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REVIEW

The potential drivers in forming avian biodiversity hotspots in the East Himalaya Mountains of Southwest China

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Abstract

Little has been published to describe or interpret Asian biodiversity hotspots, including those in the East Himalayan Mountains of Southwest China (HMSC), thus making necessary a review of the current knowledge. The Pliocene and Pleistocene geological and glacial histories of the Asian continent differ from those of Europe and North America, suggesting different mechanisms of speciation and extinction, and, thus, different responses to climate changes during the Quaternary glaciations. This short review summarizes potential drivers in shaping and maintaining high species richness and endemism of birds in the HMSC. The geographical location at the junction of different biogeographical realms, the wide range of habitats and climates along the extensive elevational range, the complex topography and the distinct geological history of this region have probably contributed to the evolution of an exceptionally species-rich and endemic-rich, specialized montane avian fauna. The Mountain systems in the HMSC may have provided refugia where species survived during the glacial periods and barriers for preventing species dispersal after the glacial periods. More studies are required to further test this refugia hypothesis by comparing more cold-tolerent and warm-tolerent species.

Key words: biodiversity hotspots, East Himalayan Mountains of Southwest China, phylogeographical divergence, Pleistocene glaciations, species richness and endemism

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INTRODUCTION

Species richness and endemism have been widely used for prioritization of biodiversity conservation at both regional and global scales (Stattersfield *et al.* 1998; Myers *et al.* 2000). Comparisons of distribution patterns among different vertebrates (Lamoreux *et al.* 2006), and between the richness and endemism of birds, have been reported at a global scale (Orme *et al.* 2005). The concept of endemism is central to the study of biogeogra-

phy (Crisp *et al.* 2001), with the level of endemism well explained by the climate-change velocity index (Sandel *et al.* 2011). Thus, species inhabiting montane regions may adapt and speciate locally, as despite global climate change, they can remain in the same climate zone by making short altitudinal movements. This may be the case in particular where wind systems from thermally stable tropical oceans can interact with the inland topography to provide extraordinary stability in certain places (Fjeldså *et al*. 2012). Thus, historical processes and spatial differences in climate impacts should be compared to explain the mountain endemism (Jetz *et al.* 2004; Graham *et al.* 2006; Lei 2012).

Over the past several decades, a number of hypotheses have been formulated to explain the large-scale variation in species diversity, notably energy-related variables (Wright 1983; Currie 1991) and landscape complexity (Rosenzweig 1995; Kerr & Packer 1997; Rahbek & Graves 2001). Energy and water are good biodiversity predictors for bird species richness (McCain 2009), although it has been suggested that this correlation is mainly driven by the large number of data points for widespread species (Jetz & Rahbek 2002; Rahbek *et al*. 2007). It has been much more difficult to explain the distributions of small-range (local endemic) species, whose distributions are possibly influenced by topography and, presumably, historical opportunities for isolation of populations and adaptation to local environments (Jetz *et al*. 2004). There is a strong role for eco-climatic stability in explaining the variation of species rich-

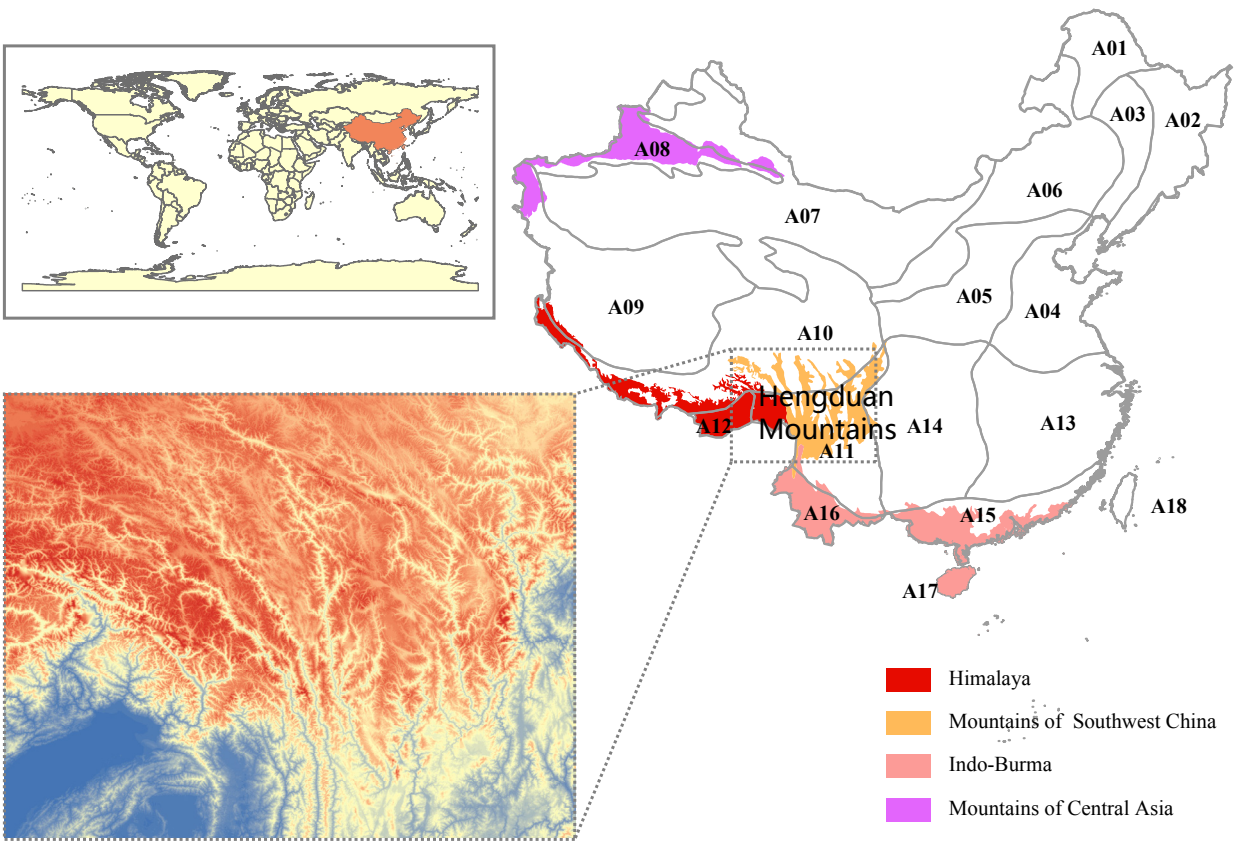

Figure 1 Map of the East Himalayan Mountains of Southwest China (HMSC) range: (a) highlights the locality China; and (b) highlights the distribution of East-Himayan and Zoogeographical regions and locations of biodiversity hotspots. Different color patches represent different hotspots. The subregional codes A01 to A18 indicate 18 of 19 zoogeographical subregions of China (e.g. A10 = Qinghai–Zangnan Subregion; A11 = Southwest Mountainous Subregion; A12 = Himalaya subregion). (c) Enlarged map to show approximately the HMSC and to indicate the locations of East Himalaya and Hengduan Mountains. The figure was modified from figure 1 in Huang *et al*. (2010) and Conservation International's website (http://www.conservation.org/where/priority_areas/hotspots/Pages/hotspots_main.aspx).

ness (Graham *et al.* 2006), for example, in Pleistocene refugia (Gomez *et al.* 2000), in areas characterized by low climate-change velocity (Jansson 2003; Davies *et al.* 2009; Loarie *et al.* 2009; Sandel *et al.* 2011), in stable cloud forest zones resulting from marine impacts (Fjeldså *et al*. 2012), and for dispersal combined with spatial niche conservatism (Wiens & Graham 2005). Most analyses of such relationships have been based on data for American and African birds, and have rarely dealt with Asian species, or, notably, the biodiversity hotspots of the east Himalayan Mountains of southwest China (HMSC). This HMSC region is located mainly in the joint areas among the Southwest Mountainous Subregion, the Qinghai–Zangnan Subregion and the Himalaya Subregion of China zoogeographical regionalization (see Fig. 1). The shortage of high-resolution digital data resources has, until recently, limited the amount of analysis of diversification patterns at Asian continental level (Ding *et al.* 2006; Rull 2011a; Lei 2012; Fjeldså 2013) or global level. However, a recent study of all Himalayan songbirds, with a focus on the eastern Himalayas, concluded that competition for niche space limits species accumulation, and that elevational distributions are determined by resources, especially the abundance of arthropods (Price *et al*. 2014). Srinivasan *et al.* (2014) emphasize the importance of the eastern Himalaya as a reservoir of diversity and as a significant unit with immense potential as a biodiversity hotspot through long time-scales. This review aims to briefly summarize what we presently know about the potential drivers shaping the current distribution pattern of birds, and highlight the underlying historical mechanisms forming the HMSC biodiversity hotspots.

THE IMPORTANCE OF THE EAST HIMALAYA: MOUNTAINS OF SOUTHWEST CHINA IN GLOBAL BIODIVERSITY CONSERVATION CONTEXT

China has high species richness and endemism of terrestrial vertebrate groups. It is a large country that covers both the Palaearctic and the Oriental realms and has a complex habitat mosaic. As one of the most important centers of global biodiversity (Myers *et al.* 2000; Orme *et al.* 2005; Huang *et al.* 2010), the Southwest mountainous range of China contains three global biodiversity hotspots (i.e. Himalaya, Mountains of Southwest China and Indo-Burma, see Fig. 1). Studies on geographic distribution patterns of larger taxonomic groups reveal the generally concordant patterns of the high species richness and endemism, for example in birds (Lei *et al.* 2003a; Lei *et al.* 2007), amphibians (Fu *et al.* 2006; Chen & Bi 2007), mammals (Wu *et al.* 2005; Tang *et al.* 2006), grasshoppers (Xu 2005), spiders (Meng *et al.* 2008) and aphids (Huang *et al.* 2008). This may reflect the similar response of different organisms to environmental conditions and climate history. These studies also reveal the role of mountain systems in forming China's biotic endemism because the mountainous areas at such low latitudes provide relatively stable environmental conditions, in spite of Quaternary climatic oscillations. The Hengduan Mountains located within HMSC are the most important mountain system in China, and are considered the 'evolutionary powerhouse' of Chinese avifauna (Zhao *et al.* 2007; Huang *et al.* 2010).

SPECIES RICHNESS AND ENDEMISM OF BIRDS IN EAST HIMALAYAN MOUNTAINS OF SOUTHWEST CHINA

With 1371 species, China has high species richness of birds, accounting for nearly 14% of the world's total number of bird species. The highest species richness is in the Southwest Mountainous, the Qinghai–Zangnan and the Himalaya Subregions in southwestern China (Zheng 2011). Both endemic species and endemic genera have the highest richness and endemism in the Hengduan Mountain hotspot (Lei *et al.* 2003 a,b), where the peak diversity for passerines in a grid-cell of 1 × 1 geographical degrees is 337 species, and large neighborhood heterogeneity in species assemblages between adjacent grid-cells suggests high local species replacement and beta diversity (Fjeldså *et al*. 2012 Fig. 1). Parsimony analysis of endemicity has identified the South-west Mountainous Subregion as 1 of the 4 areas of endemism (AOE) in China (Huang *et al*. 2010). This suggests that historical and ecological vicariant events may have acted as important factors in shaping the dramatically different avian fauna compositions between the Southwest Mountainous Subregion and its neighboring Qinghai–Zangnan Subregion (Huang *et al.* 2010). Southwest Mountainous Subregion AOE was suggested to be caused by evolutionary and ecological isolation due to the highly diversified habitats and environments. It is also possibly caused by the subregional geographical isolation due to complex topography (Lei *et al.* 2007). Furthermore, the Southwest Mountainous Subregion and its vicinities may have harbored both the

'primitive relics' and the 'newcomers' (Lei *et al.* 2007). Such hypotheses remain to be tested using phylogenetic and phylogeographic approaches. Ecological and evolutionary approaches integrated in the comprehensive model are needed in interpretations of the endemism (Lei 2012).

POTENTIAL DRIVERS IN SHAPING THE HIGH RICHNESS PATTERNS AND ENDEMISM

Mountain systems and ecological stability explains high species richness and endemism

Conditions for speciation may have differed significantly among European, American and Asian continents since the late Miocene, as illustrated by the relative differences in the occurrence of recently derived species inhabiting the northern parts of these regions (Fjeldså 2013). During the late Miocene we see diversification of many birds lineages that continued towards the Pliocene and burst in the Pleistocene when glacial and interglacial cycles altered species geographic range. In this context, areas such as Siberia and Beringia represented interglacial refugia due to their relatively stable mesophilus biome that expanded during the Pleistocene–Holocene boundary while at moderate latitudes woodland and more temperate forests were formed. Such 'mammoth steppe' stability provided opportunities for many birds to maintain local breeding populations in the north, and to move south into the mountain ranges of Central Asia and China, where a rich cold-adapted avifauna (partly of northern origin) can now be found along the high mountain ridges (Allen *et al*. 2010; Päckert *et al*. 2011; Fjeldså *et al*. 2012). The connectivity between the northern biomes, the forest-covered mid-latitude mountain ranges and wintering habitats in the mesic tropics, may have offered more opportunities for continued diversification than the situation in Europe, which is bounded towards the south by the Saharo-Arabian desert region.

The opportunity for accumulation of species, and speciation, in Asia is intimately associated with the uplift of the Qinghai Tibetan Plateau (QTP) and Himalayas. Because of such opportunities, a very large diversity of species could build up along the borderline between the tropical Asian lowlands and the uplifted QTP (Lei *et al*. 2014).

Climatic stability may promote both high species diversity and endemism because of local speciation, as local populations could persist and specialize in local environments (Fjeldså & Lovett 1997a,b), and because of the accumulation of immigrants. In tropical South America and Africa, the richness of both paleoendemic and neoendemic species always peaks in montane forest areas characterized by high climatic stability (Fjeldså 1994, 1995; Fjeldså & Lovett 1997b; Fjeldså *et al.* 1999). Altitudinal range was also considered a strong predictor in centers of endemism (Jetz & Rahbek 2002; Jetz *et al.* 2004), like species richness in South American birds (e.g. Rahbek & Graves 2001). Mountain systems facilitate speciation and maintain high species richness. Neotropical mountains have been considered decisive for Plio-Pleistocene avian evolution by acting as 'species pumps' for their surrounding midlands and lowlands (Fjeldså & Rahbek 2006; Sedano & Burns 2010). Old populations from Pleistocene refugia usually show deep genetic structure and population divergence, which may lead to the high local endemism (Gomez *et al.* 2000).

In China, the HMSC range is characterized by high species richness and endemism, as the climate was stable during the Quaternary glacial periods (Adams & Faure 1997; Liu *et al*. 2002; Shi 2002). Globally, montane hotspots are quite restricted to low latitudes and mountains near thermally stable coasts (Fjeldså *et al*. 2012), and the Sino–Himalayan area is one of the few areas where high endemism extends deeper into the continent. This may be related to the north–south direction of the mountain ranges in Yunnan channeling the monsoon winds deep into the continent. Ecological niche model analyses have suggested that the distribution ranges of several bird species in the HMSC remained stable from the Last Interglacial, through the Last Glacial Maximum (LGM) to present day (Dai *et al.* 2011; Liu *et al.* 2012; Zhao *et al.* 2012; Wang *et al.* 2013). These results inferred an 'ecological stability hypothesis' for explaining the high diversification pattern in HMSC, which was tested by comparing the HMSC and other non-hotspot regional avifaunas (Qu *et al*. 2014). Comparative phylogeography of four bird species (*Alcippe morrisonia* Swinhoe, 1863, *Stachyridopsis ruficeps* Blyth, 1847, *Parus monticolus* Vigors, 1831 and *Aegithalos concinnus* Gould, 1855) found that the high genetic diversity in HMSC might have resulted from both long-term *in situ* diversification and environmental stability of montane habitats (Qu *et al*. 2014).

In China, four currently identified AOEs are all located in the mountain area, which invoked the 'mountain

barrier hypothesis' suggesting that "mountainous environment may act as historical and ecological barriers preventing population gene flow, promoting speciation and maintaining a high endemism" (Huang *et al.* 2010, P. 2013). In the Hengduan Mountains, multiple intra-specific genetic lineages were detected in several bird species, suggesting high regional genetic diversity and endemicity (Lei *et al.* 2007; Song *et al.* 2009; Liu *et al.* 2012; Qu *et al*. 2014).

During the glacial periods, the deep valleys of the Hengduan Mountains played an important role in maintaining the local fauna, by providing refuge for many species and acting as a species pump for expansion during interglacials (Song *et al.* 2009). Consequently, the mountain system may have an effect in two ways. On one hand, it directly prevents the dispersal of species, reducing gene flow among populations (mountain barrier hypothesis). On the other hand, low altitudes of the mountains provide suitable habitats during glaciations (mountain refugia hypothesis). During the glacial periods, the central area of the high Tibetan Plateau was covered by ice, while glaciers in the Southwest Mountainous Subregion were restricted to high altitudes (Liu *et al.* 2002; Shi 2002; Zhou *et al.* 2006). In contrast, the eastern Himalayas might have had similar vegetation during glaciations as in the present time (Adams & Faure 1997), or at least species may have found benign and suitable climates by making small local translocations. It is likely that the climatic stability maintained high richness of species during the Pleistocene glacial periods (Li *et al.* 2009; Qu *et al.* 2011).

Geometric constraints, climate and productivity are frequently suggested to explain variation in species richness (Colwell *et al.* 2004; Sanders & Rahbek 2012). An analysis of species richness in the Hengduan Mountains revealed that the richness pattern for all breeding birds along the elevational gradient is hump-shaped with a peak at 800–1800 m (Wu *et al*. 2013). This peak coincided with an altitudinal range where the climate is neither too cold nor too arid and relatively stable throughout the year, and where high band area and weak geometric constraints augment the effects of climate (Wu *et al.* 2013). When comparing endemic or non-endemic taxa, it was found that endemic richness peaking at mid-elevations was explained partly by spatial factors, whereas non-endemic richness peaking at lower elevation was best explained by climatic and energy factors. These patterns are consistent with many previous studies, which inferred that endemics are more constrained by evolutionary adaptations to local conditions than more widespread, non-endemic species (Jetz & Rahbek 2002; Colwell *et al.* 2004; Dunn *et al.* 2007; Wu *et al.* 2013). In a recent study of the eastern Himalayas (Price *et al*. 2014), the peak elevation of breeding bird distributions was at approximately 1800 m, and this was found to be attributable to insectivorous species and to correlate mainly with the abundance of arthropods (i.e. food resources).

Glacial effect left evolutionary imprint on the process of diversification

Pleistocene climatic fluctuations have long been considered to have profound effects on the geographic distribution and genetic diversity of extant species (Hewitt 1996; Hewitt 2000). Among the global peak concentrations of biodiversity, several are identified as Pleistocene glacial refugia, including those in Asia, North America, South America and Africa (Adams & Faure 1997; Dobrovolski *et al*. 2012). Climate amelioration and disappearance of glaciated dispersal barriers allowed dispersal out of refugia (Taberlet *et al.* 1998; Hortal *et al.* 2011; Sandel *et al.* 2011). European and Asian continents span almost the same latitudinal bands on the Northern Hemisphere, but they have different late Pliocene and Pleistocene glacial histories (Hewitt 2000), and populations in the two regions may have responded differently to the global climate shifts (Zink *et al.* 2003; Zhao *et al.* 2012). Many Western Palearctic species underwent large-scale expansions after the LGM (Hewitt 2004), but most Asian species expanded early before LGM, or some kept stable in eastern Himalayas (Li *et al.* 2009; Song *et al.* 2009; Zhao *et al.* 2012). These differences resulted in mixing of populations and large-scale erosion of local adaptations in the west (Fjeldså 2013). This pre-LGM population expansion mode might suggest the long history and more accumulation for its population divergence. The spatial distribution pattern of Elliot's Laughing thrush (*Trochalopteron elliotii* J. Verreaux, 1870) in HMSC has evidently reflected the 'sky island' effect in promoting the spatial population divergence and maintaining the regional endemism (Qu *et al.* 2011). The 'Ecological Adaptation Hypothesis' suggested that diversified habitats, climatic heterogeneity and ecological separation might have reinforced the isolation of populations in maintaining the genetic diversity or species endemism.

Population divergence in contact zone facilitating diversification

Contrary to the high degree of introgression seen in unstable climatic regions (Jansson & Dynesius 2002),

the contact zones between recently diverged species in the HMSC may have enhanced the regional species richness. More than 50 species analyzed previously demonstrated that the southwestern China mountain system, especially the Himalayan Mountains, harbor some strongly differentiated populations (Wikramanayake *et al*. 2001; Päckert *et al.* 2012). Moreover, a clear faunal transition from lower to higher elevations in the Himalayas was found, with the avifauna of the subalpine coniferous forest related to the northern Palaearctic fauna, whereas the low elevation birds' affinities were more with the southern Indo-Malayan avifauna (Wikramanayake *et al*. 2001; Päckert *et al.* 2012). The discovery of lineage splits within seven families (Aegithalidae, Certhiidae, Fringillidae, Paridae, Phylloscopidae, Regulidae and Timaliidae) provided evidence for geographical processes of diversification and speciation. In the Sino–Himalayan mountain forests, the transition zones among Southeast Asian and north Palaearctic passerines seem to be relatively young, and might have formed due to the invasion of north Palaearctic elements into the subalpine ecozone largely during the Pliocene (Päckert *et al.* 2012). In the contact zones, populations from different refugia may remain separate, with parapatric sutures maintained across environmental gradients (Moritz *et al.* 2009), or with wandering contact/hybrid zones getting caught on a shared contemporary environmental barrier (Pyron & Burbrink 2010). The secondary contact zones may also shift around until they stabilize where there is a physical barrier. There are lots of hypotheses explaining how to generate the contact zone patterns, for example, fusion of glacial refugia, opening of mountain passes and anthropogenic influences (Anderson 1948; Hewitt 2000). HMSC comes out on top of a long historical process of faunal interchange between the north and south, right on the borderline between the biogeographic regions outlined by Holt *et al*. (2013).

The phylogeographical divergence is an early step in the speciation process. It may facilitate the process of diversification or speciation. Many phylogeographic break zones are spatially consistent with contact zones between populations after glacial expansion from refugia, few of which are characterized by lineage divergence due to glacial driving (Taberlet *et al.* 1998; Moritz *et al.* 2009; Sersic *et al.* 2011; Fouquet *et al.* 2012). Such regions have often been considered 'hotspots' in studies of evolutionary processes (Whinnett *et al.* 2005; Moritz *et al.* 2009; Rissler & Smith 2010; Hewitt 2011; April *et al.* 2013). However, few studies have so far tried to compare phylogeographic break zones to detect drivers of the diversification in the regional fauna (Pyron & Burbrink 2010).

Around the HMSC range, hybridization has been detected in the contact zones of some species, for example, between the Silver Pheasant (*Lophura nycthemera* Linnaeus, 1758) and the Kalij Pheasant (*Lophura leucomelanos* Latham, 1790) in Yingjiang, both demonstrated by combined evidence from mitochondrial DNA (mtDNA) and nuclear DNA (nu DNA) (Dong *et al.* 2013). Dai *et al*. (2011) suggest that the 2 highly divergent populations of the Black-throated Tit (*Aegithalos concinnus talifuensis* and *A. c. concinnus*) diverged during Pleistocene glaciations, mostly by isolation in separated refugia. This period of allopatric divergence allowed genetic fixation in two populations, which became admixed when they came in to contact during postglacial expansion (Dai *et al.* 2013). The Pleistocene climate changes and male-biased gene flow have been proposed to contribute to the discordant phylogeographic patterns between mtDNA and nuDNA (Dai *et al.* 2013). Furthermore, the Grey-cheeked Fulvetta (*A. morrisonia*) and the Green-backed Tit (*P. monticolus*) showed a similar phylogeographical division at this mountain region (Song *et al.* 2009; Wang *et al.* 2013). In addition, the Great Tit (*P.*) (Zhao *et al.* 2012), the Black-throated Tit (Dai *et al.* 2011), Elliot's Laughing Thrush (Qu *et al.* 2011) and some other passerines (Päckert *et al.* 2012) have concordant phylogeographical breaks within the HMSC range. The strong geographical structure of 4 passerines within the MSC region in comparison with other non-hotspot regions suggested that lineage diversification has proceeded *in situ* within this region, which resulted in divergence in the conspecific populations and sister species (Qu *et al*. 2014). These phylogeographical breaks revealed the historical geographical isolation between populations, which increased the genetic diversity within the region, which may potentially facilitate species diversification or incipient speciation.

CONCLUSION

To identify the real drivers forming the hotspots of biodiversity and endemism, especially in the HMSC, interpretations based on integrated ecological and evolutionary approaches are much needed (Lei 2012). Understanding the underlying process requires synergy between the different research disciplines across a wide range of spatial and temporal scales, while diversification related to local persistence and accumulation of species over time should not be neglected (Rull 2011b).

High species richness and endemism in the HMSC may be rooted in many factors, such as the geographical location at the junction of different biogeographical realms, the wide range of habitats and climates along the extensive elevational range, the complex topography, the ecological stability, the food resources, the glacial movements and the pre-LGM mode population history. Both 'cradles' ('species pump') and 'museums' (Stenseth 1984; Gaston & Blackburn 1996) may explain the high species richness, because both 'primitive relics' and 'newcomers' are encountered (Fjeldså & Lovett 1997). During the Pleistocene, mountain systems in the HMSC confined species into pockets of stable habitats and restricted dispersal among them, which, in turn, contributed to high genetic diversity in this region (Qu *et al*. 2014). The mountain system in the HMSC may have acted as a refuge for species during the glacial periods, but also as a barrier for expansions after glacial periods. More studies are required to further test this refugia hypothesis by comparing more cold-tolerent and warm-tolerent species. Immigration into the area is also important, at least for some groups (Johansson *et al.* 2007). Phylogeographical breaks may invoke the speciation process (Song *et al.* 2009; Wang *et al.* 2013). Population divergence followed by secondary contact after population expansion, resulting in co-occurrence of different genetic lineages, has contributed to high genetic diversity and species richness.

The conservation implications of such processes have hardly been studied in the context of Asian mountains, although similar patterns and congruences between museum and cradle conditions have been studied elsewhere and have been interpreted as having great potential for conservation. However, the prospects for conserving phylogeographical lineages under changing climate and environment have rarely been studied (D'Amen *et al.* 2013). The frequent phylogeographic lineage divergence within species motivated a reconsideration of conservation strategies for intra-specific diversity (Crandall *et al.* 2000). Distinct phylogeographic lineages within the HMSC range should be considered in assessments of conservation priorities in these biodiversity hotspots.

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