



Glacial Expansion or Interglacial Expansion? Contrasting Demographic Models of Four Cold-Adapted Fir Species in North America and East Asia

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Understanding and forecasting species' response to climate change is a critical need for future conservation and management. Two expansion hypotheses, the glacial expansion versus the interglacial expansion, have been proposed to interpret how cold-adapted organisms in the northern hemisphere respond to Quaternary climatic fluctuations. To test these two hypotheses, we originally used two pairs of high-low elevation firs from North America (*Abies lasiocarpa* and *Abies balsamea*) and East Asia (*Abies chensiensis* and *Abies nephrolepis*). *Abies lasiocarpa* and *Abies chensiensis* are widely distributed in high-elevation regions of western North America and central China. *Abies balsamea* and *Abies nephrolepis* occur in central North America and northeast China, with much lower elevations. These fir species are typical cold-adapted species and sensitive to climate fluctuations. Here, we integrated the mtDNA and cpDNA polymorphisms involving 44 populations and 585 individuals. Based on phylogeographic analyses, recent historical range expansions were indicated in two high-elevation firs (*Abies lasiocarpa* and *Abies chensiensis*) during the last glaciation (43.8–28.4 or 21.9–14.2 kya, 53.1–34.5 or 26.6–17.2 kya). Such glacial expansions in high-elevation firs were further confirmed by the evidence of species distribution modelling, geographic-driven genetic patterns, palynological records, and current distribution patterns. Unlike the north American firs, the SDM models indicated unremarkable expansion or contraction in East Asia firs for its much more stable conditions during different historical periods. Taken together, our findings highly supported that high-elevation firs experienced glacial expansion during the Quaternary climate change in East Asia and North America, as interglacial expansion within low-elevation firs. Under this situation, the critically endangered fir species distributed in high elevation would have no enough higher elevational space to migrate. Facing the increasing global warming, thus we proposed *ex-situ* conservation of defining conservation units as the most meaningful strategy.

Keywords: conservation, global climate change, phylogeography, species distribution modelling, endangered species

INTRODUCTION

Understanding and predicting species distribution range shifts in response to climate change, especially Quaternary glacial and interglacial cycles, is critical for conservation and management (Betancourt et al., 1990; Hewitt, 1996, 2004). For cold-adapted taxa in the northern hemisphere, two common hypotheses are proposed to explain their demographic shifts to historical climate change cycles (Theodoridis et al., 2017). The first hypothesis is the interglacial expansion of cold-adapted organisms at lower elevations (Lascoux et al., 2004; Theodoridis et al., 2017). Under this hypothesis, historical glaciations were generally a driver of range contraction, with large-scale latitudinal shifts into glacial refugia at the lower latitudes (Figures 1 A–C; Birks, 2008; Luzmm et al., 2020). These rapidly latitudinal shifts were characterized by low genetic diversity at higher latitudes than lower ones (Hewitt, 1996). The alternative hypothesis is the glacial expansion of cold-adapted species in higher elevations. Under this hypothesis, cold-adapted species shifted along an altitudinal gradient due to glacial-interglacial fluctuations (Petit et al., 2005; Awad et al., 2014; Inoue and Berg, 2016; Oliveira et al., 2021). They moved downslope and generated wider distribution during the various glacial maxima, and collapsed into several small high-elevation sky-islands during the interglaciations (Figures 1D–F; Galbreath et al., 2009; Inoue and Berg, 2016; Oliveira et al., 2021). Such glacial expansion hypothesis may result in multiple genetic diversity centres, and lacking genetic diversity decreasing along latitude (Hewitt, 1996). Thus, the glacial expansion hypothesis differs from the interglacial expansion hypothesis in both expansion periods and spatial distribution of genetic diversity.

The glacial expansion hypothesis has been validated by various studies on alpine and arctic species (Brown and Hebda, 2002; Cinget et al., 2015b; Shao et al., 2017, 2020; Wyatt et al., 2021). Besides, several studies have sought to support the interglacial expansion hypothesis (Cinget et al., 2015a; Theodoridis et al., 2017). Till now, the two proposed contrasting hypotheses have never been simultaneously documented in closely related species, presenting comparable high-low elevations or distinct continents (Liu et al., 2012; Theodoridis et al., 2017; Lin et al., 2021). In fact, the cold-adapted species in East Asia, Europe, and North America might respond to the Quaternary climatic fluctuations via different demographic hypotheses. In North America and Europe, northern regions have been repeatedly covered by large continuous ice sheets during glaciations. And only a few montane glaciers or valley glaciers occurred in East Asia regions (Shi et al., 1987; Shi, 2002). Thus further research concerning comparable high-low elevations and distinct continents is significant in understanding cold-adapted species' response to Quaternary glacial-interglacial cycles.

Firs are widely distributed in the montane region among the northern hemisphere, and North America and East Asia are two well-known diversity centres (Farjon, 2001; Fan, 2006). Because of their cold-adapted distribution and sensitivity to temperature changes, these plants are commonly used as paleoclimatic indicators, and make them an ideal model system for investigating the proposed contrasting hypotheses (Xu et al., 1980; Shi, 1996). Here, we selected four cold-adapted firs from

North America [*Abies lasiocarpa* Endl. and *Abies balsamea* (L.) Mill.] and East Asia (*Abies chensiensis* Tiegh. and *Abies nephrolepis* Maxim.), presenting comparable high-low elevations and distinct continents (Figure 2). These four fir species present not only distinct continents but also comparable ecozones (Halliday and Brown, 1943; Liu, 1971; Fan, 2006). *Abies lasiocarpa* and *Abies chensiensis* are typical of the montane ecozone, with an altitude of 1100–2300 and 2100–3500 m, respectively (Cheng and Fu, 1978). However, *Abies balsamea* and *Abies nephrolepis* are instead found in the boreal plain ecozone, with a much lower elevation of 0–1700 and 0–1200 m, respectively (Little, 1971; Frank, 1990). These fir species are disjunctly distributed in cold and moist high latitudes or altitudes (Alexander et al., 1990; Stewart et al., 2010). These two high-low elevation species pairs thus provide an excellent system to simultaneously evaluate the proposed contrasting hypotheses in North America and East Asia by comparing interspecific phylogeography.

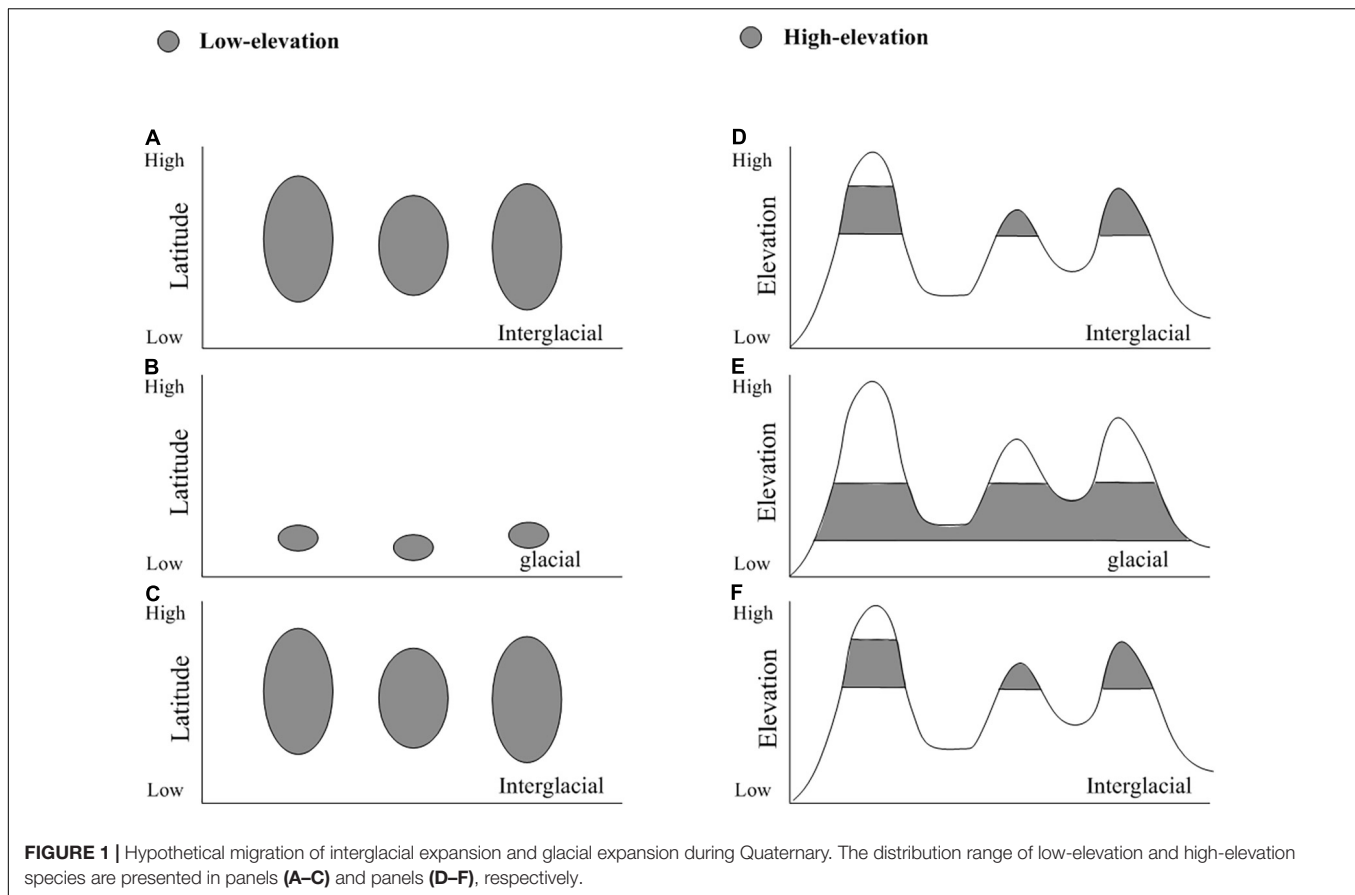
Statistical phylogeographic, by integrating phylogeographic and climatic data, is now proposed as one of the most efficient ways to inform and test alternative evolutionary hypotheses (Combe et al., 2016; Ersmark et al., 2016; Theodoridis et al., 2017; Yan et al., 2020). To reconstruct historical range shifts, the phylogeographic analysis by using population-based genealogical data is the most effective way (Avice, 2004). Another widely used method is species distribution modelling (SDM), which is widely used to understand biogeographic patterns and the processes generating them through studies of spatial-geographic variation by providing independent, but complementary, information (Waltari et al., 2007; Avice, 2009; Shao et al., 2020; Brodie et al., 2021). The statistical phylogeography thus provides a robust approach to explain current species distributions and genetic structure in relation to historical climate oscillations (Gavin et al., 2014; López-Pujol et al., 2016).

Here, we conducted statistical phylogeographic analyses and species distribution modelling on four fir species, presenting comparable high-low elevations and distinct continents, with aims: (i) original test the significance of the two contrasting hypotheses in North America and East Asia, (ii) explore the conservation strategy of fir species under increasing global warming.

MATERIALS AND METHODS

Study Species, Sampling, and Genomic Data

Four firs, presenting comparable high-low elevations and distinct continents, were used in this study. *Abies lasiocarpa* and *Abies balsamea* are widely distributed in North America (Figure 2; Hosie, 1969). These two species were located in a monophyletic clade according to mtDNA and cpDNA phylogeny (Aguirre-Planter et al., 2012; Xiang et al., 2015, 2018). *Abies lasiocarpa* tends to grow in the montane region of New Mexico and Arizona, more extensively in Utah and Colorado (Alexander et al., 1990). It is typically found at 1100–2300 m elevation in coastal subalpine conifer forests,



and grows to the alpine treeline in most of its range (Little, 1971). *Abies balsamea* always occurred in cold regions (around 4°C) of northeastern America and eastern Canada, and the northeastern United States, at 0–1700 m elevation in boreal and north temperate forests (Little, 1971; Frank, 1990). It often forms clumps, where branches from an older central stem have layered, developed apical dominance. *Abies chensiensis*, as an endangered species, is distributed in Qinling-Daba and Hengduan mountains region of central China (Cheng and Fu, 1978; International Union for Conservation of Nature [IUCN], 2021). It grows in cold, moist forests at 2100–3500 m elevation, in regions with annual precipitation of 1000–2000 mm. *Abies nephrolepis* is a species occurring in Northeast Asia. Its elevation ranges from 0 to 1200 m, characterized by short, cool summers, and long cold winters with much snow (Cheng and Fu, 1978). *Abies lasiocarpa* and *Abies chensiensis* are widely distributed in high-elevation regions, as *Abies balsamea* and *Abies nephrolepis* occur in much lower elevations (Figure 2).

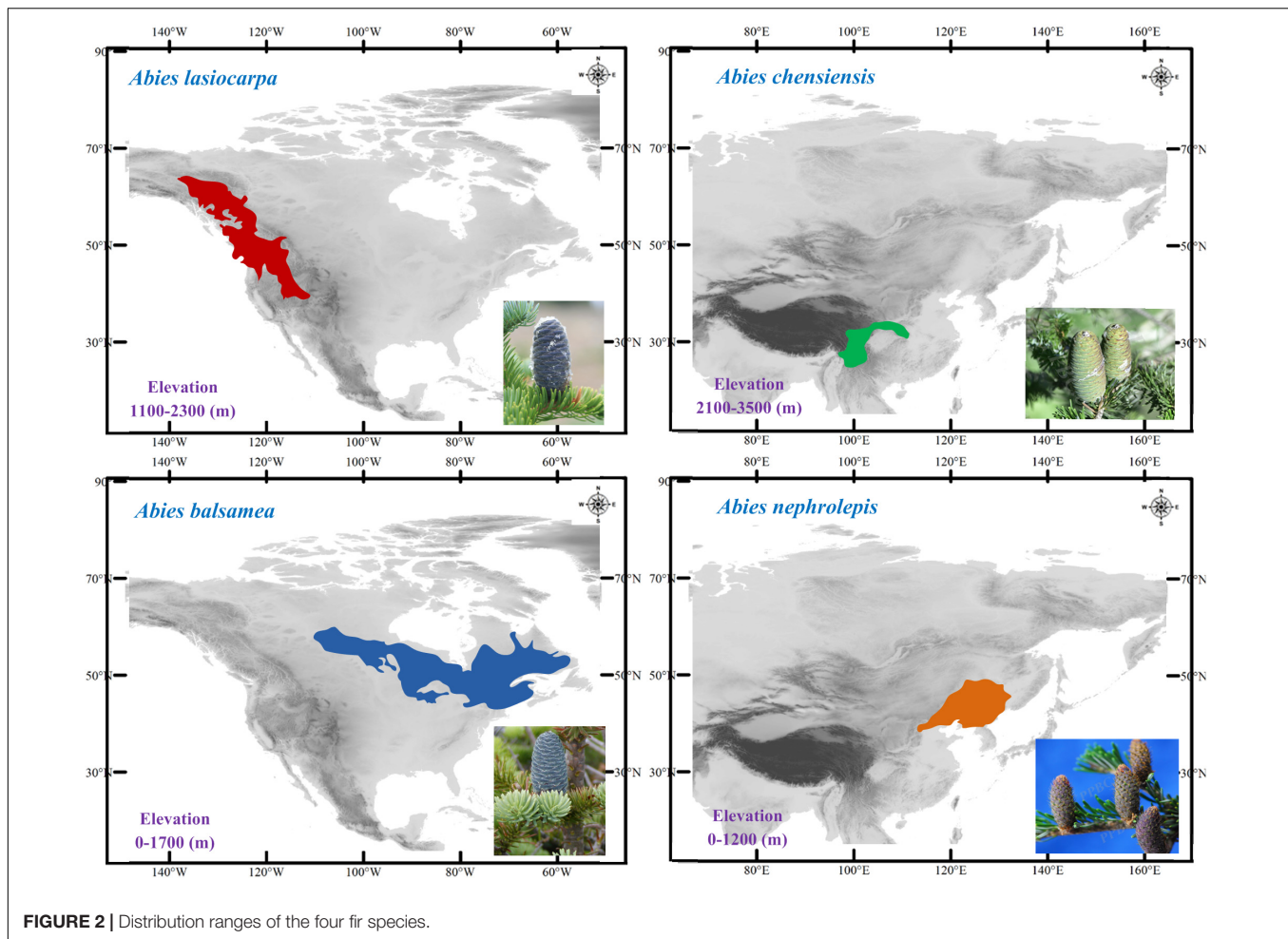
Here, the species sampling and genomic data were derived from three published studies (Jiang et al., 2011; Wang et al., 2011; Cinget et al., 2015b). Altogether, we sampled 585 individuals from 44 natural populations, including seven *A. lasiocarpa* populations, 12 *A. balsamea* populations, ten *A. chensiensis* populations, and 15 *A. nephrolepis* populations (Supplementary Table 1). Our sampling well presented the current distribution of these species. Field sampling was strictly conducted following

international rules. *Tsuga canadensis* and *Keteleeria evelyniana* were chosen as outgroups.

In total, one mtDNA fragment (nad5-4) and one cpDNA fragment (trnL-trnF) were derived from three published studies (Jiang et al., 2011; Wang et al., 2011; Cinget et al., 2015b). Even all previous population-based studies in the genus *Abies* were widely investigated, only these two fragments and four firs could be recognised. To be mentioned, even though only two makers were used, they were almost the most informative sites available in the phylogeographical analyses of the genus *Abies* so far (Cinget et al., 2015a,b; Shao and Xiang, 2015; Shao et al., 2017, 2020). In these studies, more than ten mtDNA (e.g., nad1-2, nad5-1, nad5-4, nad7-1, and cox1) and cpDNA (e.g., trnS-trnF, trnL-trnF, and trnS-trnG) had been surveyed, nad5-4 and trnL-trnF were the most informative markers. Thus the markers used could be sufficient to test the relevant phylogeographical history. The relevant Genbank numbers were recorded in Supplementary Tables 2, 3.

Population Structure and Demographic History Analyses

We used DNASP version 4.10 to calculate the genetic diversity values, including h (genotype diversity) and π (differences between genetic sequences) (Nei, 1987; Rozas et al., 2003). We run the DNASP for each species and population. We used the



molecular diversity values to explore the spatial distribution patterns by using GDivPAL (Dellicour and Mardulyn, 2014). Such analyses in Spads were not performed using mtDNA, because of its extremely low diversity in each species. By using the software NETWORK, we further inferred the network relationships within mitotypes and chlorotypes (Bandelt et al., 1999). Moreover, each gap was treated as one mutation.

To survey the population differentiation, we used the PERMUT to calculate N_{ST} and G_{ST} , the genetic diversity within populations (H_S), and the total gene diversity (H_T) (Pons and Petit, 1996). A phylogeographic structure could be indicated if G_{ST} was significantly lower than the N_{ST} . Using the program ARLEQUIN 3.5, we run the AMOVA (molecular variance analysis) to survey the genetical variation (Excoffier and Lischer, 2010). We performed the Mantel test to estimate the correlation between genetic distance and geographical distances (Mantel, 1967; Nei and Li, 1979; Dupanloup et al., 2002).

To detect historical distribution range expansions, the mismatch distribution analyses were performed in Arlequin 3.5. If recent expansions were indicated, further analyses could estimate potential periods. The estimated formula was $s = 2 ut$ (t means expansion age), $u = \mu kg$ (μ means the substitution rates of each nucleotide site every year, k means the average length

of nucleotide sequences, and g means the potential generation years in *Abies*) (Rogers and Harpending, 1992). Here, we designed the value of μ as $2.61\text{--}4.02 \times 10^{-10} \text{ ss}^{-1} \text{ y}^{-1}$, the value of k as 1111 bp, according to numerous published studies in Pinaceae and *Abies* (e.g., Gernandt et al., 2008; Shao et al., 2020). The g was designed as 25 years (option 1) or 50 years (option 2) for the occurrence of two different effective generation times of *Abies* (Xiang, 2001; Brown et al., 2004; Fan, 2006). Furthermore, such mismatch distribution analyses were performed in three species except for *A. nephrolepis*, because the chlorotype diversity within all the populations of *A. nephrolepis* was relatively low, which was fixed by C8 (Figure 3B).

Species Distribution Modelling

The occurrence data for the whole of geographic distribution range were calculated from field observations, the Global Biodiversity Information Facility,¹ and the Chinese Virtual Herbarium.² Although many herbarium records did not specify latitude and longitude, we were able to geo-reference detailed locations, using only locations specified in the label information.

¹www.gbif.org

²www.cvh.ac.cn

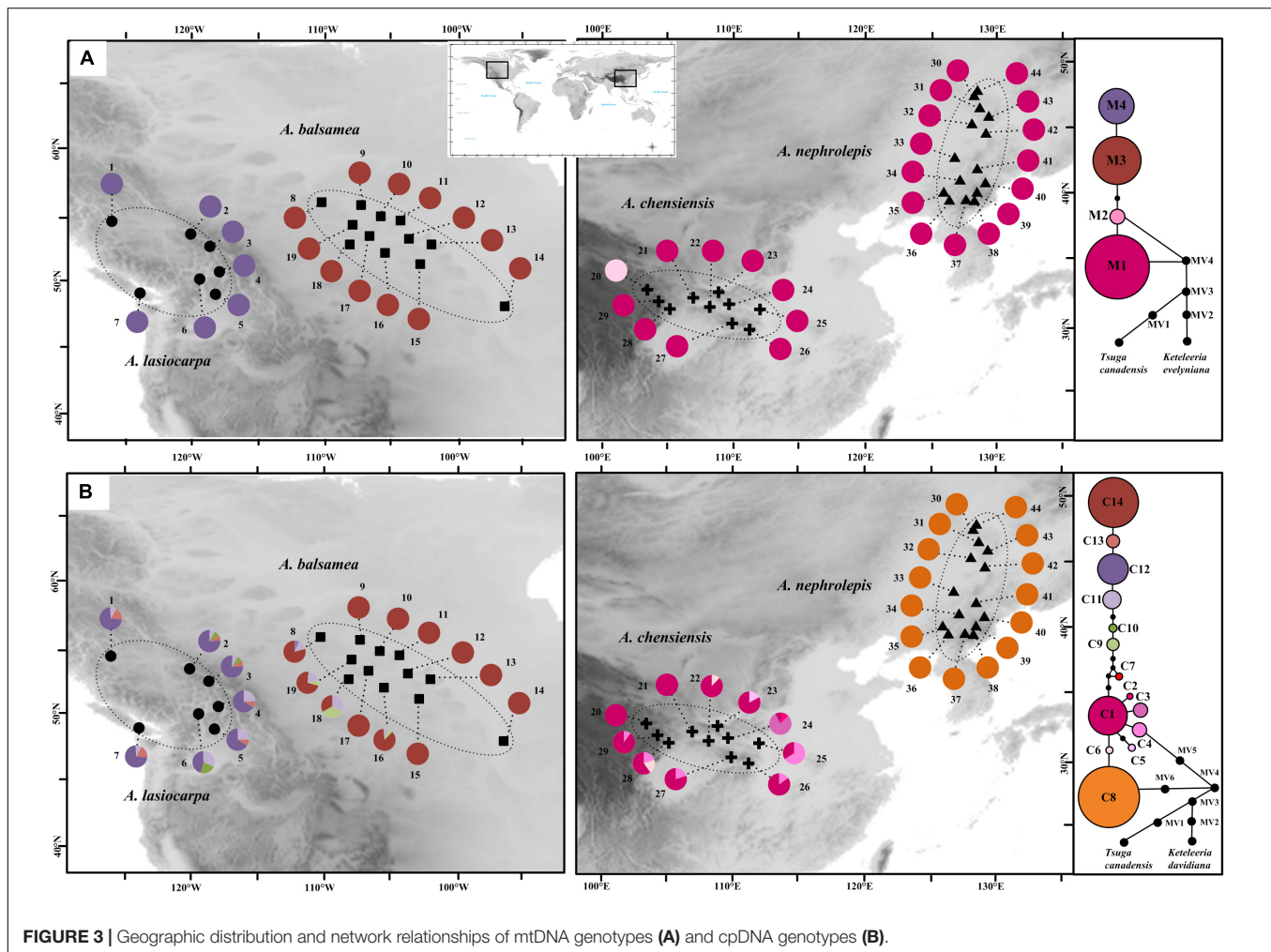


FIGURE 3 | Geographic distribution and network relationships of mtDNA genotypes (A) and cpDNA genotypes (B).

In total, after removing duplicate records within each pixel (30 arc s, ca. 1 km), we obtained 267 presence records (see **Supplementary Table 4** for the list of all occurrences). These records involved 53 *A. lasiocarpa* records, 107 *A. balsamea* records, 64 *A. chensiensis* records, and 43 *A. nephrolepis* records.

The species distribution modelling (SDM) of these four firs was modelled using the MAXENT (version 3.2.1; Phillips et al., 2006). The environmental data were provided by the WorldClim database³ (Fick and Hijmans, 2017), including 19 BIOCLIM variables and three different periods in 30 arc s resolution. These different periods are current (for the period 1,950~2,000) at a spatial resolution of 30 arc s, the last glacial maximum (LGM; ~21,000 years BP) with a spatial resolution of 2.5 arc min resolution simulated under the CCSM and MIROC models, and the last interglacial period (LIG; ~120,000–140,000 years BP) with spatial resolution in 30 arc s resolution. Following Zurell et al. (2020) and Nualart et al. (2021), we removed those highly correlated BIOCLIM variables (pairwise Pearson correlations, r greater than 0.8), seven variables were retained for subsequent analysis (bio2: mean diurnal range of temperature,

bio4: temperature seasonality, bio5: the max temperature of warmest month, bio9: mean temperature of driest quarter, bio11: mean temperature of coldest quarter, bio16: precipitation of warmest quarter, bio17: precipitation of driest quarter). The pairwise Pearson correlations among 19 BIOCLIM variables were illustrated in **Supplementary Table 5**. Finally, the SDMs of these four firs under different periods were conducted in 100 replicate runs, maximum iterations (1500). To ensure the consistency of the model prediction, 70% of the localities were used to train the model and 30% were used to test it. The area under the curve (AUC) value was estimated to evaluate the model performance (Phillips et al., 2006). All predictions were visualised in ArcGIS v. 10.2 (ESRI, Redlands, CA, United States). The suitable areas (in km²) (logistic value > 0.25) for all models at each time slice were also calculated in ArcGIS.

RESULTS

Mitochondrial DNA Genealogy

The mtDNA *nad5-4* was 246 bp in length. Four distinct mitotypes resulted from three point mutations and two indels (M1-4)

³www.worldclim.org

TABLE 1 | The results of molecular variance analyses.

Region	Species	Variation type	Mt DNA			Cp DNA	
			df	Variation (%)	Fixation index	Variation (%)	Fixation index
North America	<i>A. lasiocarpa</i>	Among populations	6	0.00	$F_{ST} = 0.00000$	2.03	$F_{ST} = 0.02033$
		Within populations	74	0.00		97.97	
		Total	95				
	<i>A. balsamea</i>	Among populations	11	0.00	$F_{ST} = 0.00000$	29.21	$F_{ST} = 0.29212^{**}$
		Within populations	158	0.00		70.79	
		Total	169				
East Asia	<i>A. chensiensis</i>	Among populations	9	100.00	$F_{ST} = 1.00000^{**}$	24.99	$F_{ST} = 0.24988^{**}$
		Within populations	86	0.00		75.01	
		Total	95				
	<i>A. nephrolepis</i>	Among populations	14	0.00	$F_{ST} = 0.00000$	0.00	$F_{ST} = 0.00000$
		Within populations	206	0.00		0.00	
		Total	220				
In total	Among species	4	95.17	$F_{SC} = 1.00000^{**}$	94.43	$F_{SC} = 0.24155^{**}$	
	Among populations within species	42	4.83	$F_{ST} = 1.00000^{**}$	1.34	$F_{ST} = 0.95778^{**}$	
	Within populations	538	0.00	$F_{CT} = 0.95170^{**}$	4.22	$F_{CT} = 0.94433^{**}$	
	Total	584					

******, $P \leq 0.001$.

TABLE 2 | The results of genetic diversity estimates and Mantel tests.

Region	Species		H_T	H_S	G_{ST}	N_{ST}	Mantel test
North America	<i>A. lasiocarpa</i>	mtDNA	NC	NC	NC	NC	$r = 0.923, p = 0.327$
		cpDNA	0.886 (0.028)	0.596 (0.098)	0.328 (0.222)	0.491 (0.157)	$r = 0.979, p = 0.174$
	<i>A. balsamea</i>	mtDNA	NC	NC	NC	NC	NC
		cpDNA	NC	NC	NC	NC	NC
East Asia	<i>A. chensiensis</i>	mtDNA	0.528 (0.109)	0.185 (0.085)	0.650 (0.130)	0.655 (0.1055)*	$r = 0.254, p = 0.115$
		cpDNA	0.700 (0.058)	0.365 (0.104)	0.479 (0.155)	0.508 (0.173)*	$r = 0.490, p = 0.006$
	<i>A. nephrolepis</i>	mtDNA	0.710 (0.108)	0.055 (0.030)	0.922 (0.045)	0.969 (0.019)*	$r = 0.525, p = 0.001$
		cpDNA	0.488 (0.102)	0.369 (0.087)	0.245 (0.035)	0.220 (0.033)*	$r = 0.249, p = 0.105$
In total	mtDNA	0.588 (0.070)	0.119 (0.030)	0.798 (0.051)	0.901 (0.033)*	$r = 0.201, p = 0.037$	
	cpDNA	0.827 (0.019)	0.387 (0.041)	0.532 (0.049)	0.597 (0.047)*	$r = 0.226, p = 0.010$	

*****, $P < 0.05$; **NC**, not calculated.

(**Supplementary Table 2**). These four mitotypes were fixed in single species. Based on the NETWORK results, M1 and M2 were probably the ancestral haplotypes (**Figure 3A**). M1 and M2 were fixed in the East Asia species (*A. chensiensis* and *A. nephrolepis*) (**Figure 3A**). M3 and M4, which derived from M1 and M2, were exclusive to *A. balsamea* (Pop. 1–7) and *A. lasiocarpa*, respectively (Pop. 8–19).

The values of π and h were recorded in **Supplementary Table 1**. In AMOVA analyses, 95.17% mtDNA variation was scattered among species, and the H_T was much higher than H_S (**Tables 1, 2**). A significant phylogeographic structure of isolated geographic distributions were indicated ($G_{ST} < N_{ST}$; $P < 0.05$), and the geographic distances were remarkably related to mtDNA genetic diversity ($r = 0.201, p = 0.037$) (**Table 2**). In the SAMOVA analyses, there was no significant geographic division.

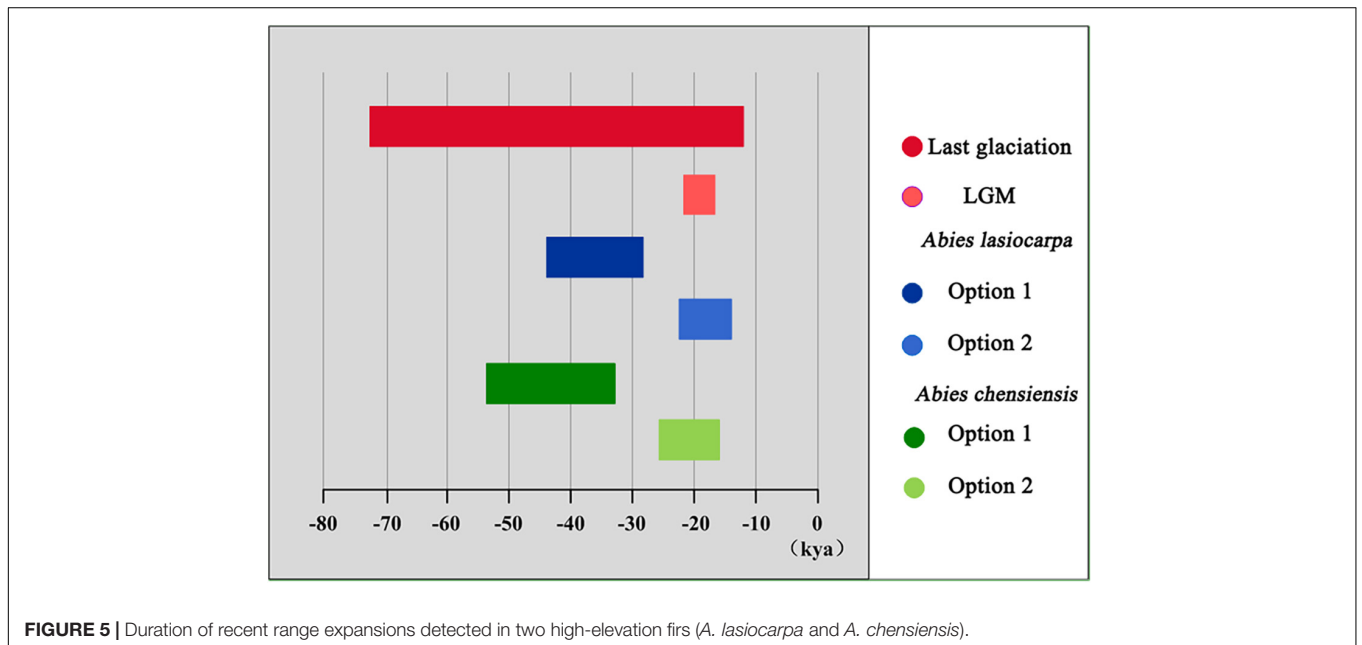
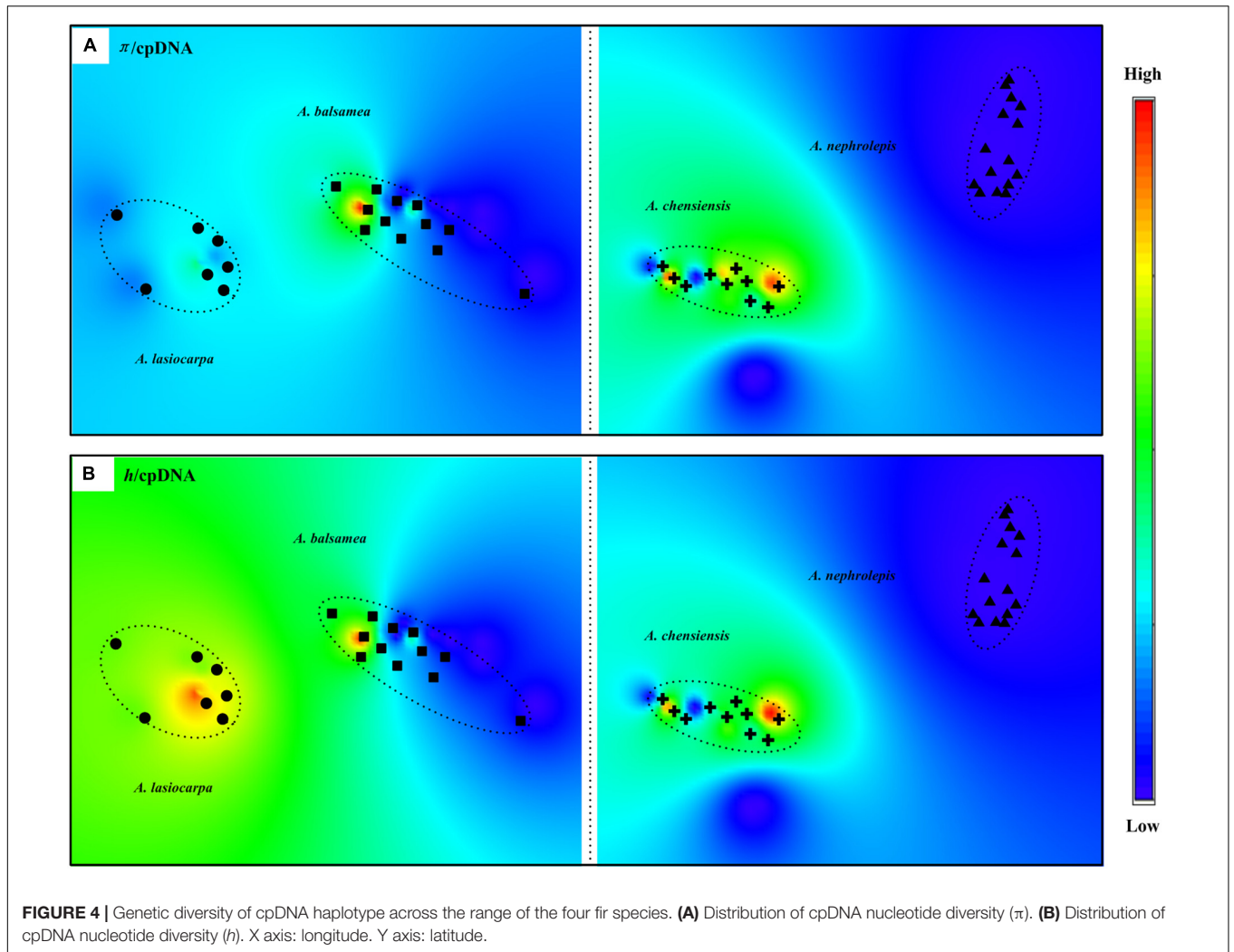
Chloroplast DNA Genealogy

In total, fourteen chlorotypes were resulted by nine substitutions and three indels (C1–14) (**Supplementary Table 3**). Among them, four chlorotypes had a frequency above 5% (C1, C8, C12, and C14), while twelve chlorotypes (C1–10 and C13–14) were fixed in single taxa. Moreover, C11 and C12 are shared

two North American species (*A. lasiocarpa* and *A. balsamea*) (**Figure 3B**). Based on the NETWORK analysis, C1 and C8 might be the ancestral haplotypes (**Figure 3B**). In *A. lasiocarpa* and *A. chensiensis*, only one or two step mutations lain in the “star-like” network (**Supplementary Figure 1**).

In AMOVA analyses, 94.43% of the mtDNA variation was located among species, and the H_T was much higher than H_S (**Tables 1, 2**). A significant phylogeographic structure isolated geographic distributions were also indicated ($G_{ST} < N_{ST}$; $P < 0.05$). In our SAMOVA analyses, there was no significant geographic division, but the results of Mantel analyses indicated remarkable correlations between geographic distances and genetical distribution ($r = 0.226, P = 0.010$) (**Table 2**).

Compared to the mtDNA, higher genetic diversity appeared in the cpDNA genealogy (**Figure 3** and **Supplementary Table 1**). Based on the Spads analyses on the species level, the mtDNA diversity did not show any latitudinal trend (**Supplementary Table 1** and **Figure 4**). Based on π and h diversity, only one diversity centre was recognised in two low-elevation species (*A. balsamea* and *A. nephrolepis*), as three or two diversity centres were revealed in high-elevation species (*A. lasiocarpa* and *A. chensiensis*) (**Figure 4**).



Species Demographic History

The analyses of mismatch distribution were performed on species level using cpDNA sequences. In total, three species were included in the comments (*A. lasiocarpa*, *A. balsamea*, and *A. chensiensis*), excluded *A. nephrolepis* because of the low cpDNA variation (Variation of cpDNA = 0; **Table 1**).

Our mismatch distribution results did not support the historical expansion hypothesis of *A. balsamea* ($P_{SSD} = 0.020$) (**Supplementary Figure 2**). Unlike *A. balsamea*, the expansion hypothesis was supported in two high-elevation firs, including *A. lasiocarpa* ($P_{SSD} = 0.147$) and *A. chensiensis* ($P_{SSD} = 0.734$) (**Supplementary Figure 2**). Further, our results estimated the relevant expansion periods of *A. lasiocarpa* in 43.8–28.4 kya (option 1: $g = 25$ years) or 21.9–14.2 kya (option 2: $g = 50$ years) (**Figure 5** and **Table 3**). Moreover, the historical expansion of *A. chensiensis* probably occurred in 53.1–34.5 kya (option 1) or 26.6–17.2 kya (option 2).

Species Distribution Modelling

The SDMs were built for four firs, separately, based on seven environmental variables under the present climate, the LGM (CCSM), the LGM (MIROC) and the LIG, respectively. All SDMs had high AUC values (greater than 0.9), indicating that the model predictions were much better than the chance (AUC = 0.5). The area of potential habitats, after accounting for uncertainty, was calculated using the logistic value > 0.25 (**Table 4**).

In North America, models for *A. lasiocarpa* showed a heavily decrease of suitable habitats while global warming, from the LGM (CCSM) (6,568,140 km²) to the present (4,710,507 km²) to the LIG (1,158,792 km²) (**Figure 6A** and **Table 4**). The potential habitats for the LGM (MIROC) (4,872,627 km²) were almost the same as the habitats under the current climate. These models predicted the lowest distribution areas under the warmest climate during the LIG. Models for *A. balsamea* showed obviously range expansion when global warming, from the LGM (CCSM) (172,001 km²) and LGM (MIROC) (1,789,170 km²) compared to the LIG (6,672,244) and present (5,995,647 km²) (**Figure 6B** and **Table 4**). In addition, the suitable habitat of *A. balsamea* during the LGM was distributed more southerly than the LIG and present models.

Compared to *A. lasiocarpa* and *A. balsamea* in North America, the suitable habitat shifting within *A. chensiensis* and *A. nephrolepis* in East Asia were unremarkable. For *A. chensiensis*, the models showed a slightly decreasing of suitable habitat while global warming, from the LGM (CCSM) (1,868,430 km²) to the present (1,823,649 km²) to the LIG (1,670,956 km²) (**Figure 6C** and **Table 4**). However, the LGM (MIROC) model (1,216,388 km²) was relatively smaller than others. And its potential habitats shifted along latitude during different periods. For *A. nephrolepis*, the models showed a slightly expansion of suitable habitat while global warming, from the LGM (CCSM) (2,324,014 km²) to the present (2,363,103 km²) to the LIG (2,537,519 km²) (**Figure 6D** and **Table 4**). But the LGM (MIROC) model (1,513,332 km²) was also relatively smaller than others. Moreover, the LGM (MIROC) models were quite different from the LGM (CCSM) models in three firs except for *A. balsamea*. Unlike the LGM

(MIROC) models, the LGM (CCSM) models were consistent with the expansion or contraction trends from the LIG to the present models.

DISCUSSION

Glacial Expansion of High-Elevation Firs and Interglacial Expansion of Low-Elevation Firs

Previous studies concerning arctic-alpine species in Northern Hemisphere indicate two distinct expansion hypotheses in response to global climate change. These two proposed hypotheses have never been simultaneously documented in comparable high-low elevations or distinct continents (Moritz and Agudo, 2013; Theodoridis et al., 2017; Lin et al., 2021). Using four closely related firs, this study evaluated their significance on distinct elevations and continents for the first time.

Our results certainly supported the glacial expansion of high-elevation firs and interglacial expansion of low-elevation firs, either in North America or East Asia. Firstly, recent expansions were revealed in two high-elevation firs (*A. lasiocarpa*, $P_{SSD} = 0.147$; *A. chensiensis*, $P_{SSD} = 0.734$), but not in *A. balsamea* ($P_{SSD} = 0.020$) (**Supplementary Figure 2**). Similar analyses were not performed in *A. nephrolepis* because of its extremely low cpDNA variation (**Table 1**). Such recent expansions were confirmed by the Networks of chlorotypes. The chlorotypes of *A. lasiocarpa* and *A. chensiensis* showed a “star-like” pattern, which could be interpreted as characteristic of recent population expansions (**Supplementary Figure 1**; Hwang et al., 2003; Shao et al., 2020). Furthermore, the recent expansions’ age of *A. lasiocarpa* and *A. chensiensis* were estimated to be around 43.8–28.4 kya and 53.1–34.5 kya (option 1: $g = 25$ years), or 21.9–14.2 and 26.6–17.2 kya (option 2: $g = 50$ years), respectively (**Table 3**). It should be noted that the above time durations were highly consistent with the last glaciation of East Asia and North America (**Figure 5**). In East Asia and North America, the last glaciation was believed to occur around 73–10.4 kya, accompanied by maximum glacial around 21–18 kya (Hewitt, 1996, 2000, 2004; Yi et al., 2004). To be mentioned, potential genetic variation within continuous range species (*A. balsamea* and *A. nephrolepis*) might be difficult to capture for the generally low-variable in plastid markers. However, even though only two makers were used, they were almost the most informative sites available in the phylogeographical analyses of the genus *Abies* so far (Cinget et al., 2015a,b; Shao and Xiang, 2015; Shao et al., 2017, 2020). Similar analyses had all been successfully conducted in previous related studies (Cun and Wang, 2010; Shao and Xiang, 2015; Shao et al., 2017, 2020).

Our SDM models also depicted historical glacial expansions in high-elevation firs and interglacial expansions in low-elevation firs. The LGM (MIROC) models were quite different from the LGM (CCSM) models in three firs except for *A. balsamea* (**Figure 6** and **Table 4**). Till now, the incongruence between the LGM (MIROC) and LGM (CCSM) had been widely

TABLE 3 | The results of mismatch distribution analysis based on cpDNA sequence.

Species	SSD (P value)	RAG (P value)	τ	Option 1		Option 2	
				t_{min} (kya)	t_{max} (kya)	t_{min} (kya)	t_{max} (kya)
<i>A. lasiocarpa</i>	0.007 (0.147)	0.125 (0.292)	0.635 (0.381–0.967)	28.441 (17.065–43.311)	43.802 (26.281–66.703)	14.221 (8.533–21.656)	21.901 (13.141–33.352)
<i>A. balsamea</i>	0.042 (0.020)	NC	NC	NC	NC	NC	NC
<i>A. chensiensis</i>	0.003 (0.734)	0.162 (0.696)	0.770 (0.000–1.514)	34.488 (0.000–67.811)	53.114 (0.000–104.435)	17.244 (0.000–33.906)	26.557 (0.000–52.218)
<i>A. nephrolepis</i>	0.000 (0.000)	NC	NC	NC	NC	NC	NC

SSD, sum of squared deviations; RAG, the Harpending's Raggedness index; NC, not calculated. Option 1, 25 years. Option 2, 50 years.

TABLE 4 | Predicted potential distribution of four fir species during different time periods.

Species	Predicted area (km ²)*			
	LIG	Present	LGM-CCSM	LGM-MIROC
<i>Abies lasiocarpa</i>	1,158,792	4,710,507	6,568,140	4,872,627
<i>Abies balsamea</i>	6,672,244	5,995,647	172,001	1,789,170
<i>Abies chensiensis</i>	1,670,956	1,823,649	1,868,430	1,216,388
<i>Abies nephrolepis</i>	2,537,519	2,363,103	2,324,014	1,513,332

*: logistic value > 0.25.

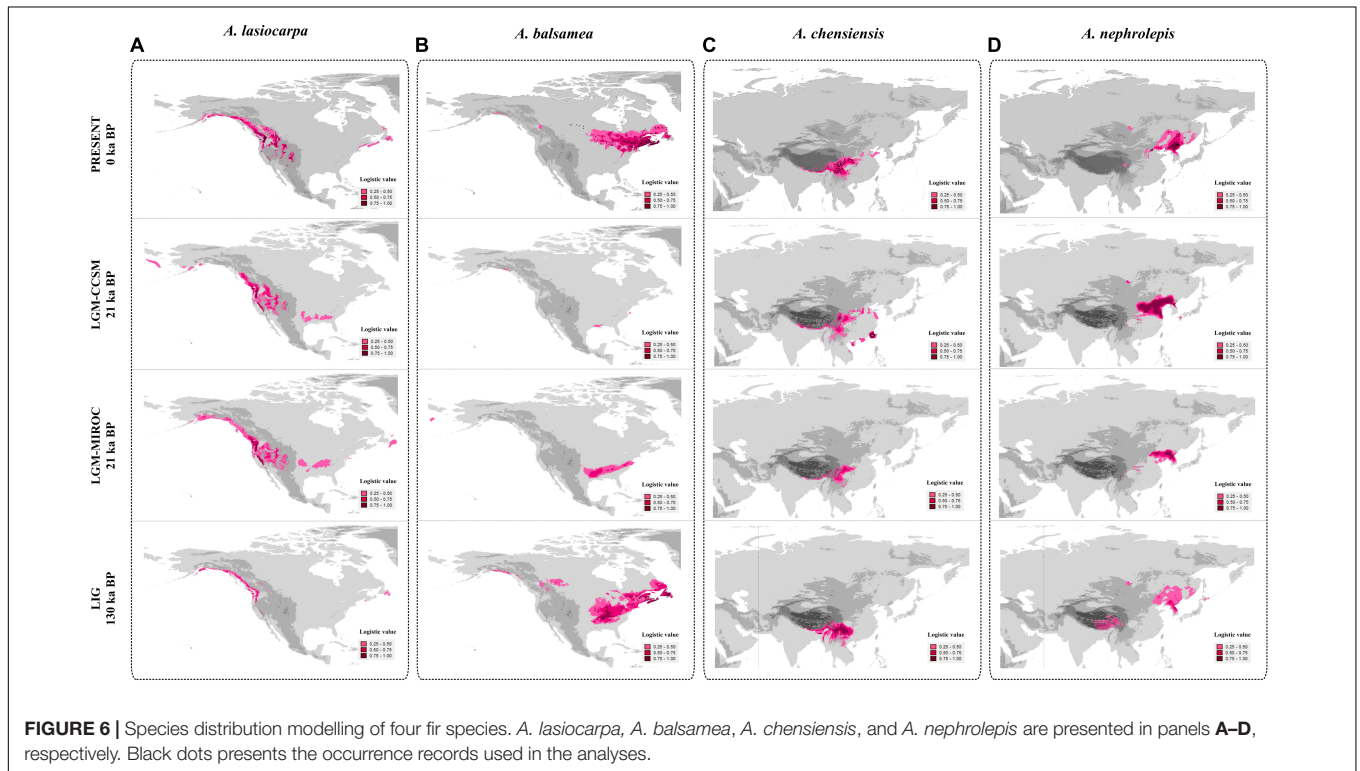


FIGURE 6 | Species distribution modelling of four fir species. *A. lasiocarpa*, *A. balsamea*, *A. chensiensis*, and *A. nephrolepis* are presented in panels **A–D**, respectively. Black dots presents the occurrence records used in the analyses.

surveyed (Guevara et al., 2019). The MIROC estimated noticeably more different climatic conditions than CCSM and suggested a remarkable different prediction of potential distribution

(Rico et al., 2021). Compared to the LGM (MIROC), the LGM (CCSM) model was much more effective and widely used in related Pinaceae species, such as the East Asian white pines

(Liu et al., 2022). In this study, the LGM (CCSM) models were highly consistent with the expansion or contraction trends from the LIG to the present models. For *A. lasiocarpa* and *A. chensiensis*, the distribution area estimations showed that the distribution range was more extensive in glacial period (the LGM CCSM) than in interglacial periods (the LIG and present) (Figures 6A,C). For *A. balsamea* and *A. nephrolepis*, the distribution range was reduced in glacial period (the LGM CCSM) than in interglacial periods (the LIG and present) (Figures 6B,D). These results suggested that *A. lasiocarpa* and *A. chensiensis* underwent expansions from the LIG till the LGM during global cooling and extensive reconstructions from the LGM to the present. Such patterns were also determined in the future geographic distribution modelling of four endemic fir species in Japan (Tanaka et al., 2012). In the context of global warming, three Japanese higher-elevation distributed firs (*Abies mariesii*, *Abies veitchii*, and *Abies homolepis*) were predicted to lose 45% suitable habitat but greater than 73% for lower-elevation distributed firs (*Abies firma*). Moreover, unlike North America, the habitat shifting in East Asia were unremarkable (Figure 6 and Table 4). For *A. chensiensis* and *A. nephrolepis*, the models showed slightly expansion or contraction of suitable habitats during different time periods. Such distinct spatial patterns could be explained by the difference in Quaternary climate between East Asia and North American (Shi et al., 1987; Shi, 2002). During Quaternary climatic fluctuations, North America has been repeatedly covered by large continuous ice sheets during glaciations, and only a few montane glaciers or valley glaciers occurred in East Asia regions. Our models indicated that the Asian range of the genus *Abies* was characterised by much more stable conditions, which might have facilitated the survival of many woody species that represent genera with highly disjunct distribution (e.g., *Aesculus*, *Pterocarya*, *Fagus*, *Castanea*) survived in East Asia (Zhang et al., 2020; Song et al., 2021).

The geographical distribution of genetic diversity could be another direct independent evidence. To distinguish interglacial and glacial expansion hypotheses, Hewitt (1996) proposed two different expansions models. One is the model of pioneer expansions, characterised by interglacial expansion hypothesis, which predicted along-latitude decreasing of genetic diversity while historical expansion (Hewitt, 2004). Another is the model of phalanx expansions, characterised by glacial expansion hypothesis, indicated along-elevation historical expansions, resulting in multiple diversity centres and no latitude trends (Oliveira et al., 2021; Wyatt et al., 2021). Based on current phylogeographical patterns, multiple diversity centers were revealed in only *A. lasiocarpa* and *A. chensiensis*, indicating no latitude decreasing trends (Figure 4). Thus the phalanx expansion model was probably activated in these two high-elevation firs. It should be noted that such pattern could also result from the fact that the isolation between potential refugia in the lowlands was less than in the mountains, which may have resulted in homogenization after the expansion period (Liu et al., 2022).

Moreover, the palynological records could be another convincing proof of species' preferred past climatic conditions. In North America, the southernmost paleo records of *A. lasiocarpa*

were US Rockies and Oregon, and could be its putative glacial refugia (Barnosky, 1981). Based on published macrofossils, *A. lasiocarpa* was originated in the Pleistocene and much common in the lower elevation regions, including Vancouver Island and Washington state (Bartlein et al., 1998; Cinget et al., 2015b). Nowadays, those lower elevation regions are dominated by *Abies amabilis* and *Abies grandis* (Farjon, 2001). For *Abies balsamea*, the palynological records reflected post-glacial migration from the refugium in southern and western Great Lakes towards central Alberta (Cinget et al., 2015a). In East Asia, numerous published palynological researches inferred a similar pattern (Xu et al., 1980, 2002; Cook et al., 2011). During interglacial periods, the pollen abundance in the high-elevation regions was obviously decreased in Eastern Asia (Tang et al., 2007; Yong et al., 2020). Indeed, those high-elevation fir species in central China (e.g., *A. chensiensis*) distributed more commonly in lowland forests during the LGM as the temperature decreased about 6–10°C (e.g., Li et al., 2019). Zhao et al. (2014) reported several remarkable impacts of repeating climate fluctuations since the LGM on the distribution of *Abies* in the mountaintop regions of central China, with obviously decreasing continuously with climate change from humid and cold (glacial) to dry and warm (interglacial). In addition, almost all the critically endangered *Abies* worldwide are restricted in the mountain top (Farjon, 2001; Xiang, 2001). Such current distribution pattern could be living evidence of interglacial fragmentation in high-elevation firs. Even though the significant deforestation during past decades, these critically endangered *Abies* species had never been the main targets for their high-elevation distribution in mountain tops and far away from human settlements (Fan, 2006). Thus climate-driven distribution changes and low seed viability could be the most critical factors.

In summary, the above results of five independent evidence lines, involving geographic-driven genetic patterns, mismatch distribution analysis, species distribution modelling, palynological records, and current distribution pattern, were highly uniform and reliable. Our findings supported the glacial expansion hypotheses of high-elevation firs and interglacial expansion hypotheses latitudinal of low-elevation firs during the Quaternary climate change in North America and East Asia.

The *ex-situ* Conservation of Critically Endangered Firs

The genus *Abies* Mill. (Pinaceae) discontinuous distributed in North America, Eastern Asia, and Europe (Xiang et al., 2018). Fir species are ecologically, and economically important plants that are dominant in Taiga and mountain conifer forests which maintain water and soil, protect the ecological environment, and conserve the biodiversity in the region (Farjon and Rushforth, 1989). However, eleven firs had been listed as endangered or critically endangered species (Xiang, 2001; International Union for Conservation of Nature [IUCN], 2021). Thus it is urgent to develop efficient conservation planning.

The primary goal in conservation biology is to determine how species respond to climate change, which generated conservation units to define (Petit et al., 1998). At present, all the endangered

fir species had an extremely high elevation habitat (>1000 m), which was quite different from the two low-elevation firs used in this study (*A. balsamea*: 0–1700 m, *A. nephrolepis*: 0–1200 m) (Farjon, 2001). Furthermore, six fir species were listed as critically endangered (*Abies beshanzuensis*, *Abies yuanbaoshanensis*, *Abies fanjingshanensis*, *Abies ziyuanensis*, *Abies fansipanensis*, and *Abies numidica*) (Fu, 1992; Xiang, 2001; International Union for Conservation of Nature [IUCN], 2021). Their distribution ranges were restricted in limited mountain tops and extremely low effective breeding size. The critically endangered status might be resulted by historical rapid recolonization *via* elevational shifting *in situ*, following severe bottleneck effects (Cinget et al., 2015a,b; Jiang et al., 2015; Shao et al., 2020). Such evolutionary progress should not be constrained. For high-elevation firs, with *A. lasiocarpa* and *A. chensiensis* as example, more than one diversity centers were depicted (Figure 4). These different diversity centers and genotypes drawn from different populations cannot be ignored. For conservation purposes, it is necessary to define conservation units on an evolutionary level for these endangered firs.

In the context of global warming, our results showed that the high-elevation firs in Northern Hemisphere had undergone glacial expansion *via* elevational shift, which led to massive habitat fragmentation or isolation. Under this situation, the suitable habitat of high-elevation *Abies* could have begun to lose continually since the LGM and quicken steps, as depicted in the SDMs of *A. lasiocarpa* and *A. chensiensis* (Figure 6). Suitable habitats of these endangered *Abies* species continued to deteriorate, and the surviving individual numbers were continuously decreased (Xiang, 2001; Peng et al., 2012; International Union for Conservation of Nature [IUCN], 2021). At present, these critically endangered firs were vulnerable to the verge of extinction, for no enough elevational space to up-migrate in respond to future climate warming (Habel et al., 2011). By analysing available studies of latitudinal and elevation range shifts for multiple taxonomic groups, most species' range shifting rate, in responding to climate change, were located around eleven meters along elevation per decade or 16.9 kilometres along latitudes per decade (Chen et al., 2011). As stated above, the endangered *Abies* species would be forced to contract up the slope by elevation shifting at a relatively high speed during the foreseeable global warming. However, these fir species have almost reached the mountaintop while no enough space to continue up-migrate, for example, *Abies beshanzuensis* located in Baishanzu Mountain (1857 m) at 1750 m, *Abies fanjingshanensis* restricted in Fanjing Mountain (2494 m) with altitudes from 2100 to 2350 m, *Abies yuanbaoshanensis* distributes in Yuanbao Mountain (2081 m) at 1900–2000 m, and *Abies ziyuanensis* occurred in Shunhuang Mountain (1882 m) at 1700 m (Fan, 2006). To protect these critically threatened *Abies*, their up-migrate along elevation must be persisted and demanded critical attention by the government managements and protection organizations.

Till now, the general government protections of these critically endangered firs were fixed by *in-situ* conservation, but it was found to be not an effective and practical program. Indeed, the continued up-migrate of the six highly endangered firs was

unsustainable. Facing the ongoing climate warming, they were believed to be near extinction or heavily contracted (Xiang, 2001; Xiang et al., 2009). Thus, we propose that the most helpful and urgent strategy was *ex-situ* management in more suitable areas, accompanied by breeding programs in botanical gardens. Even though these critically endangered firs were not included in our SDMs, the tendency was still reliable and they could be well represented for their conservative ecological niche requirement (Shao et al., 2017). As for the five critically endangered firs in China and Vietnam, the southern Hengduan Mountains region was always the suitable and ideal habitat during the whole Quaternary according to the SDMs results (Figure 6). And more than 35 National Botanical Reserves were constructed in the Heng-duan Mountains region and could play a meaningful role in the *ex-situ* conservation (Chen et al., 2009; Shao et al., 2020). Similar specific gardens and existing programs in other countries should be activated and strengthened the *ex-situ* conservation of defining conservation units. Our results are timely and significant to biodiversity conservation for endangered firs at current and future global climate change.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

AUTHOR CONTRIBUTIONS

YC and QW conceived and designed the experiments. Y-ZS and Y-YL analysed the data. Z-LY, Y-YZ, R-CX, and Y-ZY contributed reagents, materials, and analysis tools. Y-ZS, YC, and QW wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.844354/full#supplementary-material>

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