



温带亚洲特有维管植物时空格局的宏观演化与宏观生态视角

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摘要 19世纪博物学家的整体论自然观为生物多样性研究奠定基础。20世纪初种群生物学范式的兴起导致生态与演化研究分离, 宏观尺度研究被弱化。为解析宏观时空尺度上的多样性格局, 宏观演化与宏观生态的整合研究逐渐兴起。该领域借助大数据与分析方法的革新, 整合系统发育、分化时间及生态演化推断, 从“深时远距”视角揭示多样性的形成机制, 并为生物多样性保护提供科学支撑。温带亚洲作为重点区域, 拥有超过67%的维管植物特有种, 其“东亚-北美间断分布”和“第三纪孑遗植物区系”两大区系特征, 反映地质历史与气候变迁下的隔离分化与避难所存续过程。本文综述该区域特有维管植物研究的关键进展, 包括特有性量化、博物馆/摇篮理论及气候避难所假说, 以期为该区生物多样性保护与深入研究提供依据。

关键词 温带亚洲, 维管植物, 特有性, 宏观演化, 宏观生态

19世纪的博物学家们在整体论自然观下, 开启探索世界生物多样性起源奥秘的征程。达尔文在《物种起源》中对物种问题的解答, 始终交织着对生态与演化过程的观察与分析^[1,2]。这种广阔的研究视野, 在达尔文之前的研究者如洪堡的著作中已有体现^[3-5]。生物多样性研究本应是一个统一的领域, 其演化与生态、宏观与微观尺度之间并无绝对界限。然而, 20世纪初种群生物学范式的兴起, 使微观尺度过程占据主导, 导致生态与演化研究逐渐割裂。两大学科均过度聚焦

微观视角, 客观上削弱宏观尺度研究的重要性和相关性^[1]。随着科学进步, 研究者逐渐意识到, 微观尺度研究难以充分解释宏观时空尺度上的多样性现象^[6,7]。例如, 生物多样性空间分布的高度异质性^[8-10], 就需要在广阔的空间尺度、漫长的演化历史以及多样化的类群或谱系(lineages)中综合考量。

在此背景下, 宏观演化与宏观生态的整合研究应运而生, 成为生物多样性领域的新发展。这一趋势由“大数据”语境驱动, 得益于数据汇编与分析方法的革

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新^[11~13]。二者共享统一的知识框架、核心概念和分析工具^[1,11], 催生了诸如系统发育群落生态学(phylogenetic community ecology)^[14~16]、系统发育生态位保守性(phylogenetic niche conservatism, pnc)^[17~19]以及空间系统发育系统学(spatial phylogenetics)^[20~24]等交叉方向。

宏观演化和生态相结合的研究, 提供一种“深时远距”的视角来观察和分析多样性时空分布模式。该视角聚焦于整体(overall)模式和涌现(emergent)属性, 而非特异性和局部尺度变化, 并尝试在科学视角主义哲学框架下(scientific perspectivism)^[25], 理解驱动这些普遍模式的生态与演化过程^[26]。这为人类世(Anthropocene)背景下^[27~29]的生物多样性保护奠定更坚实的科学基础^[30~34]。正如学者所言, 这种整体性科学视角意味着“以新方法解答老问题(new ways to answering the old questions)”^[11]。

温带亚洲^[35]作为生物多样性研究的重点区域, 涵盖45个国家和地区, 面积约3445万平方公里, 包含环北方、东亚、伊朗-图兰和青藏高原四大植物地理单元, 各具独特的生态特征与演化历史, 拥有维管植物6.3万种, 特有种比例高达67%, 包含4个特有科和614个特有属。该区域植物多样性时空格局研究历史悠久。早在19世纪中期, 美国植物学家Asa Gray^[36,37]就注意到北美东部与日本植物区系的联系, 并系统比较日本、北美以及北温带其他地区(如欧洲、亚洲中北部)植物区系的相互关系^[38]。得益于古植物学、分子系统学和生态学证据的不断积累, 以及研究方法的多样化与整合, “东亚-北美间断分布(eastern Asian and eastern North American disjunct distribution)”^[39,40]和“第三纪孑遗植物区系(Tertiary relict floras)”^[41,42]成为阐述温带亚洲植物多样性时空格局的两大经典主题^[43~47]。分子系统学、地质学和化石证据均支持这一解释: 东亚与北美东部的间断分布, 是第三纪北半球温带森林鼎盛时期的孑遗; 其格局形成涉及北大西洋和白令陆桥, 并在第三纪有过多次起源事件^[39]。对北半球洲际间断分布现象的研究, 揭示东亚、北美东部、北美西部、亚洲西部和欧洲东南部物种间复杂的生物地理联系^[48], 表明东亚-北美模式是一个更宏大图景的组成部分^[49]。东亚-北美间断分布与第三纪孑遗植物区系, 共同刻画北半球温带植物多样性演化的时空特征, 前者侧重空间维度, 后者则强调时间维度。

本文综述温带亚洲特有维管植物多样性研究领域的关键方法与理论进展, 重点涵盖特有性量化评估、生物多样性博物馆/摇篮理论及气候避难所假说, 旨在为该区域植物多样性时空格局的综合研究与保护提供科学依据, 并促进后续深入研究。

1 特有性量化评估需要全球标准

特有性作为评估生物独特性核心指标的“生物地理学专属性(biogeographic specificity)”^[50], 其科学内涵自20世纪初便备受关注, 对揭示生物多样性形成机制及制定保护策略至关重要^[51,52]。研究特有性(endemism)首先需要界定其分布范围, 并量化其在特定研究区域的分布局限程度。

过去受限于数据匮乏, 研究常采用描述性术语界定特有现象, 例如, 根据物种相对于研究区域(如特定生境类型、生物群系或生态区)的分布范围大小, 将其划分为狭域特有(narrow endemics)、地区特有(regional endemics)、大陆特有(continental endemics)、准特有/半特有/近特有(semi-/near endemics)或真特有(true/pure endemics)等^[53,54]。此方法虽具实用性, 但未能充分考虑特有物种间分布范围大小(range size)的显著差异。缺乏量化标准易导致对区域特有性水平评估结果不一: 严格限定特有分布虽可避免边际效应, 但会低估边界及近边界区域(尤其当边界存在山地、生态交错带等高异质性生境时)的特有物种丰富度, 造成显著偏差。然而, 研究边界选择的主观性对边际效应的影响程度, 尚缺乏全面量化比较研究^[55,56]。

物种的分布范围在时空上具有动态性^[57~59]。实践中, 研究者常使用多种方法确定物种分布范围, 如直接观测、网格制图、凸包、克里金插值、物种分布模型或者其组合^[60,61]。界定分布范围的核心数据均为物种在特定区域的历史观测记录(系统或随机收集)。观测、网格制图、凸包和克里金法仅需物种出现数据(occurrence data)。鉴于大范围物种数据常非系统采样, 需采用概括化(网格制图)或内插(克里金法)方法克服数据偏差。除出现数据外, 网格制图、凸包和克里金法还需预设规则与算法(如网格大小、网格内物种存在判定规则)。这些方法虽可预测物种出现范围等总体模式, 但物种分布常呈斑块状而非均匀连续, 因此难以刻画真实的分布空间结构, 可能导致特有性评估误差。

尽管特有性及热点研究在生态、演化和保护生物学中广泛存在, 但对其定量定义仍缺乏科学共识^[62-66]. 众多特有性量化指标被提出^[66-70], 最近的中文综述见文献^[71]. 常用指标主要提供以下四类信息: (i) 特有种的数量或比例(丰富度指标); (ii) 特有种密度(密度指标); (iii) 分布范围限制程度(分布范围大小指标); (iv) 演化独特性(系统发育指标)^[62]. 近年来在大尺度网格研究中, (iii)、(iv)类指标应用较多^[72,73], 包括加权特有性(weighted endemism, WE)^[68,74]、校正加权特有性(corrected weighted endemism, CWE)^[68,69,75]、系统发育特有性(phylogenetic endemism, PE)和加权系统发育特有性(weighted phylogenetic endemism, WPE)^[70,76]. 系统发育多样性的相关指数见文献^[77]的综述.

WE的计算核心在于根据物种分布范围大小对网格单元“计分”(亦称“加权”): (i) 计算每个物种分布的网格数; (ii) 依据分布网格数为每个物种赋权重(如, 仅1个网格出现则权重=1, 2个网格则权重=0.5, 100个网格则权重=0.01); (iii) 网格内所有物种权重值之和即为该网格的WE值^[68]. CWE则用WE值除以网格的总物种丰富度, 以消除物种多样性对特有性评估的潜在影响(因物种丰富度与特有丰富度常呈空间正相关, 尽管此关系随尺度变化且非普遍)^[51,78-81]. 这些指标的核心是对物种分布范围(网格数)进行倒数加权(即“逆分布范围大小之和(sum of inverse range size)”), 其概念与范围大小稀有性(range-size rarity)^[82]和特有稀有性(endemic rarity)^[83]密切相关, 常导致术语混淆^[84,85]. 甚至有观点认为, 全球尺度上所有植物皆具特有性(即特有性是相对概念), 狭域应视为范围局限的稀有性(range-restricted rarity)^[86-88].

无论选用何种指标, 均可能忽视特有性的其他维度. Shipley和McGuire^[63]对中美洲哺乳动物的综合研究表明, 不同特有性指标蕴含的生物学、保护及生物地理学意义各异, 识别的热点区域也不一致, 可能反映不同的生态与演化过程. 定义多样且有时矛盾, 导致关于特有物种生物学、地理学及保护的关键问题悬而未决. 指标间的差异如何体现在热点空间分布上, 也缺乏详细比较研究. 正因如此, 特有物种空间分布的形成机制尚不明晰, 对高特有性区域的认知仍不全面^[51,89,90].

近年来, 高质、大尺度物种分布数据、地理信息

系统、R软件包及经纬度/公里网格的普及^[61,91], 促进物种分布范围确定与特有性评估的定量比较研究^[57,58,92,93]. 例如, De Lima等人^[62]利用公开物种分布数据(>300万条记录), 对南美洲东部大西洋森林生物多样性热点区的乔木植物进行保护评估研究. 他们通过数据驱动分析, 量化物种在研究区内的分布状态(常见、偶遇、严格特有或近特有种), 并将其定义为“特有性水平(endemism level)”, 结果与专家名录定义的特有性具有较高一致性. 尽管上述研究方法仍需要在不同尺度与类群中验证并解决潜在概念问题, 其重要性在于尝试建立量化标准定义特有性, 并仿效IUCN红色名录进行等级划分. 此类尝试极具价值, 因为物种分布范围及其变化是评估受威胁物种的关键科学标准, 量化等级也反映特有性尺度效应本质^[56,80,94,95]. 然而, 网格法量化物种分布范围时, 不可避免地面临可修改的面积单位问题(modifiable areal unit problem, MAUP)^[55,96]. 最简单情形下, 网格单元大小的选择会影响物种分布范围的估计(高估或低估), 进而影响景观中特有性的表现分布. 在任意或非生物学定义的研究区域中, MAUP还可能会导致识别的特有性热点区域存在差异^[56]. 遗憾的是, MAUP对特有性评估的影响研究甚少.

2 古新特有聚集区-博物馆/摇篮: 隐喻解释的尴尬

特有性中心(centers of endemism)^[97]形成涉及复杂的演化和生态过程, 是气候、地质和生物地理历史相互作用的结果^[9,98-100], 并与气候变化速率(velocity of climate change)^[101,102]及植物响应方式^[59,103]密切相关. 其中, 气候在演化过程中的稳定性与变化模式, 是解释高度特有性中心起源与维持的关键^[101,104,105]. 历史上气候稳定、少有冰川或极端温度波动的区域, 即气候避难所(climatic refugia)^[99,106], 常庇护演化历史古老、分布狭窄的古特有种^[107]. 而气候稳定性(亦包括地形和新栖息地的形成)^[108,109]则可能促进演化上相对年轻的新特有种^[107]的形成^[110-112]. 气候及其相关干扰机制还驱动生态位和生命史性状(如草本植物的一年生习性)的演化, 进而通过影响物种形成与灭绝速率塑造特有性格局^[113-115]. 据此, 富含古老特有种的区域被喻为“演化博物馆”, 而年轻特有种富集的区域则称为

“演化摇篮”^[72,116~122]。因此,长期的气候稳定性以及气候、地形造成的隔离,被认为是古特有和新特有分布格局的形成的关键因素^[99,123]。值得注意的是,文献中“演化摇篮/博物馆(evolutionary cradles/museums)”^[117,124,125]和“生物多样性摇篮/博物馆(biodiversity cradles/museums)”^[119,120,126]等细微差别术语也时有出现。

然而,明确历史过程对塑造当代特有性生物地理格局的作用仍具有挑战性。直接定量检验历史假说依赖于完整的化石或历史记录,而这对于许多生物类群并不可得。此外,物种形成、灭绝、扩散等历史过程对当前格局的影响也一直是争论的焦点^[127~131]。将某些区域界定为“起源中心”(演化摇篮)或“积累中心”(演化博物馆)的尝试,恰恰凸显了仅凭现存类群分布推断历史过程所面临的固有难题^[132]。将“气候避难所”直接等同于“演化摇篮”的解释面临挑战。主要困难在于区域气候稳定性缺乏跨时间尺度的量化标准,且其与物种形成-灭绝动态过程间存在复杂耦合关系。Fordham等人^[133]基于高分辨率古气候模拟发现,晚更新世和全新世期间,所谓的气候稳定区位置在千年尺度上变动显著,很少长期固定。气候稳定性与生物多样性摇篮的联系,仅在稳定区能跨越多个米兰科维奇气候振荡周期(Milankovitch climate oscillations)^[104,134,135]时才有意义。这促使研究者重新审视晚第四纪气候稳定区对当代物种丰富度、分布范围、特有性中心及生物多样性热点形成的实际作用。

更新世米兰科维奇气候周期所体现的环境不稳定性,在生命演化史上可能普遍存在并扮演重要角色^[104,136]。例如,高纬度地区若经历较高的环境不稳定性,其物种形成率可能更高^[137~139],新适应性辐射出现的可能性也就更大。这些在不稳定区起源的谱系中,能迁移至灭绝率较低的稳定区的幸存者可能得以存续^[140]。若植物能有效追踪气候变化,即使现代温带类群系统发育上嵌套于热带类群中,随时间推移,迁入热带内稳定栖息地的比例也可能高于迁出热带的比例。此观点虽与史旦宾斯(George Ledyard Stebbins)^[141]的摇篮-博物馆比喻一致,却可能与“热带外迁假说(out of the tropics, OTT)”^[142]和“热带生态位保守假说(tropical niche conservatism, TNC)”^[19,143,144]相矛盾。OTT假说认为谱系优先起源于热带并持续存在于热带,同时向高纬扩散;非热带辐射通常较年轻且嵌套于热带主干支

系中,在科属水平表现最强^[142,145,146]。TNC假说则强调物种分布主要由祖先对温暖潮湿环境的保守适应性决定^[19,143,144]。关键在于演化摇篮区可能长期存在,但其空间位置易变且消逝速度快于博物馆区,加之摇篮区较高的就地灭绝率、较低的化石保存率以及持续向稳定区的迁移,使得起源于摇篮区的谱系信号易被掩盖。相反,摇篮-博物馆隐喻提示,某类栖息地中古老基部类群或化石的高频出现,不应简单解释为起源中心,而需警惕幸存者偏差。事实上,“好的博物馆”与“好的摇篮”常共存于同一纬度带^[126,142]。摇篮与博物馆的并存,驱动着新适应性辐射的循环出现及在邻近区域的续存,这可能是全球某些地区,如低地热带雨林、安第斯山脉、亚马孙地区^[147~149];青藏高原、横断山和东亚^[108,150~153]生物多样性异常积累的关键机制之一。

目前,“演化摇篮”和“演化博物馆”最常指代新特有种(摇篮)或古特有种(博物馆)占优势的地理区域^[119,126],或分别对应高物种形成率(起源)与低物种灭绝率(存续)的区域。但这隐含物种形成率与灭绝率相互独立的假设。事实上,古生物学证据^[154]表明两者常协同变化^[155]:促进物种形成的因素也可能增加灭绝风险。因此,将高物种形成率与低灭绝率简单二分可能存在问题。更合理的指标或许是“更替率”(turnover,物种形成率+灭绝率),它能衡量演化事件发生的整体频率^[136,156]。此概念不同于净多样化速率(物种形成率-灭绝率)或灭绝分数(灭绝率/形成率),但类似于古生物学中的“支系波动性(clade volatility)”^[157]。可以说,更替率本身(而非其组分)是理解宏观演化模式的关键指标。其被忽视的原因可能是方法学限制,难以在同一框架中同时估算物种形成与灭绝速率。有趣的是,实证研究常发现符合史旦宾斯^[141]描述的摇篮区,如山地^[158];地中海气候区^[159]具有高物种形成率,而博物馆区如热带雨林^[160]则较低,但也存在例外^[161,162]。然而,仅凭区域间物种形成率差异难以完全解释宏大的生物多样性梯度^[163~165]。同时考虑物种形成速率、灭绝率,尤其是更替率,将使结论更契合宏观演化的动态视角。

George Ledyard Stebbins^[141]在提出“摇篮”与“博物馆”概念时,着重强调特定生物群落或生境类型(如热带雨林、山地、沙漠、地中海气候区)的生态背景对宏观演化过程的影响。然而,许多后续研究将其简

单等同于现代地理区域. 事实上, 这一概念最初并非指特定具体的地理位置或现存群落, 而是指能加速或减缓演化速率的特定生态环境条件. 例如, 气候多变、不稳定的地区常以年轻辐射类群为主, 但这并不意味着此类区域在过去地质时期就不存在. 即使在更温暖湿润的时期, 造山运动、山地侵蚀、海陆变迁及干旱化等过程, 也可能在全球多地不同演化历史阶段引发环境不稳定性 and 生态分异. 值得注意的是, George Ledyard Stebbins^[141]的原始论述比当前领域常用的论据更为丰富和综合, 它不仅涉及物种的演化和灭绝速率, 还包含迁移和化石保存等因素. 其诸多观点在被后续研究引用时, 往往脱离原始语境而改变含义, 甚至丢失关键论点. 对“摇篮”和“博物馆”这一隐喻的探讨, 引出一个核心问题: 在宏观演化和生态研究中, 简单的二元分类(如将地区标记为摇篮或博物馆)是否仍然适用? 事实上, 该隐喻的扩展, 如“赌场”^[166]与“坟墓”^[116], 以及特定区域兼具摇篮和博物馆功能的结论^[142,151,167]频繁出现, 恰恰说明简单的二分法难以涵盖形成空间生物多样性梯度所涉及的复杂变量组合. Araujo等人^[168]基于系统发育更替率对全球哺乳动物摇篮和博物馆的研究, 为此提供有力注解. 其研究发现, (i) 水能动态是主要驱动力: 水分供应高于能量需求环境(如热带雨林)主要充当摇篮; 而干旱环境则主要充当博物馆. (ii) 气候变化历史的影响: 经历更高历史气候变化的地区(如高纬度北方地区)成为摇篮; 气候稳定的地区则成为博物馆. (iii) 山脉的双重角色: 在不同的海拔带, 山脉既能促进新谱系的产生(摇篮功能), 又能为古老谱系提供气候避难所(博物馆功能). 因此, “摇篮”与“博物馆”并非二元对立, 而是存在于一个演化的连续体之中, 其分布和功能受多重环境因子动态塑造.

3 讨论

在20世纪中晚期, 宏观演化(macroevolution)^[169]和宏观生态(macroecology)^[170]相继作为独立的研究领域出现. 尽管二者在核心概念上有所重叠, 但由于数据来源和方法论的差异, 它们之间存在着深层次的分歧. 宏观演化主要关注时间尺度上的过程, 核心问题集中于物种形成、灭绝和净多样化等速率及其在谱系内和谱系间的时间变化. 而宏观生态则侧重空间尺度, 其核心

问题聚焦于丰富度、分布范围和特征等水平在空间和类群间的变异. 尽管整合这两个领域的呼声持续不断^[1,2,6,7,171-173], 其根本差异——时间过程与空间过程的侧重——仍然显著.

特有植物的时空分布格局受宏观演化(物种形成与灭绝)和宏观生态过程(扩散历史与环境筛选)的共同塑造^[89,98,174], 同时也与区域地质历史、气候演变、生态地理隔离、环境异质性、水热资源、气候季节性与长期气候稳定性以及植物内在的生物学特征等多重互动因素密切相关^[86,87,99,175]. 随着栖息地丧失、城市化和气候变化的加剧, 物种分布范围普遍萎缩, 使得分布范围和特有性动态研究在生态学与保护生物学研究中的重要性日益凸显^[59,176-179]. 全球环境变化的深化, 进一步增加分布受限物种生态学与保护实践的复杂性和不确定性. 因此, 要在当前及未来开展有效的全球性研究, 亟需采用综合、全面的视角理解特有性, 这要求纳入不同尺度和多种特有性指标. 单一特有性指标往往难以全面刻画特有性的空间格局. 整合评估多种量化指标, 并将其应用于全球、区域、国家等不同空间尺度, 识别基于多指标——多尺度重叠的“共识热点区”(consensus hotspots)^[63,180,181], 对于生物多样性热点区域的精准识别与制图具有重要的科学和实践价值.

研究不同尺度(全球、区域、国家)上的特有性格局, 对优化全球保护策略至关重要, (i) 尺度效应: 分析尺度和范围的差异会显著影响特有性格局的呈现和热点区域的识别精度. 尽管空间偏差对生物多样性格局解释的影响已被广泛探讨, 但其对特有性(尤其跨大洲尺度)的影响研究仍相对匮乏. (ii) 指标选择: 所采用的特有性定义指标会深刻影响格局的解释和热点区域的分布. 不同的特有性指标常具有一定独立性, 它们分别衡量物种分布范围大小、演化新颖性或地理独特性的不同方面. 因此, 有效研究特有性的趋势与驱动因素, 必须明确研究问题, 并理解不同指标与该问题的关联性.

德国植物学家恩格勒最早提出应在演化时间尺度上区分“古老”与“年轻”的特有类群^[87]. 随后这一概念被广泛采纳, 并被Cain^[182]在其经典植物地理学著作中确立为定义特有性的三个关键标准之一. 自George Ledyard Stebbins在其开创性研究——《加州植物区系的特有性和物种形成》《有花植物: 种以上水平的

演化》^[107,141]——中提出核心问题: 热带地区物种丰富性源于其作为高物种形成率的“摇篮”, 还是低灭绝的“博物馆”? 关于物种快速近期起源(新特有)与古老谱系的续存(古特有)的讨论, 便构成特有性研究的基本框架^[99]。尽管当时受限于化石证据、系统发育信息和相关分析方法的不足, 难以清晰界定特定区域中古特有与新特有类群的数量。这也是近年来系统发育特有性研究日益受到重视的原因^[70,73,76,183~188]。相关研究已从概念探讨逐渐深化为对系统发育特有性空间分布结构及其决定性环境因素的比较分析^[20~23,189~200]。在此背景下, 通过新特有和古特有的等级分析(categorical analysis of neo- and paleo-endemism, CANAPE)方法识别古特有、新特有和混合特有区域的空间分布^[70,123,201], 已成为揭示全球及区域植物多样性历史聚集模式的重要途径。

这一研究趋势的兴起得益于两方面: (i) 公开可用的物种分布数据及古植物化石记录的快速增长; (ii) 系统发育数据的积累及其分析方法和工具的飞速发展。传统特有性概念主要关注物种地理分布范围的空间局限性, 对时间维度则缺乏有效度量方法。系统发育多样性(phylogenetic diversity, PD)概念的提出和应用^[20,70,201~204]恰好填补这一长期的知识空白, 更完整地揭示特有性本质上是物种地理分布在时空上动态变化的属性^[57~59]。

过去数十年间, 针对温带亚洲特有植物的研究在多领域取得显著进展, 涵盖诸多主题, 例如, (i) 第三纪孑遗植物区系的分子系统学比较研究^[41,42,46,47,205]; (ii) 东亚种子植物特有属的古植物地理学^[206,207]; (iii) 东亚与北美植物区系的比较^[208~211]; (iv) 亚热带常绿阔叶林的起源和演化^[212~217]; (v) 干旱区代表类群的生物地理学研究^[124,218]; (vi) 高山植物区系的历史聚集特征^[150,219~223]; (vii) 多样性的时空演化模式^[108,151,152]等。

伴随生态与演化研究的深入, 一些多样性时空分布的关键问题认识不断深化。以东亚-北美植物区系比较为例, 传统观点认为, 东亚极高的物种多样性(多样性异常, diversity anomalies)源于地形异质性驱动的辐射式异域物种形成, 导致净多样化速率差异^[210,224], 系统发育多样性的空间格局也支持此模式^[225,226]。然而, 基因组比较研究显示两地类群分子演化速率相近, 选择压力亦相似, 表明多样化速率差异并非主因, 暗示

其他因素的作用^[227]。尽管如此, 现有研究仍存在明显局限。关于生物多样性热点(包括系统发育多样性分布)及历史多样化进程的重建, 大多聚焦于单一系统发育分支或特定地理区域, 缺乏在更广阔时空尺度(尤其是整合古植物化石证据)上的综合分析。鲜有研究将多源数据结合, 系统探讨温带亚洲特有植物区系的起源年代、多样化进程模式, 并检验其分布格局与古地质历史、古气候及现代气候因子的关联。虽然追踪如此丰富植物群的多样化历史具有复杂性, 但通过多谱系数据的比较分析, 仍可揭示普适性模式^[116,228~230]。鉴于温带亚洲悠久的历史与极高的多样性, 唯有通过跨谱系、跨区域的长期多样化模式与驱动因子的综合比较研究, 方能获得更具普遍性的洞见。然而, 广泛系统发育与生态背景下深时比较数据的整合不足, 阻碍对该问题的全面理解。未来的深入研究需建立全球标准以统一特有性量化、克服尺度效应。“演化摇篮/博物馆”假说虽有助于理解古特有种聚集机制, 但受限于物种形成-灭绝速率的耦合及气候动态变化, 应结合系统发育特有性分析(如CANAPE)与多指标综合评估。未来应加强宏观生态-演化整合视角, 结合机理模型与机器学习, 跨学科揭示温带亚洲特有植物格局的驱动机制。

3.1 孑遗植物间断分布的模式与成因

孑遗植物包含第三纪或更早时期广泛分布于北半球的植物群幸存者^[231~233]。根据其历史和起源可分为前第三纪、间冰期或后冰期孑遗植物^[234]。过去6500万年(65 Ma, 即第三纪和第四纪)的气候波动和地理剧变, 深刻塑造北半球现代生物群落的分布格局。随着全球气候变冷, 在第三纪早中期(65~15 Ma)适应环北方分布的植物类群, 被限制在气候适宜的有限区域, 并在其他地区走向灭绝^[233,235,236], 最终形成现今仅存于北美东南部、北美西部、东亚和欧亚西南部温暖潮湿区域的第三纪孑遗植物区系^[41,42]。

温带亚洲第三纪孑遗植物的间断分布格局, 是地质历史不同时期, 在地质构造与气候变迁背景下, 迁移扩散、适应分化、物种形成与灭绝等演化与生态过程共同作用的结果。隔离分化(vicariance)被认为是主要成因, 尽管通过白令陆桥或北大西洋陆桥的长距离扩散事件亦不可完全排除^[41,42]。第四纪冰川作用导致的生境隔离对此格局形成至关重要。冰期引发北半球

物种的大规模灭绝, 而北美东部、北美西部、东亚及欧亚西南部的复杂地形, 为孑遗植物提供多样化的避难所(refugia)^[101,237]. 这些避难所不仅是孑遗植物在冰期得以存续的关键, 也是间冰期气候波动下其分布范围扩张、适应分化及新多样性产生的重要源头. 这些孑遗植物涉及生命树上的不同谱系, 涵盖密切相关的属或种对、属下等级(如组、系), 乃至单系分支^[39,41,42,44,238]. 然而, 除少数深入研究的类群外, 目前尚不完全清楚有多少类群或谱系遵循这种“时空异步同域”的演化模式(即在空间上一致但时间上不一致地形成当前分布).

3.2 数据洪流下的机遇与挑战

DNA序列数据的爆炸式增长, 极大地推动利用分子系统学解析谱系起源与多样化模式的研究^[20,77]. 分子数据与植物分布、环境特征数据库及古生物数据库^[239~241]的整合, 正广泛应用于探究生物多样性起源^[242,243]、空间分布格局^[98,183,244,245]、灭绝风险评估^[246]、特有植物分布格局与历史演变^[101,123]、动植物区系区划^[247~252]、岛屿植物多样性形成过程^[253], 乃至植物抗逆响应的时空模式^[254].

大量可开放获取的生物多样性基础数据的涌现, 促使生态与演化生物学家日益采用“大数据”方法, 在大空间、大分类群及长时间尺度上解决问题. 典型应用包括: (i) 基于机器学习模型的全球植物多样性分布预测^[255]; (ii) 全球动植物地理区划研究^[247,250,256~258]; (iii) 系统发育多样性的空间格局分析^[183,184,259,260]; (iv) 全球生态区边界的验证^[261]等. 然而, 面对数据洪流, 必须清醒认识到数据本身在分类学、地理空间和时间(尤其是系统发育深度)维度上存在的覆盖不全、不确定性及偏差问题^[262~264]. 这些问题直接影响对真实生物多样性模式的识别与解读^[265~267]. 因此, 在利用这些强大工具的同时, 审慎评估数据质量与局限至关重要.

4 展望

展望未来, 理解生物地理格局的关键问题需要融合宏观演化与宏观生态的视角和变量. 这是因为大尺度空间过程通常在长时间尺度上发挥作用, 反之亦然^[268,269]. 具体而言, 特有性的空间分布是植物多样性

在地理空间上随时间变化的体现, 从宏观演化和生态角度看, 它是解读区域多样性来源和历史聚集过程的核心内容. 深入探究此问题需整合系统发育、谱系地理、生态、古生物、构造和气候学等多学科知识^[109], 并应用现代计算技术^[270,271].

地貌特征深刻影响生物群落的多样性与分布. 陆地和海洋中地形复杂区域常为生物多样性热点^[272~276], 这体现地质过程对生态与演化的塑造. 复杂地形由构造活动形成, 并受气候与地表过程相互作用的进一步雕琢. 这些过程促进物种分化, 并通过强化环境梯度增加物种丰富度, 从而提升区域多样性. 随时间推移(数百万年尺度), 地形多样性梯度(topographic diversity gradients)此消彼长, 记录着构造与气候的历史变迁. 这些梯度既可源于物种的地理隔离分化, 也可能来自物种向高环境梯度区域的扩散积累. 要重建多样化历史并确定驱动机制, 必须结合化石与现代数据, 因为单一数据源难以完全揭示其模式与过程^[277]. 因此, 生物学与地质学方法需紧密结合, 以检验沿地形多样性梯度的多样化模型^[229]. 通过综合分析化石记录^[278,279]和区域地形演化的地球物理模型, 研究者能直接量化过去多样性变化与地貌动态之间的耦合关系^[280]. 这种多学科(系统发育、谱系地理、生态、古生物、构造、气候学)的交叉融合正是生物地理学的新兴前沿^[109].

在研究方向上, 目前呈现两大趋势: (i) 机理模型模拟与预测的兴起. Rangel等人^[116]构建空间明确的机理模型, 模拟过去80万年气候驱动下南美洲鸟类、哺乳动物和植物的丰富度分布. 该模型采用“自下而上”策略, 整合关键生态与演化过程(如适应、地理范围变化、物种形成/灭绝、扩散、竞争)的机制及其公认运作原理. 尽管模拟未参考现实分布且时间跨度有限, 其生成的丰富度格局却惊人地逼真. 研究证实适应性生态位演化在地形和气候驱动的多样化与灭绝中作用显著, 并成功通过模拟的持久性(“博物馆”)物种丰富度历史模式捕捉现代格局的关键特征. 参数敏感性分析揭示不同演化生态过程对物种丰富度时空格局(摇篮、博物馆、坟墓)的相对影响. 当然, 这种还原论方法在宏观演化与生态研究中的适用性仍需深入探讨^[281,282]. (ii) 机器学习技术的广泛应用. 该方法已在多个领域发挥作用, 包括全球维管植物多样性分布预测^[255]、系统发育关系推断^[283]、系统发育多样性趋

势分析^[284]和整合分类学物种界定^[285,286]。上述研究进展(机理模型模拟与机器学习应用)为未来深入广泛地研究温带亚洲特有植物时空格局提供重要的方法论参考。

参考文献

- 1 McGill B J, Chase J M, Hortal J, et al. Unifying macroecology and macroevolution to answer fundamental questions about biodiversity. *Glob Ecol Biogeogr*, 2019, 28: 1925–1936
- 2 Reznick D N, Ricklefs R E. Darwin's bridge between microevolution and macroevolution. *Nature*, 2009, 457: 837–842
- 3 Humboldt A v, Bonpland A. Personal Narrative of Travels to the Equinoctial Regions of the New Continent: During the Years 1799–1804. Cambridge: Cambridge University Press, 2011
- 4 Hoorn C, Ebersbach J, Muellner-Riehl A. Humboldt, biogeography, and the dimension of time. In: Falk G C, Strecker M R, Schneider S, eds. Pollen: Alexander von Humboldt: Multiperspective Approaches. Cham: Springer International Publishing, 2022. 61–95
- 5 Rahbek C, Borregaard M K, Colwell R K, et al. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science*, 2019, 365: 1108–1113
- 6 Ricklefs R E, Schluter D. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. Chicago: University of Chicago Press, 1993
- 7 Hunter J P. Key innovations and the ecology of macroevolution. *Trends Ecol Evol*, 1998, 13: 31–36
- 8 Jetz W, McPherson J M, Guralnick R P. Integrating biodiversity distribution knowledge: toward a global map of life. *Trends Ecol Evol*, 2012, 27: 151–159
- 9 Igea J, Tanentzap A J. Multiple macroevolutionary routes to becoming a biodiversity hotspot. *Sci Adv*, 2019, 5: eaau8067
- 10 Schluter D, Pennell M W. Speciation gradients and the distribution of biodiversity. *Nature*, 2017, 546: 48–55
- 11 Bromham L, Cardillo M. Origins of Biodiversity: An Introduction to Macroevolution and Macroecology. Oxford: Oxford University Press, 2019
- 12 Liow L H, Uyeda J, Hunt G. Cross-disciplinary information for understanding macroevolution. *Trends Ecol Evol*, 2023, 38: 250–260
- 13 Wüest R O, Zimmermann N E, Zurell D, et al. Macroecology in the age of Big Data—where to go from here? *J Biogeogr*, 2020, 47: 1–12
- 14 Webb C O, Ackerly D D, McPeck M A, et al. Phylogenies and community ecology. *Annu Rev Ecol Syst*, 2002, 33: 475–505
- 15 Emerson B C, Gillespie R G. Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol Evol*, 2008, 23: 619–630
- 16 Cavender-Bares J, Kozak K H, Fine P V A, et al. The merging of community ecology and phylogenetic biology. *Ecol Lett*, 2009, 12: 693–715
- 17 Ackerly D D. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int J Plant Sci*, 2003, 164: S165–S184
- 18 Peterson A T, Soberón J, Sánchez-Cordero V. Conservatism of ecological niches in evolutionary time. *Science*, 1999, 285: 1265–1267
- 19 Wiens J J, Graham C H. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Evol Syst*, 2005, 36: 519–539
- 20 Mishler B D. Spatial phylogenetics. *J Biogeogr*, 2023, 50: 1454–1463
- 21 Thornhill A H, Mishler B D, Knerr N J, et al. Continental-scale spatial phylogenetics of Australian angiosperms provides insights into ecology, evolution and conservation. *J Biogeogr*, 2016, 43: 2085–2098
- 22 Thornhill A H, Baldwin B G, Freyman W A, et al. Spatial phylogenetics of the native California flora. *BMC Biol*, 2017, 15: 1–8
- 23 Scherson R A, Thornhill A H, Urbina-Casanova R, et al. Spatial phylogenetics of the vascular flora of Chile. *Mol Phylogenet Evol*, 2017, 112: 88–95
- 24 Morlon H, Schwikl D W, Bryant J A, et al. Spatial patterns of phylogenetic diversity. *Ecol Lett*, 2011, 14: 141–149
- 25 Giere R N. Scientific Perspectivism. Chicago: University of Chicago Press, 2006
- 26 Diniz-Filho J A F. The Macroecological perspective. In: Diniz-Filho J A F, ed. Pollen: The Macroecological Perspective: Theories, Models and Methods. Cham: Springer International Publishing, 2023. 1–13
- 27 Lewis S L, Maslin M A. Defining the Anthropocene. *Nature*, 2015, 519: 171–180
- 28 Steffen W, Grinevald J, Crutzen P, et al. The Anthropocene: conceptual and historical perspectives. *Phil Trans R Soc A*, 2011, 369: 842–867

- 29 Zhou W J, Zhao X, Chen N. New progress in the Anthropocene science in China (in Chinese). *Adv Earth Sci*, 2024, 39: 1–11 [周卫健, 赵雪, 陈宁. 中国人类世科学研究新进展. *地球科学进展*, 2024, 39: 1–11]
- 30 Pimiento C, Antonelli A. Integrating deep-time palaeontology in conservation prioritisation. *Front Ecol Evol*, 2022, 10: 959364
- 31 Dietl G P, Flessa K W. Conservation paleobiology: putting the dead to work. *Trends Ecol Evol*, 2011, 26: 30–37
- 32 Barnosky A D, Hadly E A, Gonzalez P, et al. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, 2017, 355: eaah4787
- 33 Kemp M E, Boville A E, Carneiro C M, et al. Looking back for the future: the ecology of terrestrial communities through the lens of conservation paleobiology. *Annu Rev Ecol Evol Syst*, 2023, 54: 259–282
- 34 Lawing A M. The geography of phylogenetic paleoecology: integrating data and methods to better understand biotic response to climate change. *Paleobiology*, 2021, 47: 178–197
- 35 Brummitt R K. World geographical scheme for recording plant distributions. ed. 2 ed. Pittsburgh: Hunt Inst. for Botanical Documentation, 2001
- 36 Gray A. Analogy between the flora of Japan and that of the United States. *Am J Sci*, 1846, 2: 135–136
- 37 Gray A. Dr. Siebold, Flora Japonica: sectio prima. plantas ornatui vel usui inservientes digessit Dr. J. G. Zuccarini: fasc. 1–10. fol. (review). *Am J Sci*, 1840, 39: 175–176
- 38 Gray A. Diagnostic characters of new species of phaenogamous plants collected in Japan by Charles Wright. With observations upon the relations of the Japanese flora to that of North America and of other parts of the Northern temperate zone. *Am J Sci*, 1857, 6: 377–452
- 39 Wen J. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Annu Rev Ecol Syst*, 1999, 30: 421–455
- 40 Boufford D E, Spongberg S A. Eastern Asian-eastern North American phytogeographical relationships—a history from the time of linnaeus to the twentieth century. *Ann Missouri Bot Gard*, 1983, 70: 423–439
- 41 Milne R I, Abbott R J. The origin and evolution of Tertiary relict floras. *Adv Bot Res*, 2002, 38: 281–314
- 42 Ian Milne R. Northern hemisphere plant disjunctions: a window on tertiary land bridges and climate change? *Ann Bot*, 2006, 98: 465–472
- 43 Lin H Y, Sun M, Hao Y J, et al. Phylogenetic diversity of eastern Asia-eastern North America disjunct plants is mainly associated with divergence time. *Plant Divers*, 2023, 45: 27–35
- 44 Wen J, Nie Z, Ickert-Bond S M. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. *J Syst Evol*, 2016, 54: 469–490
- 45 Kubota Y, Kusumoto B, Shiono T, et al. Phylogenetic properties of Tertiary relict flora in the east Asian continental islands: imprint of climatic niche conservatism and *in situ* diversification. *Ecography*, 2017, 40: 436–447
- 46 Tang C Q, Matsui T, Ohashi H, et al. Identifying long-term stable refugia for relict plant species in East Asia. *Nat Commun*, 2018, 9: 4488
- 47 Tang C Q. Endemism and Tertiary relict forests. In: Tang C Q, ed. *Pollen: The Subtropical Vegetation of Southwestern China: Plant Distribution, Diversity and Ecology*. Dordrecht: Springer Netherlands, 2015. 185–273
- 48 Pennington P T, Cronk Q C B, Richardson J A, et al. Patterns in the assembly of temperate forests around the Northern Hemisphere. *Phil Trans R Soc Lond B*, 2004, 359: 1633–1644
- 49 Yih D. Land bridge travelers of the tertiary: the eastern Asian-eastern North American floristic disjunction. *Arnoldia*, 2012, 69: 14–23
- 50 Assunção-Silva C C, Assis L C S. Areas of endemism of Lauraceae: new insights on the biogeographic regionalization of the Espinhaço Range, Brazil. *Cladistics*, 2022, 38: 246–263
- 51 Orme C D L, Davies R G, Burgess M, et al. Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 2005, 436: 1016–1019
- 52 Bonn A, Rodrigues A S L, Gaston K J. Threatened and endemic species: are they good indicators of patterns of biodiversity on a national scale? *Ecol Lett*, 2002, 5: 733–741
- 53 Drury W H. Rare species of plants. *Rhodora*, 1980, 82: 3–48
- 54 Stebbins G L. Rarity of plant species: a synthetic viewpoint. *Rhodora*, 1980, 82: 77–86
- 55 Jelinski D E, Wu J. The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecol*, 1996, 11: 129–140
- 56 Ferreira P M A, Boldrini I I. Potential reflection of distinct ecological units in plant endemism categories. *Conserv Biol*, 2011, 25: 672–679
- 57 Gaston K J. *The Structure and Dynamics of Geographic Ranges*. New York: Oxford University Press, 2003
- 58 Gaston K J. Measuring geographic range sizes. *Ecography*, 1994, 17: 198–205

- 59 Sheth S N, Morueta-Holme N, Angert A L. Determinants of geographic range size in plants. *New Phytol*, 2020, 226: 650–665
- 60 Yalcin S, Leroux S J. Diversity and suitability of existing methods and metrics for quantifying species range shifts. *Glob Ecol Biogeogr*, 2017, 26: 609–624
- 61 Graham C H, Hijmans R J. A comparison of methods for mapping species ranges and species richness. *Glob Ecol Biogeogr*, 2006, 15: 578–587
- 62 de Lima R A F, Souza V C, de Siqueira M F, et al. Defining endemism levels for biodiversity conservation: tree species in the Atlantic Forest hotspot. *Biol Conserv*, 2020, 252: 108825
- 63 Shipley B R, McGuire J L. Interpreting and integrating multiple endemism metrics to identify hotspots for conservation priorities. *Biol Conserv*, 2022, 265: 109403
- 64 Fattorini S. Endemism in historical biogeography and conservation biology: concepts and implications. *Biogeographia*, 2017, 32: 47–75
- 65 Anderson S. Area and endemism. *Q Rev Biol*, 1994, 69: 451–471
- 66 Hobohm C, Tucker C M. How to Quantify Endemism. In: Hobohm C, ed. *Pollen: Endemism in Vascular Plants*. Dordrecht: Springer Netherlands, 2014. 11–48
- 67 Laffan S W, Rosauer D F, Di Virgilio G, et al. Range-weighted metrics of species and phylogenetic turnover can better resolve biogeographic transition zones. *Methods Ecol Evol*, 2016, 7: 580–588
- 68 Crisp M D, Laffan S, Linder H P, et al. Endemism in the Australian flora. *J Biogeogr*, 2001, 28: 183–198
- 69 Laffan S W, Crisp M D. Assessing endemism at multiple spatial scales, with an example from the Australian vascular flora. *J Biogeogr*, 2003, 30: 511–520
- 70 Rosauer D, Laffan S W, Crisp M D, et al. Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Mol Ecol*, 2009, 18: 4061–4072
- 71 Huang J H, Zhang J L, Yang Y, et al. Advances in methods for measuring patterns of endemic plant diversity (in Chinese). *Biodiv Sci*, 2013, 21: 99–110 [黄继红, 张金龙, 杨永, 等. 特有植物多样性分布格局测度方法的新进展. 生物多样性, 2013, 21: 99–110]
- 72 Sosa V, De-Nova J A, Vásquez-Cruz M. Evolutionary history of the flora of Mexico: dry forests cradles and museums of endemism. *J Syst Evol*, 2018, 56: 523–536
- 73 Sanbonmatsu K K, Spalink D. A global analysis of mosses reveals low phylogenetic endemism and highlights the importance of long-distance dispersal. *J Biogeogr*, 2022, 49: 654–667
- 74 Linder H P, Olmstead R. On areas of endemism, with an example from the African restionaceae. *Syst Biol*, 2001, 50: 892–912
- 75 Laffan S W, Ramp D, Roger E, et al. Using endemism to assess representation of protected areas African the family Myrtaceae in the Greater Blue Mountains World Heritage Area. *J Biogeogr*, 2013, 40: 570–578
- 76 Rosauer D F, Jetz W. Phylogenetic endemism in terrestrial mammals. *Glob Ecol Biogeogr*, 2015, 24: 168–179
- 77 Tucker C M, Cadotte M W, Carvalho S B, et al. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol Rev*, 2017, 92: 698–715
- 78 Lamoreux J F, Morrison J C, Ricketts T H, et al. Global tests of biodiversity concordance and the importance of endemism. *Nature*, 2006, 440: 212–214
- 79 Storch D, Keil P, Jetz W. Universal species-area and endemics-area relationships at continental scales. *Nature*, 2012, 488: 78–81
- 80 Daru B H, Farooq H, Antonelli A, et al. Endemism patterns are scale dependent. *Nat Commun*, 2020, 11: 2115
- 81 Albuquerque F, Beier P, Sueur C. Rarity-weighted richness: a simple and reliable alternative to integer programming and heuristic algorithms for minimum set and maximum coverage problems in conservation planning. *PLoS One*, 2015, 10: e0119905
- 82 Knapp S. Assessing patterns of plant endemism in neotropical uplands. *Bot Rev*, 2002, 68: 22–37
- 83 Richards A E, Shapcott A, Playford J, et al. Physiological profiles of restricted endemic plants and their widespread congeners in the North Queensland wet tropics, Australia. *Biol Conserv*, 2003, 111: 41–52
- 84 Guerin G R, Lowe A J. ‘Sum of inverse range-sizes’ (SIR), a biodiversity metric with many names and interpretations. *Biodivers Conserv*, 2015, 24: 2877–2882
- 85 Guerin G R, Ruokolainen L, Lowe A J, et al. A georeferenced implementation of weighted endemism. *Methods Ecol Evol*, 2015, 6: 845–852
- 86 Cowling R M. Endemism. In: Levin S A, ed. *Pollen: Encyclopedia of biodiversity Volume 3*. San Diego: Academic Press, 2013. 228–236
- 87 Kruckeberg A R, Rabinowitz D. Biological aspects of endemism in higher plants. *Annu Rev Ecol Syst*, 1985, 16: 447–479
- 88 Rabinowitz D. Seven forms of rarity In: Synge H, ed. *Pollen: The Biological Aspects of Rare Plant Conservation*. Cambridge: John Wiley &

- Sons, 1981. 205–217
- 89 Keppel G, Ottaviani G, Harrison S, et al. Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Ann Bot*, 2018, 122: 927
 - 90 Hobohm C. Endemism in Vascular Plants. Dordrecht: Springer Dordrecht, 2014. 348
 - 91 Dornelles M P, Heiden G, Nic Lughadha E, et al. Quantifying and mapping angiosperm endemism in the *Araucaria* Forest. *Bot J Linn Soc*, 2021, 199: 449–469
 - 92 Gaston K J, Fuller R A. The sizes of species' geographic ranges. *J Appl Ecol*, 2009, 46: 1–9
 - 93 Gaston K J. How large is a species' geographic range? *Oikos*, 1991, 61: 434–438
 - 94 García-Llamas P, Calvo L, De la Cruz M, et al. Landscape heterogeneity as a surrogate of biodiversity in mountain systems: what is the most appropriate spatial analytical unit? *Ecol Indicators*, 2018, 85: 285–294
 - 95 Rahbek C. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Lett*, 2005, 8: 224–239
 - 96 Dark S J, Bram D. The modifiable areal unit problem (MAUP) in physical geography. *Prog Phys Geog*, 2007, 31: 471–479
 - 97 Nelson G. From Candolle to croizat: comments on the history of Biogeogr. *J History Biol*, 1978, 11: 269–305
 - 98 Kier G, Kreft H, Lee T M, et al. A global assessment of endemism and species richness across island and mainland regions. *Proc Natl Acad Sci USA*, 2009, 106: 9322–9327
 - 99 Harrison S, Noss R. Endemism hotspots are linked to stable climatic refugia. *Ann Bot*, 2017, 119: 207–214
 - 100 Hobohm C, Barker N. Centers of endemism and the potential of zoos and botanical gardens in conservation of endemics. *JZBG*, 2023, 4: 527–548
 - 101 Sandel B, Arge L, Dalsgaard B, et al. The influence of late quaternary climate-change velocity on species endemism. *Science*, 2011, 334: 660–664
 - 102 Loarie S R, Duffy P B, Hamilton H, et al. The velocity of climate change. *Nature*, 2009, 462: 1052–1055
 - 103 Dawson T P, Jackson S T, House J I, et al. Beyond predictions: biodiversity conservation in a changing climate. *Science*, 2011, 332: 53–58
 - 104 Dynesius M, Jansson R. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc Natl Acad Sci USA*, 2000, 97: 9115–9120
 - 105 Feng G, Mao L, Sandel B, et al. High plant endemism in China is partially linked to reduced glacial-interglacial climate change. *J Biogeogr*, 2016, 43: 145–154
 - 106 Gavin D G, Fitzpatrick M C, Gugger P F, et al. Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytol*, 2014, 204: 37–54
 - 107 Stebbins G L, Major J. Endemism and speciation in the California flora. *Ecol Monogr*, 1965, 35: 1–35
 - 108 Chang Y, Gelwick K, Willett S D, et al. Phytodiversity is associated with habitat heterogeneity from Eurasia to the Hengduan Mountains. *New Phytol*, 2023, 240: 1647–1658
 - 109 Badgley C, Smiley T M, Terry R, et al. Biodiversity and topographic complexity: modern and geohistorical perspectives. *Trends Ecol Evol*, 2017, 32: 211–226
 - 110 Linder H P. Plant species radiations: where, when, why? *Phil Trans R Soc B*, 2008, 363: 3097–3105
 - 111 Winkworth R. Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Org Divers Evol*, 2005, 5: 237–247
 - 112 Verboom G A, Archibald J K, Bakker F T, et al. Origin and diversification of the Greater Cape flora: ancient species repository, hot-bed of recent radiation, or both? *Mol Phylogenet Evol*, 2009, 51: 44–53
 - 113 Hopper S D, Gioia P. The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annu Rev Ecol Evol Syst*, 2004, 35: 623–650
 - 114 Gremer J R. Looking to the past to understand the future: linking evolutionary modes of response with functional and life history traits in variable environments. *New Phytol*, 2022, 237: 751–757
 - 115 Smith S A, Beaulieu J M. Life history influences rates of climatic niche evolution in flowering plants. *Proc R Soc B*, 2009, 276: 4345–4352
 - 116 Rangel T F, Edwards N R, Holden P B, et al. Modeling the ecology and evolution of biodiversity: biogeographical cradles, museums, and graves. *Science*, 2018, 361: eaar5452
 - 117 González-Orozco C E. Unveiling evolutionary cradles and museums of flowering plants in a neotropical biodiversity hotspot. *R Soc Open Sci*, 2023, 10: 230917

- 118 Chown S L, Gaston K J. Areas, cradles and museums: the latitudinal gradient in species richness. *Trends Ecol Evol*, 2000, 15: 311–315
- 119 Dagallier L M J, Janssens S B, Dauby G, et al. Cradles and museums of generic plant diversity across tropical Africa. *New Phytol*, 2020, 225: 2196–2213
- 120 Sonne J, Dalsgaard B, Borregaard M K, et al. Biodiversity cradles and museums segregating within hotspots of endemism. *Proc R Soc B*, 2022, 289: 20221102
- 121 Thorne R F. Eastern Asia as a living museum for archaic angiosperms and other seed plants. *Taiwania*, 1999, 44: 413–422
- 122 López-Pujol J, Zhang F M, Sun H Q, et al. Mountains of southern China as “Plant Museums” and “Plant Cradles”: evolutionary and conservation insights. *Mountain Res Dev*, 2011, 31: 261–269
- 123 Cai L, Kreft H, Taylor A, et al. Climatic stability and geological history shape global centers of neo- and paleoendemism in seed plants. *Proc Natl Acad Sci USA*, 2023, 120: e2300981120
- 124 Wu S, Peng H, Lian L, et al. Eurasian drylands are both evolutionary cradles and museums of Nitrariaceae diversity. *J Biogeogr*, 2024, 51: 1387–1399
- 125 McKenna D D, Farrell B D. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proc Natl Acad Sci USA*, 2006, 103: 10947–10951
- 126 Azevedo J A R, Guedes T B, Nogueira C C, et al. Museums and cradles of diversity are geographically coincident for narrowly distributed Neotropical snakes. *Ecography*, 2020, 43: 328–339
- 127 Francis A P, Currie D J. Global patterns of tree species richness in moist forests: another look. *Oikos*, 1998, 81: 598–602
- 128 Francis A P, Currie D J. A globally consistent richness-climate relationship for angiosperms. *Am Nat*, 2003, 161: 523–536
- 129 Qian H, Ricklefs R E. Taxon richness and climate in angiosperms: is there a globally consistent relationship that precludes region effects? *Am Nat*, 2004, 163: 773–779
- 130 Ricklefs R E. A comprehensive framework for global patterns in biodiversity. *Ecol Lett*, 2004, 7: 1–15
- 131 Brown J H, Svenning J. Why are there so many species in the tropics? *J Biogeogr*, 2014, 41: 8–22
- 132 Goldberg E E, Roy K, Lande R, et al. Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *Am Nat*, 2005, 165: 623–633
- 133 Fordham D A, Brown S C, Wigley T M L, et al. Cradles of diversity are unlikely relics of regional climate stability. *Curr Biol*, 2019, 29: R356–R357
- 134 Jansson R. Global patterns in endemism explained by past climatic change. *Proc R Soc Lond B*, 2003, 270: 583–590
- 135 Alley R B, Marotzke J, Nordhaus W D, et al. Abrupt climate change. *Science*, 2003, 299: 2005–2010
- 136 Vrba E S. Turnover-pulses, the Red Queen, and related topics. *Am J Sci*, 1993, 293: 418–452
- 137 Rabosky D L, Chang J, Title P O, et al. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 2018, 559: 392–395
- 138 Igea J, Tanentzap A J, Davies J. Angiosperm speciation cools down in the tropics. *Ecol Lett*, 2020, 23: 692–700
- 139 Morales-Barbero J, Gouveia S F, Martinez P A. Historical climatic instability predicts the inverse latitudinal pattern in speciation rate of modern mammalian biota. *J Evol Biol*, 2021, 34: 339–351
- 140 Meseguer A S, Condamine F L. Ancient tropical extinctions at high latitudes contributed to the latitudinal diversity gradient. *Evolution*, 2020, 74: 1966–1987
- 141 Stebbins G L. *Flowering Plants: Evolution Above the Species Level*. Cambridge: Belknap Press of Harvard University Press, 1974
- 142 Jablonski D, Roy K, Valentine J W. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 2006, 314: 102–106
- 143 Romdal T S, Araújo M B, Rahbek C. Life on a tropical planet: niche conservatism and the global diversity gradient. *Glob Ecol Biogeogr*, 2013, 22: 344–350
- 144 Wiens J J, Ackerly D D, Allen A P, et al. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol Lett*, 2010, 13: 1310–1324
- 145 Judd W S, Sanders R W, Donoghue M J. Angiosperm family pairs: preliminary phylogenetic analyses. *Harvard Pap Bot*, 1994, 5: 1–51
- 146 Crame J A. Early Cenozoic evolution of the latitudinal diversity gradient. *Earth Sci Rev*, 2020, 202: 103090
- 147 Janzen D H. Why mountain passes are higher in the tropics. *Am Nat*, 1967, 101: 233–249
- 148 Gentry A H. Neotropical floristic diversity: phytogeographical connections between central and south America, pleistocene climatic fluctuations, or an accident of the andean orogeny? *Ann Missouri Bot Gard*, 1982, 69: 557

- 149 Hoorn C, Wesselingh F P, ter Steege H, et al. Amazonia through time: andean uplift, climate change, landscape evolution, and biodiversity. [Science](#), 2010, 330: 927–931
- 150 Ding W N, Ree R H, Spicer R A, et al. Ancient orogenic and monsoon-driven assembly of the world's richest temperate alpine flora. [Science](#), 2020, 369: 578–581
- 151 Lu L M, Mao L F, Yang T, et al. Evolutionary history of the angiosperm flora of China. [Nature](#), 2018, 554: 234–238
- 152 Chen Y S, Deng T, Zhou Z, et al. Is the East Asian flora ancient or not? [Natl Sci Rev](#), 2018, 5: 920–932
- 153 Harrison S P, Yu G, Takahara H, et al. Diversity of temperate plants in east Asia. [Nature](#), 2001, 413: 129–130
- 154 Stanley S M. *Macroevolution: Pattern and Process*. San Francisco: W. H. Freeman, 1979
- 155 Marshall C R. Five palaeobiological laws needed to understand the evolution of the living biota. [Nat Ecol Evol](#), 2017, 1: 0165
- 156 Beaulieu J M, O'Meara B C. Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. [Syst Biol](#), 2016, 65: 583–601
- 157 Gilinsky N L. Volatility and the Phanerozoic decline of background extinction intensity. [Paleobiology](#), 1994, 20: 445–458
- 158 Madriñán S, Cortés A J, Richardson J E. Páramo is the world's fastest evolving and coolest biodiversity hotspot. [Front Genet](#), 2013, 4: 192
- 159 Sauquet H, Weston P H, Anderson C L, et al. Contrasted patterns of hyperdiversification in Mediterranean hotspots. [Proc Natl Acad Sci USA](#), 2009, 106: 221–225
- 160 Schley R J, de la Estrella M, Pérez-Escobar O A, et al. Is Amazonia a 'museum' for Neotropical trees? The evolution of the Brownea clade (Detarioideae, Leguminosae). [Mol Phylogenet Evol](#), 2018, 126: 279–292
- 161 Koenen E J M, Clarkson J J, Pennington T D, et al. Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. [New Phytol](#), 2015, 207: 327–339
- 162 Boucher-Lalonde V, De Camargo R X, Fortin J, et al. The weakness of evidence supporting tropical niche conservatism as a main driver of current richness-temperature gradients. [Glob Ecol Biogeogr](#), 2015, 24: 795–803
- 163 Jablonski D, Huang S, Roy K, et al. Shaping the latitudinal diversity gradient: new perspectives from a synthesis of paleobiology and biogeogr. [Am Nat](#), 2017, 189: 1–12
- 164 Eisehardt W L, Couvreur T L P, Baker W J. Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. [New Phytol](#), 2017, 214: 1408–1422
- 165 Pontarp M, Bunnefeld L, Cabral J S, et al. The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. [Trends Ecol Evol](#), 2019, 34: 211–223
- 166 Arita H T, Vázquez-Domínguez E. The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. [Ecol Lett](#), 2008, 11: 653–663
- 167 Moreau C S, Bell C D. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. [Evolution](#), 2013, 67: 2240–2257
- 168 Araujo M L, Coelho M T P, Cassemiro F A S, et al. Global distribution of mammalian cradles and museums is driven by past climate dynamics and present water-energy balance. [Glob Ecol Biogeogr](#), 2024, 33: e13914
- 169 Stanley S M. A theory of evolution above the species level. [Proc Natl Acad Sci USA](#), 1975, 72: 646–650
- 170 Brown J H, Maurer B A. Macroecology: the division of food and space among species on continents. [Science](#), 1989, 243: 1145–1150
- 171 Ricklefs R E. History and diversity: explorations at the intersection of ecology and evolution. [Am Nat](#), 2007, 170: S56–S70
- 172 Jarne P, Pinay G. Towards closer integration between ecology and evolution. [Ecol Lett](#), 2023, 26: S5
- 173 Buckley Y M, Puy J. The macroecology of plant populations from local to global scales. [New Phytol](#), 2021, 233: 1038–1050
- 174 Kreft H, Jetz W. Global patterns and determinants of vascular plant diversity. [Proc Natl Acad Sci USA](#), 2007, 104: 5925–5930
- 175 Baldwin B G, Thornhill A H, Freyman W A, et al. Species richness and endemism in the native flora of California. [Am J Bot](#), 2017, 104: 487–501
- 176 Beyer R M, Manica A. Historical and projected future range sizes of the world's mammals, birds, and amphibians. [Nat Commun](#), 2020, 11: 5633
- 177 Slatyer R A, Hirst M, Sexton J P, et al. Niche breadth predicts geographical range size: a general ecological pattern. [Ecol Lett](#), 2013, 16: 1104–1114
- 178 Lenoir J, Svenning J. Climate-related range shifts—a global multidimensional synthesis and new research directions. [Ecography](#), 2014, 38: 15–28

- 179 Struebig M J, Aninta S G, Beger M, et al. Safeguarding imperiled biodiversity and evolutionary processes in the Wallacea center of endemism. *Bioscience*, 2022, 72: 1118–1130
- 180 Zhang Y, Wang G, Zhuang H, et al. Integrating hotspots for endemic, threatened and rare species supports the identification of priority areas for vascular plants in SW China. *For Ecol Manag*, 2021, 484: 118952
- 181 Yu H, Deane D C, Zhang Y, et al. Integrating multiple indices of geobiodiversity reveals a series of regional species-rich areas worthy of conservation in the region of the Qinghai-Tibetan Plateau. *Biol Conser*, 2021, 261: 109238
- 182 Cain S A. *Foundations of Plant Geography*. New York: Harper & Brothers, 1944
- 183 Qian H, Mishler B D, Zhang J, et al. Global patterns and ecological drivers of taxonomic and phylogenetic endemism in angiosperm genera. *Plant Divers*, 2024, 46: 149–157
- 184 Qian H, Kessler M, Qian S, et al. Patterns and drivers of taxonomic and phylogenetic endemism in regional fern floras across the world. *Biol Conserv*, 2024, 291: 110506
- 185 Sandel B, Weigelt P, Kreft H, et al. Current climate, isolation and history drive global patterns of tree phylogenetic endemism. *Glob Ecol Biogeogr*, 2020, 29: 4–15
- 186 Feng G, Ma Z, Sandel B, et al. Species and phylogenetic endemism in angiosperm trees across the Northern Hemisphere are jointly shaped by modern climate and glacial-interglacial climate change. *Glob Ecol Biogeogr*, 2019, 28: 1393–1402
- 187 Guo W Y, Serra-Diaz J M, Eiserhardt W L, et al. Climate change and land use threaten global hotspots of phylogenetic endemism for trees. *Nat Commun*, 2023, 14: 6950
- 188 Cheikh Albassatneh M, Escudero M, Monnet A, et al. Spatial patterns of genus-level phylogenetic endemism in the tree flora of Mediterranean Europe. *Divers Distrib*, 2021, 27: 913–928
- 189 Folk R A, Siniscalchi C M, Doby J, et al. Spatial phylogenetics of Fagales: investigating drivers of temperate forest distributions. *J Biogeogr*, 2024, 51: 1518–1532
- 190 Zhang X, Ye J, Laffan S W, et al. Spatial phylogenetics of the Chinese angiosperm flora provides insights into endemism and conservation. *J Integr Plant Biol*, 2022, 64: 105–117
- 191 Earl C, Belitz M W, Laffan S W, et al. Spatial phylogenetics of butterflies in relation to environmental drivers and angiosperm diversity across North America. *iScience*, 2021, 24: 102239
- 192 Aragón-Parada J, Carrillo-Reyes P, Rodríguez A, et al. Spatial phylogenetics of the flora in the Sierra Madre del Sur, Mexico: evolutionary puzzles in tropical mountains. *J Biogeogr*, 2023, 50: 1679–1691
- 193 Nitta J H, Mishler B D, Iwasaki W, et al. Spatial phylogenetics of Japanese ferns: patterns, processes, and implications for conservation. *Am J Bot*, 2022, 109: 727–745
- 194 Mishler B D, Guralnick R, Soltis P S, et al. Spatial phylogenetics of the North American flora. *J Syst Evol*, 2020, 58: 393–405
- 195 Zhu Z, Harris A J, Nizamani M M, et al. Spatial phylogenetics of the native woody plant species in Hainan, China. *Ecol Evol*, 2021, 11: 2100–2109
- 196 Zhang Y, Qian L, Spalink D, et al. Spatial phylogenetics of two topographic extremes of the Hengduan Mountains in southwestern China and its implications for biodiversity conservation. *Plant Divers*, 2021, 43: 181–191
- 197 Spalink D, Kriebel R, Li P, et al. Spatial phylogenetics reveals evolutionary constraints on the assembly of a large regional flora. *Am J Bot*, 2018, 105: 1938–1950
- 198 Allen J M, Germain-Aubrey C C, Barve N, et al. Spatial phylogenetics of florida vascular plants: the effects of calibration and uncertainty on diversity estimates. *iScience*, 2019, 11: 57–70
- 199 Song W, Li Y, Luo A, et al. The phylogenetic structure patterns of angiosperm species and their determinants in East Eurasia. *Glob Ecol Biogeogr*, 2024, 33: e13897
- 200 Murali G, Gumbs R, Meiri S, et al. Global determinants and conservation of evolutionary and geographic rarity in land vertebrates. *Sci Adv*, 2021, 7: eabe5582
- 201 Mishler B D, Knerr N, González-Orozco C E, et al. Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian Acacia. *Nat Commun*, 2014, 5: 4473
- 202 Faith D P. Conservation evaluation and phylogenetic diversity. *Biol Conserv*, 1992, 61: 1–10
- 203 Faith D P. Quantifying biodiversity: a phylogenetic perspective. *Conserv Biol*, 2002, 16: 248–252

- 204 Forest F, Grenyer R, Rouget M, et al. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, 2007, 445: 757–760
- 205 Hao Q, Liu H, Cheng Y, et al. The LGM refugia of deciduous oak and distribution development since the LGM in China. *Sci China Earth Sci*, 2023, 66: 80–91
- 206 Manchester S R, Chen Z, Lu A, et al. Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. *J Syst Evol*, 2009, 47: 1–42
- 207 Zhou Z H, Momohara A. Fossil history of some endemic seed plants of East Asia and its phytogeographical significance (in Chinese). *Acta Bot Yunnan*, 2005, 5: 3–24 [周浙昆, Momohara A. 一些东亚特有种子植物的化石历史及其植物地理学意义. *云南植物研究*, 2005, 5: 3–24]
- 208 Guo Q, Ricklefs R E, Cody M L. Vascular plant diversity in eastern Asia and North America: historical and ecological explanations. *Bot J Linn Soc*, 1998, 128: 123–136
- 209 Qian H. A Comparison of generic endemism of vascular plants between East Asia and North America. *Int J Plant Sci*, 2001, 162: 191–199
- 210 Qian H, Ricklefs R E. Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, 2000, 407: 180–182
- 211 Guo Q, Ricklefs R E. Species richness in plant genera disjunct between temperate eastern Asia and North America. *Bot J Linn Soc*, 2000, 134: 401–423
- 212 Zhu H, Tan Y. The origin of evergreen broad-leaved forests in East Asia from the evidence of floristic elements. *Plants*, 2024, 13: 1106
- 213 Zhang Q, Yang Y, Liu B, et al. Meta-analysis provides insights into the origin and evolution of East Asian evergreen broad-leaved forests. *New Phytol*, 2024, 242: 2369–2379
- 214 Ye J, Li D. Diversification of East Asian subtropical evergreen broadleaved forests over the last 8 million years. *Ecol Evol*, 2022, 12: e9451
- 215 Ye J W, Tian B, Li D Z. Monsoon intensification in East Asia triggered the evolution of its flora. *Front Plant Sci*, 2022, 13: 1046538
- 216 Ashton P, Zhu H. The tropical-subtropical evergreen forest transition in East Asia: an exploration. *Plant Divers*, 2020, 42: 255–280
- 217 Zhao J, Li S, Huang J, et al. Heterogeneous occurrence of evergreen broad-leaved forests in East Asia: evidence from plant fossils. *Plant Divers*, 2024, 47: 1–12
- 218 Wu S D, Zhang L J, Lin L, et al. Insights into the historical assembly of global dryland floras: the diversification of Zygophyllaceae. *BMC Evol Biol*, 2018, 18: 166
- 219 Xing Y, Ree R H. Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proc Natl Acad Sci USA*, 2017, 114: E3444
- 220 Favre A, Päckert M, Pauls S U, et al. The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biol Rev*, 2015, 90: 236–253
- 221 Stokstad E. Mountains and monsoons created Tibetan biodiversity. *Science*, 2020, 369: 493
- 222 Li Q, Sun H, Boufford D E, et al. Grade of Membership models reveal geographical and environmental correlates of floristic structure in a temperate biodiversity hotspot. *New Phytol*, 2021, 232: 1424–1435
- 223 Muellner-Riehl A N, Favre A. Mountain biogeography coming full circle: a new ‘3D’ floristic approach provides units for reconstructing evolutionary trajectories. *New Phytol*, 2021, 232: 964–966
- 224 Qian H, Ricklefs R E. A comparison of the taxonomic richness of vascular plants in China and the United States. *Am Nat*, 1999, 154: 160–181
- 225 Qian H, Jin Y, Ricklefs R E. Phylogenetic diversity anomaly in angiosperms between eastern Asia and eastern North America. *Proc Natl Acad Sci USA*, 2017, 114: 11452–11457
- 226 Hu H, Ye J, Liu B, et al. Temporal and spatial comparisons of angiosperm diversity between eastern Asia and North America. *Natl Sci Rev*, 2021, 9: nwab199
- 227 Melton A E, Chen S, Zhao Y, et al. Genetic insights into the evolution of genera with the eastern Asia-eastern North America floristic disjunction: a transcriptomics analysis. *Am J Bot*, 2020, 107: 1736–1748
- 228 Vasconcelos T N C, Alcantara S, Andrino C O, et al. Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. *Proc R Soc B*, 2020, 287: 20192933
- 229 Meseguer A S, Michel A, Fabre P H, et al. Diversification dynamics in the Neotropics through time, clades, and biogeographic regions. *eLife*, 2022, 11: e74503
- 230 Velasco J A, Pinto-Ledezma J N. Mapping species diversification metrics in macroecology: prospects and challenges. *Front Ecol Evol*, 2022, 10: 951271
- 231 Fryxell P A. The “relict species” concept. *Acta Biotheor*, 1962, 15: 105–118

- 232 Denk T, Frotzler N, Davitashvili N. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). *Biol J Linn Soc*, 2001, 72: 287–332
- 233 Calleja J A, Benito Garzón M, Sainz Ollero H. A Quaternary perspective on the conservation prospects of the Tertiary relict tree *Prunus lusitanica* L. *J Biogeogr*, 2009, 36: 487–498
- 234 Shang K K, Song K, Da L J. Ecology of relict tertiary deciduous trees in subtropical China. In: Box E O, ed. *Pollen: Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales*. Cham: Springer International Publishing, 2016. 149–167
- 235 Wolfe J A. Some aspects of plant geography of the Northern Hemisphere during the late cretaceous and Tertiary. *Ann Missouri Bot Gard*, 1975, 62: 264–279
- 236 Tzedakis P C, Lawson I T, Frogley M R, et al. Buffered tree population changes in a quaternary refugium: evolutionary implications. *Science*, 2002, 297: 2044–2047
- 237 Hewitt G. The genetic legacy of the Quaternary ice ages. *Nature*, 2000, 405: 907–913
- 238 Wen J. Evolution of eastern Asian-eastern North American biogeographic disjunctions: a few additional issues. *Int J Plant Sci*, 2001, 162: S117–S122
- 239 Zhang S H, Shen S Z, Wang X D, et al. A perspective on reconstructing the spatial and temporal patterns of Earth’ biodiversity in deep time (in Chinese). *Chin Sci Bull*, 2024, 69: 3252–3267 [张书涵, 沈树忠, 王向东, 等. 重建深时地球生物多样性时空分布模式的思考. 科学通报, 2024, 69: 3235–3267]
- 240 Huang B. A brief discussion on paleontology research in the context of Big Data (in Chinese). *Acta Palaeontol Sin*, 2023, 62: 516–530 [黄冰. 浅谈大数据语境下的古生物学研究. 古生物学报, 2023, 62: 516–530]
- 241 Miao L Y. Big data applications in paleobiogeography and macroevolutionary studies (in Chinese). *Science*, 2020, 72: 22–25 [缪璐漪. 古生物地理学和宏演化研究中的大数据应用. 科学, 2020, 72: 22–25]
- 242 Sauquet H, Magallón S. Key questions and challenges in angiosperm macroevolution. *New Phytol*, 2018, 219: 1170–1187
- 243 Zuntini A R, Carruthers T, Maurin O, et al. Phylogenomics and the rise of the angiosperms. *Nature*, 2024, 629: 843–850
- 244 Gaston K J. Global patterns in biodiversity. *Nature*, 2000, 405: 220–227
- 245 Economo E P, Narula N, Friedman N R, et al. Macroecology and macroevolution of the latitudinal diversity gradient in ants. *Nat Commun*, 2018, 9: 1778
- 246 Davies T J. The macroecology and macroevolution of plant species at risk. *New Phytol*, 2019, 222: 708–713
- 247 Liu Y, Xu X, Dimitrov D, et al. An updated floristic map of the world. *Nat Commun*, 2023, 14: 2990
- 248 Qian H. Reassessing data quality underlying the recently updated floristic map of the world. *Nat Commun*, 2024, 15: 3674
- 249 Liu Y, Xu X, Dimitrov D, et al. Reply to: reassessing data quality underlying the recently updated floristic map of the world. *Nat Commun*, 2024, 15: 3673
- 250 Holt B G, Lessard J P, Borregaard M K, et al. An update of Wallace’s zoogeographic regions of the world. *Science*, 2013, 339: 74–78
- 251 Holt B G, Lessard J P, Borregaard M K, et al. Response to comment on “An Update of Wallace’s Zoogeographic Regions of the World”. *Science*, 2013, 341: 343
- 252 Krefl H, Jetz W. Comment on “An Update of Wallace’s Zoogeographic Regions of the World”. *Science*, 2013, 341: 343
- 253 Craven D, Knight T M, Barton K E, et al. Dissecting macroecological and macroevolutionary patterns of forest biodiversity across the Hawaiian archipelago. *Proc Natl Acad Sci USA*, 2019, 116: 16436–16441
- 254 Bromham L, Hua X, Cardillo M. Macroevolutionary and macroecological approaches to understanding the evolution of stress tolerance in plants. *Plant Cell Environ*, 2020, 43: 2832–2846
- 255 Cai L, Krefl H, Taylor A, et al. Global models and predictions of plant diversity based on advanced machine learning techniques. *New Phytol*, 2022, 237: 1432–1445
- 256 Carta A, Peruzzi L, Ramírez-Barahona S. A global phylogenetic regionalization of vascular plants reveals a deep split between Gondwanan and Laurasian biotas. *New Phytol*, 2021, 233: 1494–1504
- 257 Antonelli A. Biogeography: drivers of bioregionalization. *Nat Ecol Evol*, 2017, 1: 0114
- 258 Vilhena D A, Antonelli A. A network approach for identifying and delimiting biogeographical regions. *Nat Commun*, 2015, 6: 6848
- 259 Qian H, Qian S, Zhang J, et al. Effects of climate and environmental heterogeneity on the phylogenetic structure of regional angiosperm floras worldwide. *Nat Commun*, 2024, 15: 1079

- 260 Qian H, Kessler M, Zhang J, et al. Evolutionary causes of global patterns of species richness in regional fern floras across the world. *J Biogeogr*, 2024, 51: 1429–1437
- 261 Smith J R, Letten A D, Ke P J, et al. A global test of ecoregions. *Nat Ecol Evol*, 2018, 2: 1889–1896
- 262 Meyer C, Weigelt P, Kreft H, et al. Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecol Lett*, 2016, 19: 992–1006
- 263 Hortal J, de Bello F, Diniz-Filho J A F, et al. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu Rev Ecol Evol Syst*, 2015, 46: 523–549
- 264 Qian H. Are species lists derived from modeled species range maps appropriate for macroecological studies? A case study on data from BIEN. *Basic Appl Ecol*, 2020, 48: 146–156
- 265 Hughes A C, Orr M C, Ma K, et al. Sampling biases shape our view of the natural world. *Ecography*, 2021, 44: 1259–1269
- 266 Sandall E L, Maureaud A A, Guralnick R, et al. A globally integrated structure of taxonomy to support biodiversity science and conservation. *Trends Ecol Evol*, 2023, 38: 1143–1153
- 267 Hughes A C, Dorey J B, Bossert S, et al. Big data, big problems? How to circumvent problems in biodiversity mapping and ensure meaningful results. *Ecography*, 2024, 2024: e07115
- 268 Levin S A. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, 1992, 73: 1943–1967
- 269 Wiens J A. Spatial scaling in ecology. *Funct Ecol*, 1989, 3: 385–397
- 270 Pichler M, Hartig F. Machine learning and deep learning—a review for ecologists. *Methods Ecol Evol*, 2023, 14: 994–1016
- 271 Olden J D, Lawler J J, Poff N L R. Machine learning methods without tears: a primer for ecologists. *Q Rev Biol*, 2008, 83: 171–193
- 272 Myers N. Threatened biotas: “Hot spots” in tropical forests. *Environmentalist*, 1988, 8: 187–208
- 273 Myers N, Mittermeier R A, Mittermeier C G, et al. Biodiversity hotspots for conservation priorities. *Nature*, 2000, 403: 853–858
- 274 Noss R F, Platt W J, Sorrie B A, et al. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Divers Distrib*, 2015, 21: 236–244
- 275 Habel J C, Rasche L, Schneider U A, et al. Final countdown for biodiversity hotspots. *Conserv Lett*, 2019, 12: e12668
- 276 Mittermeier R, Turner W, Larsen F, et al. Global biodiversity conservation: the critical role of hotspots. In: Zachos F E, Habel J C, eds. *Pollen: Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas*. Berlin: Springer-Verlag Berlin Heidelberg, 2011. 3–22
- 277 Fritz S A, Schnitzler J, Eronen J T, et al. Diversity in time and space: wanted dead and alive. *Trends Ecol Evol*, 2013, 28: 509–516
- 278 Benton M J. Exploring macroevolution using modern and fossil data. *Proc R Soc B*, 2015, 282: 20150569
- 279 Flannery-Sutherland J T, Silvestro D, Benton M J. Global diversity dynamics in the fossil record are regionally heterogeneous. *Nat Commun*, 2022, 13: 2751
- 280 Smiley T M, Bahadori A, Rasbury E T, et al. Tectonic extension and paleoelevation influence mammalian diversity dynamics in the Basin and range province of western North America. *Sci Adv*, 2024, 10: eadn6842
- 281 Gaston K, Blackburn T. *Pattern and Process in MacroEcology*. Hoboken: Wiley-Blackwell, 2000
- 282 McGill B J, Algar A. The what, how and why of doing macroecology. *Glob Ecol Biogeogr*, 2019, 28: 6–17
- 283 Mo Y K, Hahn M W, Smith M L. Applications of machine learning in phylogenetics. *Mol Phylogenet Evol*, 2024, 196: 108066
- 284 Park D S, Willis C G, Xi Z, et al. Machine learning predicts large scale declines in native plant phylogenetic diversity. *New Phytol*, 2020, 227: 1544–1556
- 285 Alexander Pyron R. Unsupervised machine learning for species delimitation, integrative taxonomy, and biodiversity conservation. *Mol Phylogenet Evol*, 2023, 189: 107939
- 286 Saryan P, Gupta S, Gowda V. Species complex delimitations in the genus *Hedychium*: a machine learning approach for cluster discovery. *Appl Plant Sci*, 2020, 8: e11377

Macroevolutionary and macroecological perspectives on the spatiotemporal patterns of endemic vascular plants in temperate Asia

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The holistic view of nature held by 19th-century naturalists laid the foundation for biodiversity research. The rise of population biology paradigms in the early 20th century led to a separation between ecological and evolutionary studies, weakening macro-scale research. To analyze diversity patterns across broad spatiotemporal scales, integrative research in macroevolution and macroecology has gradually emerged. Leveraging advancements in big data and analytical methods, this field integrates phylogenetic reconstruction, divergence time estimation, and eco-evolutionary inference to uncover the mechanisms driving biodiversity from a “Deep Time and Broad Scale” perspective, thereby providing scientific support for biodiversity conservation. Temperate Asia, a key region with over 67% of endemic vascular plant species, exhibits two major floristic characteristics: “eastern Asian and eastern North American disjunct distributions” and “Tertiary relict floras”. These features reflect processes of isolation, divergence, and refuge survival upon geological and climatic changes. This review summarizes key advances in the study of endemic vascular plants in this region, including quantification of endemism, the museum/cradle, and the climate refuge hypothesis, aiming to provide a basis for biodiversity conservation and further research in the area.

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