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云南香格里拉亚高山寒温性针叶林优势种空间分布格局及种内种间关联性

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摘 要 植物种群空间分布格局是散布限制和环境过滤等多种生态过程综合作用的结果。分布在高山树线交错带的植物因其特殊的生境, 对气候变化表现出高度的敏感性。因此, 研究这些植物的空间分布格局及其相互关系, 对理解和预测高山林线森林群落的动态和发展趋势至关重要。该研究基于云南香格里拉亚高山寒温性针叶林20 hm^{2}动态监测样地的调查数据, 以样地内优势种长苞冷杉(*Abies georgei*)、亚乔木层优势种红棕杜鹃(*Rhododendron rubiginosum*)和西南花楸(*Sorbus rehderiana*)、灌木层优势种唐古特忍冬(*Lonicera tangutica*)和云南双盾木(*Dipelta yunnanensis*)为研究对象, 采用空间点格局方法分析各优势种的空间分布格局、长苞冷杉不同发育阶段间的种内关联性、长苞冷杉与其他优势种间的种间关联性, 以及其他优势种种间关联性, 并使用Torus-translation方法检验这些植物与地形因子的关联性。结果表明: (1)长苞冷杉的幼树和中树均呈现聚集分布, 这主要由散布限制和生境异质性驱动; 而成树主要呈随机分布, 表明密度依赖性的竞争对大径级个体分布的主导作用。亚乔木层和灌木层的优势种均呈聚集分布, 但剔除环境异质性后部分优势种转变为随机分布, 说明环境过滤驱动了树种空间分布模式。(2)长苞冷杉的幼树与中树呈正关联, 可能是小径级个体通过集群作用来提高抵御外界环境胁迫的能力。幼树和中树与成树呈负关联, 这主要受由密度制约引起的专一性病原菌和植食性昆虫的侵害以及大个体对小个体的不对称竞争的影响。(3)长苞冷杉的幼树与亚乔木层和灌木层的优势种分别呈正关联和负关联; 中树与其他优势种大多表现为负关联, 而成树则多表现为正关联; 乔木层和灌木层优势种之间多表现为正关联。说明亚高山寒温性针叶林优势种之间存在复杂的动态平衡。各优势种通过独特的生存策略和资源利用方式来实现长期共存, 最终形成以长苞冷杉为主导的相对稳定的顶极群落。(4)坡度与长苞冷杉的幼树和中树的密度显著负相关, 与红棕杜鹃和云南双盾木显著正相关, 说明长苞冷杉与其他优势种发生了坡度生态位的分化。此外, 由于冬季积雪时间较长等不利因素, 凹凸度也对优势种的分布具有显著的影响。总体而言, 地形驱动的生境过滤可能是维持亚高山寒温性针叶林群落构建的主要驱动力。

关键词 长苞冷杉; 点格局; 空间关联性; 生境关联

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Spatial distribution patterns and intraspecific and interspecific associations of dominant species in subalpine cold-temperate coniferous forests of Shangri-La, Yunnan, China

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Abstract

Aims The spatial distribution patterns of plant populations result from the combined effects of multiple

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ecological processes, such as dispersal limitation and environmental filtering. The plants distributed in alpine treeline ecotones are highly sensitive to climate change due to their unique habitats. Therefore, studying the spatial distribution patterns of these plants and their correlations is critical for understanding and predicting the dynamics and trends of forest communities in alpine treelines.

Methods This study is based on the inventory data collected from a 20 hm^2 dynamics plot of a subalpine cold-temperate coniferous forest in Shangri-La, Yunnan, China. The dominant tree species identified were *Abies georgei*, *Lonicera tangutica*, *Dipelta yunnanensis*, *Rhododendron rubiginosum*, and *Sorbus rehderiana*. The spatial point pattern method was used to analyze the spatial distribution pattern of each dominant species, the intraspecific association of *A. georgei* at different developmental stages, the interspecific association between *A. georgei* and the other dominant species, and the interspecific association among the other dominant species. Additionally, the Torus-translation method was applied to test the associations between these plants and topographic factors.

Important findings (1) Sapling and juvenile trees of *A. georgei* demonstrated aggregated distributions, primarily driven by dispersal limitation and habitat heterogeneity. In contrast, adult trees exhibited a predominantly random distribution, suggesting that density-dependent competition may be the primary factor influencing the distribution of individuals in large-diameter classes. The dominant species in both the subtree layer and shrub layer also demonstrated aggregated distribution. However, the posterior partial advantage of the environmental heterogeneity transformed into a random distribution, indicating that environmental filtering might be responsible for driving the spatial distribution pattern of these tree species. (2) Positive associations were observed between sapling and juvenile trees of *A. georgei* indicating that small-diameter individuals tend to congregate due to an enhanced capacity to cope with external environmental stresses. Conversely, saplings and juvenile trees were negatively correlated with adult trees. This was mainly due to the infestation of specific pathogens and phytophagous insects caused by density constraints and asymmetric competition of large individuals against smaller ones. (3) There were positive and negative correlations between the saplings and the dominant species in the subtree layer and the shrub layer, respectively. The juvenile trees and other dominant species revealed predominantly negative correlation, while the adult trees showed predominantly positive correlation. The majority of the dominant species in the tree layer and shrub layer exhibited positive correlation, indicating a complex dynamic balance within the dominant species in the subalpine cold-temperate coniferous forest. The long-term coexistence of each dominant species in the plot is achieved through their unique survival strategies and resource utilization, and ultimately leading to the formation of a relatively stable successional climax community dominated by *A. georgei*. (4) Slope was found to be significantly negatively correlated with sapling and juvenile trees of *A. georgei*, and significantly positively related to *R. rubiginosum* and *D. yunnanensis*. This suggests that the slope ecological niche differentiation occurred between *A. georgei* and other dominant species. Additionally, convexity was found to exert a significant effect on the distribution of dominant species due to adverse conditions such as prolonged snowpack in winter. In conclusion, the habitat filtering driven by topography is the main driver that maintains community assembly in subalpine cold-temperate coniferous forests.

Key words *Abies georgei*; spatial point pattern; spatial association; habitat association

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IPCC第六次评估报告指出, 在未来20年内, 全球平均气温的上升幅度可能会超过1.5 ℃, 其中高海拔和高纬度地区受气候变化的影响尤为显著和迅速(Lee et al., 2021)。气候变化对森林生态系统构成了严重的威胁, 尤其是对山地森林生态系统。树线作为山体达到一定高度时森林分布的上限, 被视为高海拔生态系统中承受环境压力最大的地区之一(Hermes, 1955)。随着全球温度的持续升高, 树线位置可能会上移, 这一变化不仅改变了树线植物种群的分布格局, 也对整个山地生态系统的结构和功能造成影响(Körner & Paulsen, 2004; Adams et al., 2009)。高山树线交错带作为森林与高山草甸之间的生态过渡带, 由于其结构相对简单且对气候变化高度敏感, 正面临着日益加剧的气候变化威胁

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(Gauthier et al., 2015)。因此, 高山树线交错带的植物群落组成、结构以及动态变化逐渐成为研究者们关注的焦点(Barros et al., 2017)。

研究植物种群空间格局对揭示种群结构及其生态学过程至关重要(Getzin et al., 2008)。种群的空间分布格局通常可分为聚集、随机和均匀3种类型。其中聚集分布主要由基于生态位理论的生境异质性和基于中性理论的扩散限制所驱动(Condit et al., 2000; Wiegand & Moloney, 2014), 尤其是小尺度上的聚集多由扩散限制所致(Harms et al., 2001; 李立等, 2010)。相反, 均匀分布通常由自疏效应和种内竞争引起的密度制约所引发(Sterner et al., 1986; 安璐等, 2021)。空间关联性分析可以进一步探讨物种在空间上的相互作用, 包括正关联、负关联和不相关3种类型(张金屯, 1998)。正关联表明物种之间相互依赖或生态位重叠, 负关联则反映了物种间存在竞争或密度制约效应, 不相关则说明物种能够在资源充足的环境中共存, 彼此间无明显的相互影响(张金屯, 1998; 祝燕等, 2011)。点格局分析(spatial-point-pattern-analysis, SPPA)是研究种群空间格局的一种常用方法(Brown et al., 2011), 通过将每个个体的位置视为二维空间中的点, 允许在任意尺度上分析空间分布格局和关联性。与传统的样方法、距离法和角尺度法相比, 点格局分析能够更充分地利用空间信息, 为揭示种群空间分布特征与生态过程之间的联系提供了强有力的工具(Ripley, 1977; Wiegand & Moloney, 2004)。因此, 通过点格局分析, 能够更好地揭示种群的空间分布和维持机制(Nathan, 2006)。

环境因子特别是地形因子, 在塑造植物的空间格局方面起着决定性作用(Palmer, 1990)。地形因子通过改变土壤湿度、土壤养分和光照等综合环境条件, 从而影响物种分布(Balvanera et al., 2011)。例如, 沟谷生境因水分条件较好且资源可获得性高, 往往能够支撑更多的植物种类和数量。相反, 在资源相对匮乏的山脊生境, 仅能支撑有限的植物种群(Gibbons & Newbery, 2003)。研究显示, 由不同地形因子引起的生境异质性变化, 是塑造局域尺度上不同树种的空间分布格局的主要因素。例如, 梁爽等(2014)在对海南岛尖峰岭60 hm^2热带山地雨林优势种空间分布的研究中发现, 坡度与不同生活史阶段的个体分布呈显著正相关关系, 海拔主要影响幼树的分布, 而凹凸度对幼树和中树的分布有显著影响。He等(2022)在研究秦岭皇冠25 hm^2暖温性落叶阔叶林优势树种的空间分布格局时发现, 坡度和凹凸度主要与乔木层树种分布呈正相关关系, 而与亚乔木层和灌木层树种分布呈负相关关系。这说明不同地形因子在塑造种群空间分布格局中的相对重要性在不同森林类型间存在显著差异。

长苞冷杉(*Abies georgei*)是我国特有的松科冷杉属植物, 是组成寒温性针叶林的主要树种, 也是青藏高原东南缘主要的高山林线树种(刘庆等, 2001)。该树种种群的动态变化可能对当地的物种组成、群落结构以及区域生物多样性产生深远影响。目前对长苞冷杉林的研究主要集中在种子的特征与变异(王丹等, 2023)、幼苗的生长存活动态(刘庆, 2004)、树干的径向生长动态(张贇等, 2018; 张慧等, 2022), 以及小尺度上的分布格局(张桥英等, 2008; 顾荣等, 2021)等方面。然而, 在较大空间尺度上, 关于长苞冷杉群落优势树种的分布格局、种内和种间关联性及其影响因素的研究仍相对不足。

本研究基于长苞冷杉为优势种的云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地的调查数据, 旨在探讨以下问题: (1)亚高山寒温性针叶林优势种的空间分布格局具有哪些特征? (2)长苞冷杉不同发育阶段的种内关联性如何? 长苞冷杉与其他优势种之间的种间关联性如何? (3)地形因子如何影响亚高山寒温性针叶林优势种的空间分布? 以期为揭示驱动亚高山寒温性针叶林物种多样性维持机制提供理论基础, 为普达措国家公园寒温性针叶林的经营规划提供科学依据。

1 材料和方法

1.1 研究区概况

普达措国家公园(99.90°–100.19° E, 27.73°–28.08° N)位于云南省迪庆藏族自治州香格里拉县, 是青藏高原东南缘的一部分, 位于横断山脉高寒峡谷区北段(Chen et al., 2022), 海拔范围为3 200–4 159 m, 年平均气温为4.2 ℃, 4–10月降水量为817.3 mm (杨迎花等, 2021)。该地区主要受高原季风气候的影响, 形成具有明显季节性的雪被, 降雪期至融雪期长达4–6个月。独特的气候条件孕育了高山草甸、针叶林、阔叶林和湿地等多种植被类型(赵玉堂, 2023), 是亚热带常绿阔叶林向青藏高原高寒植被的重要过渡区域(张菊梅等, 2021)。位于低纬

度高海拔的普达措国家公园保存着大片以长苞冷杉为优势种的寒温性针叶林。

1.2　样地调查

2022年, 按照全球森林观测网络(Forest Global Earth Observatory, Forest GEO)的技术规范(Condit, 1998), 在普达措国家公园内建立了一块20 hm^2的寒温性针叶林生物多样性长期监测样地。样地东西宽500 m, 南北长400 m, 使用全站仪把样地分成500个20 m × 20 m的样方, 每个20 m × 20 m的样方又分成16个5 m × 5 m的小样方, 记录并鉴定所有胸径≥1 cm的木本植物个体。记录信息包括植物编号、物种名称、在样方内的位置(坐标*x*和*y*)、胸径、分枝情况以及生长状况(如枯立、倒伏和倾斜)等。样地共有39 106株活立木, 分属于10科15属28种。其中, 长苞冷杉为样地内优势度最高的物种, 有27 463株, 占总株数的70%。亚乔木层优势种为红棕杜鹃(*Rhododendron rubiginosum*), 有1 839株, 其次是西南花楸(*Sorbus rehderiana*), 有1 026株。灌木层优势种为唐古特忍冬(*Lonicera tangutica*), 有3 663株, 其次是云南双盾木(*Dipelta yunnanensis*), 有1 920株(顾荣等, 2025)。

1.3　地形因子测量

地形因子主要包括海拔、凹凸度、坡度和坡向(Harms et al., 2001)。平均海拔由样方4个顶点处的海拔平均后得到。坡度以每个样方的任意三个角构成的平面与水平面夹角的平均值来表示。凹凸度值则由该样方的平均海拔减去与该样方相邻的8个样方平均海拔的平均值, 处于边缘的样方的凹凸度为样方中心的海拔值减去4个顶点海拔的平均值。坡向使用正弦坡向和余弦坡向分别代表东西方向和南北方向(Lin et al., 2013)。

1.4　数据分析

1.4.1　发育阶段划分

采用径级结构代替年龄结构分析种群分布格局动态, 虽然径级和龄级不同, 但在相同的环境条件下, 同一树种的径级和龄级对环境的反应规律具有一致性(Frost & Rydin, 2000)。参照寒温性针叶林相关研究中对林冠层林木径级结构的划分标准(顾荣等, 2021), 同时结合样地内长苞冷杉种群的实际情况及生活史特征。在此基础上, 将其分为3个发育阶段: 径级I (幼树, 1 cm ≤ DBH < 5 cm)、径级II (中树, 5 cm ≤ DBH < 15 cm)、径级III (成树, DBH ≥ 15 cm)。

1.4.2　种群空间分布格局及种内种间的空间关联性

该研究以Ripley (1977)提出的Ripley's *K* (*K*(*r*))函数为基础, 采用单变量成对相关函数($g(r)$), 以样地中每个个体的空间坐标为基础, 分析长苞冷杉及其他4种优势种种群的空间格局。采用Monte-Carlo拟合检验, 计算上下包迹线, 即置信区间的范围, 拟合次数为999次, 得到99%的置信区间。若$g(r)$值高于上包迹线, 种群呈聚集分布; 若$g(r)$值低于下包迹线, 种群呈均匀分布; 若$g(r)$值在包迹线之间, 种群则呈随机分布。为检验生境异质性对空间分布格局形成的作用, 使用异质性泊松过程为零模型来分析长苞冷杉及其他4种优势种种群的空间格局, 本研究以地形因子作为模拟异质泊松点过程的协变量。

采用双变量成对相关函数($g_{12}(r)$), 分析长苞冷杉不同发育阶段个体间及其与优势种之间的关联性。同理, 采用Monte-Carlo拟合检验, 随机模拟999次, 得到99%的置信区间, 并生成上下两条包迹线。$g_{12}(r)$值高于上包迹线, 则两者为正相关; $g_{12}(r)$值在包迹线之间, 则两者无相关性; $g_{12}(r)$值低于下包迹线, 则两者为负相关。此外, 使用拟合优度(Goodness of Fit, GoF)测试来评估实际点格局与零模型模拟的差异显著性(Loosmore & Ford, 2006)。

1.4.3　物种-地形生境的关联性

本研究采用Torus-translation方法检验亚高山寒温性针叶林优势种与4类地形因子之间的相关性(Harms et al., 2001)。该方法主要通过比较实际生境图和模拟生境图上物种在各类地形因子上的相对密度来确定其与地形因子的相关性。如果某个物种在某种地形因子上的实际相对密度落在最大的2.5%区间内, 则认为该物种与该地形因子呈正相关关系; 反之, 若实际相对密度落在最小的2.5%区间内, 则认为该物种与该地形因子呈负相关关系。本研究的所有数据分析和作图均在R 4.3.2软件中完成, 利用"spatstat"包分析种群的空间分布格局及其关联性, 利用"ggplot2"包作图。

2　结果和分析

2.1　寒温性针叶林优势种的空间分布格局

基于完全空间随机零模型(CSR)的分析表明, 长苞冷杉不同发育阶段的空间分布格局有所差异

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(图1)。幼树和中树的空间分布格局总体呈聚集分布，聚集度随着尺度的增大逐渐降低(图1A、1B); 成树在空间尺度0–8 m范围上呈均匀分布，但随着尺度的增大呈微弱的聚集分布，最终趋向于随机分布(图1C)。基于异质泊松零模型(HP)的点格局分析发现，幼树和中树从小尺度的随机分布最终转变为聚集分布，成树则从随机分布最终转变为均匀分布(附录I)。

对亚乔木层和灌木层的优势种进行空间分布格局分析，结果表明亚乔木层的西南花楸在空间尺度0–70 m范围内呈聚集分布，随着尺度的增大最终趋向于随机分布(图2B)。亚乔木层的红棕杜鹃、灌木层的唐古特忍冬和云南双盾木均呈聚集分布，且聚集程度随着尺度的增大逐渐降低(图2A、2C、2D)。当剔除环境异质性后红棕杜鹃从随机分布转变为聚集分布，而西南花楸、唐古特忍冬和云南双盾木整体呈随机分布(附录II)。

2.2 寒温性针叶林优势种长苞冷杉种群不同发育阶段的种内关联性

基于完全空间随机零模型的分析发现，长苞冷杉的幼树与中树在整个空间尺度上呈正关联(图3A); 幼树与成树呈负关联，随着尺度的增大转变为不相关(图3B); 中树与成树在整个空间尺度上呈负关联(图3C)。

2.3 寒温性针叶林优势种的种间关联性

对长苞冷杉种群的3个发育阶段与4种优势种之间进行关联性分析，结果表明幼树与亚乔木层的红棕杜鹃和西南花楸之间均主要呈正关联，与灌木层的唐古特忍冬和云南双盾木在整个尺度上均呈负关联(图4A、4B; 附录III)。中树除了与灌木层的唐古特忍冬表现出无关联外，与其他3种优势种之间均主要呈负关联(图4A、4B; 附录III)。成树与亚乔木层的西南花楸在小尺度上呈负关联，随着尺度的增大转变为无关联，而与其他3种优势种之间均主要呈正关联(图4A、4B; 附录III)。

对亚乔木层和灌木层的优势种进行种间空间关联性分析，结果表明红棕杜鹃在小尺度上与西南花楸和云南双盾木表现出不关联，但随尺度增大其转变为正关联，而与唐古特忍冬呈负关联(图5; 附录IV)。西南花楸与唐古特忍冬之间主要呈负关联，与云南双盾木呈正关联，但最终转变为无关联(图5; 附录IV)。灌木层的两个优势种唐古特忍冬与云南双盾木之间主要呈正关联(图5; 附录IV)。

2.4 地形对寒温性针叶林优势种空间分布格局的影响

Torus-translation检验结果表明，长苞冷杉种群及其他优势种的密度至少与一种地形因子存在显著相关性关系(表1)。具体来说，长苞冷杉幼树和中树的密度均与坡度显著负相关，成树则与海拔、凹凸度显著正相关。亚乔木层的优势种红棕杜鹃的密度与坡度、凹凸度显著正相关，西南花楸与海拔显著负相关(表1)。灌木层的优势种唐古特忍冬的密度与除坡度以外的地形因子显著正相关，云南双盾木与坡度和坡向显著正相关(表1)。Spearman相关检验显示，大部分物种的密度与海拔、凹凸度、坡度呈显著正相关或负相关(表1)。

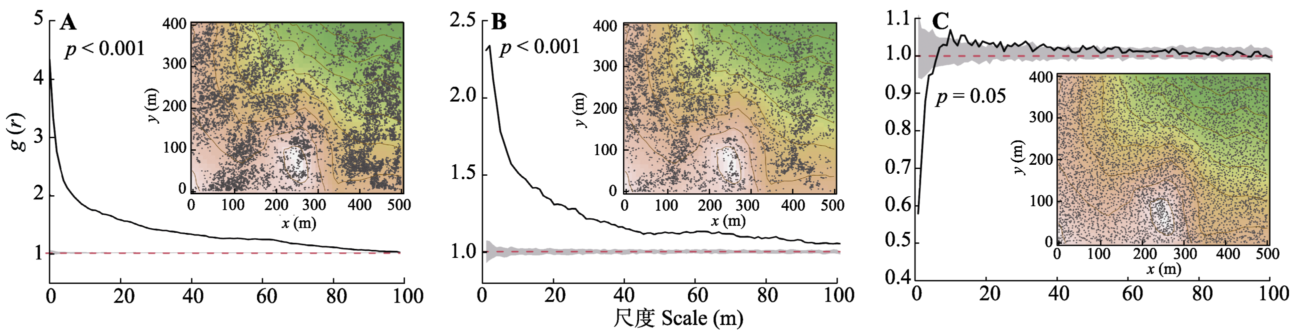

图1 云南香格里拉亚高山寒温性针叶林20 hm^{2}动态监测样地中长苞冷杉种群不同发育阶段的空间分布格局。**A,** 幼树。**B,** 中树。**C,** 成树。黑色实线表示单变量成对相关函数$g(r)$的函数值，红色虚线表示单变量成对相关函数$g(r)$的期望值，灰色阴影部分表示99%的置信区间。地图中绿色表示低海拔，红色表示高海拔。p值为拟合优度检验结果。

Fig. 1 Spatial distribution pattern of *Abies georgei* at different developmental stages in the 20 hm^2 dynamics plot of subalpine cold-temperate coniferous forest in Shangri-La, Yunnan. **A,** Saplings. **B,** Juvenile trees. **C,** Adult trees. Solid black lines represents the value of the univariate pair-correlation $g(r)$ function, the dashed red line represents the expected value of the univariate pair-correlation $g(r)$ function, and the gray shaded part represents the 99% confidence interval. Green on the map indicates low altitudes and red indicates high altitudes. The p-value is the goodness of fit test result.

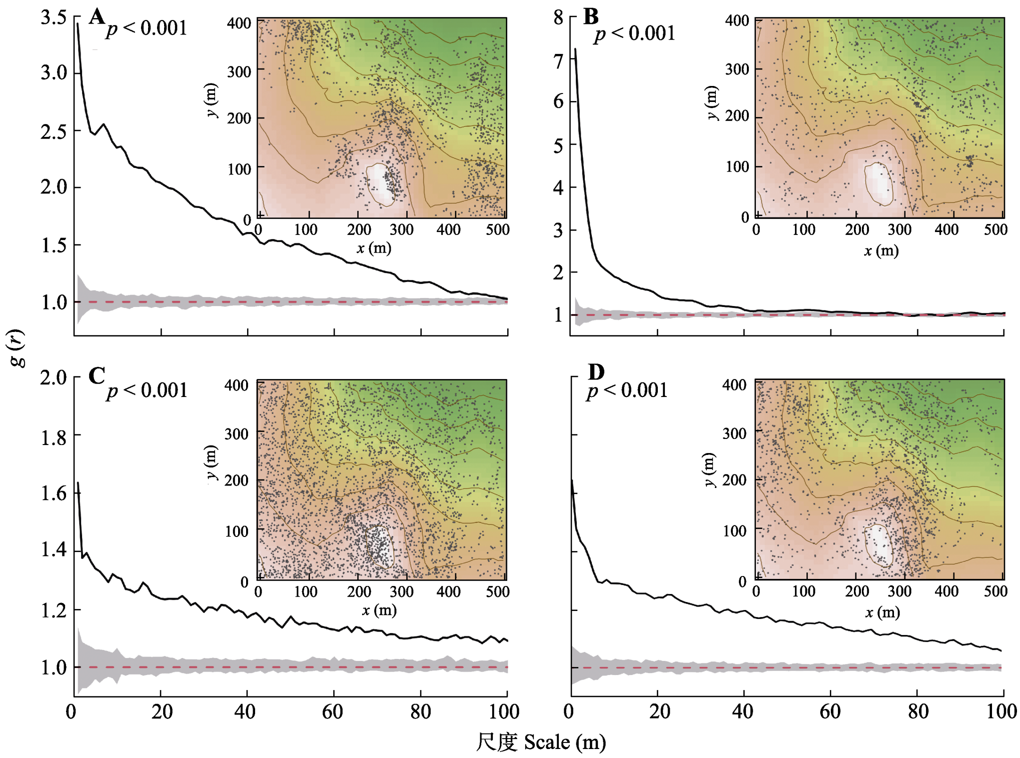

图2　云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地中亚乔木层和灌木层优势种的空间分布格局。**A,** 红棕杜鹃。**B,** 西南花楸。**C,** 唐古特忍冬。**D,** 云南双盾木。黑色实线表示单变量成对相关函数$g(r)$的函数值, 红色虚线表示单变量成对相关函数$g(r)$的期望值, 灰色阴影部分表示99%的置信区间。地图中绿色表示低海拔, 红色表示高海拔。p值为拟合优度检验结果。

Fig. 2　Spatial distribution pattern of dominant species in the subtree layer and shrub layer in the 20 hm^2 dynamics plot of subalpine cold-temperate coniferous forest in Shangri-La, Yunnan. **A,** *Rhododendron rubiginosum*. **B,** *Sorbus rehderiana*. **C,** *Lonicera tangutica*. **D,** *Dipelta yunnanensis*. Solid black lines represent the value of the univariate pair-correlation $g(r)$ function, the dashed red lines represent the expected value of the univariate pair-correlation $g(r)$ function, and the gray shaded parts represent the 99% confidence interval. Green on the map indicates low altitudes and red indicates high altitudes. The p-value is the goodness of fit test result.

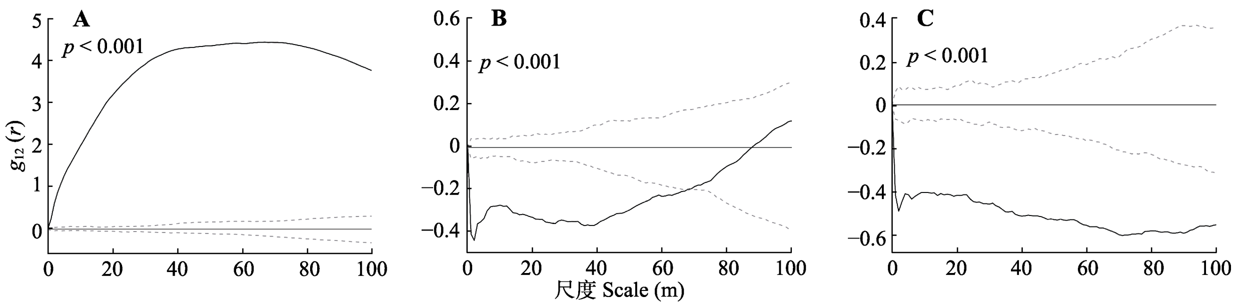

图3　云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地中长苞冷杉种群不同发育阶段的种内关联性。**A,** 幼树和中树。**B,** 幼树和成树。**C,** 中树和成树。黑色曲线表示双变量成对相关函数$g_{12}(r)$的函数值, 黑色直线表示双变量成对相关函数$g_{12}(r)$的期望值, 灰色虚线表示99%的置信区间。p值为拟合优度检验结果。

Fig. 3　Intraspecific correlation of *Abies georgei* population at different developmental stages in the 20 hm^2 dynamics plot of subalpine cold-temperate coniferous forest in Shangri-La, Yunnan. **A,** Sapling and juvenile trees. **B,** Sapling and adult trees. **C,** Juvenile and adult trees. The black curve represents the function value of the bivariate pair-correlation function $g_{12}(r)$, and the black straight line represents the expected value of the bivariate pair-correlation $g_{12}(r)$ function. The dashed gray line indicates a 99% confidence interval. The p-value is the goodness of fit test result.

3　讨论

3.1　寒温性针叶林优势种的空间分布格局

本研究中, 云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地内的长苞冷杉种群的幼树和中树主要呈聚集分布模式, 且聚集度随着尺度的增大而减小, 而成树的空间分布格局由均匀分布逐渐转变为随机分布(图1)。这一结果与国内外大多数关于

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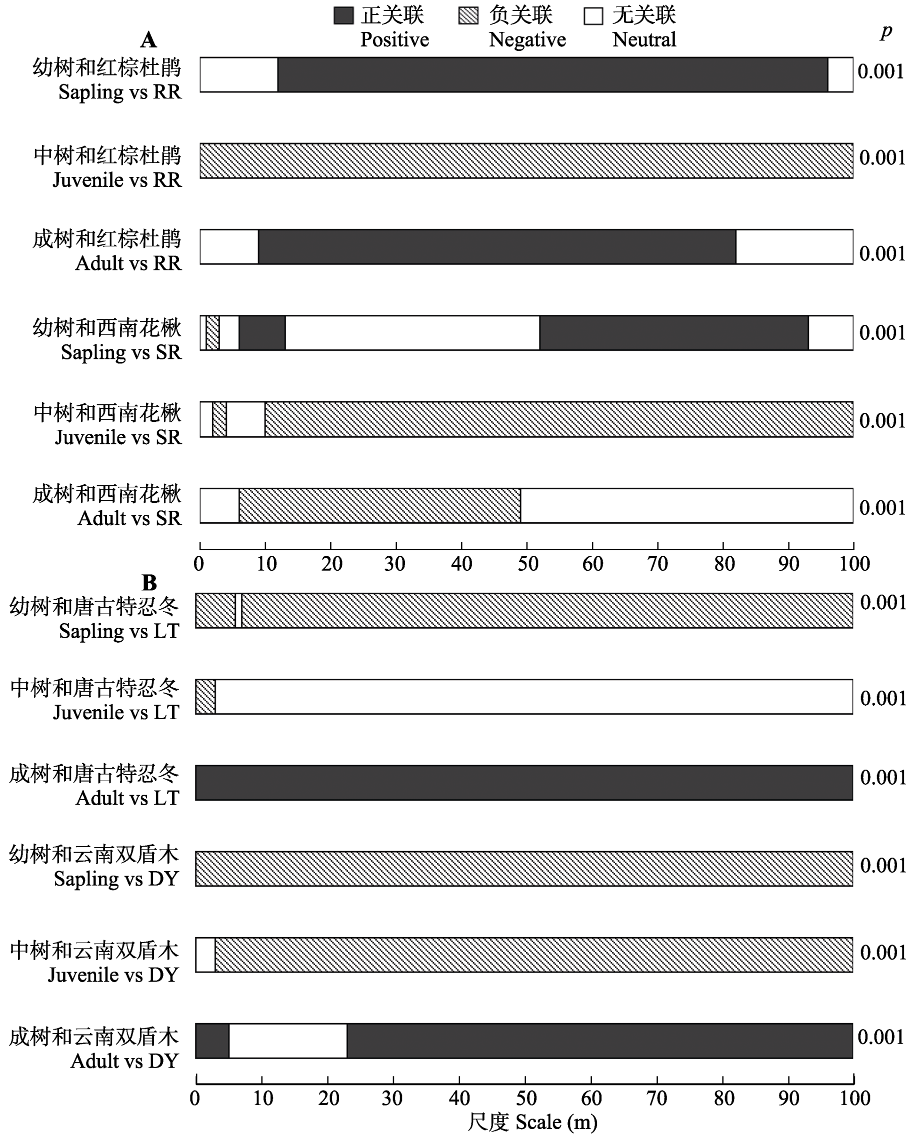

图4 云南香格里拉亚高山寒温性针叶林20 hm^{2}动态监测样地中长苞冷杉种群不同发育阶段与其他优势种的种间关联性。**A,** 长苞冷杉与亚乔木层优势种之间的关联性。**B,** 长苞冷杉与灌木层优势种之间的关联性。*p*值为拟合优度检验结果。

Fig. 4 Interspecific relationship between *Abies georgei* at different developmental stages and other dominant species in the 20 hm^2 dynamics plot of subalpine cold-temperate coniferous forest in Shangri-La, Yunnan. **A,** Relationship between *Rhododendron rubiginosum* and dominant species in subtree layers. **B,** Relationship between *Rhododendron rubiginosum* and dominant species in shrub layers. DY, *Dipelta yunnanensis*; LT, *Lonicera tangutica*; RR, *Rhododendron rubiginosum*; SR, *Sorbus rehderiana*. The *p*-value is the goodness of fit test result.

自然森林优势种群空间格局的研究结果(兰国玉等, 2008; Liu et al., 2020; 顾荣等, 2021)一致。聚集分布是小径级个体最常见的分布类型, 主要受散布限制和环境过滤这两种生态过程驱动(Getzin et al., 2008)。长苞冷杉的种子以球果形式存在, 种子的散布主要靠重力的作用, 所以早期的聚集分布模式可能是受扩散限制的影响(朱文婷等, 2021)。此外, 本样地所在的海拔较高, 环境条件比较严酷, 例如11月至次年4月长时间的冬季积雪覆盖, 以及年平均气温低于4.2 ℃的低温环境(杨迎花等, 2021)。因此, 温度和湿度等环境因子引起的生境过滤也是长苞冷杉的幼树和中树呈现聚集分布的原因之一。种群通过聚集分布能够调节微气候和小生境, 增加种群优势, 增加个体存活的机会(韩路等, 2007)。随着个体径级的增大和对资源需求的增加, 种内竞争加剧, 竞争中处于劣势的个体逐渐死亡, 负密度制约引起的自疏作用最终导致长苞冷杉的成树个体从均匀分布最终转变为随机分布(Stoll & Bergius, 2005;

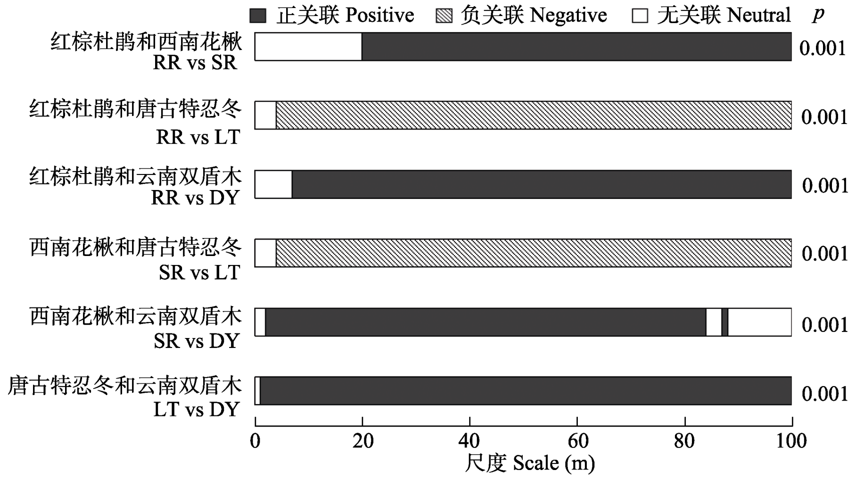

图5 云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地中亚乔木层和灌木层优势种的种间关联性。*p*值为拟合优度检验结果。

Fig. 5 Interspecific relationship of dominant species in subtree layer and shrub layer in 20 hm^2 dynamics plot of subalpine cold-temperate coniferous forest in Shangri-La, Yunnan. DY, *Dipelta yunnanensis*; LT, *Lonicera tangutica*; RR, *Rhododendron rubiginosum*; SR, *Sorbus rehderiana*. The *p*-value is the goodness of fit test result.

表1 云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地长苞冷杉种群及其他优势种与地形因子的Torus-translation检验及物种密度与地形因子的Spearman相关系数

Table 1 Torus-translation test and Spearman correlation coefficient of species density and topographic factors of *Abies georgei* and other dominant species in the 20 hm^2 dynamics plot of subalpine cold-temperate coniferous forest in Shangri-La, Yunnan

发育阶段/物种 Development stage/species	海拔 Altitude	坡度 Slope	凹凸度 Convex	正弦坡向 Sin (aspect)	余弦坡向 Cos (aspect)
幼树 Sapling	0.16	–0.41*	0.08	–0.13	–0.13
中树 Juvenile	0.07	–0.30*	–0.08	0.06	0.08
成树 Adult	0.27*	0.04	0.34*	0.07	0.08
红棕杜鹃 *Rhododendron rubiginosum*	–0.17	0.39*	0.28*	–0.07	–0.07
西南花楸 *Sorbus rehderiana*	–0.26*	0.15	–0.08	–0.07	–0.10
唐古特忍冬 *Lonicera tangutica*	0.50*	–0.04	0.17*	0.35*	0.38*
云南双盾木*Dipelta yunnanensis*	0.05	0.49*	0.08	0.50*	0.51*

*, $p < 0.05$.

Wang et al., 2010)。本研究的结果与青藏高原的岷江冷杉(*Abies fargesii* var. *faxoniana*)和色季拉山的急尖长苞冷杉(*Abies georgei* var. *smithii*)所呈现的随机分布格局, 以及米亚罗地区岷江冷杉的聚集分布结果有所差异(赵常明等, 2004; 赵广东等, 2022; 朱文婷等, 2022)。这一差异可能是由于不同研究样地的空间异质性及其面积大小的不同引起的, 较小的样地面积可能会掩盖环境过滤对物种分布的真实作用。此外, 本研究发现亚乔木层和灌木层的优势种的空间分布格局同样以聚集分布为主(图2), 这和以往的研究结果一致, 即群落内个体数量较少的物种往往聚集程度较高(Condit et al., 2000; Wang et al., 2010)。本研究样地内长苞冷杉个体数量占总株数的70%, 相比之下, 即使为各层优势种的红棕杜鹃、西南花楸、唐古特忍冬和云南双盾木在整个样地中的数量仍较少, 它们通过聚集分布来增加周围的同种个体的数量, 减少异种邻体, 减弱种间竞争, 从而实现与长苞冷杉在局域尺度上的稳定共存(Chacón-Labella et al., 2017; 毛子昆等, 2020)。剔除环境异质性的影响后, 西南花楸、唐古特忍冬和云南双盾木的空间分布格局显著地由聚集分布转变为随机分布(附录II), 这与大多数研究结果(Condit et al., 2000; Wang et al., 2010; 顾荣等, 2021; 邱婧等, 2022)一致。表明这3种物种的空间分布格局主要受环境异质性的调控。

3.2 寒温性针叶林优势种的种内、种间的关联性

空间关联描述了植物个体之间的关系, 可以反映种群的状态以及种内种间及其与环境的相互作用(Wang et al., 2010)。本研究发现长苞冷杉的幼树与中树整体呈正关联(图2), 说明两者对生境的选择具

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有一致性。小径级个体由于对资源的需求较少、种间竞争相对较弱，倾向于通过集群作用来提高抵御外界环境胁迫的能力，从而提高其生存能力(Cavieres et al., 2014; Liu et al., 2020)。然而，幼树与成树间的负关联可能是受Janzen-Connell假说的距离制约效应影响，主要受有害生物侵害和资源限制的影响，靠近成树的幼树更易受专一性病原菌和植食性昆虫的攻击，从而降低幼树存活率(Connell, 1971; Liu et al., 2012)。此外，同种个体对资源的需求相似，尤其在母树附近，由于成树已经占据了大量资源，幼树在资源竞争中处于劣势地位(祝燕等, 2009)。因此，幼树在分布上倾向于远离母树，寻找资源相对丰富、竞争压力较小的生境，以提高自身的生存机会。中树与成树之间的负相关可能是大径级个体通过不对称竞争限制了中径级个体对空间、养分、光照等资源的获取(韩豪等, 2021)，尤其是长苞冷杉大径级个体树冠庞大，占据较大的空间，且对光照、水分和土壤养分具有更强的竞争能力，限制了周围中径级个体的生长。

本研究还发现，长苞冷杉的幼树与亚乔木层优势种红棕杜鹃、西南花楸呈正关联(图3)，一方面可能与长苞冷杉是耐荫树种的生物学特性有关，亚乔木层树种的树冠为其提供适度的遮阴环境有利于幼树的生长(Wang et al., 2010; Liu et al., 2020)。另一方面，亚乔木层的树冠能够分散并承载部分积雪，为林下长苞冷杉幼树的生长提供了更好的生存条件。相反，长苞冷杉的幼树与灌木层、中树与亚乔木层和灌木层的优势树种呈负关联(图3)，这说明长苞冷杉中小径级个体与灌木层树种存在激烈的种间竞争，可能原因是两者具有相似的生态需求和资源利用策略，导致林下更新和生长能力较强的灌木能够与长苞冷杉的幼树和中树争夺光照、水分和养分等限制性资源，并抢占长苞冷杉小径级个体的生态位空间(Yang et al., 2018; 董雪等, 2020)。长苞冷杉的成树与各层优势种之间普遍呈正关联(图3)，这表明长苞冷杉的成树可能通过改善微环境，减少竞争压力，从而为其他树种提供了有利条件。乔木层和灌木层优势种之间也普遍表现出正关联，这可能是因为这些优势种通过其生态位特化来促进资源的互补利用。因此，在亚高山寒温性针叶林中，不同优势种之间的相互作用构成了一个错综复杂的动态平衡系统。随着森林群落的演替，本样地最终形成以长苞冷杉为代表的相对稳定的顶极群落。在这一过程中，长苞冷杉种群与其他优势种通过各自的生态策略形成互利共生或互补的种间关系，有效利用和补充资源，最终实现长期稳定共存(叶权平等, 2018)。

3.3 地形对寒温性针叶林优势种空间分布格局的影响

在较小尺度上，种群分布格局主要受周围同种和异种邻体相互作用的影响，而在较大空间尺度上，生境过滤作用更加显著(HilleRisLambers et al., 2012; Shen et al., 2013)。地形在塑造植物局域尺度物种分布中起着重要作用(Webb & Peart, 2000; Chuyong et al., 2011)。通过Torus-translation检验发现，本样地的优势树种的密度至少与一种地形因子显著关联性(表1)。高海拔地区具有低温、低氧和紫外线辐射强等恶劣条件，这对许多物种的生存构成了巨大的挑战(Sun et al., 2018)。本样地的优势种大多与海拔呈正相关关系，其经过长期的自然选择和进化过程，已经形成了适应高海拔环境的能力和生存策略。然而，西南花楸与海拔呈负相关关系，说明随着海拔的升高，其植株数量逐渐减少，可能原因是作为落叶型植物的西南花楸对环境变化较为敏感，其更倾向于利用环境变化相对缓慢的低海拔区域(Xing et al., 2023; 邢红爽等, 2024)。长苞冷杉的幼树和中树与坡度呈显著负相关关系，说明这些中小径级个体更偏好较缓的坡度。其中幼树的这种偏好可能与其繁殖策略有关，因为陡峭坡面不利于长苞冷杉种子的萌发和幼苗的定植，相反，在相对平缓的地形中，脱落的球果更易于在土壤中停留，增加了定植的机会。中树阶段的长苞冷杉，随着其根系和树冠的扩展，对养分和水分等资源的需求量增加，坡度较大的区域可能会因为土壤浅薄和养分供应不足而不利于中树生长。红棕杜鹃和云南双盾木偏好坡度较陡的生境，与长苞冷杉发生坡度生态位的分化，从而减少了种间竞争，促进了这些物种的稳定共存(朱文婷等, 2021)。长苞冷杉成树、红棕杜鹃和唐古特忍冬的密度与凹凸度的正相关可能反映了较凹区域积雪较厚且覆盖时间较长，土壤温度过低而不利于树种的更新。此外，本研究还发现灌木层的优势种唐古特忍冬和云南双盾木对坡向的偏好，暗示坡向引起的光照和水分等生态位分化对亚高山针叶林物种共存的重要性(Punchi-Manage et al., 2013)。总之，地形通过影响生境异质性，对植物空间分布

格局产生作用, 为不同生活史策略和生态需求的物种提供了相应的定居机会, 从而有利于生物多样性的维持(Palmer, 1990)。

4 结论

云南香格里拉亚高山寒温性针叶林20 hm^2动态监测样地内的优势种整体表现出强烈的聚集分布, 聚集程度随着尺度的增加而逐渐降低。而不同优势种的聚集模式受不同的生态学过程所驱动。但随着径级的增大, 自疏作用的增强, 导致长苞冷杉的成树最终趋于随机分布。本研究的种内和种间关联性表现出了正关联、负关联和不关联3种关系, 其中以正、负关联为主, 表明物种间的相互作用(如竞争和互惠等)在群落构建中共同发挥作用。此外, 优势种的空间分布主要受地形因子(海拔、坡度和凹凸度)的显著影响, 说明地形异质性是引起长苞冷杉林优势种间分布格局差异的主要原因。研究表明幼苗空间格局是影响森林群落组成的重要因素。因此, 需要进行长期的动态监测, 进一步探讨幼苗的空间格局, 以揭示更新阶段的潜在生态学机制。

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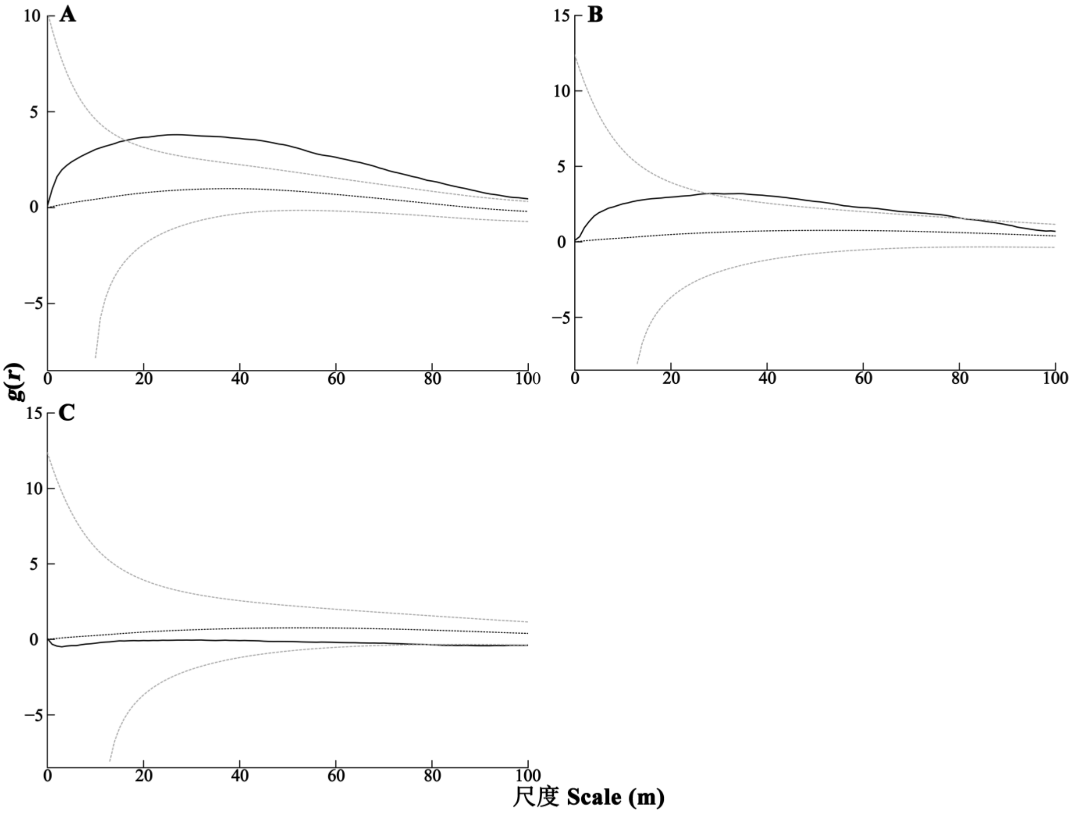

A, 幼树。**B,** 中树。**C,** 成树。黑色曲线表示单变量成对相关函数($g(r)$)的函数值, 中间黑色虚线表示$g(r)$的期望值, 灰色虚线表示99%的置信区间。

A, Sapling. **B,** Juvenile trees. **C,** Adult trees. Solid lines represent the value of the univariate pair-correlation function ($g(r)$), the black dashed line represents the expected value of the $g(r)$ function, and the gray dashed lines represent the 99% confidence interval.

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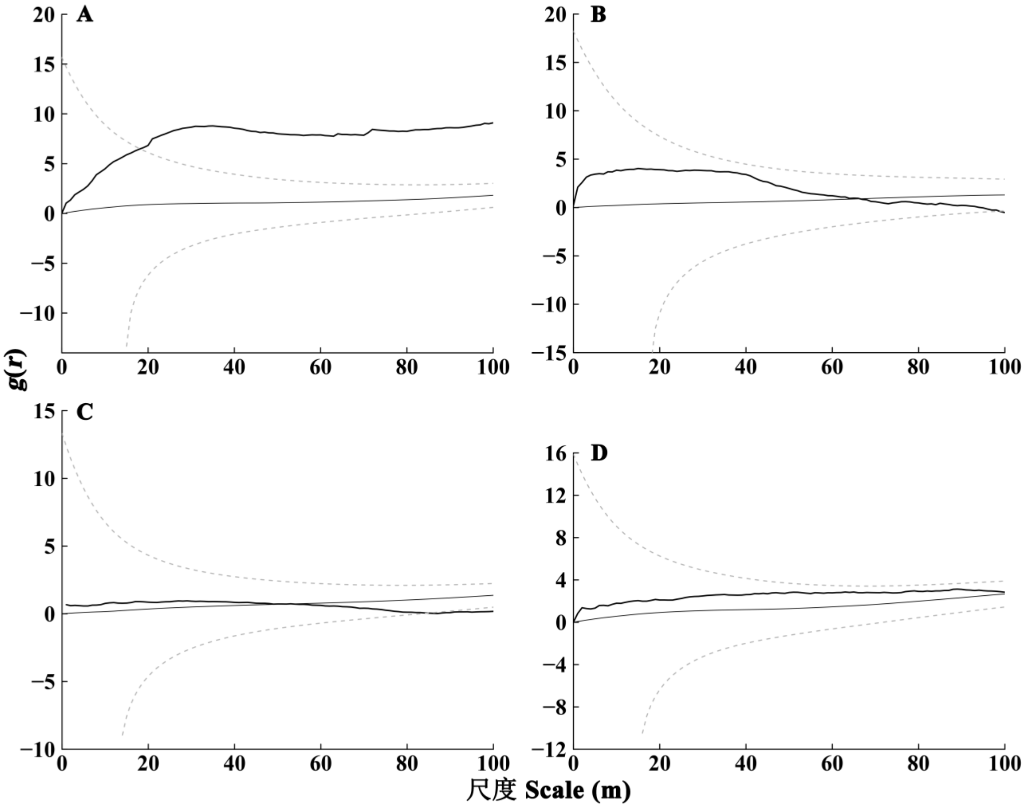

A, 红棕杜鹃。**B,** 西南花楸。**C,** 唐古特忍冬。**D,** 云南双盾木。黑色曲线表示单变量成对相关函数$g(r)$的函数值, 中间黑色较直的线表示$g(r)$的期望值, 灰色虚线表示99%的置信区间。

A, *Rhododendron rubiginosum*. **B,** *Sorbus rehderiana*. **C,** *Lonicera tangutica*. **D,** *Dipelta yunnanensis.* Solid black line represents the value of the univariate pair-correlation $g(r)$ function, the black solid line in the middle represents the expected value of the $g(r)$ function, and the gray dashed lines represent the 99% confidence interval.

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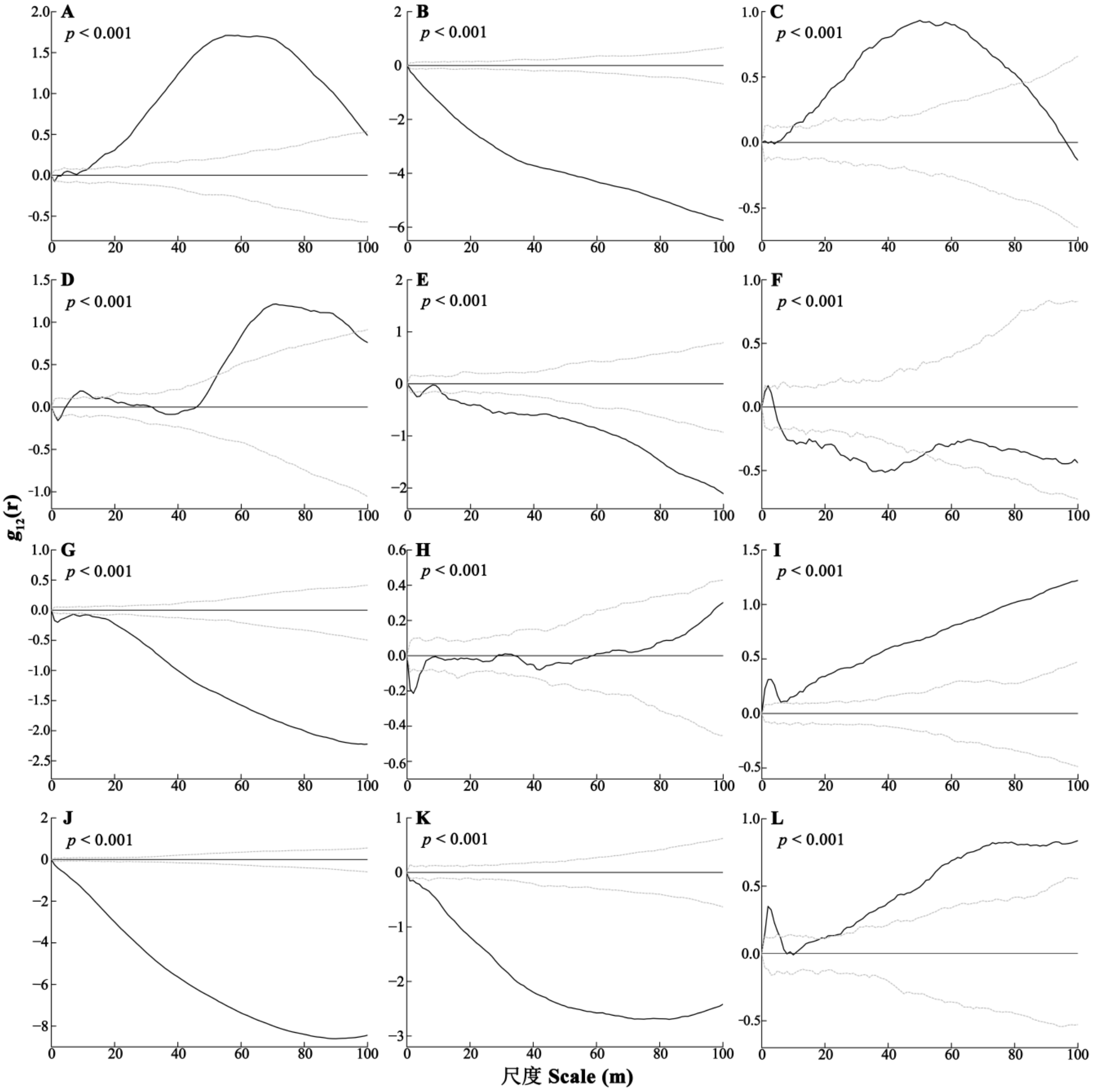

亚乔木层: **A,** 幼树和红棕杜鹃。**B,** 中树和红棕杜鹃。**C,** 成树和红棕杜鹃。**D,** 幼树和西南花楸。**E,** 中树和西南花楸。**F,** 成树和西南花楸。灌木层: **G,** 幼树和唐古特忍冬。**H,** 中树和唐古特忍冬。**I,** 成树和唐古特忍冬。**J,** 幼树和云南双盾木。**K,** 中树和云南双盾木。**L,** 成树和云南双盾木。黑色曲线表示双变量成对相关函数($g_{12}(r)$)的函数值, 中间黑色直线表示$g_{12}(r)$的期望值, 灰色虚线表示99%的置信区间。p值为拟合优度检验结果。

Subtree layer: **A,** Sapling and *Rhododendron rubiginosum*. **B,** Juvenile trees and *Rhododendron rubiginosum*. **C,** Adult trees and *Rhododendron rubiginosum*. **D,** Sapling and *Sorbus rehderiana*. **E,** Juvenile trees and *Sorbus rehderiana*. **F,** Adult trees and *Sorbus rehderiana.* Shrub layer **G,** Sapling and *Lonicera tangutica*. **H,** Juvenile trees and *Lonicera tangutica*. **I,** Adult trees and *Lonicera tangutica*. **J,** Sapling and *Dipelta yunnanensis*. **K,** Juvenile trees and *Dipelta yunnanensis*. **L,** Adult trees and *Dipelta yunnanensis.* The black curve represents the function value of the bivariate pair-correlation function ($g_{12}(r)$), and the black line represents the expected value of the $g_{12}(r)$ function. The dashed gray lines indicate a 99% confidence interval. The p-value is the goodness of fit test result.

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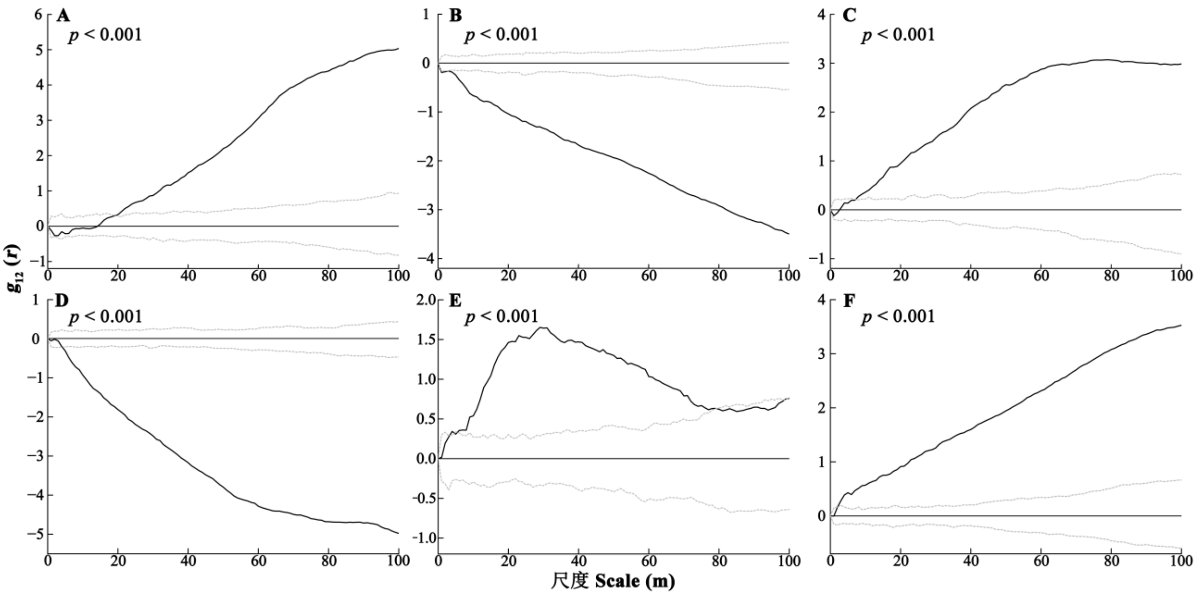

A, 红棕杜鹃和西南花楸。**B,** 红棕杜鹃和唐古特忍冬。**C,** 红棕杜鹃和云南双盾木。**D,** 西南花楸和唐古特忍冬。**E,** 西南花楸和云南双盾木。**F,** 唐古特忍冬和云南双盾木。黑色曲线表示双变量成对相关函数($g_{12}(r)$)的函数值，中间黑色直线表示$g_{12}(r)$的期望值，灰色虚线表示99%的置信区间。p值为拟合优度检验结果。

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