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·综述·

青藏高原及毗邻区植物多样性演化与维持机制: 进展及展望

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摘要: 生物多样性演化和维持受遗传和环境的共同影响。环境要素中, 地质和气候的影响最大。地质和气候过程对青藏高原及毗邻区植物多样性的演化和维持的影响尤为强烈。本文从不同时空尺度综述了青藏高原隆升、亚洲季风气候演变、冰期旋回的气候波动及偶联的环境变化对青藏高原及毗邻区植物多样性起源、演化、群体动态及维持机制的影响。总结了当前植物多样化和物种分布格局变迁和维持研究的最新进展和存在的不足, 展望了气候变化对植物遗传多样性的影响、杂交带及其群体动态和维持机制、植物多样性格局及其成因、季风气候演变对植物多样性维持的影响以及植物群落构建机制等五个值得深入的热点研究方向。

关键词: 气候变化; 杂交; 植物多样性; 群体历史; 青藏高原

Evolution and maintenance mechanisms of plant diversity in the Qinghai-Tibet Plateau and adjacent regions: retrospect and prospect

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Abstract: The evolution and maintenance of biodiversity is largely determined by the interaction of genetics and environmental factors. Geological and climatic histories, which played pivotal roles in the evolution and maintenance of plant diversity in the Qinghai-Tibet Plateau (QTP) and adjacent regions, are the most important environmental aspects. We review the major effects of QTP environmental changes associated with geological uplift, Asian monsoon evolution, and Pleistocene climatic oscillation on the origin, evolution, population demography, and maintenance mechanisms of plant diversity in the QTP and adjacent regions across spatiotemporal scales. Furthermore, we summarize the current progress and knowledge gaps on mechanisms of diversification and maintenance of plant diversity, and outline the effect of climate change on plant genetic diversity, hybrid zone dynamics, plant diversity patterns, the effect of Asian Monsoon evolution on plant diversity maintenance, and mechanisms of community assembly, the five additional future research hotspots.

Key words: climate change; hybridization; plant diversity; population demography; Qinghai-Tibet Plateau

区域生物多样性的时空演化除受物种本身固有的生物学特性决定外, 还受地质事件、气候历史等多种环境要素的影响(Godfray & Lawton, 2001), 涉及突变、遗传漂变和自然选择, 是物种形成、灭绝、迁移的耦合过程。其中与地质过程偶联的环境变化, 在长时间尺度上的作用更加明显, 对生物多样性在物种及以上阶元的宏进化(macroevolution)具有重要的驱动作用。通过系统发育学、生物地理学和古生物学等学科手段可以解析长时间尺度上地质过程对区域生物多样性形成、演化和维持机制

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的影响。近缘种及种内遗传格局及其变迁过程则主要受更新世以来(≤2.6 Ma, Ma即百万年)冰期旋回的气候波动影响(Avise, 2000; Hewitt, 2000), 通常表现为种群分布区在冰期收缩、间冰期扩张, 涉及到遗传变异格局、冰期避难所、冰期后的群体扩散路线以及群体历史等方面, 可利用分子谱系地理学、物种分布区模拟等学科方法进行探究。

素有“世界屋脊”和地球“第三极”之称的青藏高原是世界上面积最大、海拔最高的高原。大约在40–50 Ma, 印度板块和欧亚板块持续碰撞、挤压和拆沉, 导致了青藏高原的隆升和喜马拉雅山脉的形成(Molnar, 1986; Bouilhol et al, 2013; Jagoutz et al, 2015; Tada et al, 2016); 高原隆升的同时, 印度板块向东侧挤压, 形成了横断山(Harrison et al, 1992; 郑度和姚檀栋, 2004; Royden et al, 2008)。关于青藏高原隆升的时间、幅度和次数等问题一直存在争议。一些学者根据同位素、古磁学等方法, 认为青藏高原的西藏中部或北部部分地区在40 Ma已经到达了现在的海拔高度或比现在还高, 随后逐渐下降(Lippert et al, 2014); 但是这些测定方法本身存在很多缺陷, 其结论还有待进一步探讨(Deng & Ding, 2015)。但是, 也有学者根据这些部分地点有争议性的年代标记结果, 认为整个青藏高原在40 Ma已经达到了现在平均4,000 m的海拔高度, 同时坚称第四纪冰期存在大冰盖(Renner, 2016)。尽管青藏高原哪些地区达到现有的海拔高度还需要进一步研究, 但是, 更多的地质学、地理学以及古生物学等证据表明, 从整个青藏高原(包括部分喜马拉雅山脉、横断山、昆仑山等)来说, 似乎不是一次隆升导致的, 隆升存在时间和空间的异质性, 多数地区在第三纪中晚期以来才隆升到现有高度。

青藏高原的隆升是中生代以来地球上最重大的地质历史事件之一, 高原隆升导致了其自身及周边环境的剧烈变化, 如亚洲季风气候形成和加强以及中亚干旱化等。一般认为亚洲季风形成于25–22 Ma, 此后在~14 Ma, 9–7 Ma, ~5 Ma和3.6 Ma等时期发生过显著的变化, 然而这种变化与青藏高原的阶段性隆升并不完全同步(Clift et al, 2008; An et al, 2014; Lu & Guo, 2014; Tada et al, 2016)。伴随着青藏高原的隆升及环境变化, 古近纪(66–23 Ma)由西向东横跨中国大陆宽阔的干旱带, 自新近纪(23–2.6 Ma)以来退缩至中国西北部地区(Sun & Wang, 2005)。更新世以来, 青藏高原地区经历了4次主要的冰期过程(施雅风等, 1998; Zheng et al, 2002; 易朝路等, 2005), 但未形成过大规模的统一冰盖(施雅风等, 1998; Shi, 2002; Owen et al, 2008), 这一假说也得到谱系地理学证据支持(见2.2节)。

综合考虑青藏高原及周边地区的地质构造, 植物多样性分布格局和特征(Mao et al, 2013; Yan et al, 2013; Zhang et al, 2016)及相关研究的关注区域, 本文所指的青藏高原及毗邻区域主要指青藏高原台面, 南部的喜马拉雅山脉, 东南部的横断山地区。这个区域是中国生物多样性重要的特有中心之一(López-Pujol et al, 2011; Huang et al, 2012), 也是生物多样性保护的优先地区(Huang et al, 2016；Zhang et al, 2017b)。该地区是地球上生物多样性最为富集的区域, 植被类型多样, 区系成分来源复杂, 是生态系统的脆弱区和气候变化的敏感区, 包含喜马拉雅(Himalaya)、中国西南山地(Mountains of Southwest China)和印度–缅甸(Indo-Burma) 3个全球生物多样性热点地区(Mittermeier et al, 2001)。

实际上, 不同时间尺度的地质、气候历史事件通常耦合在一起, 共同影响着青藏高原及毗邻区的生物多样性起源、演化和维持。近年来, 基于分子系统学、生物地理学、谱系地理学和古生物学等学科手段, 学者们对青藏高原及毗邻区植物多样性在不同时空尺度的演化历史与维持机制开展了深入研究(Liu et al, 2012, 2014b; Wen et al, 2014; Favre et al, 2015), 揭示了一些类群生物多样性起源、演化和维持机制。然而, 在科学发展与交叉的新形势下, 尚存在许多亟待探究的科学问题和值得深入的热点。本文以时间轴为序列, 试图对青藏高原及毗邻区植物多样性起源、演化与维持机制的研究进展进行综述, 在此基础上, 对未来值得深入的研究热点进行了展望, 以期为该地区植物多样性演化和维持机制的相关研究提供参考。

1 高原隆升及偶联的环境变化驱动了植物多样化

青藏高原隆升及偶联的季风气候演化, 造成了地表格局和环境的异质化, 形成了物种扩散的隔离障碍或通道, 扩展了生态、环境梯度, 提供了新生态位, 驱动了植物多样性演化。从源头上讲, 随着青藏高原隆升, 古地中海逐渐退却, 早期青藏高原

植物区系主要由第三纪残存的古地中海植物区系发展演化而来(孙航, 2002b), 后来高山植物区系的发展吸纳了北极的第三纪成分(孙航, 2002a), 同时也接受了来自中亚、东亚以及南半球等地区迁入的类群(Wen et al, 2014)。在环境变化的驱动下, 该地区孕育了许多特有成分, 很多类群发生了快速辐射演化, 同时有一些类群灭绝(见3.4节)。近年来, 分子系统学和生物地理学分析为此提供了有力证据, 以下将进行简要论述。

板块运动和高原隆升形成的高山、峡谷等地理障碍, 限制了物种基因流, 促进了植物异域分化。Zhao等(2016b)通过姜科距药姜属(*Cautleya*)和象牙参属(*Roscoea*)的演化历史分析, 发现两个属大约起源于44 Ma, 在32 Ma发生分化, 而随着喜马拉雅–青藏高原的第三次隆升(23 Ma)及其相伴的中南半岛快速侧向滑动, 两个属的祖先分布区被“撕裂”成两个不连续的区域, 此后异域分化为完全不同的类群。这两个属的演化历史正好映射了喜马拉雅–青藏高原早期不同隆升阶段的地质过程及其对植物多样性演化的影响。绣线菊属(*Spiraea*)的系统发育和生物地理分析也显示该属起源于13.4 Ma, 在4 Ma发生多样化, 这个过程与青藏高原前两次隆升密切相关(Khan et al, 2016)。基于报春花属(*Primula*)的*Armerina*组(Ren et al, 2015)和葱属(*Allium*)的*Cyathophora*亚属(Li et al, 2016)的研究表明, 两个类群的分化事件大约在4–3 Ma, 推测是最后一次青藏高原隆升和横断山隆起形成的地理隔离障碍促进了属内物种分化。

更多研究显示, 地质和气候过程对植物多样化的影响程度难以准确地单独量化, 通常认为在地质和气候事件的共同作用下, 生态位多样化驱动了区域内植物类群的快速辐射演化(rapid radiation) (Liu et al, 2012, 2014b; Wen et al, 2014; Favre et al, 2015; Hughes & Atchison, 2015)。橐吾属–垂头菊属–蟹甲草属(*Ligularia-Cremanthodium-Parasenecio*)复合体是以青藏高原及毗邻区为分布中心的类群, Liu等(2006)通过分子钟估算发现, 伴随着青藏高原从中新世到上新世的快速隆升, 新的生态位和地理隔离促成了异域物种形成, 导致该类群发生了快速的辐射演化。相似的结果也发现于如下类群中: 毛冠菊属(*Nannoglottis*) (Liu et al, 2002)、风毛菊属(*Saussurea*) (Wang et al, 2009c)、大黄属(*Rheum*) (Sun et al, 2012)、景天属(*Rhodiola*) (Zhang et al, 2014)和葱属的*Cyathophora*亚属(Li et al, 2016)等。值得一提的是, Favre等(2016)通过龙胆属(*Gentiana*)的进化分析发现, 该属多样化速率随时间推移平稳增加, 在青藏高原地区未发生过快速辐射演化, 在中新世/上新世(约7 Ma)的生态位转换促进了物种多样化。

2　更新世以来物种分布格局的变迁和维持

谱系地理学解析的尺度多在更新世以来至末次冰盛期(Last Glacial Maximum, LGM), 通常基于群体遗传学、地理分布和气候数据的统计分析, 探讨物种分化历史和遗传格局、冰期避难所和冰期后扩散路线、分布格局变迁和群体历史等问题(Avise, 2000; Knowles, 2009; Avise et al, 2016)。通过不同植被类型、生活史和繁育系统的代表性类群的分子谱系地理学研究, 揭示了青藏高原及毗邻区植物类群的分布格局变迁和群体历史的基本式样(Qiu et al, 2011; Liu et al, 2012)。

2.1　地理隔离塑造了物种遗传格局

青藏高原的快速隆升, 极大地改变了该区域的地表格局, 包括主要山系的形成、“空中岛屿”(sky island)的出现、河流袭夺改道等, 这种地形地貌的变化驱动了植物近缘种及种内群体的遗传分化。

2.1.1　地理障碍促进了种内群体间的遗传分化

高原隆升形成的主要山系阻碍了植物群体间的基因流, 促进了物种群体间的分化。如碧罗雪山(湄公河–萨尔温江的分水岭)是喜马拉雅红豆杉(*Taxus wallichiana*) (Gao et al, 2007; Liu et al, 2013)和桃儿七(*Sinopodophyllum hexandrum*) (Li et al, 2011)东西向基因流的重要地理障碍, 导致了山脉东西两侧植物群体的遗传分化。喜马拉雅南坡和横断山区的高山峡谷促进了柏木属(*Cupressus*) (Xu et al, 2010)和川滇高山栎(*Quercus aquifolioides*) (Du et al, 2017)的异域分化。他念他翁山和念青唐古拉山的形成, 也导致了西藏沙棘(*Hippophaë tibetana*)、丝叶眼子菜(*Stuckenia filiformis*)和穗状狐尾藻(*Myriophyllum spicatum*)种内的遗传分化(Wang et al, 2010; Du & Wang, 2016; Wu et al, 2016)。

2.1.2　“空中岛屿”限制了物种的基因流

伴随着青藏高原隆升, 喜马拉雅–横断山区形成了大量的“空中岛屿”(He & Jiang, 2014), 这些“岛屿”上的气候、植被和物种与其周边低海拔地区完

全不同(Heald, 1951)。与此同时，低海拔的生境构成了扩散的隔离障碍，限制了“岛屿”间群体的基因流，分布于其上的高山植物群体通过自然选择和遗传漂变等过程发生遗传分化。Yue等(2009)发现分布于横断山区“空中岛屿”上的丛菔属(*Solms-laubachia*)特有物种大约在0.87 Ma发生分化，尽管这些物种间遗传距离相对较小，但遗传差异显著，推测是“空中岛屿”隔离所致。类似的结果也在风毛菊属(Wang et al, 2009c)和大黄属(Sun et al, 2012)中报道。在物种层面，Luo等(2016a)通过对4种高山冰原带植物的谱系地理学研究，发现物种的遗传格局呈“岛屿”状分异样式，不同“岛屿”上的群体间遗传分化十分明显。由此可见，该地区的“空中岛屿”对种间和种内的基因流都具有重要的限制作用。

2.1.3 河流改道扰动了物种遗传格局

历史上，西南山地的水系格局与目前相比有很大差异，伴随着青藏高原隆升和横断山脉的形成，这些河流发生过袭夺和改道(Clark et al, 2004)。水系的变迁改变了植物的扩散通道，促进了群体间遗传分化。基于干热河谷植物滇榄仁(*Terminalia franchetii*) (Zhang et al, 2011)和皱叶醉鱼草(*Buddleja crispa*) (Yue et al, 2012)的物种演化分析发现，当前物种的遗传格局很好地支持古红河河流系统南北走向的漏斗状结构假说，反映出河流袭夺之后的河流系统对植物群体遗传结构产生的影响。

2.2 冰期旋回对物种群体历史的影响

基于对已报道研究的整合分析，初步确定了青藏高原及邻近地区避难所的可能的位置(Qiu et al, 2011; Liu et al, 2012)。横断山地区是植物冰期的重要避难所之一，很多植物冰期退缩到该地区，随着冰期后气候回暖，又向外扩散，如长花马先蒿(*Pedicularis longiflora*) (Yang et al, 2008)、祁连圆柏(*Juniperus przewalskii*) (Zhang et al, 2005)和青海云杉(*Picea crassifolia*) (Meng et al, 2007)等。

分布在青藏高原台面和喜马拉雅山地的一些耐寒植物，在末次冰盛期时在微避难所中存活下来，冰期后又向外扩散，形成现今的分布格局。如西藏沙棘(Wang et al, 2010)、露蕊乌头(*Aconitum gymnandrum*) (Wang et al, 2009a)、大果圆柏复合群(*Juniperus tibetica* complex) (Opgenoorth et al, 2010)、银露梅(*Potentilla glabra*) (Wang et al, 2009b)和西藏报春(*Primula tibetica*) (Ren et al, 2017)等。分布于喜马拉雅山脉的一些类群，可能在最大冰期(1.2–0.6 Ma)后从横断山区扩散而来，而末次冰盛期对其遗传结构影响不大，如云南铁杉(*Tsuga dumosa*) (Cun & Wang, 2010)、喜马拉雅红豆杉(Liu et al, 2013)和西藏报春(Ren et al, 2017)等。

多数物种的种群扩张历史符合“冰期收缩，间冰期扩张”的式样，但也有一些物种的种群扩张历史与此相反，在冰期扩张，间冰期收缩，如喜马拉雅红豆杉(Liu et al, 2013)、丽江云杉(*Picea likiangensis*) (Li et al, 2013)、华西小石积(*Osteomeles schwerinae*) (Wang et al, 2015)等，最近基于简化基因组数据对西藏报春的研究也支持了该假说(Ren et al, 2017)。此外，一些物种没有发生过大范围的分布区变迁，可能随着气候变化，就地沿海拔上下迁移，如云南铁杉(Cun & Wang, 2010)、川滇高山栎(Du et al, 2017)和部分呈“空中岛屿”分布的类群(Luo et al, 2016a)。

3 研究展望

随着DNA测序技术的发展和测序成本的降低，基因组数据被大规模用于系统发育基因组学(phylogenomics) (Delsuc et al, 2005; Pyron, 2015; Barrett et al, 2016)和群体基因组学(population genomics) (Luikart et al, 2003; Ellegren, 2014)等研究中。加之大数据处理方法的开发应用和计算能力的不断提高，使得基于基因组数据的系统发育、生物地理和群体遗传学分析方便易行(Abbott et al, 2016; Avise et al, 2016; Payseur & Rieseberg, 2016)。与此同时，伴随着生物多样性信息学(biodiversity informatics)的快速发展，大量的标本数据库(如GBIF和NSII等)、性状数据库(如TRY)和遗传数据库(如NCBI和iBOL等)在线共享，可以比较便捷地同时获取和分析大量物种的分布和遗传数据。此外，通过气象和环境数据库(如WorldClim和IPCC网站等)可获得物种分布点的气候和环境数据。因此，当前生物多样性演化和维持机制研究，趋向于将上述部分或全部数据耦合分析，综合探讨生物多样性演化与维持机制的相关科学问题。

就青藏高原及毗邻区基于系统发育和谱系地理学开展的生物多样性起源与演化机制研究而言，受限于系统发育关系的分辨率以及分歧时间估算的准确度，此前的多数工作仅基于少数DNA片段构建系统发育关系和推断物种演化历史，分歧时间的

估算也常常基于有限的化石记录和DNA平均进化速率, 也缺乏详细的多样化机制分析。现在, 叶绿体基因组、转录组、简化基因组(如RAD-seq)乃至全基因组测序已成为常规手段, 更为可喜的是有可能通过基因组测序, 获得不同世代间准确的DNA序列突变速率(如Xie et al, 2016)。因此, 未来的工作需要尽可能实现类群和基因组的全面取样, 通过系统发育基因组学构建更可靠的系统发育关系, 利用更多的可靠化石点或者准确突变速率进行分歧时间估算和群体历史分析。此外, 也应该充分考虑性状数据, 在可能的情况下整合古孢粉和化石中的古DNA数据, 以实现对青藏高原及毗邻区植物多样性起源、演化和灭绝的综合分析。通过区域内不同门类(动物、植物和微生物)特征类群的综合研究, 也将有助于阐明区域多样性起源的时空格局和维持机制(如Merckx et al, 2015)。同时针对更多特征类群, 通过宏进化和微进化(microevolution)的有机结合, 开展从属级到物种水平的整合研究, 提供更为完整的物种演化时间序列(如报春花属, Ren et al, 2015, 2017), 将有助于阐明较长时间尺度上不同地质和气候事件对植物多样性不同层次的演化和维持机制的影响。如果能基于多个物种的转录组或基因组数据的比较谱系地理学(comparative phylogeography)和群体基因组学研究, 将得出更为准确的物种分歧时间和群体历史过程, 有助于揭示物种水平的演化格局。

除此之外, 我们进一步展望了青藏高原及毗邻区未来研究中值得关注的5个热点科学问题。

3.1　气候变化对植物遗传多样性的影响

随着空间数据越来越容易获取以及分析方法的发展, 物种分布区模拟(species distribution modeling)给谱系地理学研究带来了新视角(Alvarado-Serrano & Knowles, 2014)。基于物种分布区模拟, 可以探讨气候变化对植物多样性可能产生的影响。此前, 青藏高原及邻近区域的研究主要关注历史气候变化对物种分布格局的影响(如Liu et al, 2013; Sun et al, 2014), 也有少量工作关注未来气候变化对物种分布的潜在影响(如Poudel et al, 2014; Wan et al, 2016), 但尚未有探讨气候变化对区域物种多样性和系统发育多样性(phylogenetic diversity) (如Pio et al, 2014; Zhang et al, 2017a)和种内遗传多样性(intraspecific genetic diversity) (如Alsos et al, 2012; Yannic et al, 2014; Inoue & Berg, 2017)的影响。将来的工作需要侧重多物种的整合分析(meta-analysis), 以及在分析中融入遗传数据(Fordham et al, 2014; Ikeda et al, 2017), 以便更准确地预测气候变化对植物遗传多样性可能产生的影响, 为生物多样性的保护提供科学证据。

3.2　杂交带及其群体动态和维持机制

杂交带(hybrid zone)往往是近缘物种交汇的区域, 是生物多样性演化研究的天然实验室(Hewitt, 1988), 对物种的维持具有重要意义(Harrison, 1990)。目前欧洲和北美杂交带的位置及动态已比较清楚。

在青藏高原及毗邻区, 伴随着青藏高原隆升, 新形成的生境为杂交种提供了生态位, 许多植物类群发生了快速辐射演化, 在冰期–间冰期气候波动的驱动下, 一些物种发生杂交而后产生新的物种。自然杂交和基因渐渗在橐吾属(*Ligularia*) (Liu et al, 2006; Yu et al, 2014)、杜鹃属(*Rhododendron*) (Ma et al, 2010; Zha et al, 2010)、绿绒蒿属(*Meconopsis*) (Yang et al, 2012)和红景天属(*Rhodiola*) (Zhang et al, 2014)等类群中都有报道。同域分布的丝叶眼子菜(*Stuckenia filiformis*)和蓖齿眼子菜(*S. pectinata*) (Du & Wang, 2016), 黑杨(*Populus nigra*)和苦杨(*P. laurifolia*) (Jiang et al, 2016)也发生了杂交, 而同域分布的紫果云杉(*Picea purpurea*)和丽江云杉中也检测到了频繁的基因渐渗(Du et al, 2011)。此外, 一些物种经历了同倍体杂交物种形成, 如高山松(*Pinus densata*) (Ma et al, 2006; Gao et al, 2012)、丽江云杉(Sun et al, 2014)、居中虎榛子(*Ostryopsis intermedia*) (Liu et al, 2014a)和江孜沙棘(*Hippophaë gyantsensis*) (Jia et al, 2016)。由此可见杂交和基因渐渗在该地区植物多样性演化和维持中扮演着重要角色。

然而在青藏高原及毗邻区, 杂交带的位置、群体的动态和维持机制等问题尚不清楚。此外, 该地区典型的山地地貌中, 在海拔梯度上是否存在杂交带及其动态机制也亟待探索。与此同时, 近年来研究发现, 物种形成伴随基因流存在可能是一种普遍式样(Nosil, 2008; Feder et al, 2012; 李忠虎等, 2014), 但在上述杂交带的近缘物种中基因流在物种分化初期是否存在、其在时空层面的变化式样, 以及在基因组中维持生殖隔离的分子机制(多少基因位点? 哪些位点以及如何决定？如Poelstra et al,

2014)等仍不清楚。此前的多数研究基于单亲遗传的质体DNA的遗传证据(叶绿体、线粒体), 缺乏双亲遗传的核基因证据, 主要探讨物种的谱系历史, 将来的研究需要基于生态、形态、质体和核基因组等证据, 并结合同质园(common garden)以及基因功能验证实验进行杂交带及群体动态与维持机制的综合研究。

3.3 植物多样性格局及其成因

有关青藏高原及毗邻区植物多样性格局及成因, 在不同空间尺度上已有一些研究。在区域尺度上, 基于志书、标本数据的分析显示青藏高原的东部和南部是物种多样性和系统发育多样性的分布中心(Mao et al, 2013; Yan et al, 2013), 也是特有物种的分布中心(López-Pujol et al, 2011; Huang et al, 2012; Zhang et al, 2016); 分析发现物种丰富度与气候之间有强烈的关联, 但不同生活型的植物关联程度不同(Mao et al, 2013; Yan et al, 2013)。基于群落调查数据, Wang等(2006)发现物种多样性随着海拔升高而降低, 水平梯度上从东南向西北逐渐降低。然而, Shimono等(2010)并未发现植物多样性与海拔和维度之间存在紧密的相关性。在局域尺度上, Wang等(2007)对高黎贡山海拔梯度植物多样性格局进行了研究, 发现植物多样性水平(科、属、种)随海拔升高呈偏峰分布, 在中海拔最高, 这种式样得到了独龙江流域(Li et al, 2015)和玉龙雪山(Xu et al, 2016)相关研究的支持。然而基于海拔梯度样方调查的数据则显示, 随着海拔的升高, 高黎贡山木本植物物种丰富度逐渐下降, 而草本则先下降再上升(徐成东等, 2008), 而两者在玉龙雪山都随海拔上升而下降(冯建孟等, 2006; Luo et al, 2016b, c)。

上述研究由于数据来源、研究尺度及调查方法和标准等不尽相同, 得出的植物多样性格局及环境解释的主导因子差异较大, 加之多数研究并未考虑系统发育多样性和功能性状多样性的格局, 也未运用更准确的遗传数据(如DNA条形码)构建系统发育树。此外, 也未能考虑更多的环境变量, 如末次冰盛期以来的气候变化、环境异致性等, 这些要素对欧洲、北美植物(Montoya et al, 2007; Svenning & Skov, 2007)以及东亚植物类群(Liu et al, 2017; Wang et al, 2017)分布格局形成有重要影响, 然而这些要素如何影响青藏高原及毗邻区的植物多样性格局, 尚待深入研究。因此将来有必要以整个青藏高原及毗邻区为研究对象, 在区域物种库构建中考虑地衣、苔藓、维管植物等类群, 综合利用志书、标本、群落、遗传、功能性状等数据源, 并考虑更多的环境变量, 开展不同时空尺度上植物多样性水平梯度和海拔梯度格局及成因的耦合分析。

此外, 在物种水平, 种内遗传变异的格局及成因也值得关注。地理和环境等要素耦合造就了植物的遗传格局, 解析它们对植物遗传格局的影响程度将有助于阐明遗传多样性的形成机制。此前, 该地区的研究仅限于利用一代测序和常规分子标记获得遗传变异数据, 进而与环境做关联分析。如Wu等(2016)发现穗状狐尾藻(*Myriophyllum spicatum*)的遗传格局在区域尺度上主要受环境要素制约, 然而在具有明显的环境梯度的局域尺度上, 地理要素更重要(Wu et al, 2015), 而地理和环境要素的耦合塑造了云南松(*Pinus yunnanensis*)的遗传变异格局(Wang et al, 2013a)。目前, 基因组数据(如全基因组或简化基因组)获取在非模式植物中变得简单可行(Ellegren, 2014), 将来的研究, 一方面需要考虑更多的环境变量, 进一步量化每个环境要素的贡献(Wang et al, 2013b), 开展更深入的遗传与环境关联分析(Rellstab et al, 2015), 同时挖掘其中可能和生态环境适应相关的基因, 揭示物种生态适应和形成的分子机制; 另一方面需要从生态学的角度考虑生物要素的影响, 同时结合物种的丰富度、适合度等开展综合研究(Pironon et al, 2015), 阐明物种遗传多样性的维持机制。

3.4 季风气候演变对植物多样性维持的影响

青藏高原的隆升和亚洲季风气候的演变并非完全同步(Clift et al, 2008; An et al, 2014; Lu & Guo, 2014; Tada et al, 2016), 亚洲季风演化更多受全球变冷的影响, 并且印度季风先于东亚季风形成(Tada et al, 2016)。这意味着除了高原隆升的地质过程外, 季风气候的转变可能是该地区植物演化的另一重要驱动力(Liu et al, 2013)。但此前的研究将物种演化笼统地归因于高原隆升促进了物种分化, 缺少对季风气候对物种形成演化影响的讨论和评估。古生物学证据显示, 晚上新世以来, 伴随着青藏高原快速隆升和亚洲季风气候加强, 西南地区冬春季降水显著减少, 这导致了雪松属(*Cedrus*) (Su et al, 2013)和红杉属(*Sequoia*) (Zhang et al, 2015b)等植物类群在东亚消失。分子谱系地理学的结果也表明,

更新世(46–16 ka, ka为千年)亚洲季风气候减弱促进了华西小石积群体间的遗传分化(Wang et al, 2015)。而群体遗传学证据显示, 自2.96 Ma以来, 亚洲季风气候促进了红砂(*Reaumuria soongarica*)的生境片断化和物种分化, 同时冬季风促进了物种纬向的基因流(Yin et al, 2015)。

高原隆升和季风演变可能耦合影响植物的演化, 地表格局的变化会导致生境的异质化, 而季风的变化会进一步加剧生境的异质化(Liu et al, 2013)。这些要素综合影响现存物种的演化, 表现为现存物种间显著的生态位分化(Mao & Wang, 2011; Liu et al, 2013; Sun et al, 2014; Zhao et al, 2016a)。将来基于基因组数据和更准确的演化模型(如ABC、∂a∂i和SFS等模型), 有可能估算出更为准确的物种分歧时间和群体动态历史, 进而结合植物生理生态特征的演化分析(如Pittermann et al, 2012)和更准确的季风演化过程重建(如Cheng et al, 2016), 有望解析季风气候演变对植物多样性维持机制的影响。

3.5　植物群落构建机制

生物群落的构建机制是生态学研究的核心问题。学者们普遍认为群落构建机制是由区域过程和局域过程共同决定的(Taylor & Aarssen, 1990; Zobel, 1997)。其中, 区域过程包括地质历史事件、物种形成、迁移扩散以及灭绝等, 决定了现有区域物种库的数量, 同时限制进入局域群落内的物种数量。局域过程则包括种间相互作用、生境过滤、扩散限制等, 它们最终影响局域群落内物种的组成。目前, 结合系统发育和功能性状维度为探讨群落构建机制如何沿时空格局的变化提供了新的思路(Webb et al, 2002; Kraft & Ackerly, 2010; Cavender-Bares et al, 2016)。

青藏高原及毗邻区区域尺度上群落构建的研究结果表明, 系统发育结构在多数区域呈聚集结构(Yan et al, 2013), 而在海拔梯度上, 系统发育结构在不同海拔间存在显著差异(Li et al, 2014; Li et al, 2015)。全新世以来, 人类活动对生物多样性及其赖以生存的地球环境产生了显著影响(Vitousek et al, 1997), 青藏高原及毗邻区也不例外(Chen et al, 2013)。人类活动的影响可能波及群落的物种、系统发育和功能多样性及群落构建机制, 如青藏高原地区持续的放牧改变了高寒草甸的群落性状结构(Niu et al, 2016), 不同演替阶段的高寒草甸群落的功能多样性和群落结构相反(Zhang et al, 2015a)。然而, 如前所述(见3.3节), 上述研究存在数据源不同和研究尺度各异等缺陷, 难以耦合分析出全面格局和一般规律, 将来的研究需要基于大尺度(水平和海拔梯度)的森林及高寒草甸群落的地面监测(样地、环境), 空中观测(卫星、无人机等), 结合遗传、性状和环境等多维度数据, 综合研究自然过程和人类活动下的群落构建的时空变化格局。

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参考文献

Abbott RJ, Barton NH, Good JM (2016) Genomics of hybridization and its evolutionary consequences. Molecular Ecology, 25, 2325–2332.

Alsos IG, Ehrich D, Thuiller W, Eidesen PB, Tribsch A, Schönswetter P, Lagaye C, Taberlet P, Brochmann C (2012) Genetic consequences of climate change for northern plants. Proceedings of the Royal Society B: Biological Sciences, 279, 2042–2051.

Alvarado-Serrano DF, Knowles LL (2014) Ecological niche models in phylogeographic studies: applications, advances and precautions. Molecular Ecology Resources, 14, 233–248.

An Z, Sun Y, Chang H, Zhang P, Liu X, Cai Y, Jin Z, Qiang X, Zhou W, Li L (2014) Late Cenozoic climate change in monsoon-arid Asia and global changes. In: Late Cenozoic Climate Change in Asia, pp. 491–581. Springer, Berlin.

Avise JC (2000) Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, Massachusetts.

Avise JC, Bowen BW, Ayala FJ (2016) In the light of evolution X: comparative phylogeography. Proceedings of the National Academy of Sciences, USA, 113, 7957–7961.

Barrett CF, Bacon CD, Antonelli A, Cano Á, Hofmann T (2016) An introduction to plant phylogenomics with a focus on palms. Botanical Journal of the Linnean Society, 182, 234–255.

Bouilhol P, Jagoutz O, Hanchar JM, Dudas FO (2013) Dating the India-Eurasia collision through arc magmatic records. Earth and Planetary Science Letters, 366, 163–175.

Cavender-Bares J, Ackerly DD, Hobbie SE, Townsend PA (2016) Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. Annual Review of Ecology, Evolution, and Systematics, 47, 433–462.

Chen H, Zhu Q, Peng C, Wu N, Wang Y, Fang X, Gao Y, Zhu D, Yang G, Tian J (2013) The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. Global Change Biology, 19, 2940–2955.

Cheng H, Edwards RL, Sinha A, Spötl C, Yi L, Chen S, Kelly

M, Kathayat G, Wang X, Li X, Kong X, Wang Y, Ning Y, Zhang H (2016) The Asian monsoon over the past 640,000 years and ice age terminations. Nature, 534, 640–646.

Clark MK, Schoenbohm LM, Royden LH, Whipple KX, Burchfiel BC, Zhang X, Tang W, Wang E, Chen L (2004) Surface uplift, tectonics, and erosion of eastern Tibet from large-scale drainage patterns. Tectonics, 23, TC1006.

Clift PD, Hodges KV, Heslop D, Hannigan R, Van Long H, Calves G (2008) Correlation of Himalayan exhumation rates and Asian monsoon intensity. Nature Geoscience, 1, 875–880.

Cun YZ, Wang XQ (2010) Plant recolonization in the Himalaya from the southeastern Qinghai-Tibetan Plateau: geographical isolation contributed to high population differentiation. Molecular Phylogenetics and Evolution, 56, 972–982.

Delsuc F, Brinkmann H, Philippe H (2005) Phylogenomics and the reconstruction of the tree of life. Nature Reviews Genetics, 6, 361–375.

Deng T, Ding L (2015) Paleoaltimetry reconstructions of the Tibetan Plateau: progress and contradictions. National Science Review, 2, 417–437.

Du FK, Hou M, Wang W, Mao K, Hampe A (2017) Phylogeography of *Quercus aquifolioides* provides novel insights into the Neogene history of a major global hotspot of plant diversity in south-west China. Journal of Biogeography, 44, 294–307.

Du FK, Peng XL, Liu JQ, Lascoux M, Hu FS, Petit RJ (2011) Direction and extent of organelle DNA introgression between two spruce species in the Qinghai-Tibetan Plateau. New Phytologist, 192, 1024–1033.

Du ZY, Wang QF (2016) Allopatric divergence of *Stuckenia filiformis* (Potamogetonaceae) on the Qinghai-Tibet Plateau and its comparative phylogeography with *S. pectinata* in China. Scientific Reports, 6, 20883.

Ellegren H (2014) Genome sequencing and population genomics in non-model organisms. Trends in Ecology & Evolution, 29, 51–63.

Favre A, Michalak I, Chen CH, Wang JC, Pringle JS, Matuszak S, Sun H, Yuan YM, Struwe L, Muellner-Riehl AN (2016) Out-of-Tibet: the spatio-temporal evolution of the temporal evolution of *Gentiana* (Gentianaceae). Journal of Biogeography, 143, 1967–1978.

Favre A, Packert M, Pauls SU, Jahnig SC, Uhl D, Michalak I, Muellner-Riehl AN (2015) The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. Biological Reviews, 90, 236–253.

Feder JL, Egan SP, Nosil P (2012) The genomics of speciation-with-gene-flow. Trends in Genetics, 28, 342–350.

Feng JM, Wang XP, Xu CD, Yang YH, Fang JY (2006) Altitudinal patterns of plant species diversity and community structure on Yulong Mountains, Yunnan. Journal of Mountain Science, 24, 110–116. (in Chinese with English abstract) [冯建孟, 王襄平, 徐成东, 杨元合, 方精云 (2006) 玉龙雪山植物物种多样性和群落结构沿海拔梯度的分布格局. 山地学报, 24, 110–116.]

Fordham DA, Brook BW, Moritz C, Nogués-Bravo D (2014) Better forecasts of range dynamics using genetic data. Trends in Ecology & Evolution, 29, 436–443.

Gao J, Wang B, Mao JF, Ingvarsson P, Zeng QY, Wang XR (2012) Demography and speciation history of the homoploid hybrid pine *Pinus densata* on the Tibetan Plateau. Molecular Ecology, 21, 4811–4827.

Gao LM, Möller M, Zhang XM, Hollingsworth ML, Liu J, Mill RR, Gibby M, Li DZ (2007) High variation and strong phylogeographic pattern among cpDNA haplotypes in *Taxus wallichiana* (Taxaceae) in China and North Vietnam. Molecular Ecology, 16, 4684–4698.

Godfray HCJ, Lawton JH (2001) Scale and species numbers. Trends in Ecology & Evolution, 16, 400–404.

Harrison RG (1990) Hybrid zones: windows on evolutionary process. Oxford Surveys in Evolutionary Biology, 7, 69–128.

Harrison TM, Copeland P, Kidd WSF, Yin A (1992) Raising Tibet. Science, 255, 1663–1670.

He K, Jiang X (2014) Sky islands of southwest China. I. An overview of phylogeographic patterns. Chinese Science Bulletin, 59, 585–597.

Heald WF (1951) Sky islands of Arizona. Natural History, 60, 56–63.

Hewitt GM (1988) Hybrid zones: natural laboratories for evolutionary studies. Trends in Ecology & Evolution, 3, 158–167.

Hewitt GM (2000) The genetic legacy of the Quaternary ice ages. Nature, 405, 907–913.

Huang JH, Chen B, Liu CR, Lai JS, Zhang JL, Ma KP (2012) Identifying hotspots of endemic woody seed plant diversity in China. Diversity and Distributions, 18, 673–688.

Huang JH, Huang JH, Liu CR, Zhang JL, Lu XH, Ma KP (2016) Diversity hotspots and conservation gaps for the Chinese endemic seed flora. Biological Conservation, 198, 104–112.

Hughes CE, Atchison GW (2015) The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. New Phytologist, 207, 275–282.

Ikeda DH, Max TL, Allan GJ, Lau MK, Shuster SM, Whitham TG (2017) Genetically informed ecological niche models improve climate change predictions. Global Change Biology, 23, 164–176.

Inoue K, Berg DJ (2017) Predicting the effects of climate change on population connectivity and genetic diversity of an imperiled freshwater mussel, *Cumberlandia monodonta* (Bivalvia: Margaritiferidae), in riverine systems. Global Change Biology, 23, 94–107.

Jagoutz O, Royden L, Holt AF, Becker TW (2015) Anomalously fast convergence of India and Eurasia caused by double subduction. Nature Geoscience, 8, 475–478.

Jia DR, Wang YJ, Liu TL, Wu GL, Kou YX, Cheng K, Liu JQ (2016) Diploid hybrid origin of *Hippophaë gyantsensis* (Elaeagnaceae) in the western Qinghai-Tibet Plateau. Biological Journal of the Linnean Society, 117, 658–671.

Jiang D, Feng J, Dong M, Wu G, Mao K, Liu J (2016) Genetic origin and composition of a natural hybrid poplar *Populus* × *jrtyschensis* from two distantly related species. BMC Plant

Biology, 16, 1–12.

Khan G, Zhang FQ, Gao QB, Fu PC, Xing R, Wang JL, Liu HR, Chen SL (2016) Phylogenetic analyses of *Spiraea* (Rosaceae) distributed in the Qinghai-Tibetan Plateau and adjacent regions: insights from molecular data. Plant Systematics and Evolution, 302, 11–21.

Knowles LL (2009) Statistical phylogeography. Annual Review of Ecology, Evolution, and Systematics, 40, 593–612.

Kraft NJB, Ackerly DD (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs, 80, 401–422.

Li L, Abbott RJ, Liu BB, Sun YS, Li LL, Zou JB, Wang X, Miehe G, Liu JQ (2013) Pliocene intraspecific divergence and Plio-Pleistocene range expansions within *Picea likiangensis* (Lijiang spruce), a dominant forest tree of the Qinghai-Tibet Plateau. Molecular Ecology, 22, 5237–5255.

Li MJ, Tan JB, Xie DF, Huang DQ, Gao YD, He XJ (2016) Revisiting the evolutionary events in *Allium* subgenus *Cyathophora* (Amaryllidaceae): insights into the effect of the Hengduan Mountains Region (HMR) uplift and Quaternary climatic fluctuations to the environmental changes in the Qinghai-Tibet Plateau. Molecular Phylogenetics and Evolution, 94, 802–813.

Li R, Kraft NJB, Yu H, Li H (2015) Seed plant phylogenetic diversity and species richness in conservation planning within a global biodiversity hotspot in eastern Asia. Conservation Biology, 29, 1552–1562.

Li XH, Zhu XX, Niu Y, Sun H (2014) Phylogenetic clustering and overdispersion for alpine plants along elevational gradient in the Hengduan Mountains Region, southwest China. Journal of Systematics and Evolution, 52, 280–288.

Li Y, Zhai SN, Qiu YX, Guo YP, Ge XJ, Comes HP (2011) Glacial survival east and west of the “Mekong-Salween Divide” in the Himalaya-Hengduan Mountains region as revealed by AFLPs and cpDNA sequence variation in *Sinopodophyllum hexandrum* (Berberidaceae). Molecular Phylogenetics and Evolution, 59, 412–424.

Li ZH, Liu ZL, Wang ML, Qian ZQ, Zhao P, Zhu J, Yang YX, Yan XH, Li YJ, Zhao GF (2014) A review on studies of speciation in the presence of gene flow: evolution of reproductive isolation. Biodiversity Science, 22, 88–96. (in Chinese with English abstract) [李忠虎, 刘占林, 王玛丽, 钱增强, 赵鹏, 祝娟, 杨一欣, 阎晓昊, 李银军, 赵桂仿 (2014) 基因流存在条件下的物种形成研究述评: 生殖隔离机制进化. 生物多样性, 22, 88–96.]

Lippert PC, van Hinsbergen DJJ, Dupont-Nivet G (2014) Early Cretaceous to present latitude of the central proto-Tibetan Plateau: a paleomagnetic synthesis with implications for Cenozoic tectonics, paleogeography, and climate of Asia. In: Toward an Improved Understanding of Uplift Mechanisms and the Elevation History of the Tibetan Plateau: Geological Society of America Special Paper 507 (eds Nie J, Horton BK, Hoke GD), pp. 1–21.

Liu BB, Abbott RJ, Lu ZQ, Tian B, Liu JQ (2014a) Diploid hybrid origin of *Ostryopsis intermedia* (Betulaceae) in the Qinghai-Tibet Plateau triggered by Quaternary climate change. Molecular Ecology, 23, 3013–3027.

Liu J, Möller M, Provan J, Gao LM, Poudel RC, Li DZ (2013) Geological and ecological factors drive cryptic speciation of yews in a biodiversity hotspot. New Phytologist, 199, 1093–1108.

Liu JQ, Duan YW, Hao G, Ge XJ, Sun H (2014b) Evolutionary history and underlying adaptation of alpine plants on the Qinghai-Tibet Plateau. Journal of Systematics and Evolution, 52, 241–249.

Liu JQ, Gao TG, Chen ZD, Lu AM (2002) Molecular phylogeny and biogeography of the Qinghai-Tibet Plateau endemic *Nannoglottis* (Asteraceae). Molecular Phylogenetics and Evolution, 23, 307–325.

Liu JQ, Sun YS, Ge XJ, Gao LM, Qiu YX (2012) Phylogeographic studies of plants in China: advances in the past and directions in the future. Journal of Systematics and Evolution, 50, 267–275.

Liu JQ, Wang YJ, Wang AL, Hideaki O, Abbott RJ (2006) Radiation and diversification within the *Ligularia-Cremanthodium-Parasenecio* complex (Asteraceae) triggered by uplift of the Qinghai-Tibetan Plateau. Molecular Phylogenetics and Evolution, 38, 31–49.

Liu YP, Shen ZH, Wang QG, Su XY, Zhang WJ, Shrestha N, Xu XT, Wang ZH (2017) Determinants of richness patterns differ between rare and common species: implications for Gesneriaceae conservation in China. Diversity and Distributions, 23, 235–246.

López-Pujol J, Zhang FM, Sun HQ, Ying TS, Ge S (2011) Centres of plant endemism in China: places for survival or for speciation? Journal of Biogeography, 38, 1267–1280.

Lu HY, Guo ZT (2014) Evolution of the monsoon and dry climate in East Asia during late Cenozoic: a review. Science China: Earth Sciences, 57, 70–79.

Luikart G, England PR, Tallmon D, Jordan S, Taberlet P (2003) The power and promise of population genomics: from genotyping to genome typing. Nature Reviews Genetics, 4, 981–994.

Luo D, Yue JP, Sun WG, Xu B, Li ZM, Comes HP, Sun H (2016a) Evolutionary history of the subnival flora of the Himalaya-Hengduan Mountains: first insights from comparative phylogeography of four perennial herbs. Journal of Biogeography, 43, 31–43.

Luo YH, Liu J, Tan SL, Cadotte MW, Wang YH, Xu K, Li DZ, Gao LM (2016b) Trait-based community assembly along an elevational gradient in subalpine forests: quantifying the roles of environmental factors in inter- and intraspecific variability. PLoS ONE, 11, e0155749.

Luo YH, Liu J, Tan SL, Cadotte MW, Xu K, Gao LM, Li DZ (2016c) Trait variation and functional diversity maintenance of understory herbaceous species coexisting along an elevational gradient in Yulong Mountain, Southwest China. Plant Diversity, 38, 303–311.

Ma XF, Szmidt AE, Wang XR (2006) Genetic structure and evolutionary history of a diploid hybrid pine *Pinus densata* inferred from the nucleotide variation at seven gene loci. Molecular Biology and Evolution, 23, 807–816.

Ma YP, Zhang CQ, Zhang JL, Yang JB (2010) Natural hybridization between *Rhododendron* delavayi and *R. cyano-*

carpum (Ericaceae), from morphological, molecular and reproductive evidence. Journal of Integrative Plant Biology, 52, 844–851.

Mao JF, Wang XR (2011) Distinct niche divergence characterizes the homoploid hybrid speciation of *Pinus densata* on the Tibetan Plateau. The American Naturalist, 177, 424–439.

Mao LF, Chen SB, Zhang JL, Hou YH, Zhou GS, Zhang XS (2013) Vascular plant diversity on the roof of the world: spatial patterns and environmental determinants. Journal of Systematics and Evolution, 51, 371–381.

Meng LH, Yang R, Abbott RJ, Miehe G, Hu TH, Liu JQ (2007) Mitochondrial and chloroplast phylogeography of *Picea crassifolia* Kom. (Pinaceae) in the Qinghai-Tibetan Plateau and adjacent highlands. Molecular Ecology, 16, 4128–4137.

Merckx VSFT, Hendriks KP, Beentjes KK, Mennes CB, Becking LE, Peijnenburg KTCA, Afendy A, Arumugam N, de Boer H, Biun A, Buang MM, Chen P-P, Chung AYC, Dow R, Feijen FAA, Feijen H, van Soest CF, Geml J, Geurts R, Gravendeel B, Hovenkamp P, Imbun P, Ipor I, Janssens SB, Jocque M, Kappes H, Khoo E, Koomen P, Lens F, Majapun RJ, Morgado LN, Neupane S, Nieser N, Pereira JT, Rahman H, Sabran S, Sawang A, Schwallier RM, Shim P-S, Smit H, Sol N, Spait M, Stech M, Stokvis F, Sugau JB, Suleiman M, Sumail S, Thomas DC, van Tol J, Tuh FYY, Yahya BE, Nais J, Repin R, Lakim M, Schilthuizen M (2015) Evolution of endemism on a young tropical mountain. Nature, 524, 347–350.

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Global biodiversity conservation: the critical role of hotspots. In: Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas (eds Zachos FE, Habel JC), pp. 3–22. Springer, Berlin, Heidelberg.

Molnar P (1986) The geologic history and structure of the Himalaya. American Scientist, 74, 144–154.

Montoya D, Rodríguez MA, Zavala MA, Hawkins BA (2007) Contemporary richness of holarctic trees and the historical pattern of glacial retreat. Ecography, 30, 173–182.

Niu K, He JS, Lechowicz MJ (2016) Grazing-induced shifts in community functional composition and soil nutrient availability in Tibetan alpine meadows. Journal of Applied Ecology, 53, 1554–1564.

Nosil P (2008) Speciation with gene flow could be common. Molecular Ecology, 17, 2103–2106.

Opgenoorth L, Vendramin GG, Mao KS, Miehe G, Miehe S, Liepelt S, Liu JQ, Ziegenhagen B (2010) Tree endurance on the Tibetan Plateau marks the world's highest known tree line of the Last Glacial Maximum. New Phytologist, 185, 332–342.

Owen LA, Caffee MW, Finkel RC, Seong YB (2008) Quaternary glaciation of the Himalayan-Tibetan orogen. Journal of Quaternary Science, 23, 513–531.

Payseur BA, Rieseberg LH (2016) A genomic perspective on hybridization and speciation. Molecular Ecology, 25, 2337–2360.

Pio DV, Engler R, Linder HP, Monadjem A, Cotterill FPD, Taylor PJ, Schoeman MC, Price BW, Villet MH, Eick G, Salamin N, Guisan A (2014) Climate change effects on animal and plant phylogenetic diversity in southern Africa. Global Change Biology, 20, 1538–1549.

Pironon S, Villellas J, Morris WF, Doak DF, García MB (2015) Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? Global Ecology and Biogeography, 24, 611–620.

Pittermann J, Stuart SA, Dawson TE, Moreau A (2012) Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. Proceedings of the National Academy of Sciences, USA, 109, 9647–9652.

Poelstra JW, Vijay N, Bossu CM, Lantz H, Ryll B, Müller I, Baglione V, Unneberg P, Wikelski M, Grabherr MG, Wolf JBW (2014) The genomic landscape underlying phenotypic integrity in the face of gene flow in crows. Science, 344, 1410–1414.

Poudel RC, Moller M, Liu J, Gao LM, Baral SR, Li DZ (2014) Low genetic diversity and high inbreeding of the endangered yews in Central Himalaya: implications for conservation of their highly fragmented populations. Diversity and Distributions, 20, 1270–1284.

Pyron RA (2015) Post-molecular systematics and the future of phylogenetics. Trends in Ecology & Evolution, 30, 384–389.

Qiu YX, Fu CX, Comes HP (2011) Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of Quaternary climate and environmental change in the world's most diverse temperate flora. Molecular Phylogenetics and Evolution, 59, 225–244.

Rellstab C, Gugerli F, Eckert AJ, Hancock AM, Holderegger R (2015) A practical guide to environmental association analysis in landscape genomics. Molecular Ecology, 24, 4348–4370.

Ren G, Conti E, Salamin N (2015) Phylogeny and biogeography of *Primula* sect. *Armerina*: implications for plant evolution under climate change and the uplift of the Qinghai-Tibet Plateau. BMC Evolutionary Biology, 15, 161.

Ren G, Mateo RG, Liu J, Suchan T, Alvarez N, Guisan A, Conti E, Salamin N (2017) Genetic consequences of Quaternary climatic oscillations in the Himalayas: *Primula tibetica* as a case study based on restriction site-associated DNA sequencing. New Phytologist, 213, 1500–1512.

Renner SS (2016) Available data point to a 4-km-high Tibetan Plateau by 40 Ma, but 100 molecular-clock papers have linked supposed recent uplift to young node ages. Journal of Biogeography, 43, 1479–1487.

Royden LH, Burchfiel BC, van der Hilst RD (2008) The geological evolution of the Tibetan Plateau. Science, 321, 1054–1058.

Shi YF (2002) Characteristics of late Quaternary monsoonal glaciation on the Tibetan Plateau and in East Asia. Quaternary International, 97/98, 79–91.

Shi YF, Li JJ, Li BY (1998) Uplift and environmental changes of Qinghai-Xizang (Tibetan) in the late Cenozoic. Guangdong Science and Technology Press, Guangzhou. (in Chinese) [施雅风, 李吉均, 李炳元 (1998) 青藏高原晚新生代隆升与环境变化. 广东科技出版社, 广州.]

Shimono A, Ueno S, Gu S, Zhao X, Tsumura Y, Tang Y (2010) Range shifts of *Potentilla fruticosa* on the Qinghai-Tibetan Plateau during glacial and interglacial periods revealed by chloroplast DNA sequence variation. Heredity, 104, 534–542.

Su T, Liu YS, Jacques FMB, Huang YJ, Xing YW, Zhou ZK (2013) The intensification of the East Asian winter monsoon contributed to the disappearance of *Cedrus* (Pinaceae) in southwestern China. Quaternary Research, 80, 316–325.

Sun H (2002a) Evolution of Arctic-Tertiary flora in Himalayan-Hengduan Mountains. Acta Botanica Yunnanica, 24, 671–688. (in Chinese with English abstract) [孙航 (2002a) 北极–第三纪成分在喜马拉雅–横断山的发展及演化. 云南植物研究, 24, 671–688.]

Sun H (2002b) Tethys retreat and Himalayas-Hengduanshan Mountains uplift and their significance on the origin and development of the Sino-Himalayan elements and alpine flora. Acta Botanica Yunnanica, 24, 273–288. (in Chinese with English abstract) [孙航 (2002b) 古地中海退却与喜马拉雅–横断山的隆起在中国喜马拉雅成分及高山植物区系的形成与发展上的意义. 云南植物研究, 24, 273–288.]

Sun XJ, Wang PX (2005) How old is the Asian monsoon system? Palaeobotanical records from China. Palaeogeography, Palaeoclimatology, Palaeoecology, 222, 181–222.

Sun YS, Abbott RJ, Li LL, Li L, Zou JB, Liu JQ (2014) Evolutionary history of purple cone spruce (*Picea purpurea*) in the Qinghai-Tibet Plateau: homoploid hybrid origin and Pleistocene expansion. Molecular Ecology, 23, 343–359.

Sun YS, Wang AL, Wan DS, Wang Q, Liu JQ (2012) Rapid radiation of *Rheum* (Polygonaceae) and parallel evolution of morphological traits. Molecular Phylogenetics and Evolution, 63, 150–158.

Svenning J-C, Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters, 10, 453–460

Tada R, Zheng H, Clift PD (2016) Evolution and variability of the Asian monsoon and its potential linkage with uplift of the Himalaya and Tibetan Plateau. Progress in Earth and Planetary Science, 3, 4.

Taylor DR, Aarssen LW (1990) Complex competitive relationships among genotypes of three perennial grasses: implications for species coexistence. The American Naturalist, 136, 305–327.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science, 277, 494–499.

Wan DS, Feng JJ, Jiang DC, Mao KS, Duan YW, Miehe G, Opgenoorth L (2016) The Quaternary evolutionary history, potential distribution dynamics, and conservation implications for a Qinghai-Tibet Plateau endemic herbaceous perennial, *Anisodus tanguticus* (Solanaceae). Ecology and Evolution, 6, 1977–1995.

Wang BS, Mao JF, Zhao W, Wang XR (2013a) Impact of geography and climate on the genetic differentiation of the subtropical pine *Pinus yunnanensis*. PLoS ONE, 8, e67345.

Wang H, Qiong L, Sun K, Lu F, Wang YG, Song ZP, Wu QH, Chen JK, Zhang WJ (2010) Phylogeographic structure of *Hippophae tibetana* (Elaeagnaceae) highlights the highest microrefugia and the rapid uplift of the Qinghai-Tibetan Plateau. Molecular Ecology, 19, 2964–2979.

Wang IJ, Glor RE, Losos JB (2013b) Quantifying the roles of ecology and geography in spatial genetic divergence. Ecology Letters, 16, 175–182.

Wang LY, Abbott RJ, Zheng W, Chen P, Wang YJ, Liu JQ (2009a) History and evolution of alpine plants endemic to the Qinghai-Tibetan Plateau: *Aconitum gymnandrum* (Ranunculaceae). Molecular Ecology, 18, 709–721.

Wang LY, Ikeda H, Liu TL, Wang YJ, Liu JQ (2009b) Repeated range expansion and glacial endurance of *Potentilla glabra* (Rosaceae) in the Qinghai-Tibetan Plateau. Journal of Integrative Plant Biology, 51, 698–706.

Wang QG, Su XY, Shrestha N, Liu YP, Wang SY, Xu XT, Wang ZH (2017) Historical factors shaped species diversity and composition of *Salix* in eastern Asia. Scientific Reports, 7, 42038.

Wang W, Wang Q, Li S, Wang G (2006) Distribution and species diversity of plant communities along transect on the northeastern Tibetan Plateau. Biodiversity and Conservation, 15, 1811–1828.

Wang YJ, Susanna A, Von Raab-Straube E, Milne R, Liu JQ (2009c) Island-like radiation of *Saussurea* (Asteraceae: Cardueae) triggered by uplifts of the Qinghai-Tibetan Plateau. Biological Journal of the Linnean Society, 97, 893–903.

Wang ZH, Tang ZY, Fang JY (2007) Altitudinal patterns of seed plant richness in the Gaoligong Mountains, south-east Tibet, China. Diversity and Distributions, 13, 845–854.

Wang ZW, Chen ST, Nie ZL, Zhang JW, Zhou Z, Deng T, Sun H (2015) Climatic factors drive population divergence and demography: insights based on the phylogeography of a riparian plant species endemic to the Hengduan Mountains and adjacent regions. PLoS ONE, 10, e0145014.

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33, 475–505.

Wen J, Zhang J, Nie ZL, Zhong Y, Sun H (2014) Evolutionary diversifications of plants on the Qinghai-Tibetan Plateau. Frontiers in Genetics, 5, 4.

Wu Z, Yu D, Li X, Xu X (2016) Influence of geography and environment on patterns of genetic differentiation in a widespread submerged macrophyte, Eurasian watermilfoil (*Myriophyllum spicatum* L., Haloragaceae). Ecology and Evolution, 6, 460–468.

Wu Z, Yu D, Wang Z, Li X, Xu X (2015) Great influence of geographic isolation on the genetic differentiation of *Myriophyllum spicatum* under a steep environmental gradient. Scientific Reports, 5, 15618.

Xie ZQ, Wang L, Wang LR, Wang ZQ, Lu ZH, Tian DC, Yang SH, Hurst LD (2016) Mutation rate analysis via parent-progeny sequencing of the perennial peach. I. A low rate in woody perennials and a higher mutagenicity in hybrids. Proceedings of the Royal Society B: Biological Sciences,

283, 20161016.

Xu CD, Feng JM, Wang XP, Yang X (2008) Vertical distribution patterns of plant species diversity in northern Mt. Gaoligong, Yunan Province. Chinese Journal of Ecology, 27, 323–327. [徐成东, 冯建孟, 王襄平, 杨雪 (2008) 云南高黎贡山北段植物物种多样性的垂直分布格局. 生态学杂志, 27, 323–327.]

Xu TT, Abbott RJ, Milne RI, Mao K, Du FK, Wu GL, Ciren ZX, Miehe G, Liu JQ (2010) Phylogeography and allopatric divergence of cypress species (*Cupressus* L.) in the Qinghai-Tibetan Plateau and adjacent regions. BMC Evolutionary Biology, 10, 194.

Xu X, Zhang H, Tian W, Zeng X, Huang H (2016) Altitudinal patterns of plant diversity on the Jade Dragon Snow Mountain, southwestern China. SpringerPlus, 5, 1566.

Yan Y, Yang X, Tang Z (2013) Patterns of species diversity and phylogenetic structure of vascular plants on the Qinghai-Tibetan Plateau. Ecology and Evolution, 3, 4584–4595.

Yang FS, Li YF, Ding X, Wang XQ (2008) Extensive population expansion of *Pedicularis longiflora* (Orobanchaceae) on the Qinghai-Tibetan Plateau and its correlation with the Quaternary climate change. Molecular Ecology, 17, 5135–5145.

Yang FS, Qin AL, Li YF, Wang XQ (2012) Great genetic differentiation among populations of *Meconopsis integrifolia* and its implication for plant speciation in the Qinghai-Tibetan Plateau. PLoS ONE, 7, e37196.

Yannic G, Pellissier L, Ortego J, Lecomte N, Couturier S, Cuyler C, Dussault C, Hundertmark KJ, Irvine RJ, Jenkins DA (2014) Genetic diversity in caribou linked to past and future climate change. Nature Climate Change, 4, 132–137.

Yi CL, Cui ZJ, Xiong HG (2005) Numerical periods of Quaternary glaciations in China. Quaternary Sciences, 25, 609–619. [易朝路, 崔之久, 熊黑钢 (2005) 中国第四纪冰期数值年表初步划分. 第四纪研究, 25, 609–619.]

Yin H, Yan X, Shi Y, Qian C, Li Z, Zhang W, Wang L, Li Y, Li X, Chen G, Li X, Nevo E, Ma XF (2015) The role of East Asian monsoon system in shaping population divergence and dynamics of a constructive desert shrub *Reaumuria soongarica*. Scientific Reports, 5, 15823.

Yu J, Kuroda C, Gong X (2014) Natural hybridization and introgression between *Ligularia cymbulifera* and *L. tongolensis* (Asteraceae, Senecioneae) in four different locations. PLoS ONE, 9, e115167.

Yue JP, Sun H, Baum DA, Li JH, Al-Shehbaz IA, Ree R (2009) Molecular phylogeny of *Solms-laubachia* (Brassicaceae) s.l., based on multiple nuclear and plastid DNA sequences, and its biogeographic implications. Journal of Systematics and Evolution, 47, 402–415.

Yue LL, Chen G, Sun WB, Sun H (2012) Phylogeography of *Buddleja crispa* (Buddlejaceae) and its correlation with drainage system evolution in southwestern China. American Journal of Botany, 99, 1726–1735.

Zha HG, Milne RI, Sun H (2010) Asymmetric hybridization in *Rhododendron agastum*: a hybrid taxon comprising mainly F_1s in Yunnan, China. Annals of Botany, 105, 89–100.

Zhang DC, Ye JX, Sun H (2016) Quantitative approaches to identify floristic units and centres of species endemism in the Qinghai-Tibetan Plateau, south-western China. Journal of Biogeography, 43, 2465–2476.

Zhang H, Qi W, John R, Wang W, Song F, Zhou S (2015a) Using functional trait diversity to evaluate the contribution of multiple ecological processes to community assembly during succession. Ecography, 38, 1176–1186.

Zhang J, Nielsen SE, Chen Y, Georges D, Qin Y, Wang SS, Svenning J-C, Thuiller W (2017a) Extinction risk of North American seed plants elevated by climate and land-use change. Journal of Applied Ecology, 54, 303–312.

Zhang JQ, Meng SY, Allen GA, Wen J, Rao GY (2014) Rapid radiation and dispersal out of the Qinghai-Tibetan Plateau of an alpine plant lineage *Rhodiola* (Crassulaceae). Molecular Phylogenetics and Evolution, 77, 147–158.

Zhang JW, D'Rozario A, Adams JM, Li Y, Liang XQ, Jacques FM, Su T, Zhou ZK (2015b) *Sequoia maguanensis*, a new Miocene relative of the coast redwood, *Sequoia sempervirens*, from China: implications for paleogeography and paleoclimate. American Journal of Botany, 102, 103–118.

Zhang MG, Slik JWF, Ma KP (2017b) Priority areas for the conservation of perennial plants in China. Biological Conservation. http://dx.doi.org/10.1016/j.biocon.2016.06.007.

Zhang Q, Chiang TY, George M, Liu JQ, Abbott RJ (2005) Phylogeography of the Qinghai-Tibetan Plateau endemic *Juniperus przewalskii* (Cupressaceae) inferred from chloroplast DNA sequence variation. Molecular Ecology, 14, 3513–3524.

Zhang TC, Comes HP, Sun H (2011) Chloroplast phylogeography of *Terminalia franchetii* (Combretaceae) from the eastern Sino-Himalayan region and its correlation with historical river capture events. Molecular Phylogenetics and Evolution, 60, 1–12.

Zhao JL, Gugger PF, Xia YM, Li QJ (2016a) Ecological divergence of two closely related *Roscoea* species associated with late Quaternary climate change. Journal of Biogeography, 43, 1990–2001.

Zhao JL, Xia YM, Cannon CH, Kress WJ, Li QJ (2016b) Evolutionary diversification of alpine ginger reflects the early uplift of the Himalayan-Tibetan Plateau and rapid extrusion of Indochina. Gondwana Research, 32, 232–241.

Zheng BX, Xu QQ, Shen YP (2002) The relationship between climate change and Quaternary glacial cycles on the Qinghai-Tibetan Plateau: review and speculation. Quaternary International, 97/98, 93–101.

Zheng D, Yao TD (2004) Uplifting of Tibetan Plateau with Its Environmental Effects. Science Press, Beijing. (in Chinese) [郑度, 姚檀栋 (2004) 青藏高原隆升与环境效应. 科学出版社, 北京.]

Zobel M (1997) The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology & Evolution, 12, 266–269.

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