•研究报告•

欧亚大陆东部毛茛科植物多样性格局及主导因子

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摘要: 毛茛科是真双子叶植物的基部类群之一, 包含多种药用植物, 具有较高的保护价值, 但关于毛茛科物种多样性和谱系多样性大尺度格局及其影响因子的研究还比较匮乏, 特别是以较高分辨率分布数据为基础的物种多样性格局研究尚未见报道。本文旨在: (1)建立欧亚大陆东部毛茛科植物分布数据库, 估算不同生活型物种多样性和谱系多样性格局, 并探究格局的形成机制。(2)分析毛茛科物种多样性和谱系多样性的相关关系, 确定多样性热点地区, 为毛茛科保护规划提供依据。根据中国、哈萨克斯坦、吉尔吉斯斯坦、塔吉克斯坦、土库曼斯坦、乌兹别克斯坦、蒙古和俄罗斯等国家的区域和地方植物志, 建立了“欧亚大陆东部地区毛茛科物种分布数据库”。该数据库包含了欧亚大陆东部地区1,688种毛茛科物种的分布数据, 空间分辨率为100 km × 100 km。在此基础上, 估算了毛茛科全部及不同生活型的物种多样性和谱系多样性格局, 并利用广义线性模型和等级方差分离方法分析了毛茛科物种和谱系多样性格局与环境因子的关系。最后比较了物种多样性和谱系多样性的相关关系, 确定了毛茛科的古热点地区。结果显示: (1)欧亚大陆东部毛茛科植物物种和谱系多样性均呈明显的纬度格局, 且在山区具有较高的多样性。(2)毛茛科植物物种和谱系多样性受现代气候、地形异质性和末次冰期以来的气候变化的共同影响, 但不同影响因子的相对贡献率在物种和谱系多样性及不同生活型之间差异显著。(3)中高纬度地区的谱系多样性高于给定物种数的预期, 是毛茛科的古热点地区, 在毛茛科保护规划中应受到重视。

关键词: 毛茛科; 草本植物; 木本植物; 物种多样性; 谱系多样性; 生物多样性热点地区

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Patterns and environmental drivers of Ranunculaceae species richness and phylogenetic diversity across eastern Eurasia

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ABSTRACT

Aims: Ranunculaceae, one of the basal clades in eudicots of angiosperms, has a variety of medicinal plants and is of

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high conservation value. However, large-scale patterns in species richness and phylogenetic diversity of Ranunculaceae based on high-resolution distribution data and their environmental determinants remain poorly understood. We aims to: (1) establish a Ranunculaceae distribution database in eastern Eurasia, estimate the species diversity and phylogenetic diversity pattern of different life forms, and explore the formation mechanism of the pattern; (2) analysis the relationship between species diversity and phylogenetic diversity of Ranunculaceae, and determine the diversity hot spots to provide basis for Ranunculaceae conservation planning.

Methods: Here, we established the first species distribution database for 1,688 Ranunculaceae species across eastern Eurasia by compiling distribution data from regional and local floral records from across China, Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan, Mongolia, and Russia at a spatial resolution of 100 km × 100 km. Using this database, we mapped large-scale patterns in species richness and phylogenetic diversity for species with different life forms and explored the mechanisms underlying these patterns. We also quantified the relationship between species richness and phylogenetic diversity and identified hotspots of Ranunculaceae phylogenetic diversity.

Results: We found a latitudinal gradient in both species richness and phylogenetic diversity and revealed that Ranunculaceae in eastern Eurasia have particularly high levels of species and phylogenetic diversity in mountainous areas. Contemporary climate, habitat heterogeneity, and climate changes since the Last Glacial Maximum (LGM) all influenced spatial patterns in species richness and phylogenetic diversity, but their relative contributions varied across life forms. Phylogenetic diversity at mid and high latitudes was higher than expected when controlling for species richness, which suggests that these latitudes may represent a paleo-biodiversity hotspot of Ranunculaceae.

Conclusion: Consequently, these regions should be considered a key conservation priority for this important family.

Key words: herbaceous plants; woody plants; biodiversity hotspots; conservation; species distribution; spatial database

全球生物多样性正面临生境破坏、过度利用、全球变化等多重威胁,有效保护生物多样性已成为挑战之一。物种多样性大尺度格局及其形成机制是宏观生态学和生物地理学研究的核心问题之一(Colwell & Lees, 2000),也是生物多样性保护规划的基础(Stuart-Smith et al, 2013)。随着物种分布数据的积累,以往研究已对多个类群(特别是脊椎动物)的物种多样性大尺度格局进行了较为系统的研究,包括全球哺乳动物(Schipper et al, 2008)、两栖动物(Fritz & Rahbek, 2012)、鸟类(Jetz et al, 2012)和鱼类(Rabosky, 2020),并已绘制了其全球物种多样性格局。这些研究为全球的生物多样性保护提供了重要的数据支撑。

种子植物是陆地植物中最为繁盛的一类,是陆地生态系统的优势类群。种子植物的演化显著影响了陆生植被的演化及其对环境变化的响应(Coiffard et al, 2012; Chaboureau et al, 2014)。随着人类干扰和利用的加剧,大量陆生种子植物成为受威胁物种甚至面临灭绝风险。比如,近年来的评估显示,全球裸子植物中约40%的物种被评估为受威胁物种(包含易危、濒危和极危物种),而在已完成评估的全球被子植物中,41%被评估为受威胁物种(<https://www.iucnredlist.org/>),这说明全球种子植物正面临严峻的灭绝风险。但与大型脊椎动物相比,

有关洲际至全球尺度种子植物物种多样性格局的研究仍不足。制约种子植物物种多样性大尺度格局研究的重要瓶颈即缺乏准确详实的物种分布数据。

物种多样性地理格局受多种因素的共同影响,包括现代气候、生境异质性和地质历史上的气候变化(O'Brien, 1993; Manafzadeh et al, 2017)。现代气候(Cavender-Bares et al, 2005; Morales et al, 2013),特别是温度、降水和气候季节性,对物种多样性大尺度格局具有显著影响,其效应被以往研究广泛证实(Affenzeller et al, 2018; Kinlock et al, 2018)。例如,温度和降水可通过影响植物生理过程而影响植物分布,过高或过低的温度和水分条件都会对植物的生理过程产生限制,从而限制物种的分布(Qian & Ricklefs, 2000; Qian, 2002; 刘庆福等, 2015; 朱桂丽等, 2017)。生境异质性可以为物种共存提供更多的生态位,或者为物种提供避难所(Stein & Kreft, 2015)。比如,中国华中和西南山地地区的地形复杂,为气候适应性不同的物种提供了栖息地;同时,自第三纪以来,华中和西南山地一直是植物多样性的避难所,保存了大量珍稀孑遗植物,如水杉(*Metasequoia glyptostroboides*)、珙桐(*Davidia involucrata*)等。此外,在地形异质性较高的山区,由于受人类活动影响较小,一些山区也可以作为珍稀物种在未来全球变化背景下的避难所(Tang et al,

2018)。第四纪气候变化也会影响物种多样性格局, 一般认为, 第四纪气候变化更剧烈的地区可能拥有较低的物种多样性(Fleishman et al, 2000; Currie, 2001; Kerr, 2001)。尽管以往研究已评估了不同因子对物种多样性格局的影响, 但关于不同因子的相对重要性及其作用在不同生活型之间的差异仍存在争议。

木本植物和草本植物的茎内木质部发达程度不同, 从而造成这两种不同生活型物种具有不同的生长形态和气候生态位(Salinas & Casas, 2007; Li et al, 2010)。木本植物茎内木质部发达, 木质化组织较多, 质地坚硬, 是大多数森林生态系统的建群种(周乃富等, 2018)。相反, 草本植物茎内木质部不发达, 木质化组织较少, 茎干柔软, 是林下植被的重要组成部分(Slezák & Axmanová, 2016; Manish et al, 2017), 也是许多重要中药材的原材料(包金花等, 2018)。不同生活型的植物由于生活史策略不同, 对环境变化的响应也不同(Steinberg et al, 1990; Pretzsch, 2002; Massad, 2013)。一般认为, 草本植物的生活史较短(Gebrehiwot et al, 2019), 分化速率较高(Smith & Donoghue 2008), 因此全球草本植物区系在相对较近的地质历史中显示出更快的物种形成速率(Smith & Beaulieu, 2009; Antonelli et al, 2018)。目前, 国内外对木本植物物种多样性的大尺度格局及其成因已进行了大量研究, 并对不同影响因子的相对作用进行了比较(Weiser et al, 2007; 王志恒等, 2009; Wang et al, 2012), 但有关草本植物物种多样性格局及其成因的研究则相对较少。

生物多样性包含物种多样性、谱系多样性、功能多样性等不同维度(Villéger et al 2017)。其中, 谱系多样性是反映物种间系统进化关系的多样性测度(Faith, 1994, 2016; Jones et al, 2019), 近年来被广泛用于植物多样性分布格局的研究中(Rodrigues & Gaston, 2002; Faith, 2013; Huang et al, 2018; Lu et al, 2018)。群落内的物种组成是进化过程和生态过程共同作用的结果, 分析物种间亲缘关系可以反映现有群落形成的历史过程(Rodrigues & Gaston, 2002; Fritz & Rahbek, 2012)。谱系多样性可在一定程度上反映一个地区物种的分化历史和过去发生的扩散事件对物种组成的影响(Zhang et al, 2015; Tsirogianis & Sandel, 2016)。同时, 由于不同物种

的进化历史不同, 可能对现代气候产生不同的适应, 因此即使物种数量相同的群落, 由于其组成物种的进化历史、祖先生态位及环境适应性不同, 群落对未来气候变化的响应也可能存在差异(Faith, 1992; Zhu et al, 2006; López-Pujol et al, 2011b)。也正是因为这样的原因, 越来越多的研究提出, 保护生物多样性不应只考虑物种多样性, 还要考虑谱系多样性(陈之端和李德铎, 2018; Miller et al, 2018)。在具有较高谱系多样性的地区建立保护区可以更好地保留物种的进化特征和进化潜力。近期研究已开始关注谱系多样性的研究。比如, 基于山地植物群落的研究显示, 群落谱系多样性沿海拔梯度呈升高、降低或单峰型的变化趋势(Zhu et al, 2019; Zu et al, 2019); 而在洲际至全球尺度, 人们发现北美地区植物(Qian et al, 2017; Mishler et al, 2020)和全球两栖类(Fritz & Rahbek, 2012)的谱系多样性格局均呈明显的纬度格局, 且与物种多样性呈显著正相关。然而, 有关东亚地区植物谱系多样性大尺度格局的研究仍然不足, 制约了基于谱系多样性的植物多样性保护规划(Kareiva & Marvier, 2003; Zhang, 2015)。

毛茛科是真双子叶植物的基部类群之一, 包含多种药用植物, 具有较高的保护价值(Li et al, 2020)。毛茛科绝大多数物种是一年生、两年生或多年生草本植物(Wang et al, 2016), 全球共有约2,300多种, 其中约2/3的物种分布在亚洲温带地区(Chanderbali et al, 2016; Sramkó et al, 2019)。作为被子植物早期分化的类群之一, 毛茛科可能起源于白垩纪早期的温带地区(Ziman & Keener, 1989; Tamura, 1995), 后在亚洲温带地区特别是青藏高原东南部地区经历快速分化(Kong et al, 2017)。因此, 毛茛科是北半球高山生态系统的重要组成成分(Ziman, & Keener, 1989; Tamura, 1995), 对温带山地植物区系和植被的演化具有重要作用。探索毛茛科植物物种多样性的大尺度格局及其形成机制可以为该科物种多样性保护政策的制定提供数据和理论支撑。然而, 关于毛茛科物种多样性和谱系多样性大尺度格局及其影响因子的研究还比较匮乏, 特别是以较高分辨率分布数据为基础的物种多样性格局研究尚未见报道。基于以上背景, 我们提出了以下问题: (1)毛茛科物种多样性和谱系多样性格局如何? 相关关系如何? 主导因子是什么? (2)现代

气候、过去气候变化和地形异质对毛茛科物种多样性的相对贡献如何?在木本植物和草本植物之间是否有区别?

1 材料与方法

1.1 物种分布数据

利用中国、哈萨克斯坦、吉尔吉斯斯坦、塔吉克斯坦、土库曼斯坦、乌兹别克斯坦、蒙古和俄罗斯等国家公开的大量区域和地方植物志书,建立了“欧亚大陆东部地区毛茛科植物物种分布数据库”(完整的数据源清单见附录1)。中国物种分布的数据来源均为县级,其他国家分布数据的分辨率均低于 $100\text{ km} \times 100\text{ km}$ 。我们进一步从提供标本记录的在线数据库中收集了物种的分布数据,包括2019年5月访问的“国家标本资源共享平台”(NSII, <http://www.nsii.org.cn>)、“全球生物多样性信息网络”(GBIF, <http://www.gbif.org/>)等。

数字化后,数据源中的物种分布记录可以分为点和面两种格式。由于上述地区和地方出版物中原始地理单元的中值接近 $100\text{ km} \times 100\text{ km}$,因此在ArcGIS 10.3中,将分布图转换为具有 $100\text{ km} \times 100\text{ km}$ 空间分辨率的环行投影网格(cylinder)的分布,然后分别按点和面对结果进行整合。删除面格式的重复并叠加数据后,然后将面格式的结果与点格式的数据汇总。以Catalogue of Life (<http://www.catalogueoflife.org>)为准对来自不同数据源的物种名称进行校准,删除栽培种和外来种的记录,并将亚种单位(即亚种和变种)合并为种。

采集到的植物分为两种生活型:木本(包括灌木、矮生灌木、亚灌木和木质藤本植物)和草本(包括草本和草质藤本植物)。生活型数据从已发表的植物区系和在线数据库中收集,包括The Tropicos (<http://www.tropicos.org/Home.aspx>)、eFloras.org (http://www.efloras.org/project_list.aspx)、Scientific Database of China Plant Species (<http://db.kib.ac.cn/eflora/Default.aspx>)和Chinese Plant Subject Databases (<http://www.plant.csdb.cn>)。最终收集到毛茛科植物1,688种,隶属于49属,其中草本植物1,398种,木本植物151种。

谱系多样性的计算采用Faith谱系多样性的方法(Faith, 1994),即最小生成树的总支长。其计算通过R软件的picante程序包完成。由于当前全球毛茛

科种级系统发育树尚未成功构建,因此本文中使用了Wang等(2016)建立的全球毛茛科属级系统发育树。Wang等(2016)对全球76种毛茛科植物进行取样,并对5个质体基因(*rbcL*, *matK*, *atpB*, *atpA*, *ndhF*)和1个核基因(26S rDNA)进行测序;在此基础上,利用贝叶斯方法建立了毛茛科属级系统发育树,并利用该科3块化石对系统发育树进行了定年。该属级系统进化树涵盖全球毛茛科55属中的50属(占比约91%),很好地覆盖了毛茛科各主要分支。可见,该系统进化树在属级水平的采样率较高,取样的区域偏差较小。利用该属级系统进化树,根据毛茛科物种的属级分类系统,我们将研究区内的毛茛科物种以属基部多歧分支的形式插入所属的属级分支内;然后利用这一系统进化树计算全部毛茛科植物和草本植物的谱系多样性格局。这一方法已在以往研究中被广泛使用(如Lu et al, 2018)。由于本研究中,毛茛科木本植物只包含铁线莲属(*Clematis*) (部分为木质藤本),而我们使用的系统发育树为属级树,难以反映属内的种间关系,因此文中没有计算木本植物的谱系多样性。

1.2 环境数据

本文使用的气候数据来自WorldClim (<http://www.worldclim.org>),空间分辨率为 $2.5'$ 。使用ArcGIS 10.3计算每个网格的气候平均值,并将现代气候因子分为3类:(1)温度变量,包括年均温(MAT)和最冷季均温(月均温最低的连续3个月,在本研究区一般为12月至次年2月,MTCQ)。MAT在以往的研究中被广泛用于表征环境能量,MTCQ用于研究冬季低温对物种多样性的影响。O'Brien (1993)对非洲木本植物和Wang等(2011)对中国木本植物多样性的研究均发现,冬季温度对木本植物物种多样性有显著影响。(2)降水变量,包括年平均降水量(MAP)和最干季降水量(月降水量最低的连续3个月的降水量,PDQ)。PDQ反映了旱季降水的影响。Huang等(2015)研究认为,冬季降水对中国的孑遗植物有显著影响。(3)气候季节性,包括温度季节性(一年内月平均气温的标准差,TSN)和降水季节性(一年内月降水量的变化系数,PSN)。TSN和PSN反映了气温和降水季节变化的影响,是气候异质性的指标。

用网格内的海拔高差(ELER)反映生境异质性。海拔高差即一个网格内最高海拔与最低海拔的差。海拔数据来源于美国地质勘探局(<https://www.usgs>).

gov/)的GTOPO数据,空间分辨率为1 km × 1 km。利用ArcGIS 10.3计算每个100 km × 100 km网格单元内的海拔高差。

第四纪气候变化以末次冰期(LGM, 约公元前22,000前)以来的温度变化速率(即物种跟踪气候变化所必须的空间迁移距离)来衡量,是自末次盛冰期以来年均温变化的时间梯度和年均温变化的空间梯度之间的比率(Loarie et al, 2009),一般认为,末次冰期以来的气候变化强弱能较好地反映第四纪时期不同地区气候波动的程度(Araújo et al, 2008; Sandel et al, 2011)。由于第四纪古气候数据的全球模拟尚未完成,以往研究通常用末次冰期以来的气候变化来反映第四纪气候波动。在本文中,末次冰期时的气候数据采用MPI-ESM-P模型(Watanabe et al, 2011)的重建结果。

1.3 分析方法

利用欧亚大陆全部1,688种毛茛科的物种分布数据,结合系统发育树数据,估算欧亚大陆毛茛科全部物种、草本植物和木本植物的物种多样性和谱系多样性,并用ArcGIS 10.3绘制格局图,其中,物种多样性以每个网格内的物种数表示。使用一元线性最小二乘回归模型(ordinary least square models, OLS models)拟合谱系多样性与物种多样性的关系,然后计算二者模型的残差(实际值与预测值之间的差值)并绘制残差格局图。

绘制物种多样性和谱系多样性与环境因子之间的散点图。再利用一元广义线性模型(generalized linear models, GLMs)中的泊松回归分析物种多样性与环境因子之间的关系;利用一元线性最小二乘回归模型分析谱系多样性与环境因子之间的关系。每个变量对物种多样性或谱系多样性格局的解释率以相应GLM或OLS模型的 R^2 进行衡量。为了消除空间自相关对模型显著性(P 值)的影响,在模型显著性检验中使用修正 t 检验(Clifford et al, 1989);只有当校正后的 $P < 0.05$ 时,才认为GLM和OLS模型的 R^2 显著。

对包含2个变量的环境变量类别,以其中解释率最高的因子反映该类别变量的作用,用于多元回归分析。初步结果显示,年平均降水量、最冷季平均气温、气温季节性分别是水分、能量、气候季节性变量中解释率最高的变量,可用来反映这些类别

变量的作用。采用等级方差分离模型(hierarchical partitioning) (Mac Nally, 2000)分析各变量对物种多样性和谱系多样性的独立、共同解释率。等级方差分离模型采用R软件中的hier.part程序包完成。

2 结果

2.1 物种多样性和谱系多样性格局及其关系

欧亚大陆东部毛茛科全部物种、木本植物和草本植物的物种多样性呈明显的纬度梯度格局,随着纬度的增加,物种多样性逐渐降低。全部物种和草本植物的物种多样性在云贵高原、川桂交界、秦巴山区等山区最多(图1a、c),而木本植物物种多样性在横断山区、云南南部、云贵高原、川桂交界、秦巴山区等山区最高(图1b)。

全部物种谱系多样性与物种多样性格局有所不同,除了低纬度地区谱系多样性较高之外,中高纬度地区也有较高的谱系多样性(图1d)。草本植物谱系多样性的地理格局与物种多样性格局较为相似,在云贵高原、秦巴山区较高(图1e)。

谱系多样性与全部物种和草本植物物种多样性均呈现较强的正相关关系(图2a、c)。物种与谱系多样性关系的残差格局图显示,对于全部物种,残差在中高纬度地区为正值(图2b),对于草本植物,残差在低纬度地区为正值(图2d)。这说明,这些地区的谱系多样性高于给定物种多样性时的预期。

2.2 物种多样性和谱系多样性的影响因子

一元广义线性模型模拟结果表明,在所有环境因子中,温度季节性是木本植物物种多样性格局的主导因子,且其对木本植物的解释率高于草本植物(图3)。在温度季节性弱的地区,物种多样性较高(图3)。全部物种和草本植物物种多样性格局的主导因子是末次冰期以来的气候变化速率,且其对草本植物的解释率高于木本植物(图3)。在末次冰期以来气候变化较小的地区,物种多样性较高(图3)。地形异质性的不同生活型物种多样性均具有显著影响,在地形异质性较高的地区,物种多样性较高(图3)。等级方差分离结果与一元广义线性模型拟合结果一致,末次冰期以来的气候变化速率对全部物种、草本植物物种多样性的独立解释率和总解释率(共同解释率和独立解释率之和)最高,温度季节性对木本植物物种多样性的总解释率最高(图4)。

图1 欧亚大陆东部毛茛科全部物种(a)、木本植物(b)、草本植物(c)物种多样性及全部物种(d)、草本植物(e)谱系多样性格局
Fig. 1 Geographical patterns in the species richness of all Ranunculaceae species (a), woody species (b), and herbaceous species (c); phylogenetic diversity of all Ranunculaceae species (d) and woody species (e) in East Eurasia estimated in cyclinder grids of 100 km × 100 km

图2 欧亚大陆东部毛茛科谱系多样性与全部物种和草本植物物种多样性的关系(a, c)及残差格局图(b, d)
Fig. 2 The relationship between phylogenetic diversity and species diversity of all Ranunculaceae species (a) and herbaceous (c) species and their residual patterns (b, d) in East Eurasia

一元最小二乘回归模型拟合结果表明, 末次冰期以来的气候变化速率是全部物种谱系多样性格局的主导因子, 在末次冰期以来气候变化较小的地区, 谱系多样性较高(图3)。旱季降水是草本植物谱系多样性格局的主导因子, 在旱季降水较多的地区, 谱系多样性较高(图3)。等级方差分离结果与一元广义线性模型拟合结果一致, 末次冰期以来的气候变化速率对全部物种谱系多样性的独立解释率和总解释率最高, 旱季降水对草本植物谱系多样性的独立解释率最高(图4)。

3 讨论

3.1 毛茛科物种多样性和谱系多样性格局及其影响因素

欧亚大陆东部毛茛科全部物种的物种多样性和谱系多样性均呈现明显的纬度格局(图 1a、d), 且二者呈显著正相关关系, 这与以往有关植物和两栖

类多样性的研究结果一致(Rodrigues & Gaston, 2002; Fritz & Rahbek, 2012)。末次冰期以来的气候变化是全部植物物种多样性和谱系多样性格局的主导因子, 在末次冰期以来气候变化较小的地区多样性较高, 这与以往的研究结果也是一致的(López-Pujol et al, 2011b; Antonelli et al, 2018; Muellner-Riehl et al, 2019)。与本文结果一致, 对中亚地区木本植物狭域种(Liu et al, 2019)以及欧洲乔木(Svenning & Skov, 2007)的研究均发现, 末次冰期以来的气候变化显著影响了物种多样性格局。第四纪以来冰期和间冰期的反复交替, 特别是末次冰期以来气候的剧烈变化, 使得全球很多地区的植被分布发生改变(Wang SY et al, 2017; Li et al, 2019; 邱浩杰等, 2020)。研究显示, 第四纪特别是末次冰期以来气候变化较小的地区(也即气候较稳定的地区)为物种提供了重要的避难所, 使得大量古老孑遗类群得以保存, 从而提高这些地区的谱系多样性

图3 欧亚大陆东部毛茛科全部物种、木本植物、草本植物物种多样性及全部物种和草本植物谱系多样性与现代气候、海拔高差和过去气候变化的关系散点图, 加粗的数值表示一行中 R^2 最大的数值。

Fig. 3 The relationship between the richness of all Ranunculaceae species, woody species, and herbaceous species; and the phylogenetic diversity of all Ranunculaceae species and herbaceous species in East Eurasia and contemporary climate, elevation range, past climate change evaluated by generalized linear models, the value in bold indicates the maximum value of R^2 in a row.

图4 现代气候、海拔高差和过去气候变化对欧亚大陆东部毛茛科全部物种、木本植物和草本植物丰富度和谱系多样性的影响。图中显示了物种多样性和各类影响因子之间的等级方差分离结果。不同柱子分别代表5个不同的解释因子，分别代表水分(a)、能量(b)、温度季节性(c)、海拔高差(d)和末次冰期以来的温度变化速率(e)。深色表示独立解释量，浅色表示共同解释量。

Fig. 4 The effects of contemporary climate, elevation range and past climate change on species richness and phylogenetic diversity of all Ranunculaceae species, woody species, herbaceous species in East Eurasia. The figure shows the results of hierarchical partitioning between species richness and each selected dominant factor. Different charts respectively represent five different explanatory factors, namely, water (a), energy (b), temperature seasonality (c), elevation range (d) and temperature velocity since the Last Glacial Maximum (LGM) (e). The dark color means independent effect, light color means joint effects.

(Dupont-Nivet et al, 2007; Araújo & Rahbek, 2008; López-Pujol et al, 2011a; Sandel et al, 2011)。相反，在第四纪气候波动较大的地区，物种易发生局地灭绝；同时，较大的第四纪气候波动也可能使得部分类群进化较快，从而更易形成物种年轻且末端支长较短的分支(Weir et al, 2007)；这两个过程可能均使得第四纪气候变化剧烈地区的谱系多样性较低。这在一定程度上解释了毛茛科以及其他类群(如欧洲乔木, Skov & Svenning, 2004; 欧洲两栖和爬行动物, Araújo et al, 2008)物种多样性与末次冰期以来气候变化间的显著负相关关系。

此外，以往研究发现，亲缘关系相近的物种也倾向于具有相同的气候适应性，也即气候生态位的谱系保守性(Li et al, 2020)。气候变化倾向于将亲缘关系较近、生态位相似的物种筛选进入特定群落，使得气候变化较大地区的植物群落通常具有较低的谱系多样性，这也可能使得谱系多样性与末次冰期以来的气候变化幅度间呈显著负相关。在更长的地质历史时间尺度，气候变化也可能通过影响物种的分化过程而影响物种多样性格局。比如，近期研究显示，中新世以来的气候变化，特别是中新世中期以来的全球性变冷、变干趋势显著促进了壳斗科、桤木属(*Alnus*)植物类群在东亚亚热带的快速分化(Zhang et al, 2014; Xu et al, 2016)，进而提高了东亚温带和亚热带木本植物物种多样性。

本研究发现，在物种多样性和谱系多样性格局的影响因子中，温度和降水的作用不显著，这与以往的研究结果有所不同。比如，在中国，最冷季均温是影响木本植物物种多样性地理格局的主要因素(Sakai & Malla, 1981; Wang et al, 2012)，这主要是因为中国木本植物区系中含有较多的热带和亚热带植物区系成分(Fang & Yoda, 1988, 1989)，而这些植物对冬季低温非常敏感(Feldman et al, 2016)，冬季低温通过限制热带和亚热带物种向北扩散而形成了当前的多样性格局(Wang et al, 2011)。再如，水分因子对于中国蔷薇科植物的物种多样性格局也具有较强的作用。蔷薇科可能起源于东亚温带地区，由于有倾向于保留其祖先温带生态位的趋势，对寒冷的耐受性较强，因而冬季低温对其物种多样性影响较弱；与温度相比，水分因子对蔷薇科物种多样性的影响相对较强(邹东廷等, 2019)。而对毛茛科系统发育的研究显示，毛茛科起源于温带，并在北半球温带和寒温带地区广泛分布(Ziman & Keener, 1989; Tamura, 1995; Anderson et al, 2005)，对冬季低温和干旱环境具有较强的适应性，这可能部分解释了为什么冬季低温和年平均降水对毛茛科物种多样性和谱系多样性的作用均较弱。

3.2 不同生活型间物种多样性格局影响因子的差异

欧亚大陆东部毛茛科木本和草本植物的物种多样性格局不同：木本植物主要集中分布在低纬度地区，而草本植物分布更为广泛；在中高纬度地区，草本植物的物种多样性高于木本植物(图1b、c)。木

本植物和草本植物物种多样性格局的差异可能主要是由两类生活型不同的生活史策略和环境适应性引起的(Ferreira Ribeiro & Tabarelli, 2002)。一般来说, 草本植物的生活史比木本植物短, 因此对气候变化的敏感性比木本植物强(Francis & Currie, 1998; Smith & Beaulieu, 2009; Song et al, 2019)。

末次冰期以来的气候变化对木本植物物种多样性的影响弱于其对草本植物物种多样性的影响, 这主要是因为草本植物的世代时间通常比木本植物更短, 因而可能拥有更高的进化速率(Smith & Donoghue, 2008; Qi et al, 2014), 而这又使得草本植物拥有较快的微进化适应(Hof et al, 2011; Liu et al, 2019), 使得其适应过去气候变化的滞后时间缩短了(Smith & Donoghue, 2008; Smith & Beaulieu, 2009)。由于草本植物生活史较短, 草本植物可以快速适应新环境(Albuquerque et al, 2011; Liu et al, 2019), 因此对过去气候变化十分敏感。此外, 由于毛茛科木本植物主要分布在中国南部地区, 而这一区域在第四纪气候波动中一直是物种保存的避难所, 这可能也是末次冰期以来的气候变化对木本植物的影响弱于草本植物的原因之一。

地形异质性对木本植物和草本植物的影响都很显著。山区地形异质性和生境破碎化程度高, 复杂的生境除了为物种提供更多生态位之外, 还可以通过促进异域物种形成和生态成种过程, 促进新物种的形成(Xing & Ree, 2017)。但在两种生活型间, 地形异质性对木本植物物种多样性的影响强于其对草本植物物种多样性的影响, 这可能是由于地形异质性对于木本植物和草本植物的影响存在尺度依赖性(Hurlbert & Jetz, 2007)。草本植物由于形态低矮, 林下分布居多, 更容易受到土壤湿度、光照强度等微地形环境因素的影响, 并且与动物运输种子、人类干扰等生物因素也密切相关(Martínez, 2003; Saul-Tcherkas & Steinberger, 2011; Song et al, 2011)。虽然微地形因子在较小的空间尺度中对物种多样性具有较显著影响, 但随着空间尺度的增加, 微地形因子的作用逐渐变弱甚至被其他因子的作用所掩盖。

无论对于木本植物还是草本植物, GLMs结果都表明, 温度季节性对毛茛科物种多样性具有较强作用。在温度季节性强的地区, 平均气温在一年内

变化剧烈(Liu et al, 2019; 邹东廷等, 2019), 对植物的生理活动和生长造成影响, 从而限制植物分布和物种多样性(Jacquemyn et al, 2001; Roscher et al, 2009; Hettenbergerová et al, 2013)。

3.3 生物多样性热点地区分析

本研究显示, 位于中国的云贵高原、川桂交界山区、秦巴山区等山区是毛茛科物种多样性和谱系多样性的热点地区。这些结果说明, 毛茛科的多样性热点地区多集中在山区, 这与以往基于其他类群的研究结果一致(Wang QG et al, 2017; Antonelli et al, 2018; Muellner-Riehl et al, 2019)。这可能是由于这些地区巨大的生境异质性所导致。山脉的隆起会给这些地区带来复杂的地形和多样的生境, 为毛茛科植物的分布提供更加多样的生存环境, 从而容纳更多的物种共存(López-Pujol et al, 2011b; Antonelli et al, 2018; 邹东廷等, 2019)。同时, 复杂地形导致的较高的物种分化速率可能也是该地区形成毛茛科生物多样性热点的原因之一。

以往的研究表明, 物种多样性、谱系多样性的热点地区可能表现出不同的空间分布特征(Tucker & Cadotte, 2013)。在确定保护优先区时, 为了保护生物多样性的不同维度, 不应只考虑物种多样性, 也要考虑谱系多样性(Kareiva & Marvier, 2003; Zhang et al, 2015)。根据谱系多样性格局以及物种多样性和谱系多样性关系的残差图可知, 对于毛茛科全部物种而言, 中高纬度地区的谱系多样性较高, 残差也较高, 说明这些地区的谱系多样性高于具有相同物种数的其他地区。这可能在一定程度上说明, 这些地区保存了毛茛科物种独特的进化历史(Kareiva & Marvier, 2003)。一旦这些进化历史丢失, 将会造成某些独立支系的消失, 在生物多样性保护方面造成巨大损失(Faith, 1992)。化石和分子谱系研究显示, 毛茛科起源于白垩纪的温带地区(Tamura, 1995; Ziman & Keener, 1989), 后在欧亚大陆东部中高纬度的亚洲温带地区快速分化并向周边扩散。因此, 欧亚大陆中高纬度地区可能是毛茛科的古热点地区(Cai et al, 2021), 这一地区的毛茛科物种应在该科物种的保护规划中得到重视。

对于草本植物而言, 低纬度地区的谱系多样性较高, 残差也比较高, 这与物种多样性格局较为相似。具体而言, 草本植物谱系多样性高的地区多集

中在山区。在地质历史进程中, 山脉隆起带来的复杂地形除了提供多种生境外, 更促进了物种快速分化并改变了群落物种组成(Chaieb et al, 2019), 从而表现出更高的谱系多样性。

欧亚大陆东部毛茛科植物物种多样性、谱系多样性均呈明显的纬度梯度格局, 由南向北逐渐降低, 在山区具有较高的多样性。毛茛科植物物种和谱系多样性受现代气候、地形异质性和末次冰期以来的气候变化影响, 但不同影响因子的相对作用在物种和谱系多样性之间以及在不同生活型之间差异显著。在所有因子中, 末次冰期以来的气候变化对欧亚东部毛茛科植物物种和谱系多样性的影响最强, 且对草本植物多样性的影响大于木本植物; 现代气候对木本植物分布的影响大于草本植物。地形异质性和不同生活型物种多样性均具有显著影响。我们发现, 在中高纬度地区, 毛茛科的谱系多样性高于具有相同物种数的其他地区, 说明这些地区保存了毛茛科物种独特的进化历史。为保护毛茛科的进化历史, 这些地区在该科的保护规划中应得到重视。

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附录 Supplementary Material

附录1 物种分布记录数据来源

Appendix 1 Data sources of species distribution records

<http://www.biodiversity-science.net/fileup/PDF/2020246-1.pdf>

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