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森林结构对鸟类物种多样性的影响研究进展

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摘要:森林生态系统作为最重要的鸟类栖息地,其内部结构不仅是决定鸟类多样性组成和分布的关键因素,还在维持和提升森林生态系统功能方面发挥着重要作用。随着近年来全球范围内不同程度的森林退化和恢复、毁林和造林事件的持续发生,森林结构发生了显著而复杂的变化。鸟类多样性如何响应森林结构及其变化成为森林生态学和生物多样性保护领域研究的热点问题。梳理了常见森林水平和垂直结构特征,并对其含义和影响进行了总结。进而对不同尺度上森林结构影响鸟类多样性的现象、规律和内在机制进行了归纳。总体而言,森林结构能够通过改变食物资源、栖息地、微气候条件、种间关系等对鸟类多样性产生直接和间接影响,鸟类的生活史和生态特征在对森林结构的响应中起到了决定性作用。在不同的尺度上森林结构的影响机制也有所不同,并存在一定的不确定性。展望了新兴观测手段在推动森林结构与鸟类多样性关系研究方面的作用,并强调了开展多尺度比较研究的重要性。倡导生态学家、保护生物学家和政策制定者之间的跨学科合作以解决复杂的保护挑战,为森林管理和生物多样性保护提供科学参考。

关键词:森林生态系统; 森林结构; 鸟类多样性; 影响机制; 生物多样性保护

Review of the impact of forest ecosystem structure on avian species diversity

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Abstract: As critical habitats for birds, the structure of forest ecosystems is not only a key factor in determining the spatial patterns of bird diversity and community composition, but also plays an important role in maintaining and enhancing the functions of forest ecosystems. Over the past few decades, global forest dynamics-characterized by varying degrees of degradation, restoration, deforestation, and afforestation-have resulted in significant and complex changes to forest structure. As a result, understanding how bird diversity responds to forest structure and its changes has become a central topic in the field of forest ecology and biodiversity conservation. In this study, we first review the key characteristics of forest structure and their heterogeneity, considering both horizontal and vertical dimensions. The definitions, calculation methods, and ecological significance are also summarized. Horizontal structure refers to the composition, configuration and distribution

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patterns of vegetation community, while vertical structure describes the bottom-to-top stratification of vegetation community such as the herbaceous layer, shrub layer, and canopy. Both aspects play critical roles in shaping habitat suitability and availability for avian species. We then explore the main data collection methods and commonly used research approaches for examining forest structure and bird diversity across plot, landscape, and regional scales. This study synthesizes the phenomena, patterns, and underlying mechanisms by which forest structure affects bird diversity at different scales. The findings indicate that forest structure can influence bird diversity by altering food resources, available habitats, microclimate conditions, and interspecies interactions. The life history traits and ecological characteristics of bird species play a decisive role in determining how they respond to changes in forest structure. Birds with specialized habitat requirements may be more sensitive to forest structural changes than generalist species. However, we find that the mechanisms by which forest structure influences biodiversity differ across scales, and the conclusions are subject to a certain degree of uncertainty. In addition to summarizing existing knowledge, this study also explores the potential of emerging observational techniques, such as citizen science, UAVs (unmanned aerial vehicles), and LiDAR (light detection and ranging), in advancing research on the relationship between forest structure and bird diversity. We also emphasize the importance of multi-scale comparative studies, as the relationship between forest structure characteristics and remote sensing-derived parameters, as well as the inferred influence mechanisms, exhibits strong scale dependence. We advocate for interdisciplinary collaboration among ecologists, conservation biologists, and policymakers to address complex conservation challenges, thereby providing scientific insights for forest management and biodiversity conservation.

Key Words: forest ecosystem; forest structure; bird diversity; influence mechanism; biodiversity conservation

鸟类多样性是生物多样性的重要组成部分,也是被人类研究最多、最深入的种类之一。由于鸟类分布广泛,易于观察,且对环境尤为敏感,长期以来被认为是生境质量的指示物种[1—2],其多样性的组成和分布对于生态系统功能评价具有重要意义[3—4]。

森林生态系统是鸟类最重要的栖息地,约 80%以上的陆地鸟类依赖于森林生存[5]。很早以前研究者们就认识到,森林生态系统复杂的内部结构可以提供多样化的生态位,从而支持较高的鸟类多样性[6—7]。然而随着世界范围内不同程度的毁林、造林以及森林退化的持续发生[8—9],全球森林的分布格局和组成结构发生了剧烈变化[10—12]。以破碎化、同质化为代表的森林结构变化通过各种直接和间接影响,例如觅食和筑巢地点的丧失[13—15]、生境连通性的降低[16—17]、种间竞争的增加[18]等,成为导致鸟类多样性降低、种群数量下降甚至灭绝的重要因素[19—20]。

深入理解森林结构的影响机制,有助于掌握生物多样性的空间格局和变化规律,对于林业管理和生物多样性保护具有重要意义。近年来国内外学者就森林结构特征及获取方法[21]、激光雷达手段在获取三维结构中的应用[22—24]、人工林的生物多样性影响[25—26]、鸟类生理生态特征在响应森林变化中的作用[27—28]等方面进行了一定的归纳和总结。然而,不同研究在影响的程度、范围和方向上尚存在一定的不确定性[29]。且大多数研究关注样地和林分尺度,对于景观、区域乃至全球尺度上鸟类多样性空间分布变化规律的认识还有待深入。目前尚缺乏对森林结构特征影响鸟类多样性的内在机制的系统性总结,或局限于某一区域[16,24]和某个方面[30—31]。

随着以激光雷达为代表的观测手段的迅速发展,高精度、大尺度森林结构信息不断涌现,为森林结构相关研究提供了前所未有的精细化数据。然而森林结构的影响机制尚未得到充分认识,阻碍了对生物多样性变化格局和响应规律的进一步理解。由于森林结构本身及其生物多样性效应都具有鲜明的尺度特征,因此本文围绕森林结构对鸟类多样性的影响机制这一科学问题,从尺度的视角,对常用森林结构参数及其获取方式、森林结构变化的直接和间接影响机制等方面的研究进展和局限性进行了总结,并提出需要重点关注和有潜力的研究方向,支持在林业生态建设中推动生物多样性高质量保护。

1　森林结构特征

森林结构指植被的三维分布及其景观格局的变异性,可以由结构特征和结构复杂性两方面解释[32]。结构特征反映了森林生态系统内部的各种属性,例如物种组成和丰富度、个体大小及分布等空间或非空间指数或指标,通常分为水平和垂直两个维度[33—34]。森林垂直结构描述了植物群落在空间上的垂直分化[35],是决定森林生态过程和生态服务功能的关键因素。森林垂直分层包括地上层和地下层,根据群落组成的高度,地上部分通常分为林冠层、灌木层、草本层等[36]。森林水平结构即植被群落分布在水平维度上的景观格局[37],例如树木的大小、密度、年龄及分布、破碎度、复杂度、连通性等[34]。结构复杂性指森林水平和垂直结构特征的空间异质性[32]。通过对不同结构属性,例如不同树种的分布格局、各垂直分层的变异性等,以及它们之间的相互关系在不同尺度上进行量化,可以更全面地描述森林整体结构特征(图 1 和表 1)。

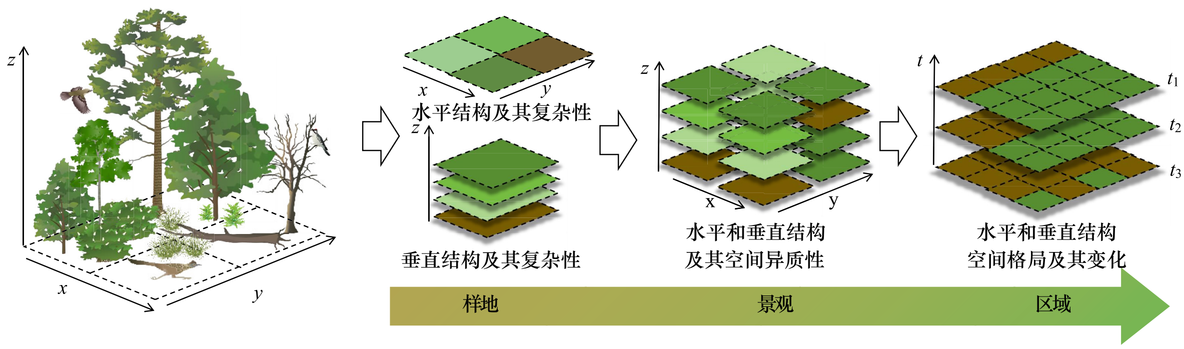

图 1　不同尺度上的森林结构特征及其空间异质性示意图

Fig.1　Forest structure characteristics and spatial heterogeneity at different scales

x, y, 水平方向; z, 垂直方向; t, 时间

表 1　常用森林垂直和水平结构变量及其对鸟类多样性的影响

Table 1　Common forest vertical and horizontal structure variables and their effects on bird diversity

类别 Category	名称 Name	定义 Definition	影响 Influence
垂直特征 Vertical characteristics	冠层高度,及其均值、中位数、众数、分位数、最值等	样地或像元内植被高度信息的最大值,通常与胸径、林龄相关。	发育良好的冠层的平均植被高度值较高,且随着林下层和中层代表量的增加而减少[38]。通常物种多样性或丰富度随冠层高度的增加而增加[39—41],但外来种或以灌丛为主要栖息地的种类下降[41—43]。种群数量的响应具有一定的不确定性[44—45]。
	冠层高度变异性	样地或像元内植被高度的标准差、方差、偏度、峰度等。	对鸟类丰富度和功能多样性有较好的解释作用[46—47],其相关性甚至比冠层高度更强[48],通常树种单一、年龄相似的人工林的垂直变异性较低[46,49]。
	叶面积密度(LAD)	叶面积指数在垂直剖面上的分布,当使用激光雷达数据时,林内空间可以被划分为高度为 Δz 的体素,并且可以通过计算垂直方向上目标体素 i 以上和以下的返回值来计算 GF_i。 $\mathrm{LAD}_i = -\frac{\ln GF_i}{k\Delta z}$; $GF_i = -\frac{N_{be}}{N_{tot}\ N_{ab}}$ 式中,N_{ab} 是体素以上的激光雷达返回数,N_{be} 是体素以下的返回数,N_{tot} 是垂直维度上的总回波数。	研究表明基于 LAD 测量的指标比基于冠层高度变化的指标对鸟类物种丰富的有更好的解释力[50]。

续表

类别 Category	名称 Name	定义 Definition	影响 Influence
	叶高多样性(FHD)	$FHD = \sum_{i=1}^{n} p_i \ln p_i$ 式中,n 为总层数,p_i 为 i 层的返回比例。当所有层具有相同的返回数时达到最大值,即 Shannon-Wiener 指数随着垂直分层上的点分布更加均匀而增加。	鸟类丰富度与叶高多样性呈正相关[51—53]。
	冠层垂直分布	冠层部分在不同高度层枝叶的结构和密度的分布情况。	鸟类种群数量和丰富度随之增加[49,54]。
水平特征 Horizontal characteristics	冠层覆盖度	冠层部分在水平地表上的投影面积,郁闭冠层的覆盖度较高。	物种丰富度随冠层覆盖而增加[39,42,54],但也有一定的不确定性[23,55]。
	分层覆盖度	单位水平地表面积上各层的垂直投影面积与森林地面面积的比率	树木覆盖度和灌木层覆盖度对鸟类丰富度有显著正向影响,灌木层覆盖度和草本层覆盖度与稀有物种呈正相关[56]。
	叶面积指数(LAI)	单位土地面积上植物叶片总面积与地面面积的比例 $LAI(z) = -\frac{\ln GF(z)}{k}$ 式中,GF 即空隙度 gap fraction, $GF(z)$ 是从冠层底部到高度 z 的总空隙度,k 是消光系数。	LAI 对鸟类丰富度有较强的解释能力[57]。

LAD: 叶面积密度 leaf area density; FHD: 叶高多样性 foliage height diversity; LAI: 叶面积指数 leaf area index

2 森林结构及其变化影响鸟类多样性的内在机制

过去几十年来,国内外学者在研究森林结构及其生物效应方面开展了深入的探索。由于森林结构本身及其对鸟类多样性的影响具有强烈的尺度依赖性[58],森林结构对生物多样性的影响也依赖于尺度[59],下面结合该领域研究发展历程从不同尺度的角度进行回顾(表 2)。

表 2 不同尺度森林结构对鸟类生物多样性影响研究

Table 2 Effects of forest structure on bird diversity at different scales

尺度 Scale	主要数据获取手段 Main data collection methods		常用研究方法 Common research methods	主要关注的科学问题 Key scientific issues of focus
	森林结构特征 Forest structure characteristics	鸟类多样性信息 Bird diversity information		
样地 Plot	样地调查法、破坏性采样法、分层收割法、光学仪器测量法(利用叶面积仪和数字半球相机等)、凋落叶法等。对不同高度进行测量则通过绳索悬吊、塔基或移动升降机等。也可通过地基或背包激光雷达、高光谱和多光谱扫描反演植被结构。	采用样点法、样线法,在停留或行进过程中记录一定时间内观察到的鸟类种类和数量。也可采用网捕法、环志法、红外触发相机自动拍摄法、声音监测法等获取鸟类分布信息。	样点对比	森林结构特征与鸟类多样性和群落组成之间的关系[41,52,60—63];森林结构特征及其异质性的影响机制[64—66];鸟类生理生态和生活史特征的作用等[67—68]。
景观 Landscape	通过无人机搭载激光雷达、高光谱和多光谱仪等获取飞行轨迹下方特定视场范围内的扫描数据,测量和反演林分、景观和区域范围的森林结构参数。		统计回归	森林结构空间异质性和景观格局对鸟类多样性的影响[23,69—71];森林管理措施的影响和人工林的生物多样性效应等[72—74]。
区域 Region	星载光学和激光雷达等。	环志标记法、雷达跟踪法、卫星追踪技术、稳定性同位素标记法等。	统计回归、物种分布模型	鸟类多样性分布格局和森林退化的影响等[19,47,75]。

2.1 样地尺度

样地—林分尺度是最早开展关于森林结构与鸟类多样性之间关系研究的尺度,也是对森林结构的影响机

制理解最为深入的尺度。早在 1935 年,科学家已经通过对具体案例的研究认识到森林结构与鸟类群落的物种组成密切相关[60]。Robert MacArthur 等在 1961 年的研究中,进一步证实了植被结构对鸟类物种多样性的影响要大于植被组成的影响[52]。由于鸟类的飞行能力使其天然地能够占据不同高度的森林空间,并且森林的垂直分层在小尺度上表现的更加明显,因此在这一尺度上,相关研究更多关注森林垂直结构对鸟类多样性的影响。前期研究力图证实结构信息在描述个体—环境关系中的有效性[41,61—62];后期探索的重点转变为评估植被结构和种群水平鸟类分布的关系[47]。随着研究的不断深入,巢址选择、扩散策略、窝卵数、体型和食性等鸟类生理生态和生活史特征的主导作用逐渐得到揭示[67—68]。

2.1.1　森林结构对鸟类的直接影响

食物作为一种鸟类丰富度的限制资源[76],是森林结构影响鸟类分布的最主要方式之一。例如 Stefan Ferger 等分析坦桑尼亚乞力马扎罗山的鸟类记录发现,鸟类丰富度与植被结构和食物可利用性(无脊椎动物生物量和果实丰度)密切相关[64]。类似的,在巴布亚新几内亚中央山脉的雨林中,通过多种野外观测方法发现食虫鸟丰富度与植被结构和食物资源高度相关,其作用甚至超过了温度这一普遍认为的生物多样性的决定性因素[65]。

森林结构提供了必要的筑巢地点和适宜的栖息生境,从而直接影响繁殖鸟类的分布、密度和筑巢成功率。例如,由于林下植被和凋落物为地面和灌木营巢的鸟类提供了重要的筑巢资源,在美国新英格兰地区林下灌木的减少导致了金翅莺(*Vermivora chrysoptera*)和草原莺(*Setophaga discolor*)的种群数量急剧下降[77]。而在美国俄亥俄州东南部的成熟森林中,研究者发现凋落物、林下层密度和冠层高度与地面和灌丛营巢鸟类的密度成正相关[66]。在波兰东南部温带落叶林中,树木死亡造成的小尺度林冠空隙为洞穴和地面筑巢鸟提供了栖息地,林隙样地的鸟类物种丰富度、多样性和相对丰度均显著高于对照样地[78]。对于能够利用桉树筑巢的和尚鹦鹉(*Myiopsitta monachus*)来说,阿根廷潘帕斯草原植被结构的变化为其创造了有利条件,造成了该种入侵鸟类的分布范围显著增加[79]。Ivan Réus Viana 等进一步发现植被结构的景观格局而非面积能够更好的解释这种入侵鸟类的出现[80]。

此外,森林结构还可以通过改变微气候条件(气温、湿度、光照、风速等)影响栖息地适宜性[81—83],进而直接影响物种分布和群落组成。例如在对森林实施间伐后,林下光照的增加使林下层湿度降低、温度升高,从而导致了一些森林鸟类的数量下降和消失[84—85]。微气候假说认为,老龄林密闭的冠层和复杂的垂直结构通过提供较为凉爽的微气候条件,为气候变暖敏感物种提供了热避难所,从而减缓了气候变暖对动物种群下降趋势的负面影响[86]。例如 Hankyu Kim 等结合长期鸟类观测和亚冠层温度数据发现多种鸟类的丰度下降趋势在微气候较冷区域比较暖区域更慢,表明由地形和植被结构构造的小型气候避难所具有缓冲对温暖气候敏感鸟类种群免受气候变化影响的潜力[81]。但也有研究认为,在美国东南部等气候相对温和的地区,植被结构仍是决定鸟类栖息地选择的决定性因素,微气候的影响则不那么重要[87]。

实际上,鸟类的食性、巢址、气候敏感性等特征往往共同决定了对森林结构的响应。研究普遍认为种群规模小、窝卵数少、营地面生活和食虫性的鸟类最容易受到森林结构变化的影响[27,68]。例如在巴西东南部森林浓密冠层栖息的通常是食虫和食果的高度森林依赖种类,而在较开阔林地发现地面觅食、食虫的低森林依赖种类较为丰富[68]。

2.1.2　森林结构对鸟类的间接影响

植被结构通过影响巢捕食风险、躲避捕食者的能力[88]、种间竞争[18]等影响鸟类的繁殖成功率[89]。对于许多地面筑巢鸟类而言,它们的巢穴很容易被捕食者接近[90]。例如 Julian Klein 等对一种开放式筑巢的针叶林鸟类——北噪鸦(*Perisoreus infaustus*)进行研究发现,由于此种鸟类的筑巢失败主要是由与人类定居点相关的视觉捕食者引起的,因此灌木密度与繁殖成功率成正相关[91]。此外,鸟类也通过种子传播等机制对植被结构产生反作用。例如,在夏威夷,适应本地树种高度结构变异性的本地鸟类,通过抵抗能够有效传播入侵树木的非本地鸟类,有助于防止结构简单的入侵树木的扩散[42]。

2.2 景观尺度

近年来激光雷达等观测手段和无人机等搭载平台的发展[92—93],以及鸟类调查活动的普及[94—95],为森林结构和鸟类多样性关系的相关研究提供了大量景观尺度的数据。研究范围从样地扩展到景观尺度,使得更多的森林结构及其异质性被包括进来。生境异质性或栖息地异质性作为生态学研究的基础,为森林结构的生物多样性效应研究从现象描述到统计分析再到机理解释的不断深入起到了重要作用。同时,景观尺度也是人类活动最为强烈的尺度。在这一尺度上,人类活动造成的森林结构变化成为关注的重点[96]。随着世界范围内的原始林、天然林逐渐被破坏,以单一种、同林龄、等间距为特点的同质化人工林、商业种植园和农业景观主导了森林覆盖的增加[97]。考虑到未来人工林的面积预计在全球会持续增加,而由此导致的森林组成和结构的变化仍将加剧[98]。因此,人工林的生物多样性效应也成为近期研究的热点。

2.2.1 森林结构异质性

生境异质性假说认为复杂的结构可以提供更多的生态位,通过增加可利用资源(如食物、庇护所等)从而支撑较高的物种丰富度和多样性[52]。随着在垂直和水平方向上各种资源的分配越复杂,生态位的密度也越高。研究表明森林结构及其复杂性对鸟类群落的影响甚至超过了植物组成和区系丰富度[99—101]。因此在物种分布模型中包括植被三维结构和垂直异质性,能够有效提升模型精度[38,102]。随着对生境异质性和物种多样性之间关系的认识的不断深入,普遍认为两者在不同尺度上都具有良好的正相关关系[69,103—104],然而这种关系也存在一定的不确定性[105—106]。例如基于 101 项研究的荟萃分析发现,景观异质性(Landscape Shannon′s Diversity Index, SHDI)与鸟类丰富度呈正相关($r = 0.31$),55.56%的研究表明斑块类型丰富度(Patch Richness, PR)对鸟类丰富度有积极影响,22.22%的研究显示负面影响或影响不显著[105]。这可以由微破碎化概念解释,即异质性的增加导致由于群落内所需资源的隔离而造成的小规模斑块[107]。由于森林专性种对于特定资源具有较高的依赖性,当复杂生境中关键资源被隔离时受到负面影响[108]。

长期以来,对于森林结构的生物多样性影响的研究大多数都集中在非结构特征的空间异质性(例如植物多样性),或者单一的垂直结构变量(例如冠层高度或者胸径)的空间异质性等[15,47,109],很少有研究涉及到多个或垂直剖面上的植被结构的水平异质性。得益于近年来激光雷达等观测手段和无人机等搭载平台的发展,越来越多的研究发现结合森林垂直和水平结构能够更好的反映鸟类的生境需求。例如 Luis Carrasco 等基于各植被高度层的叶面积密度建立了一系列激光雷达结构指标,并发现植被垂直结构的水平变异对鸟类丰富度的解释力最强[50]。

2.2.2 森林破碎化

在近几十年中,随着城市化的进展和土地利用的变化,大面积、连续的天然林不断被分解成小面积、孤立的斑块[110],当前全球有一半以上的森林受到破碎化的影响[111]。从 2000 年到 2010 年,全球森林边缘面积在短短 10 年内从森林总面积的 27%增加到 31%,预计到 2100 年,50%的热带森林面积将处于森林边缘[98]。当前普遍认为,森林破碎化对鸟类物种丰富度有严重的负面影响,是世界范围内多样性下降和物种灭绝的主要驱动力之一[112]。完整、连续、良好的森林结构可以提供连续的生境通道,促进鸟类的迁徙和交流,维持种群的稳定性和多样性。基于综合了冠层高度、树木覆盖度和干扰发生后的时间构建的森林结构状况指数[113],Rajeev Pillay 等证实了结构完整性较高的森林中鸟类种群数量下降和灭绝的风险较低[114]。相反,当空间连续的森林生境变为不连续、较小的斑块,斑块内部支持的种群数量降低、繁殖活动下降[115],斑块之间的连通性降低、移动减少[116],从而对鸟类物种多样性和种群数量造成负面影响[31,71,117—118]。基于波兰南部的鸟类调查表明,鸟类丰富度即分类学多样性随斑块面积的增加而增加,达到一定规模后趋于稳定。而功能多样性对破碎化指标和林分特征的响应最小,随着森林斑块隔离度的降低而线性降低。系统发育多样性与林分年龄呈正相关[119]。但也有研究报道相反或不显著的结果[120]。

具有不同生态学和生活史特征的鸟种对斑块大小、边缘面积、植被结构的响应有所不同[121]。Thomas Weeks 等通过将野外调查数据与表征鸟类扩散能力的形态学指标——手翼指数相结合,评估了全球 1034 种

鸟类对森林破碎化的响应,研究表明扩散能力是影响鸟类对森林破碎化敏感性的关键因素[122]。特别是对于扩散能力较弱的热带食虫鸟类,森林破碎化造成的负面影响尤为严重[31,123]。也有研究表明,当原始森林斑块被大量半自然的栖息地(如种植园或农田)所包围,仍然可以为某些鸟类,甚至是受胁或濒危种提供必要的栖息地[123—124]。而一些通常需要大面积森林才能成功繁殖的鸟类,在迁徙季节也可以使用城市和农村的小型森林斑块以及郊区的树冠作为中途停留点[125]。

森林破碎化导致斑块边缘面积增加,引起的边缘效应可能在鸟类多样性和群落组成的响应方面发挥关键作用[126]。边缘效应往往会对原本生活在森林内部的鸟类物种产生负面影响,较弱的抗干扰能力使得这些鸟类的分布变化或种群数量下降。例如 Harrison Jones 等通过在安第斯山脉森林斑块梯度开展鸟类样线调查、网捕和回放,发现森林依赖种主导了丰富度随生境数量的减少、边缘密度的增加和选择性采伐干扰的增加而下降[127]。此外,森林斑块边缘区域的鸟类更容易受到捕食者的威胁,例如 Triin Kaasiku 等基于摄像机陷阱的记录,发现边缘效应是由于捕食者赤狐(*Vulpes Vulpes*)靠近森林边缘的巢穴捕食率升高引起的[128]。而能够适应边缘区域生境特征的一些常见种、广布种、生活在开阔生境的鸟类物种往往能够受益于破碎化,导致鸟类物种组成发生变化[116]。总体而言,越小的斑块往往包含较多的广布种和边缘种,导致破碎化的森林与未受干扰的原始林之间的鸟类群落物种组成差异越大[129]。

此外,森林破碎化还会通过影响捕食者对鸟类多样性产生间接影响。中级捕食者释放假说认为,较小的森林斑块往往会失去土狼等大型捕食者,从而使浣熊、狐狸和家猫中等大小捕食者的种群规模无法受到控制。大量增加的中级捕食者捕食了更多的鸟蛋和雏鸟,从而导致鸟类种群数量的下降甚至地方性灭绝[130—131]。但这一理论目前仍存在一定的不确定性,需要开展更多研究以详细评估捕食者的行为对鸟类种群水平和物种水平分布变化的影响[132—133]。

2.2.3　人工林的鸟类多样性维持功能

面临由于人类活动和自然干扰(如农业扩张、火灾和虫害)造成的森林损失,包括我国在内许多国家实施了大规模的植树造林计划以增加碳储量、恢复退化森林、保护生物多样性和满足木材产品需求[134],导致全球范围内人工林的面积不断扩大[97]。通常认为相较于天然林,人工林树种单一、内部结构简单、垂直分层较少,难以维持较高的鸟类多样性[73]或仅能维持部分耐干扰和广布种[135]。大量观测表明人工林内鸟类多样性和丰度均低于天然林[136]。基于全球 138 个样点 361 项观测的荟萃分析表明,人工林鸟类的丰富度比原始林低 30%以上[25]。特别是对稀有种、狭布种和专性种产生严重的负面影响[72,137],不利于林下生活鸟类和濒危鸟类的生存[73,135]。

在不同研究中,对于人工林造成的负面影响仍存在一定的差异,导致当前对于人工林是生物多样性的“绿色沙漠”还是宝贵补充的科学认识尚不清晰[138]。人工林可以在一定程度上为鸟类群落提供栖息地和资源,例如在补充退化的天然林或增加连通性的地区,并可通过各种机制为生物多样性保护做出贡献[139—140]。有调查案例表明人工林和天然林在鸟类丰富度方面差异不大[50,141]。通过对亚马逊森林鸟类混合种群的移动行为研究发现,次生林的冠层高度在达到一定阈值后,其生态效益可以替代原始林[142]。然而,大量证据显示由于经济林和人工林的不断扩张导致鸟类群落组成相似性的增加[143—144]。Ruth Bennett 等在研究商业种植园对鸟类多样性的影响时发现,冠层覆盖度大于 30%的可可种植园可以支撑与附近的初级或成熟次生林相似的鸟类多样性,但鸟类群落的物种组成不同[143]。特有物种、食果鸟和食虫鸟等不适应种植业的鸟类的多样性下降,而广布种、外来种、食蜜鸟和与种植园相关的食种鸟的多样性上升。在油棕林也发现了类似规律,有一些食物选择灵活、繁殖策略多样的广布种能够较好的利用同质化的人工林结构[145]。尽管森林结构的同质化往往会导致鸟类群落物种组成的相似性增加。而增加与原始林的连通性,可以提高次生林的生物多样性保护效力[17]。

此外,有研究发现一些濒危种也出现在以木材生产为目的的人工橡树林中[140],还有食花蜜鸟的密度在桉树林中反而增加的报道[146]。这可能是由于森林管理措施的开展使得人工林或次生林内的适宜栖息地增

加。不均匀林龄(单独或小块采伐)的人工林有较高的结构异质性[147],因此研究者建议构建不同年龄组成的人工林以促进生物多样性保护[148]。但也有研究表明林龄并不能很好的代替森林结构指标[68],这是由于不同的自然和人为干扰影响,相似年龄的森林往往具有差异很大的内部结构。人工林和商业种植园对鸟类生物多样性保护的相对价值更多的取决于管理措施[68]。例如修剪间伐等能够减轻对鸟类多样性的负面影响[136],开展补植套种可以在一定程度上提高鸟类多样性[149],增加冠层开放度对某些鸣禽的繁殖成功率有促进作用[66]等。

2.3 区域尺度

近年来卫星遥感、无人机等观测手段和搭载平台的发展,为在区域或更大尺度上研究森林结构提供了大量空间连续的高分辨率栖息地特征。国内外学者结合卫星遥感数据反演的森林结构信息与地面调查获取的鸟类分布情况,通过统计回归、物种分布模型等方法构建生物—环境关系, 在多样性分布格局[37]和森林退化影响[19]等方面开展了大量研究。

2.3.1 鸟类多样性分布格局

相比较于气候、地形和植被生产力等,冠层高度、叶面积密度等森林结构特征能够更好的解释鸟类多样性和群落组成[115,150—151]。例如基于鸟类分布地图和 1km 全球森林冠层高度数据,Feng Gang 等发现冠层高度是鸟类物种丰富度和功能丰富度的最重要解释因子[47]。在利用北美繁殖鸟类调查样线数据研究美国鸟类多样性空间分布格局时,结合生境垂直结构指标(冠层高度)和水平结构指标(土地覆盖类型)的模型具有最高的 R^2,可以解释森林鸟类多样性高达 70%的变异[37]。Charles Coddington 等在巴西利用激光雷达手段检测了热带森林原始林和次生林鸟类物种丰富度和功能多样性变化与三维森林结构特征的关系,研究发现茂密的亚冠层和林下植被对混种鸟群具有重要的影响,原生林中鸟群的物种丰富度在海拔高、林下和亚冠层叶面积密度高的地区有所增加,但与次生林的生境结构不相关[151]。他们进一步量化了林下食虫混合种群的垂直觅食生态位,并发现中层植被(6—15m)的重要作用[115]。然而受限于当前除冠层高度以外的森林垂直结构信息仍然较少,在区域尺度研究上较多关注森林水平结构及其变化,并通常使用森林类型或土地覆盖类型来表征。研究者对不同结构特征变量的重要性进行了探索[37],并由此并提出标准化森林三维结构变量的重要性[152]。

在区域尺度上,森林结构的空间异质性也是决定鸟类多样性的重要因素[20,153—154]。例如 Luis Carrasco 等利用英国繁殖鸟类调查数据和随机森林模型研究了空间异质性的不同组分对鸟类丰富度的影响,发现植被结构是最重要变量,植被多样性也对丰富度有重要作用[20]。Naparat Suttidate 等利用卫星遥感图像纹理作为生境异质性的代理指标,显著地提升了模型预测鸟类分布的精度,并发现泰国热带森林中较大体型的鸟类分布对生境异质性更敏感[155],这可能是由于犀鸟、啄木鸟和野鸡等大型鸟类比小型鸟类在更大的尺度上感知和利用森林结构。

2.3.2 森林退化

森林退化的含义非常广泛[156],一般指由于火灾、边缘效应、木材开采、极端干旱等人类活动或自然过程导致森林生态系统整体质量下降的过程[157]。国际粮农组织将森林退化定义为森林总体效应供应的长期减少,其中包括木材、生物多样性和其他产品和服务[158]。遥感监测表明当前整个巴西亚马逊森林的退化的面积和程度已经超过了森林砍伐[159]。森林退化被认为是当前区域或更大尺度鸟类多样性下降和群落组成同质化的主要原因之一[19,160—162]。

与森林破碎化导致斑块面积减小、连通性下降不同,森林退化主要影响森林内部的的生物多样性和生态系统功能。森林退化过程中林下植被减少,功能和结构完整的原始林转变为次生林、草地和农田等[163],都会造成鸟类栖息地适宜性的下降甚至丧失,从而对鸟类多样性产生负面影响[19]。研究表明如果一个物种的地理范围内有大量退化的森林,那么这个物种受到威胁或种群减少的可能性要比那些其地理范围内有较少森林覆盖但质量高的物种大[114]。

食性、巢址等习性在决定鸟类对森林退化的响应中起到了重要作用。例如野外观测发现由于次生林缺乏

天然的树洞,洞穴筑巢鸟类更容易受到幼虫寄生的影响[160]。林下食虫鸟也对森林退化十分敏感,许多研究表明食虫鸟在退化森林中种群数量下降[164—166],但具有一定的不确定性[165]。研究者就鸟类(捕食者)和无脊椎动物(猎物)对森林退化的不同响应开展了广泛调查,但尚未取得一致性的结论[31,167]。

森林退化还会导致鸟类群落组成的同质化。例如 Matthew Betts 等发现在加拿大东部尽管总体森林覆盖率变化不大,但由于频繁的采伐和大规模的集约化林业转型,原始森林面积缩小、森林结构简化导致适宜鸟类栖息地大量减少。多种森林鸟类,特别是成熟原始林依赖种,例如栗胸林莺(*Setophaga castanea*)、橙胸林莺(*Setophaga fusca*)、北山雀(*Poecile hudsonicus*)、鹪鹩(*Troglodytes hiemalis*)等受到严重的负面影响[19]。通过对肯尼亚南部近自然林、退化森林、农田和外来种人工林鸟类多样性的对比也发现,退化森林与其周边农用地的鸟类群落组成基本相似,而与近天然森林的鸟类群落组成差异较大,近天然森林往往拥有较高密度的森林依赖型鸟类[161]。

3　未来研究展望

综上所述,森林结构及其变化在不同尺度上都对鸟类多样性产生了深远的影响。本文基于当前森林结构的生物多样性影响机制研究进展,概述了当前研究中存在的问题并对未来可能的研究方向提出了展望,主要包括以下三个方面:

3.1　新兴观测手段的应用

在鸟类多样性信息获取方面,尽管传统的野外调查能够为鸟类分布提供较为准确信息,但多集中在局地的个体和群落水平。在将样地尺度结果外推到景观尺度上时,不可避免的受到样本代表性和空间异质性的影响[168]。由于鸟类多样性也随研究范围和调查强度的增加发生非线性增长或变化[169],导致在不同地点之间进行鸟类多样性及其主导因素的比较存在一定的困难。当前基于大规模标准化调查的鸟类分布地图仍然较为缺乏,多使用行政区划、生态地理区域等进行表述[170],此类面状分布数据的时空分辨率也较其他环境数据集粗糙[171]。近年来观鸟活动逐渐在国内外兴起,这种公众参与的方式为研究最新的鸟类分布变化提供了大量信息。观鸟记录一般具有准确的地理坐标或较为详细的目击地点描述,便于进行地理空间分析。随着网络技术的发展和智能手机的普及,观鸟记录数量快速增长,并形成了如 eBird[172]、中国观鸟记录中心等网络数据库。Vijay Ramesh 等利用 2013 年至 2021 年间 eBird 提供的 129 万份公民科学观测数据,研究了气候和景观变量的作用及其与热带生物多样性热点(印度西高止山脉南部)鸟类物种发生的关系[173]。Auriel Fournier 等的研究表明,利用公民科学监测项目的大量数据可以改善鸟类迁徙连通性的模拟精度,从而为湿地管理决策和鸟类保护行动提供科学支持[174]。然而,半结构化的公民科学数据因其质量的不确定性而受到质疑,由于观测的不完善和持续时间的不统一,可能会使物种丰富度的估计产生偏差[175]。需要利用多种统计方法处理公民数据中的错误和偏差,从而改进半结构化和结构化数据中物种丰富度的预测[176—177]。对比公民数据和专业数据库发现两者都包含了生物多样性的宝贵信息,但侧重不同的方面:公民数据往往具有更多易于发现的、体型较大的物种,而专业数据库中的濒危种较多[178]。我国观鸟活动起步较晚、数据收集尚不完善,如何综合利用多源数据、准确还原森林结构变化过程中鸟类分布的时空演变特征仍需进一步探索[179—180]。

在森林结构信息获取方面,近年来激光雷达、无人机等探测手段和搭载平台的发展从根本上改变了我们观察和描述森林结构的方式。激光雷达以其高效、精准、穿透能力强、不受太阳高度角和阴影影响、克服光学遥感的饱和问题等优点,逐渐成为发现以前难以测量的栖息地特征的有力工具[181]。许多科学工作已经探索了激光雷达数据在特定种类的资源选择、指导濒危物种野外调查、生物多样性预测、栖息地质量评价等方面的可能性。尽管大尺度高分辨率森林结构产品不断涌现[182—183],但当前主要使用冠层高度及其变异来评估对鸟类多样性的影响[102],对于林下特征的研究仍局限于样地或林分尺度。最近发射的全球生态系统动态调查激光雷达(GEDI, Global Ecosystem Dynamics Investigation Lidar)为全球森林结构测量提供了前所未有的高密度、高精度、一致性的数据[184],基于其反演的林下结构参数已被成功应用于鸟类多样性预测[50]、估算林下可

燃物储量[185]、监测虫害导致的中下层植被死亡[186]等。然而,受限于验证数据的普遍缺乏,GEDI 产品的实际表现尚未得到充分讨论和评价。由于数据覆盖率低、空间分布不连续,如何进行点面转换、与地面调查相匹配也是制约其广泛应用的阻碍之一。因此,应用 GEDI 数据获取森林结构参数虽已展现了巨大潜力,但仍需进一步探索。

3.2 开展多尺度比较研究

尽管国内外学者已经在不同尺度上初步揭示了森林结构对鸟类多样性的影响机制,但当把样地尺度上对驱动因素的认识和内在机制的理解外推到区域尺度上时,往往存在一定的不确定性和局限性[187]。除了个体或样地研究存在背景依赖性以外[189—190],有学者认为空间尺度和粒度是导致不确定性的关键因素。这是由于森林结构指标与遥感反演参数之间的关系,以及由此推论的森林结构影响机制均具有强烈的尺度依赖性[190],生物—环境之间的关系会随着观测尺度和粒度发生变化[187]。

森林结构及其异质性在不同的时间和空间尺度上都是连续的,而用于量化森林结构及其异质性的变量却强烈依赖于观测尺度和粒度[191]。在对不同森林结构变量进行比较时,不同大小或形状的观测单位可能会导致不同或者不可比的森林结构估计,从而影响了遥感数据的预测性[192]。例如,尽管普遍认为森林结构及其异质性对生物多样性有积极影响,但研究发现环境异质性—物种多样性之间的关系并不总是正的,甚至有不显著、负相关和驼峰形状相关关系存在[188,194—195]。Collins Kukunda 等研究了地块大小在量化森林结构空间异质性中的影响,发现对于空间异质性较大的样地,各项森林结构指标所受样地大小的影响也较大。随着样地面积和分辨率的增加,更多的森林结构空间异质性被包括进来,因此较大的样地面积可以得到更可靠的森林结构异质性估计[191]。树木的空间排列同样决定了达到可靠的森林结构异质性估计所需的样地面积大小[33]。研究者对激光雷达遥感反演森林结构信息的最佳空间粒度和尺度进行了深入探索,研究发现使用 25—75 m 的空间粒度可以充分捕获多种森林类型的结构特征[195],对于空间尺度存在一个 900—2500 m^2 的阈值以完整表达森林结构异质性[191]。因此,多尺度观测有可能更好的揭示森林结构及其变化,促进对森林结构影响鸟类多样性这一生态过程的内在机制的理解。

对森林结构变化引发的生态学过程,也需要从不同尺度开展研究。例如,在总结森林破碎化的影响时,有的研究者更加关注在景观尺度下斑块间距离的缩短导致入侵和定殖概率增加、破碎化导致斑块间和板块内的异质性增加等过程,因此往往得到破碎化对生物多样性有积极影响的结论[190,196];而有的研究者在样地或斑块尺度下发现破碎化导致的栖息地丧失和隔离,一方面增加了物种灭绝风险,另一方面孤立的斑块和扩散能力的限制使得重新定殖的可能性降低,从而对生物多样性产生负面影响[198—199]。因此,需要进一步的不同尺度的实证研究以全面理解森林破碎化对生物多样性的影响及机制[187]。

3.3 进行多领域跨学科合作

研究森林结构对生物多样性的影响,需要生态学家、保护生物学家和森林管理政策制定者开展跨学科合作,将内在机制、保护方法和管理措施相结合。随着世界范围内林业发展进入从砍伐到种植,从增量到提质的新阶段[200—201],森林管理引发的结构变化比单纯的砍伐和种植更加复杂,难以使用森林类型(例如落叶/常绿、针叶/阔叶、天然/人工林等)准确描述其内部结构的差异。即使利用卫星遥感影像进行反演,一些精细尺度的森林结构变化也很难捕捉到。例如有研究发现在构建物种分布模型进行预测时,预测成功率较低的物种往往与高大孤立树木、枯立木、倒木等森林结构的细节有关[19],而这种结构的缺失对濒危物种的负面影响更大。即使野外观测发现某些森林结构特征对鸟类分布有重要影响,也难以扩展到景观水平,阻碍了在较大尺度上实行有效的生物多样性保护和森林管理行动[91]。因此需要森林生态学家开展精细时间分辨率下的大规模的森林清查,并结合激光雷达等最新手段获取森林结构特征及其变化。

尽管激光雷达技术可以提供独特的精细化植被三维结构、帮助保护生物学家更好的认识和理解生物—环境之间的影响过程及其内在机制,但目前激光雷达参数反演主要服务于森林资源调查或森林生态学的研究,有时难以准确反映鸟类的生境需求[201]。应用于生物多样性保护的森林三维结构特征信息通常是离散的,在

不同尺度上十分稀少并缺乏一致性。因此,面对激光雷达反演森林三维结构数据的巨大潜力,如何筛选出与生境质量评估和生物多样性保护密切相关的森林结构参数或格局阈值[152],对未来生物多样性保护研究有重要意义。

我国自 20 世纪 80 年代以来陆续实施的防护林建设、天然林保护、退耕还林、速生丰产林等多个大型生态工程,极大的改变了森林的种类组成和年龄结构[12,202]。最新遥感监测显示全国人工林面积增加了 44.75 万 km^2,而天然林面积减少了 21.91 万 km^2[203]。我国人工林总体质量不高,中幼林、人工纯林、低效林比重大,需要定期进行抚育、疏林和采伐等人为干预,从而影响整个尺度上的森林结构[205—207]。森林管理措施的开展也为推进生物多样性保护提供了难得的机遇[74,207]。建立和恢复具有与原始林相似特征的林分已成为森林管理最重要的目标之一[208—209],而森林结构是评价这种相似性的首选工具[22]。然而当前尚缺乏全球性的定量评估来确定哪些结构特征可以通过管理来减少对鸟类多样性的负面影响[210—211]。这需要森林管理者在明确对生物多样性有关键影响的森林结构特征的基础上,根据不同国家和地区的实际情况制定具有针对性的政策,以更加有效的保护生物多样性,在森林生态系统的多种功能价值之间的达到平衡。

4　结论

物种—环境关系及其影响机制是生态学和生物地理学长期关注的问题,研究者很早就发现了森林结构是决定鸟类群落组成的直接因素。在当前毁林和造林不断发生的背景下,森林水平和垂直结构及其空间异质性的巨大变化,在不同尺度上直接或间接的对鸟类多样性产生了深刻的影响。但受限于样地监测的局限性和数据的普遍缺乏,在目前在不同的研究中对于影响的范围、程度甚至方向不尽相同,缺乏对影响机制的综合理解。

激光雷达技术的发展和鸟类调查活动的普及使相关数据可利用性迅速增长,支持了森林结构的生物多样性影响研究方法从定量比较到统计建模的扩展,以及研究内容从机理解释到影响预测的深入。当前亟需加强新兴数据和技术的应用,并广泛开展生态学家、保护生物学家和森林管理政策制定者的跨学科合作,从而明确对鸟类多样性有重要影响的结构特征和格局,为探索生物多样性保护解决方案提供更可靠的科学支持。

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