

Review

Plant phylogeography in arid Northwest China: Retrospectives and perspectives

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Abstract Despite the absence of major Quaternary glaciations in arid Northwest China, significant climatic oscillations definitely impacted the evolution of the biota *in situ*. Phylogeography has grown as a discipline because it has provided explicit tools for the study of geographical subdivision among populations. But phylogeographical application for arid Northwest China has begun to blossom, which has provided evidence that aridification played a significant role in the increase of genetic diversity and species diversification. The time frame corresponds with Pleistocene climatic oscillations, which caused extreme aridity and the expansion of sandy deserts. In the Asian desert flora subkingdom and Eurasian forest subkingdom of Northwest China, the recurrent phylogeographical scenarios, identified by different case studies, broadly agree with longstanding biogeographic, floristic, and topographic concepts: (i) aridification promoted diversification and speciation of desert plants; (ii) desert expansion caused habitat fragmentation; (iii) the Altay–Tianshan Mountains included glacial refugia for plants; (iv) population expansion and recolonization from glacial refugia occurred during the postglacial period; and (v) desert plants persistence and alpine plants retreat during climate oscillations. We discuss the main phylogeographical findings in light of molecular and paleo-environmental evidence, emphasizing notable gaps in our knowledge and outlining future research perspectives for disentangling the evolutionary history of this arid region's flora.

Key words arid Northwest China, aridification, phylogeography, Quaternary.

With the development of molecular methods, phylogeography has grown as a popular discipline investigating geographical variation by use of molecular markers, and it has explored explosively in the recent three decades since 1987 (Avice et al., 1987). At present, it is well appreciated that global climate fluctuations, in particular the remarkable Quaternary climatic oscillations, have instigated cycles of habitat contraction and expansion, and latitudinal–altitudinal shifts of species' distributions, affecting the genetic structure of many plant and animal species in temperate zones of the Northern Hemisphere (Hewitt, 2000, 2004; Petit et al., 2003; Hickerson et al., 2010). Phylogeography has been appreciated as a major focus of evolutionary biology, using spatiotemporal distribution of genetic lineages to deduce the influence of historical processes on species' evolution. Also, it has provided

an effective approach, when detailed reconstruction of the evolutionary process of plant species has been hampered by lack of fossil data, to untangle the evolutionary history of species (Comes & Kadereit, 1998). In documentation of the effects of climatic shifts on organisms, numerous phylogeographical surveys of temperate plant species in Europe (e.g., Demesure et al., 1996; Comes & Kadereit, 1998; Schönswetter et al., 2005), North America (e.g., Shaw & Small, 2005; Brunfeldt et al., 2007; Gonzales et al., 2008), and the Japanese Archipelago (e.g., Okaura & Harada, 2002; Ikeda & Setoguchi, 2007) can be referenced. Phylogeography also addressed the topic in South America, Africa, and Australia, where research has seen exponential growth recently (e.g., Lorenz-Lemke et al., 2010; Lorenzen et al., 2012; Nakamura et al., 2012; Segovia et al., 2012). Phylogeographical surveys of plant species have been informative in resolving or further delineating the location of glacial refugia, and routes of colonization and range expansion after glacial periods (Petit et al., 2003; McLachlan et al., 2005; Ikeda & Setoguchi, 2007; Gonzales et al., 2008; Carnicer

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et al., 2012). In addition, phylogeographical results, regardless of whether pertaining to trees, shrubs, or herbs, have proved to be consistent with fossil pollen evidence in indicating extensive latitudinal range shifts, typically in the form of retreat southward and to lower altitudes during glaciation, followed by rapid expansion northward and to higher altitudes during postglacial intervals (Comes & Kadereit, 1998; Hewitt, 1999; Nason et al., 2002; Sakaguchi et al., 2011; Segovia et al., 2012; Voss et al., 2012).

In China, the progress of plant phylogeographical studies has been recently outlined (Qiu et al., 2011; Liu et al., 2012). As pointed out by these authors, most studies have focused on the Sino-Japanese flora of East Asia, in which harbors the largest amount of diversity among the world's temperate regions (Ying et al., 1993; Myers et al., 2000); it was also the most important glacial refugium for Tertiary representatives ("relics") throughout Quaternary ice-age cycles (Qiu et al., 2011). Studies have often investigated endangered or endemic species, especially those concentrated in the areas of the Hengduan Mountains and adjacent Qinghai-Tibet Plateau (QTP) regions (Cun & Wang, 2010; Li et al., 2010; Zhang et al., 2011; Jia et al., 2012; Liu et al., 2013; Wang et al., 2013a; Zhao et al., 2013). These constitute an area referred to as the core of the Himalayan hotspot, containing one of the greatest concentrations of biodiversity in the world due to its high level of species and generic richness. In contrast, very few studies have been applied to the vegetation in arid zones of China.

Development of deserts in Central Asia was a response to global climatic change (e.g., long-term cooling and drying trends) and regional factors (e.g., the environmental effects of the Himalayas and QTP rising). The India-Asia continental collision may have begun at ca. 50 Mya; uplift had become sufficient by late Eocene or early Oligocene for the appearance of abundant pollen of high altitude conifers in the north of the QTP and in sediments of the South China Sea (Wu et al., 2003; Hoorn et al., 2012). Retreat of the Tethys Ocean from the Tarim Basin also occurred at that time (Hoorn et al., 2012). A consequent increase in arid Eurasian continental interior is demonstrated by the first appearance of pollen referable to *Artemisia* L., as well as abundant chenopods (Sun & Wang, 2005; Miao et al., 2011; Hoorn et al., 2012). By the early Miocene, central parts of the QTP may have uplifted to present heights (Wang et al., 2008; Wu et al., 2008), and long-term dust deposition in the Loess Plateau and Dzungarian Basin were established (Guo et al., 2002, 2008; Sun et al., 2010). The size of the QTP appears to have been augmented through times by successive peripheral uplifts, with presumably increasing climatic

effects (Lu et al., 2004; Clark et al., 2005; Fang et al., 2005). In addition to these geologic events, the climate of temperate areas of the earth experienced a general cooling and drying trend connected with atmospheric CO₂ decrease (Dupont-Nivet et al., 2007; Miao et al., 2012), which reached their most profound minima during glacial periods of the Pleistocene. Strong episodic cooling at those times resulted in sharp increases in aridity of the Chinese deserts (Fang et al., 2002; Ding et al., 2005).

Deserts make up approximately one-third of Earth's land surface, and host a surprisingly rich biodiversity. Geological processes, such as the dynamics of sand movement, oasis formation, and river course alterations, often affect population genetic structure and speciation (Riddle et al., 2000; Nason et al., 2002; Riddle & Hafner, 2006; Garrick et al., 2009) in deserts of North America, Africa, and Australia. Geographic barriers between deserts apparently have led to vicariant speciation or population differentiation in many desert organisms (Byrne, 2008; Fehlberg & Ranker, 2009; Rebering et al., 2010). Climatic oscillations and associated environmental changes in the Quaternary promoted range fragmentation, vicariance, and population isolation, providing opportunities for allopatric speciation through the action of selection and/or genetic drift in temperate plants. So far, a growing body of studies, based on pollen cores, fossils, moraines, and deposition of loess, have begun to elucidate the possible roles of geology, multiple glaciations and climatic oscillations in shaping the current geo-ecological system occurring across these arid zones (Sun, 2002; Wu et al., 2002; Sun & Zhang, 2009; Sun et al., 2010; Guan et al., 2011). However, phylogeography of plant species spanning the arid zones of Northwest China are limited and, to the best of our knowledge, restricted to regional floras. Thus, a phylogeographical review on arid Northwest China is now needed.

Our focus is on the effects of Quaternary changes in climate and topography on the current population genetic structure of plants in these regions, especially in light of region-specific paleo-environmental evidence, but also considering major phylogeographical concepts developed in other temperate regions of the Northern Hemisphere. We begin with a brief account of the phytogeographic and vegetational features of arid Northwest China, followed by some general biogeographic hypotheses concerning the origin of plant species diversity and endemism in these regions. In this study, we want to point out the distinctive features in these regions, because the influence of the Quaternary cold and dry period on the geographical distribution of genetic diversity in arid Northwest China is still not

very clear. Based on current research, we attempted to address these questions: Did aridification resulting from climatic shifts promote the diversification and speciation in the vast deserts and steppes or not? Were there refugia distributed in the arid zones? How were the refugia and biodiversity centers distributed? Were there common phylogeographical patterns of the diversification, isolation habitat fragmentation, and colonization as in other sections (e.g., temperate regions and the QTP)? Here, we present a phylogeographical review of plants in arid Northwest China and try to elucidate general patterns to address these questions. We conclude by outlining some future challenges and research prospects, hoping it will provide future directions and stimulation for further research on the evolutionary history and biogeography of the world's arid flora, especially that of Central Asia.

1 Phylogeographic and vegetation features in arid Northwest China

From the viewpoint of phylogeographic studies, arid Northwest China belongs to the “Central Asia, West Asia–Mediterranean Kingdom,” which includes the regions surrounding the Mediterranean Sea, regions from West Asia to South Russia, and Central Asia and

Northwest China (e.g., Xinjiang, Inner Mongolia Plateau, and the QTP) (Good, 1974). Generally, we regard these regions as pertaining to (Wu & Wang, 1983): the Asian desert flora subkingdom and the Eurasian forest subkingdom (Fig. 1). Both of them are represented within the deserts and mountains of Northwest China. We omit the phylogeography of plants occurring in other parts of the QTP, as they have been reviewed elsewhere (Qiu et al., 2011).

The distribution of the Asian desert flora subkingdom is closely related to its geographic position, climate, and atmospheric circulation. The Northwest arid zones are located in the interior of Eurasia at a profound distance from the sea, and are consequently reached by little moisture. Also, the QTP rising weakens the westerlies and intensifies the Mongolian–Siberian high pressure, bringing these areas under the control of the continental dry air mass, so Asian deserts become the arid climatic center of Eurasia. Shrubs, subshrubs, and herbs (e.g., Chenopodiaceae, Lamiaceae, Fabaceae, Rosaceae, Zygophyllaceae, and Tamaricaceae) are able to withstand drought and dominate in these regions.

The Eurasian forest subkingdom in arid Northwest China, including the Altay and Tianshan Mountains, has undergone glaciation and climatic shifts during the Quaternary (Yi et al., 2004; Lehmkuhl & Owen, 2005; Xu et al., 2010), which belongs to the cold temperate

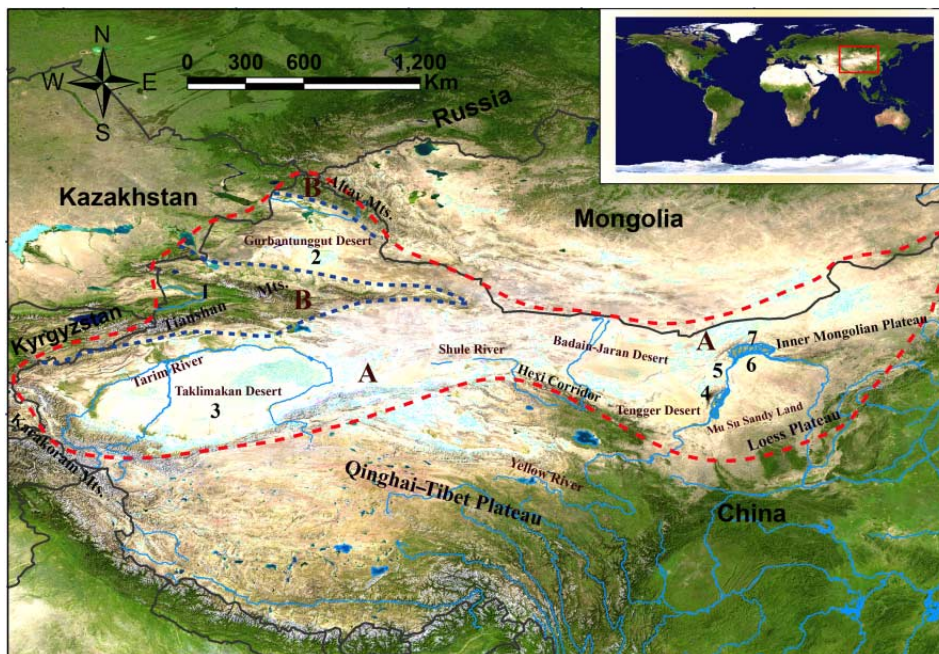


Fig. 1. Major geographical and phylogeographical features of arid Northwest China and significant locations. The red dashed line demarcates boundaries in arid Northwest China; blue dashed lines demarcate boundaries of two floristic subkingdoms according to Wu & Wang (1983). A, Asian desert flora subkingdom; B, Eurasian forest subkingdom. 1, Ili (Yili) Valley; 2, Dzungarian Basin; 3, Tarim Basin; 4, Helan Mountains; 5, Ulanbuhe Desert; 6, Kubuqi Desert; 7, Yinshan Mountains.

and temperate mountain coniferous forest. The vegetation in these areas consists of shrubs, trees, and herbs (e.g., Pinaceae, Cupressaceae, Betulaceae, Salicaceae, Rosaceae, Ranunculaceae, and Rubiaceae).

2 General biogeographic hypotheses on the origin of plants in Northwest China

The origin of plant species diversity and endemism in arid Northwest China has attracted much attention from phytogeographers and paleontologists (Wu & Wang, 1983; Liu, 1985; Wu & Zhou, 1986; An et al., 2001; Dang & Pan, 2001; Dang et al., 2002; Zhao, 2003; Zhao & Zhu, 2003). According to these published works, when the QTP was uplifted catastrophically by >3000 m in the Quaternary, the regression of the Tethys Sea, initiation of the Asian monsoons, and aridification of the Asian interior also occurred. The origins of the flora in northwestern China have frequently been discussed from this point of view, but the ideas presented may be of value even if the timelines remain highly discordant. Of course, on the basis of the viewpoints mentioned above, these geologic events would have likely affected the origin of interspecific or intraspecific taxa, or they might relate to genera.

As suggested, the flora of arid Northwest China derived primarily from Tethys coastal xerophytes (Liu, 1985, 1995; Dang et al., 2002). From the viewpoint of palynology, Xinjiang and Kazakhstan had similar paleo-environments, and were parts of the Tethys vegetational zone (Dang et al., 2002). In the late Eocene or late Pliocene, abundant pollen of Asteraceae (e.g., *Artemisia*) and Chenopodiaceae on the northern margin of the QTP illustrated that the vegetation type had been transformed from a deciduous broad-leaved forest to desert steppe (Guo & Gu, 1993; Sun & Wang, 2005). There have also been some East Asian floral elements incorporated into the desert flora, such as *Caragana* Fabricius, which originated as a forest species in East Asia in the Eocene and expanded southwestward and northwestward, with the northwest clade becoming adapted to arid environments and there forming Sect. *Microphyllae* Lam. (Zhang & Fritsch, 2010).

3 Phylogeography in temperate steppes and deserts, the Asian desert flora subkingdom

3.1 Aridification promoted diversification and speciation of desert plants

Pleistocene climatic shifts played important roles in shaping geographical patterns of intraspecific genetic

diversity (Hewitt, 1996, 2000, 2004); however, the role in driving speciation is less clear (Willis & Niklas, 2004; Futuyma, 2010), especially in Northwest China. Fortunately, the phylogeography of desert plants has been increasing to elaborate the speciation and diversification that resulted from aridity when the climate shifted in the Quaternary (Ge et al., 2011; Meng & Zhang, 2011, 2013; Su et al., 2011, 2012; Ma & Zhang, 2012; Ma et al., 2012a; Su & Zhang, 2013; Gao et al., 2014).

Lagochilus ilicifolius Bunge ex Benthams, belonging to the family Lamiaceae, and with a distribution area ranging from northern China to parts of Mongolia and Russia, provided the first molecular evidence from chloroplast DNA (cpDNA) sequence variation of desert plants. Genetic analyses revealed high diversity and significant phylogeographical signal among populations (Meng & Zhang, 2011). Furthermore, there was a high level of cpDNA haplotype diversity within the desert edge area, but mainly haplotypic uniformity across the more arid regions, indicating diversification as the desert range expanded, or perhaps the desert edge acted as a refugium. Given that presently disjunctive distribution of *L. ilicifolius* and the other species of this genus, an early period of expansion was likely followed by range fragmentation due to additional aridification, perhaps during the Pleistocene when the climate became very cold and dry. These conditions might drive rapid speciation in the mountains or at the edges of deserts, as adaptation to the environment during these geological events, especially the extreme aridity imposed by extreme weather events (Meng & Zhang, 2013).

Further evidence of diversification and speciation has come from subsequent studies in other desert plants, such as those highly drought-tolerant shrub species widely distributed across the deserts of western China, *Reaumuria soongarica* (Pall.) Maxim. (Tamaricaceae) (Li et al., 2012), *Nitraria sphaerocarpa* Maxim. (Nitrariaceae) (Su & Zhang, 2013), *Pugionium cornutum* (L.) Gaertn., and *P. dolabratum* Maxim. (Brassicaceae) (Wang et al., 2013b; Yu et al., 2013). Within *R. soongarica*, phylogeographical patterns of the cpDNA sequence variation revealed that the desert shrub occurred near to the QTP and experienced deep intraspecific divergence, which have been triggered by the latest tectonic uplift of the QTP since the Pliocene, as well as indications that recent regional expansion of *R. soongarica* followed desert development occurring during glacial periods (Li et al., 2012). Likewise, in the populations of *N. sphaerocarpa*, compared with total gene diversity, within-population gene diversity was rather insignificant, resulting in a

high level of differentiation among populations (Su & Zhang, 2013), which indicated that aridification played a part in differentiation of populations. Within *P. cornutum* and *P. dolabratum*, the combined results from single sequence repeat loci and internal transcribed spacer (ITS) sequence suggested that the two species shared numerous ancestral cpDNA polymorphisms, and pointed to the importance of nuclear DNA (ITS or accumulation of multiple genetic loci) in delimiting recently diverged species (Yu et al., 2013). The assessments of species boundaries and interspecific delimitation at different DNA loci will provide a solid basis for the further study of species identity, taxonomy, and speciation. Surveying from sequence variation within ITS, cpDNA fragments, and eight low-copy nuclear genes among individuals revealed the importance of Pleistocene climate change, especially an increase in aridity as a cause of speciation, suggested the divergence of plants in different habitats associated with the expansion of deserts (Wang et al., 2013b). The results regarding *Ammopiptanthus* suggested that genetic differentiation might be due to a possible vicariant event from a single common ancestor through the fragmentation of its natural distribution range, giving rise to *A. mongolicus* (Maxim. ex Komarov) S. H. Cheng and *A. nanus* (Popov) S. H. Cheng (Ge et al., 2005). In addition, the extrinsic factors (e.g., climate or environment factors) and the intrinsic factors also contribute to the high diversity of intraspecific genetic diversity. The dispersal ability of pollen (or seed) and/or physiological tolerance to aridity might cause the capability of adaptation to the arid environment, and this phenomenon is usual for desert plants in Northwest China.

3.2 Habitat fragmentation and recolonization in arid Northwest China

During the Pleistocene glaciations, species at high to mid-latitudes were affected by the spread of large ice sheets, whereas at lower latitudes they were subjected to extreme aridity as well as lower temperatures (Willis & Niklas, 2004), which caused sandy desert and gobi (stony desert) expansion in Northwest China. As a consequence, the geographical distribution areas of many species in the arid zones became fragmented, promoting conditions for allopatric divergence among isolated populations, and possibly speciation, such as shown in the phylogeography of *Gymnocarpus przewalskii* Maxim. (Ma & Zhang, 2012; Ma et al., 2012b). The studies suggested that regional genetic differentiation of *G. przewalskii* has resulted mainly from geographic isolation posed by the development of mountains and large deserts; it also resulted from range

contraction and population fragmentation induced by climate oscillations. The duration of glacial periods has been insufficient for speciation to occur, so speciation was more likely the outcome of repeated Pleistocene cycles of range fragmentation and reunification (Bennett, 2004). Arid conditions have caused habitat fragmentation and population isolation of many plant species in the area (Su et al., 2011; Su & Zhang, 2013; Wang et al., 2013b). Within populations of *Helianthemum songaricum* Schrenk, nested clade phylogeographical analysis diagnosed allopatric fragmentation over the total cladogram (Su et al., 2011). During the last interglacial period, a warmer and wetter climate contributed to range expansion of this species within portions of the Hexi Corridor. By contrast, based on ecological niche modeling, *N. sphaerocarpa* indicated that populations had a shrunken and more fragmented range during the Last Glacial Maximum (LGM) (Su & Zhang, 2013). Population genetic analyses of *Pugionium* showed that the species diverged within the Pleistocene, possibly as a result of adaptation to dissimilar desert habitats (Wang et al., 2013b).

Geographical barriers between deserts also caused vicariant speciation or population differentiation in many desert organisms, especially animals (Castoe et al., 2007; Phillipson & Metcalf, 2009). Repeated desert expansions and contractions, in response to glaciation cycles and the existence of Pleistocene refugia, may explain a large part of the current distribution patterns of many desert species. Fragmentation events during desert formation were also detected in populations of *Hexinia polydichotoma* (Ostenf.) H. L. Yang (Asteraceae), which indicated that, during the interglacial period of the middle Pleistocene, a large amount of snow and glacial ice melted from the mountains surrounding the Tarim Basin, causing increased water in the desert. These events and the dispersal ability of *Hex. polydichotoma* were important factors driving not only geographic range expansion, but also the current phylogeographical structure of the species (Su et al., 2012). It is possible that during the middle Pleistocene, climatic fluctuations resulted in expansion and contraction cycles of river systems and oases, and may consequently have caused population fragmentation. Deserts in Central Asia have perhaps the most complex geological history and geographic features. Few studies have focused on the influence of extensive development of the deserts on the phylogeographical and genetic structures of species in the region, although there are abundant desert plants alongside the rivers in the arid zone, such as the Yellow, Tarim, and Shule Rivers (Fig. 1). River diversion and appearance or shrinkage of oases caused the shifting of

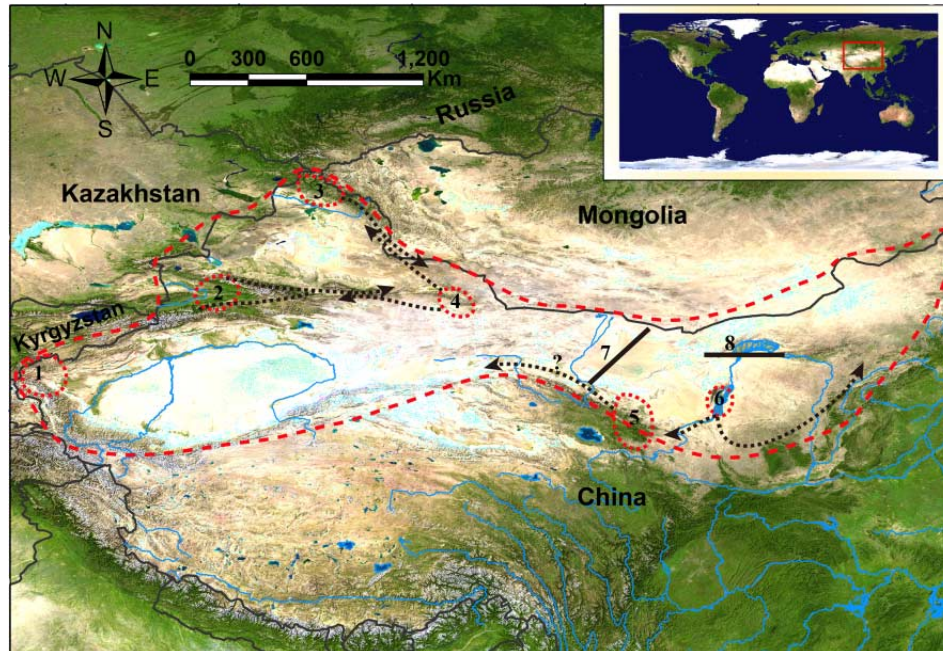


Fig. 2. Locations of potential major refugia (dashed circles) and the most common genetic discontinuities (solid lines), and putative colonization routes (dashed arrows) reported by phylogeographic studies of plant species in arid Northwest China. The red dashed lines demarcate boundaries of arid zones. 1, Karakoram–Tianshan Mountains junction; 2, Ili (Yili) Valley; 3, Altay Mountains; 4, East Tianshan Mountains; 5, Northeast Qinghai–Tibet Plateau edge; 6, Helan Mountains; 7, Badan Jaran–Tengger Desert; 8, Ulanbuhe Desert–Yinshan Mountains–Kubuqi Desert.

habitats of desert plants, playing significant roles in changing genetic structure and diversity. It will be of great interest in the future to analyze the details of how desert plants have adapted to their alternative habitats and the genetic basis of these adaptive differences.

In combination with studies of population structure and evolutionary history, phylogeography offers opportunities to elucidate the factors that affect the evolution of organisms over time and space. Migration and gene flow are important factors affecting the genetic structure and demography of populations (Templeton, 1998), playing important roles in desert plants when the plants migrated southward during ice ages and northward during interglacials. The phylogeography of *L. ilicifolius* possibly explained the migration route of desert plants in the northern arid section of China (Meng & Zhang, 2011). Physiographical heterogeneity in the Helan Mountains area gave rise to geographical and, probably, ecological isolation, which was responsible for population differentiation along the ridges and adjacent areas. To the north of the mountains are the Ulanbuhe and Kubuqi Deserts; and on the west and east are the Tengger Desert and Mu Us Sandy Land, respectively; at the southeast is the Loess Plateau (Fig. 1). Interestingly, the Loess Plateau, which presents an apparently desolate and fragmented landform with hundreds and thousands of hills and gullies, and the

Inner Mongolian Plateau, considered the flattest plateau in China, were not enough to have served as geographical barriers to *L. ilicifolius*. Instead, the Loess Plateau appears to have provided an ecological corridor for northward migration of the species during the interglacial phase (Fig. 2) (Meng & Zhang, 2011). Although no evidence of common phylogeographical histories across the arid region have been found, recolonization routes show some interesting concordances. The mountains (e.g., Tianshan, Altay, and Helan) in the vast arid zones were not only the geographical barriers, but also the migration corridors for recolonization after the cold periods.

3.3 Conservation implications of desert plants in arid Northwest China

Conservation of the genetic resources of desert plants, especially the endemic desert plants, is crucial to worldwide efforts to combat desertification, to prevent further degradation of the fragile ecosystems in arid and semi-arid regions, and to sustain desert biodiversity. Several conservation genetic and phylogeographical studies of DNA sequence variation have now also been completed in endangered and endemic desert shrubs in recent years, for example, *Tetraena mongolica* Maxim. (Zygophyllaceae) (Ge et al., 2003, 2011), *Hex. polydichotoma* (Su et al., 2012), *Hel. songaricum* (Su

et al., 2011), *G. przewalskii* (Ma & Zhang, 2012; Ma et al., 2012b), and *Ammopiptanthus* S. H. Cheng (Ge et al., 2005). Phylogeography and conservation of *T. mongolica* indicated limited seed dispersal and past fragmentation were likely associated with the Yellow River flooding (Ge et al., 2011). The endangered species are narrowly distributed and have a small population size, which would heighten the risk of extinction, especially when gene flow between populations is restricted. *Helianthemum songaricum* showed genetic drift and inbreeding within populations, indicating a significant extinction risk (Su et al., 2011).

The genealogical relationships among haplotypes of *G. przewalskii*, as well as their geographic distribution across the species range indicate that *ex situ* conservation is necessary to maximize the probability of successful reintroduction of *G. przewalskii*, because the species has become extinct in wild areas. Also, management plans would be expected to focus on the maintenance of effective population sizes and reduction of human disturbance (Ma & Zhang, 2012; Ma et al., 2012b).

In arid Northwest China, the Helan Mountains–Alxa region, considered one of eight endemic genus diversification centers in China, contains several endemic genera (Wu et al., 2010), such as *Potaninia* Maxim., *Ammopiptanthus*, *Tetraena* Maxim., *Stilpnolepis* Krasch., *Tugarinovia* Iljin, *Kaschgaria* Poljakov, *Elachanthemum* Y. Ling and Y. R. Ling, *Synstemon* Botsch., *Timouria* Roshev., *Sympegma* Bunge, *Iljinia* Korovin, and *Sarcozygium* Bunge (Zhao & Zhu, 2003). MAXENT and DOMAIN species distribution model (SDM) simulations of the distribution areas of 13 genera indicated that Alxa–Inner Mongolia is the most noticeable endemic area (Ma et al., 2012a). However, these noticeable diversification and endemic areas have not as yet been brought to conservational attention. Desert plants play a key role, as the primary producers, in maintaining these ecosystems. Desert ecosystems currently cover about 35% of the Earth's land surface (Hellden, 1991), and they are expanding. Moreover, the history of long-term human disturbance, especially human overexploitation of resource plants, has inevitably caused dramatic declines in population sizes of desert plants. The natural vegetation landscape of arid Northwest China is mainly dominated by steppes and deserts, with a relatively homogeneous overall environment, and genetic variation is usually not concentrated in a single site. Thus, effective strategy for *ex situ* conservation of the species should be carried out to protect the larger number of plants from one or two populations rather than to smaller numbers from many different sites. In order to develop an effective strategy

for conservation, Evolutionarily Significant Units (ESUs) need to be defined. Various criteria for ESUs have been suggested, including reciprocal monophyly (Moritz, 1994), adaptive variation, and reproductive separation. Recognizing ESUs as reciprocally monophyletic groups promotes maintenance of the entire evolutionary heritage within a species, and the separate management of populations belonging to different lineages. So, taking into account the very large numbers of desert plant species that are currently under threat, the immediate challenge will be to prioritize where future research efforts should be focused, and to relate research closely to the needs of conservation practitioners.

4 Phylogeography in the Altay–Tianshan Mountains, the Eurasian forest subkingdom

4.1 Glacial refugia in the Altay–Tianshan Mountains

The environments in the Mongolian Altay and Tianshan Mountains of the temperate arid zones of Central Asia were influenced by multiple Pleistocene glaciations and fluctuated between arid and semi-arid conditions due to climatic fluctuations (Grunert & Lehmkuhl, 2004; Xu et al., 2010). The extent of Pleistocene ice in the Altay is still under debate, however, in the eastern Altay, especially the northern part of the Mongolian Altay, Pleistocene glaciers were restricted to several isolated mountain systems (Lehmkuhl et al., 2004). In the Tianshan regions, glacier fluctuations (Xu et al., 2010) and fossil pollen from lake sediments (Wen & Shi, 1993) indicated climatic cycles consisting of dry glacial and humid interglacial periods during the Pleistocene. Thus, species still experienced glacial-time retreats and interglacial recolonizations in response to cold–warm climatic cycles; separate refugia during glacial episodes are hypothesized to have triggered lineage divergence in many plant species. There is now firm molecular evidence that populations of temperate plant species (Zhang & Zhang, 2012a, 2012b; Xie & Zhang, 2013; Zhang et al., 2013; Jiang et al., 2014), including alpine plants presently distributed in the Altay–Tianshan Mountains and QTP, such as *Picea* A. Dietr. (Li et al., 2010) and *Hippophae* L. (Jia et al., 2012), are derived from populations that recolonized these areas from glacial refugia located at lower elevations in valleys and/or at the mountain edges.

In Northwest China, deserts seem to have promoted allopatric divergence of the studied species, and the divergent populations must have survived in separate refugia during the LGM (Liu et al., 2012).

Phylogeographical study of *Clematis sibirica* Mill. has shown significant phylogeographical structure, and the location of refugia in the Tianshan–Altay Mountains (Fig. 2). Two independent lineages, the possible postglacial colonization routes of the two phylogeographic lineages of *C. sibirica* in the Tianshan and Altay Mountains, and a contact zone between the Tianshan Mountains and eastern Altay Mountain lineages were found (Zhang & Zhang, 2012b) (Fig. 2). In order to endure the cold-dry glacial climate, two phylogeographical groups of the forest species *C. sibirica* retreated to more mesic refugial areas (Zhang & Zhang, 2012b). Phylogeographical studies have sprung up like mushrooms after rain in China, however, plant phylogeography in arid Northwest China, especially the Tianshan and Altay Mountains abundant in alpine plants that were influenced by glacial-dry environments, are generally lacking. Thus, refugia for plant species in the regions remain rather cryptic. In the absence of an ice sheet, the flora of the area was deemed to have been influenced primarily by Pleistocene fluctuations, from glacial-dry to interglacial-humid conditions (Wen & Shi, 1993). Under the pressure of arid local climates, forest species in the mountains are expected to migrate to more humid locations. The humid valleys may provide refugial habitats for these species. For instance, the Gongnaisi valley in the western Tianshan, and the Kanasi valley in the Altay have been suggested as refugia for green toads, a widespread terrestrial vertebrate (Zhang et al., 2008). Because the valleys received moisture from westerly air movements, species in arid Northwest China were less influenced by the high barrier of the QTP and surrounding mountains, and the western portions were more humid than the eastern Tianshan and Altay Mountains. Thus, western locations in the mountains were likely to have served as refugia, allowing plant persistence during arid-glacial climates. Genetic structure of the *Delphinium naviculare* W. T. Wang species group suggested that cold and drought were primary drivers of lineage migration during glacial periods, and the humid valleys at mid-elevation served as refugia at these times in the Tianshan Mountains (Zhang & Zhang, 2012a) (Fig. 2). During the latest two glacial episodes, new refugia likely appeared, corresponding to a decreased extent of glaciation. In accordance with the glacial chronology derived from proxy data such as glacial tills, lacustrine sedimentary sequences and oxygen isotope records, the genetic structure of the *D. naviculare* species group revealed a paleoclimatic history of three glacial/interglacial cycles and an overall trend towards aridity during the course of the Pleistocene (Zhang & Zhang, 2012a).

Further evidence that plants retreated to refugia in the arid zones of China has come from subsequent studies in other alpine plants. In particular, the Ili Valley, as a biodiversity hotspot of Northwest China (Tang et al., 2006) located near the juncture between the northern and southern branches of the Tianshan Mountains, is shown to have been a biotic glacial refugium where plants persisted during glacial periods (Zhang et al., 2008; Zhang & Zhang, 2012a) (Fig. 2). In terms of genetic structure analysis of *Aconitum* L., the Ili Valley and another locality somewhat farther to the east were inferred probable glacial refugia for the *Acon. nemorum* Popov species group (Jiang et al., 2014) (Fig. 2). High intrapopulation genetic diversity within this species indicates that it contracted to several refugia of the Ili Valley during the glacial periods, with divergence *in situ*. Additional evidence for *in situ* refugia recently emerged from cpDNA data of *Ribes meyeri* Maxim. in arid Northwest China that strongly suggested glacial refugia in the Helan Mountain areas, and that the plants underwent postglacial expansion as the climate became relatively warm and moist (Fig. 2) (Xie & Zhang, 2013).

4.2 Postglacial expansion and recolonization from glacial refugia

Postglacial expansion and recolonization are significant aspects of phylogeographical study. The demographic histories of species are universally associated with the dynamics of paleoclimatic fluctuations (Hewitt, 2011), especially the Pleistocene glacial–interglacial cycles. With the onset of interglacial warming, these species would have undergone demographic expansion (Comes & Kadereit, 1998). Species migrations are thus strongly related to glacial cycles, enabling us to use the migration of a species to track how changes between glacial and interglacial climates affected their demographic history. Most parts of China are deemed to have been free of an extensive ice sheet (Shi et al., 2006); however, species experienced glacial-time retreats and interglacial recolonizations in response to cold–warm climatic cycles. During glacial episodes, separate refugia are hypothesized to have triggered lineage divergence in many species, especially the alpine plants in the Altay–Tianshan Mountains. *Clematis sibirica* suggested that Pleistocene climatic oscillations have significantly affected the current spatial genetic structure, and the separate glacial refugia led to the origin of the two phylogeographical lineages of this forest species during the Pleistocene maximum glacial stage (Zhang & Zhang, 2012b).

In the Tianshan Mountains, Pleistocene cold–dry glacial climates produced the simultaneous effects of

mountain glacier advance (Shi et al., 2006; Xu et al., 2010) and arid steppe expansion (Ni et al., 2010). Following interglacial warming and moistening, demographic expansions were identified for these phylogeographical lineages in the mountain ranges surrounding the Dzungarian Basin, which were hypothesized to have served as migration corridors for the species (Zhang & Zhang, 2012b). The evolutionary history of the *D. naviculare* species group, focused on the locations of glacial refugia and lineage divergence or expansion, indicated a stepwise demographic expansion scenario and a hierarchical structure of multiple refugia, in response to an increase in aridity in the eastern Tianshan (Zhang & Zhang, 2012a). Divergence and expansion time estimates for the *D. naviculare* species group inferred from molecular data are consistent with the Pleistocene glacial chronology of the Tianshan Mountains. With the expansion of steppes, populations of the *D. naviculare* species group in the lowlands (approximately 1290 m a.s.l.) were enabled to migrate upwards along the mountains to higher, moister areas. Thus, lowland areas did not act as glacial refugia under the pressure of aridity. The phylogeographical patterns of the *Acon. nemorum* species group in the Tianshan Mountains and their surroundings also indicate that in the intervals between glaciations during the late Quaternary (Jiang et al., 2014), *Acon. nemorum* underwent at least two periods of eastward expansion from glacial refugia. So, ancient geological and climatic events likely affected the evolution and current distribution of the *Acon. nemorum* species group. As demonstrated by the aforementioned inferences, the genetic structure of plant species can provide additional insights into the history of climatic change in the Pleistocene.

4.3 Local persistence and retreat in arid Northwest China

The phylogeography of forest and desert steppe species to climatic change in arid Northwest China showed opposite responses: persistence or retreat. Evaluation of published works show a number of phylogeographical patterns in biota of arid Northwest China. The most striking pattern is the presence of high intraspecific and interspecific diversity that is geographically structured. Studies revealed the presence and retreat of multiple divergent lineages, and their dating indicated Pleistocene divergence, most frequently in the mid-Pleistocene, in these regions (Meng & Zhang, 2011, 2013; Su et al., 2011, 2012; Ma & Zhang, 2012; Ma et al., 2012b; Zhang & Zhang, 2012a; Su & Zhang, 2013; Xie & Zhang, 2013; Jiang et al., 2014). Most of these species occupy arid and

semi-arid habitats, including alpine plants in the Altay–Tianshan Mountains. So their intra/interspecific or species group divergent lineages are geographically structured, showing high geographic structure of haplotypes. Evidence of multiple levels of persistence and retreat implied divergence through multiple glacial/interglacial cycles. In general, there is little evidence of widespread expansion of divergent lineages. The combined approach of phylogeography and SDM of the two *Clematis* species, forest species *C. sibirica* and desert steppe species *C. songorica* Bunge, indicated that the forest species would likely have experienced range reduction, though without genetic diversity loss, in the face of climate change; whereas the steppe species should maintain a consistently stable potential distribution under the LGM and future climatic conditions, in reference to its existing potential distribution (Zhang et al., 2013). Based on Mismatch analyses and Bayesian skyline plot analyses of genetic variation of *Lagochilus* Bunge ex Benth., along with the results of demographic analyses, it was proposed that regional demographic expansion of the species probably resulted from the large deserts that developed during the Pleistocene in Northwest China (Meng & Zhang, 2013). These regions were characterized by intense arid conditions and propelled the organisms to migrate from extremely cold and dry environments to warmer and more humid habitats (Zhang et al., 2000). Compared with alpine plants, which retreated when the ice expanded and the global climate cooled, while aridification intensified, the drought-tolerant desert plants might have expanded during such conditions, and therefore they have driven rapid speciation in the mountains or at the edges of deserts as an adaptation to the environment during these geological events. In addition, habitat destruction and fragmentation and misapplication of human activity may cause a decline in population size of desert plants (Ge et al., 2011; Su et al., 2011, 2012; Ma & Zhang, 2012; Ma et al., 2012b). The presence and retreat of highly divergent lineages is an indicator of major contraction to geographically isolated refugia during climatic cycles in the early to mid-Pleistocene; geographic structuring of the lineages implies subsequent expansion during favorable conditions with retreat during unsuitable conditions. However, the existence of highly localized haplotypes within lineages indicates a different pattern in later Pleistocene cycles, with multiple refugia on a microgeographic scale throughout the distribution of the species. This is consistent with expectations from a hypothesis of local persistence and extinction, with limited migration from individual populations in more

recent geological time, and divergence through repeated cycles of contraction and expansion.

5 Perspectives and future directions

Over the past three decades, phylogeography has been developing rapidly. Its perspectives have provided insights into evolutionary genetic processes, including the mitochondrial and other gene-tree systems from which these perspectives arose (Avice, 2007), and it shows no signs of slowing down. Phylogeographical study of arid Northwest China is also on the rise, so we have briefly summarized the typical phylogeographical patterns of different plant species in this region (Table 1).

With the development of molecular technology, it will be exciting to address future studies in arid zones with the development of next-generation sequencing (NGS) and extended phylogeographical analyses. The NGS (e.g., restriction-site-associated DNA sequencing, RAD-seq) approaches to the ultra-high-throughput sequencing of DNA are currently transforming the ways that phylogeographers can track the dynamics of genetic diversity in space and time. Historically, methods to identify large numbers of genetic markers and characterize their geographic distribution in natural populations were labor-intensive and cost-prohibitive for almost any species, particularly those lacking extensive resources. The appearance of RAD-seq may open new avenues to resolve these questions for the generation of large numbers of molecular markers in a panel of individuals to better characterize the ecology and evolution of traditionally non-model species (Rowe et al., 2011). The power of these approaches mainly lies in their ability to yield hundreds of millions of short sequence reads per run (Metzker, 2010), which differs from conventional Sanger sequencing that typically yields only a few hundreds of reads. So, phylogeographical studies in our reviewed area using current NGS-based biogeography and phylogeography may develop a better understanding on the evolutionary history of taxa. Through the phylogeographical patterns of multiple-species groups, integrated NGS may enable us to better understand the plant diversity in arid Northwest China, and set up concrete hypotheses for studying plant speciation and diversification mechanisms in these regions. Although the potential of RAD-seq for marker discovery and trait mapping in non-model systems remains undisputed, caution is required when applying this technique to make population genetic inferences (Arnold et al., 2013).

Most studies focus on individual species, with a preferential bias of using sequence information from

uniparentally inherited and non-recombining cpDNA, with a few using nuclear DNA (Table 1). It is worth noting that more and more cases have suggested that the phylogeographical structure of cpDNA is very different from that of nuclear DNA or mitochondrial DNA (mtDNA) in plant phylogeographical studies (Liepelt et al., 2002; Du et al., 2009; Zhou et al., 2010). That means that pollen gene flow and incomplete lineage sorting would result in the non-significant population structure of nuclear DNA. For example, mtDNA haplotypes are often shared among related conifer species, whereas cpDNA haplotypes are more species-specific, which indicates that increased intraspecific gene flow appears to decrease differentiation within species but not among species (Du et al., 2009). So, we should notice the difference between the nuclear DNA and mtDNA or cpDNA in future research.

In addition, using ecological niche models (Gugger et al., 2011), Geographic Information Systems (Chan et al., 2011), and SDM (Barve et al., 2011) will bring new power to phylogeographical studies in these regions, which use associations between environmental variables and known species' occurrence localities to define abiotic conditions within which populations can be maintained. The historical constraints on current distribution and abundance of organisms in the past are key issues for phylogeography as well as for its parent disciplines, geology and biology.

Moreover, comparative phylogeography has been proved useful for investigating biological responses to past climatic change and postglacial colonization routes in Europe (Taberlet et al., 1998). This is strong when combined with extrinsic hypotheses derived from paleoclimate, the fossil record, or geology in arid areas, because there are abundant records of fossils and palynology. However, in arid Northwest China, a comparison of phylogeography is rare. The most significant result of comparative phylogeography is that these studies will search for concordant geographical distribution among lineages within different species of close relationship and indicate the influence of the common historical factors. Interestingly, there are many parasites in this research area, for instance, the endangered desert plant *Cistanche deserticola* Ma always parasitizes on the roots of *Tamarix* L. and *Haloxylon* Bunge; *Cynomorium songaricum* Rupr. is a parasite on the roots of *Nitraria* L. The evolutionary history of the most complex parasitism is not well understood, so comparative phylogeography may reveal the cryptic speciation. Also, phylogeographical analyses not of single species but of entire communities are now possible. So we can jointly analyze plants and associated animals to induce the evolutionary history of

Table 1 Typical phylogeographical patterns of different plant species in arid Northwest China

Taxon/taxa	Family	DNA	Major inference(s)	References
<i>Nitraria sphaerocarpa</i> Maxim.	Nitrariaceae	<i>trnH-psbA</i> <i>rpl32-trnL</i>	Climate aridification impacted evolutionary processes of species, as the driver for genetic isolation and divergence.	Su & Zhang (2013)
<i>Clematis sibirica</i> Miller and <i>C. songorica</i> Bunge	Ranunculaceae	nrITS <i>psbA-trnH</i>	Forest species is more sensitive to climate changes than the steppe species.	Zhang et al. (2013)
<i>Lagochilus</i> Bunge ex Benth.	Lamiaceae	<i>psbA-trnH</i> <i>trnS-trnG</i>	Aridification spurred desert plant diversification, past fragmentation, and species range expansion, which is adaptation and response to the climatic oscillations.	Meng & Zhang (2013)
<i>Ribes meyeri</i> Maxim.	Saxifragaceae	<i>psbA-trnH</i> <i>psbK-psbI</i>	Quaternary climatic oscillations affected the spatial genetic structure, and there were glacial refugia in LGM.	Xie & Zhang (2013)
<i>Aconitum nemorum</i> Popov	Ranunculaceae	<i>psbA-trnH</i> <i>trnS-trnG</i>	Cold-dry and warm-humid climatic cycles during the late Quaternary promoted genetic divergence within the species.	Jiang et al. (2014)
<i>Pugionium</i> Gaertn.	Brassicaceae	nrITS <i>trnV-trnM</i> <i>trnS-trnF/M</i>	Pleistocene climate change increased aridity, which prompted speciation; speciation was in association with expansion of deserts in China.	Wang et al. (2013b), Yu et al. (2013)
<i>Delphinium naviculare</i> W. T. Wang	Ranunculaceae	<i>trnS-trnG</i> <i>trnL-trnF</i>	Pressures of cold and dry climates during glacial periods were primary driving forces that shaped the current spatial genetic structure of species.	Zhang & Zhang (2012a)
<i>Clematis sibirica</i> Miller	Ranunculaceae	<i>psbA-trnH</i>	Largest glaciation during the middle Quaternary may have triggered divergent lineages and promoted allopatric speciation.	Zhang & Zhang (2012b)
<i>Lagochilus ilicifolius</i> Bunge ex Benth.	Lamiaceae	<i>psbA-trnH</i> <i>trnS-trnG</i>	Helan Mountains may be the diversification center for the species, whereas the Loess Plateau was a dispersal corridor for postglacial recolonization northward.	Meng & Zhang (2011)
<i>Hexinia polydichotoma</i> (Ostenf) H. L. Yang	Asteraceae	<i>trnH-psbA</i> <i>ycf6-psbM</i>	Mid-Pleistocene climatic fluctuations resulted in expansion and contraction cycles of river systems and oases, which caused population habitat fragmentation.	Su et al. (2012)
<i>Gymnocarpus przewalskii</i> Maxim.	Caryophyllaceae	<i>psbA-trnH</i> <i>ycf6-psbM</i> <i>rpl32-trnL</i>	Independent glacial refugia were inferred; bottlenecks and postglacial recolonization were identified; human disturbance currently is the greatest threat to the species.	Ma & Zhang (2012), Ma et al. (2012b)
<i>Helianthemum songaricum</i> Schrenk	Cistaceae	<i>trnD-trnT</i> <i>rps16-trnK</i>	Dry and cold climate during early Quaternary contributed to the lineage split, which most likely led to Yili range expansion.	Su et al. (2011)
<i>Reaumuria soongarica</i> (Pall.) Maxim.	Tamaricaceae	<i>trnS-trnG</i>	Divergence and regional range expansions of species have corresponded to the development of desert ecosystems during the last glacial age in western China.	Li et al. (2012)
<i>Tetraena mongolica</i> Maxim.	Zygophyllaceae	<i>atpB-rbcL</i>	Genetic polymorphisms are losing, each population of <i>T. mongolica</i> should be recognized as a conservation unit.	Ge et al. (2011, 2003)
<i>Ammopiptanthus</i> S. H. Cheng	Leguminosae	ISSR	Significant genetic difference between two species might be due to vicariant evolutionary event from the fragmentation of their common ancestor's range.	Ge et al. (2005)

ISSR, inter-simple sequence repeat; LGM, Last Glacial Maximum; nrITS, nuclear ribosomal internal transcribed spacer.

plant species in arid Northwest China, especially co-evolution mechanisms. For instance, the pollination mutualism between pollinators and plants highlights the potential importance of host plant specificity in insect diversification (Althoff et al., 2001). Comparative phylogeography in a specific and obligate pollination indicated dissimilar distributions among the phylogeographical history of plants and pollinators (Espindola & Alvarez, 2011).

6 Conclusions

This review of plant phylogeography in arid Northwest China revealed the biotic responses to Pleistocene climatic cycling in shaping the genetic structure and phylogeographical patterns. Desert expansion, environmental aridification, and river course dynamics have significant roles in providing adequate habitats for persistence of desert plant species that could

tolerate extreme drought and cold through glacial cycles, especially as temperate plants retreated to warmer and wetter conditions. In the arid regions, there is a distinctive pattern involving range expansion of desert plants during glaciation onto the vast temperate desert and steppe due to adaptation to the extreme environment, a pattern that contrasts with many examples of plants retreating to *in situ* glacial refugia for survival, although the predominant biotic response of desert plant species to Quaternary environmental change appears to be one of range fragmentation, vicariance, and population isolation with aridification or desert expansion.

Arid Northwest China is a very extensive area; however, as we have seen, few studies have investigated this region. Thus, research in desert and desert plant species may have considerable potential in the future. This review, the first attempt to synthesize our current knowledge on the basis of the limited number of published reports, will help to define the appropriate scope for future phylogeographical studies. Here, we suggest that future progress and research on these areas are in process and advances in the field of phylogeography will clearly come from a better integration of modeling, genetics, ecology, paleontology (fossil data information and palynology), and climatology, ideally against the backdrop of robust species-level phylogenies. Such an integrated approach applied to desert plants should serve to better disentangle the evolutionary history of population demographic, biogeographic, and speciation processes that have given rise to the world's very diverse desert floras. This is encouraging as it means comparative studies of other specific regions, which would be fruitful avenues for identification of mechanisms to diversification, refugia, and detection of ancestral patterns of diversity. Understanding the drivers and mechanisms of species diversification and persistence is of central interest to biogeography, evolutionary biology, and conservation genetics (Lexer et al., 2013), and understanding ancestral patterns of diversity is a key to predicting responses of species to future climate change (Hewitt & Nichols, 2005). This will be a key feature of plant responses to historical climate change, especially the desert plants to aridification and desert expansion. Refugial areas where genomes survived and diverged over major climate oscillations can continue to sustain populations through climatic fluctuations. These are priority areas for conservation, as noted in previous studies (Hewitt & Nichols, 2005), especially the refugia in the Altay–Tianshan Mountains and Ili Valley. Persistence of steppe and desert species and retreat of alpine species will be enhanced by facilitating the

continued action of dynamic evolutionary processes during climate oscillations. The adaptive capacity of species to respond to climate oscillations will be a key component of maintaining ongoing evolutionary processes. Localized refugia indicate that a mosaic of habitats in heterogeneous landscapes is essential for species persistence while some desert plants continue to expand.

This review provides examples of the evolutionary processes that occurred during the Pleistocene, in which climate change and aridification were likely to have been the underlying cause of speciation. It will be of interest in the future to analyze in detail the ways in which desert plants adapt to habitats, and the genetic basis of those adaptive differences, especially as deserts are still spreading under the conditions of global change and the disturbance of human activities.

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