arceiz et al., 2022), the low haplotype diversity (Hd) may be a consequence of historical bottleneck events (Chen et al., 2023). In Xishuangbanna, there are five sub-reserves spanning a wide geographical range (Chen et al., 2023; Zhang et al., 2015), yet the scarcity of haplotypes in this population still suggests a potential genetic risk for this relatively large α clade population. The situation is more critical in Cangyuan (Nangunhe National Nature Reserve, Lincang), where the population is unsustainably small and fully isolated, consisting of fewer than 20 individuals belonging to four small family groups (Liu et al., 2016; Tang et al., 2023). This isolation has exacerbated genetic erosion, making genetic rescue an urgent priority (Chen et al., 2021; Chen et al., 2022). While introducing α clade elephants from Xishuangbanna to the β clade population in Cangyuan may provide a potential solution, such interventions must be carefully considered. The introduction of individuals from different clades could risk outbreeding depression or

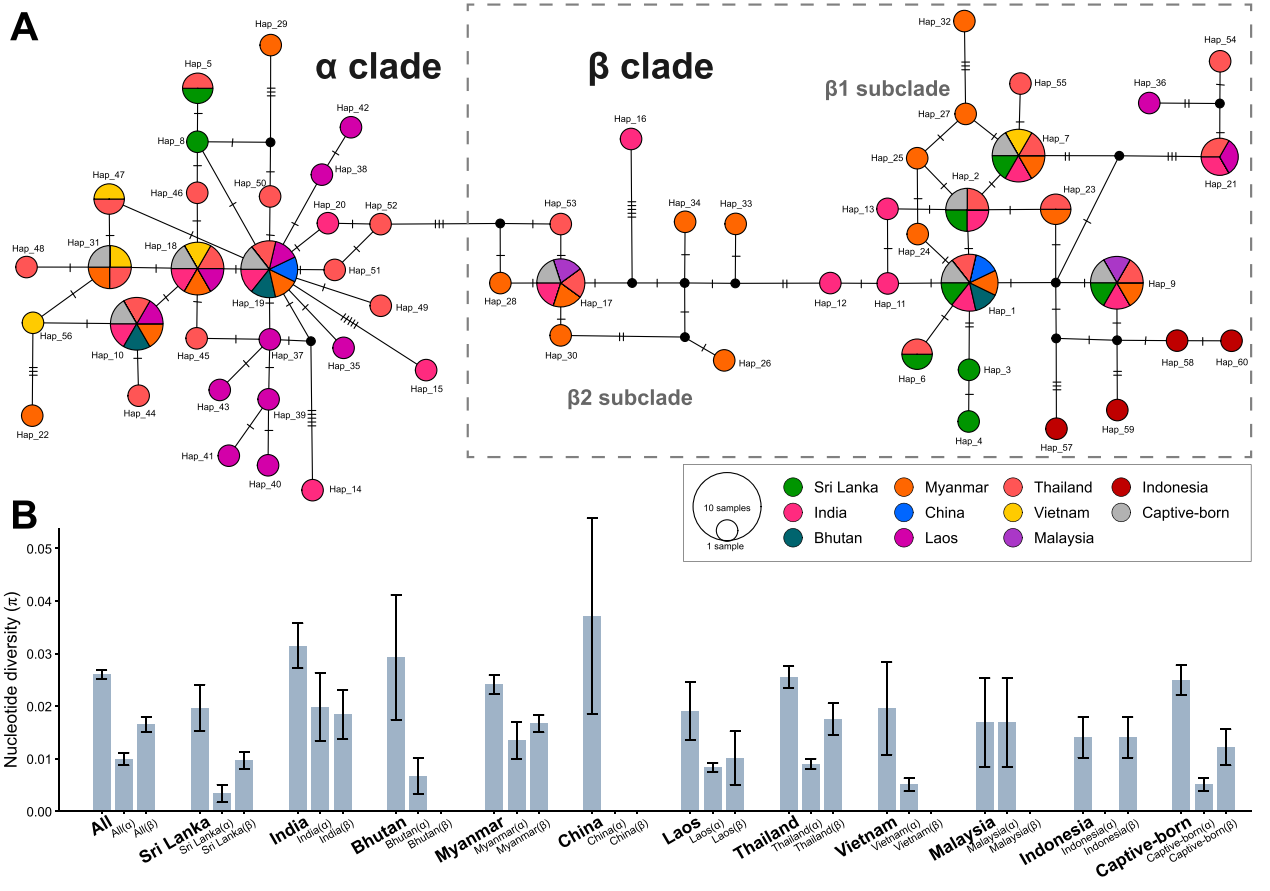

Fig. 4. Overview of the genetic diversity of Asian elephants worldwide. A. Haplotype networks of wild Asian elephants from 10 countries and captive elephants in North America (Captive-born). B. Genetic diversity of Asian elephants in each country, including the α and β clades.

disrupt local adaptations. Thus, further genetic studies involving a larger sample size are needed to assess the effectiveness and potential unintended consequences of translocation, to ensure that genetic rescue does not undermine the long-term viability of the Cangyuan population (Lan et al., 2024).

4.2. Implications for future conservation of Asian elephants in China

The mitochondrial genome provides genetic insights into the maternal lineage, while the biparentally inherited nuclear genome offers a more comprehensive picture of the population structure (Hajibabaei et al., 2007). In this study, the main topological structures corresponding to the α and β clades remained consistent in the phylogenetic tree of both the nuclear and mitochondrial DNA. However, we observed some nuclear and cytoplasmic incongruence within both the α and β clades. In the phylogenetic tree based on the mitochondrial genome, the rescued Asian elephants (EM-TP), from the Wild Elephant Valley in Xishuangbanna, clustered with the Cangyuan population. In contrast, these EM-TP individuals clustered with elephants from Myanmar in the nuclear DNA tree. The Cangyuan elephants have formed a small and isolated population for more than 50 years (Liu et al., 2016). This nuclear-cytoplasmic inconsistency could be explained by two possible scenarios: (1) the EM-TP individual and the Cangyuan population shared a common ancestor several decades ago, or (2) the two populations underwent long-term differentiation, with gene flow occurring between them more recently, which is akin to the documented genetic exchange between red wolves and coyotes (Sacks et al., 2021). Regardless of the mechanism (gene flow or shared ancestry), the genetic differences in mitochondrial DNA are small, suggesting that the divergence occurred relatively recently. Additionally, the clustering of the EM-TP individual with elephants from Myanmar in the nuclear DNA tree indicates the existence of gene flow between elephants of China and Myanmar. Individuals in the α clade also showed nuclear-cytoplasmic inconsistency, and the EM-UNO individual from Assam, India, was an example. Unlike the EM-TP, the EM-UNO showed a larger genetic distance to the Xishuangbanna population at the mitochondrial level, but fully clustered with the SM population in the nuclear phylogenetic tree. This may be caused by the recent gene flow between Asian elephants of Assam and Xishuangbanna, or historical hybridization events followed by the rapid evolution of the mitochondrial genome after their separation (Toews and Brelsford, 2012). Nonetheless, the nuclear-cytoplasmic inconsistency further supports the existence of gene flow between the Xishuangbanna population and populations outside China.

The extremely low mitochondrial genetic diversity in both Cangyuan and Xishuangbanna populations highlights the serious risk of inbreeding faced by the Asian elephant populations in China. The observed nuclear-cytoplasmic inconsistency provided potential evidence for gene flow between populations in China and neighboring countries. This finding is crucial for promoting cross-border wildlife protection and establishing transnational corridors. Notably, the distribution range of the Xishuangbanna population in the α clade borders Laos (Fig. 1A). In December 2009, China and Laos signed a joint agreement to establish an Asian elephant corridor between the Shangyong Reserve in China and Nantha Province in Laos (He et al., 2011). The establishment of this corridor effectively connects two adjacent reserves, enabling the movement of elephants across the China-Laos border, which facilitates transboundary movements and genetic exchanges, mitigating the risk of inbreeding and enhancing genetic diversity. As a result of this conservation effort, the suitable habitat area for Asian elephants within the China-Laos transboundary conservation area increased 251.26 square kilometers from 1985 to 2020 (Chen et al., 2024; Wang et al., 2021). This expansion has provided elephants with a larger, more contiguous habitat, which could in turn reduce fragmentation-induced human-elephant conflicts. Our results showed eight independent haplotypes in Laos' elephants and three haplotypes shared with elephants in China (Hap_19, Fig. 4A), supporting the long-term benefits of this transnational corridor for elephant protection in both countries.

However, promoting gene flow between the Cangyuan and Xishuangbanna populations appears difficult. Artificially assisted gene flow is a potential genetic rescue strategy for the Cangyuan population. The most suitable source for introducing genetic diversity into the Cangyuan population would be β clade elephants from other countries. Alternatively, establishing corridors between Xishuangbanna and Nangunhe may provide another viable option. Unfortunately, connecting the Xishuangbanna and Cangyuan population is difficult due to the high density of human activities and infrastructure. Furthermore, further analysis with whole genome sequencing data is needed to support such rescue plans by evaluating the benefits and risks of both inbreeding and outbreeding depression.

4.3. Limitations and future prospects

The maternal inheritance and multi-copy characteristics of mitochondrial DNA present both advantages and limitations in population genetics research (Kowalczyk et al., 2021). While mitochondrial genome analysis can effectively reflect maternal population structure and genetic diversity, it is important to recognize the significant role of paternal gene flow in Asian elephant populations. Compared to smaller mammals, Asian elephants typically have larger home ranges (Fernando et al., 2008; Hutchinson et al., 2006), which increases the likelihood of encounters and mating with males from different populations, particularly when their habitats are connected. Paternal gene flow is a key driver in enhancing the genetic diversity of Asian elephants. However, obtaining high-quality samples and overcoming the technical challenges of extracting high-quality host DNA from non-invasive samples, such as feces, has hindered research on the nuclear genome of wild Asian elephant populations, which further hampers the detailed assessment of the possible genetic consequences (e.g. accumulation of or introduction of deleterious mutations) of the translocation of individuals within or between α and β clades.

In the context of conservation, our work offers a preliminary exploration of the genetic background of Asian elephants, highlighting the need to integrate both mitochondrial and nuclear genetic data. Although we conducted extensive sampling across the elephant range in China, our sample size remains small to represent the entire population. Long-term observations indicate that there are multiple family groups of Asian elephants in the Mengla region (Campos-Arceiz et al., 2021), which may represent the most diverse

population, yet we only included three samples in this area. Future studies should aim for range-wide sampling that aligns with the distribution of Asian elephants to eliminate the issue of sampling imbalance. With ongoing advancements in sequencing technology, sequencing costs have steadily decreased (Hu et al., 2021). Furthermore, improved DNA isolation techniques for non-invasive samples are gradually becoming available (Cui et al., 2024). It is urgent to explore the population structure and genetic diversity of global Asian elephants at the whole-genome level. This includes exploring gene flow between Asian elephant populations and evaluating the effectiveness of genetic rescue measures, such as artificial gene flow between α clade and β clade, which are expected to provide robust support for future conservation efforts.

5. Conclusions

In this study, we assembled the whole mitochondrial genomes of 35 wild Asian elephant individuals from China and 13 captive Asian elephants. Population genetic analysis showed two deeply differentiated Asian elephant populations, corresponding to the α clade in Xishuangbanna and β clade in Nangunhe (Cangyuan). We found extremely low haplotype diversity in the two diverged populations, with only two and one haplotype found in the Xishuangbanna and Nangunhe, respectively. By comparing to Asian elephants from other countries, we found potential gene flow between the Xishuangbanna population and populations in neighboring countries. Unfortunately, the Nangunhe population is fully isolated and needs special conservation interventions. However, an appropriate genetic rescue plan for wild Asian elephants in China still needs more comprehensive investigation at the whole genome level.

Ethics statement

Sample collection, follow-up experiments, and research design in this study were all approved by the Laboratory Animal Management and Ethics Committee of Northeast Forestry University (No. 2024100).

CRediT authorship contribution statement

Minhui Shi: Data curation, Formal analysis, Investigation, Visualization, Writing – original draft preparation. **Yinping Tian:** Formal analysis, Investigation, Validation, Writing – original draft preparation. **Yongjing Tang:** Investigation, Resources. **Haimeng Li:** Investigation, Validation. **Jishan Wang:** Investigation, Resources. **Yue Ma:** Investigation. **Xin Liu:** Supervision, Writing – review & editing. **Ahimsa Campos-Arceiz:** Writing – review & editing. **Fei Chen:** Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing. **Tianming Lan:** Conceptualization, Funding acquisition, Project administration, Resources, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03503.

Data availability

The sequences supporting this research have been deposited in GenBank with the accession numbers PQ720719-PQ720758.

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