



•综述• 创刊30周年纪念专辑

气候变化与生物多样性之间的复杂关系和反馈机制

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摘要: 气候变化与生物多样性丧失是人类社会正在经历的两大变化。气候变化影响生物多样性的方方面面, 是导致生物多样性丧失的一个主要驱动因子; 反过来, 生物多样性丧失会加剧气候变化。因此, 阻止甚至扭转气候变化和生物多样性丧失是当前人类社会亟需解决的全球性问题, 但我们对气候变化与生物多样性之间的复杂关系和反馈机制尚缺乏清晰认识。本文总结了近年气候变化与生物多样性变化的研究进展, 重点概述了不同组织层次、空间尺度和维度的生物多样性对气候变化的响应和反馈等相关领域的研究进展和存在的主要问题。结果发现多数研究关注气候变化对生物多样性的直接影响, 涉及到生物多样性的不同组织层次、维度和营养级, 但针对气候变化间接影响的研究仍然较少, 机理研究同样需要加强; 生物多样性对生态系统功能影响的环境依赖和尺度推演、生物多样性对生态系统多功能性的作用机理和量化方法是当前研究面临的挑战; 生物多样性对生态系统响应气候变化的作用机制尚无统一的认识; 生物多样性对气候变化的正、负反馈效应是国内外研究的盲点。最后, 本文展望了未来发展方向和需要解决的关键科学问题, 包括多因子气候变化对生物多样性的影响; 减缓和适应气候变化的措施如何惠益于生物多样性保护; 生物多样性与生态系统功能的理论如何应用到现实世界; 生物多样性保护对实现碳中和目标的贡献。

关键词: 气候变化; 多维度生物多样性; 多尺度生物多样性; 生态系统多功能性; 反馈机制

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Complex relationships and feedback mechanisms between climate change and biodiversity

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ABSTRACT

Background and Aims: Climate change and biodiversity loss are two major changes that human society is experiencing. Climate change affects all aspects of biodiversity and is a major driver of biodiversity loss; in turn, biodiversity loss exacerbates climate change. Therefore, halting or even reversing climate change and biodiversity loss is a global issue that needs to be addressed by human society. However, we lack a clear understanding of the complex relationships and feedback mechanisms between climate change and biodiversity. Here, we summarize the research on climate and biodiversity change in the last decade by focusing on studies investigating the responses and feedback of biodiversity to climate change at different organizational levels, spatial scales, and diversity dimensions.

Progress: Our results showed that most studies focus on the direct impacts of climate change on biodiversity, involving different organizational levels and dimensions and trophic levels of biodiversity. Studies on the indirect impacts of

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climate change were rare, and we suggested that mechanistic studies need to be strengthened. The mechanisms and quantification of the effects of biodiversity on ecosystem multifunctionality were challenges for current research. There was no consensus on how biodiversity contributes to ecosystem response to climate change; the positive and negative feedback effects of biodiversity in the context of climate change were a blind spot in domestic and international research.

Prospects: The future direction and key scientific issues that need to be solved in the field of climate change and biodiversity change are numerous. We identify 4 main areas of future research: understanding (1) the impacts of multi-factor climate change on biodiversity, (2) how mitigation and adaptation measures to climate change can benefit biodiversity conservation, (3) how the theory of biodiversity and ecosystem function can be applied to the real-world ecosystems and (4) what is the contribution of biodiversity conservation to carbon neutrality goals.

Key words: climate change; multi-dimensional biodiversity; multi-scale biodiversity; ecosystem multifunctionality; feedback mechanisms

我们生活的世界正在经历两大变化, 并且与每个人息息相关, 这就是气候变化和生物多样性变化。这两大变化, 一个是非生物的环境变化, 一个是生物因素的变化, 它们的发生都与人类活动密切相关, 反过来又影响到人类活动。

全球气候变化是不争的事实, 鲜有异议。气候变化是指气候平均状态在较长一段时间上具有统计学意义的改变或波动。通常情况, 全球气候变化是指工业革命以来, 与大气CO₂浓度上升相联系的气温的升高和降水格局的改变。联合国气候变化政府间专家委员会(Intergovernmental Panel on Climate Change, IPCC)第6次评估报告明确指出, 大气中CO₂浓度相对于1850年工业革命前的285 ppm已经升高了47.3%, 即达到了409.9 ppm, 导致全球和陆地地表大气温度分别升高1.09°C和1.59°C, 也加剧了极端气候事件(如干旱、热浪)发生的强度、频率和持续时间(IPCC, 2021)。

相比较而言, 人们对生物多样性变化的感知并没有那么直接。这是因为, 认识生物多样性的变化, 一方面需要专业知识, 甚至依赖专业设备的分析; 另一方面需要长期的观察、监测(马克平等, 2018; 冯晓娟等, 2019)。例如人们很早就注意到一些大型动物、有花植物种群数量的变化, 制定了珍稀濒危生物的红皮书, 但对于隐花植物、昆虫、海洋生物、微生物等则关注甚少, 而这些生物往往在生态系统中扮演了重要的角色。随着气候变化和人类活动的加剧, 全球尺度上的生物多样性丧失是极其显著的。据统计, 自公元1500年以来, 约有30%的物种在全球范围内受到威胁或已经灭绝(Isbell et al, 2022)。在地球的演化历史上, 由于剧烈的环境变化曾经出现过5次生物大灭绝, 而目前由人类活动引起的生

物多样性丧失, 特别是4万年前人类走出非洲到现在, 大规模的生物灭绝, 被认为是第6次生物大灭绝(Cowie et al, 2022)。当然, 现在的生物灭绝速率要远比人类非洲起源时代大得多。

气候变化与人类活动共同作用, 塑造了地球生物多样性格局; 而不同维度和营养级上的生物多样性变化, 反过来或多或少也影响气候变化和人类活动, 也即生物多样性的反馈作用(图1)。其中, 我们了解最少的是生物多样性如何通过生态系统功能的变化间接调控气候变化。比如, 传统知识认为, 伴随着生物多样性的丧失, 生态系统固碳、抵御极端气候、抵御外来种入侵等功能也随之减弱, 甚至丧失(Díaz et al, 2009a; Tilman et al, 2014; Isbell et al, 2015), 最终会加速气候变化(Mori et al, 2021)。但因生物多样性的多维度性和多营养级, 使得准确预测生态系统功能如何响应生物多样性的变化变得异常困难(Le Bagousse-Pinguet et al, 2019; Wu et al, 2022)。

鉴于气候变化和生物多样性变化对人类社会的深刻影响, 有两个国际组织评估了适应和减缓这些变化的可能对策。IPCC是世界气象组织(World Meteorological Organization, WMO)及联合国环境规划署(United Nations Environment Programme, UNEP)于1988年联合建立的政府间机构, 其主要任务是对关于气候变化的科学、技术和社会经济知识的现状, 气候变化对社会、经济的潜在影响和未来风险, 适应和减缓气候变化的可能对策等进行评估。到目前为止, IPCC第6次气候变化评估报告已经出版(<https://www.ipcc.ch/assessment-report/ar6>)。成立于2012年的生物多样性和生态系统服务政府间科学政策平台(Intergovernmental Science-Policy Platform

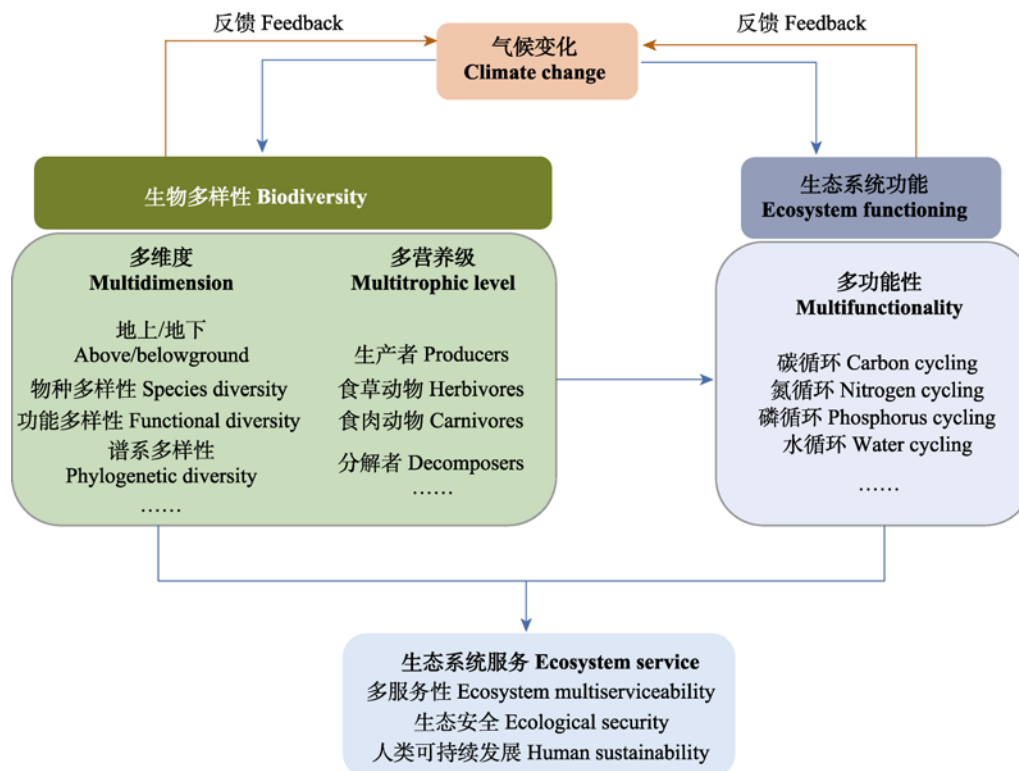


图1 气候变化对多维度、多营养级生物多样性的影响以及生物多样性对气候变化的反馈作用。人类活动和生物多样性的协同发展是维持生态系统多服务性、生态安全和人类可持续性的基础。

Fig. 1 Impacts of climate change on multi-dimensional, multi-trophic biodiversity, and the feedback of biodiversity to climate change. The coordinated development of human activities and biodiversity is the basis for maintaining ecosystem multiserviceability, ecological security and human sustainability.

on Biodiversity and Ecosystem Services, IPBES, <https://ipbes.net/global-assessment>)作为独立的政府间机构,开展全球和区域尺度的生物多样性与生态系统服务评估,涉及包括《生物多样性公约》《濒危野生动植物物种国际贸易公约》《湿地公约》等7项环境领域的国际协议,其作用类似IPCC。2021年6月,IPCC和IPBES联合发布了一份关于生物多样性和气候变化的会议报告,凸显了气候变化和生物多样性对解决目前环境问题的重要性(Pörtner et al, 2021)。

近20年,生物多样性相关研究发表文章数量呈逐年增长趋势,而同时关注生物多样性和气候变化的文章在2000–2017年呈缓慢增长,从2018年开始年增长迅速(图2a)。生物多样性和气候变化研究领域主要集中在生物多样性、生物多样性保护、生态环境科学和野生生物管理等,其次是环境科学、种群研究、生物地理学和计算生物学等领域(图2b)。

气候变化和生物多样性变化虽然得到了极大

关注,但是我们对两者之间的复杂关系和反馈机制尚缺少清晰认识(牛书丽等, 2009; Chapin III & Díaz, 2020; Mori et al, 2021)。气候变化对生物多样性的影响表现在不同的时空尺度和不同组织层次,异常复杂(图3)。在大尺度上,气候变化直接影响到物种的地理分布、迁徙模式、季节动态等。在生态系统尺度上,气候变化最重要和最直接的影响是改变群落物种组成、多样性以及与生物多样性紧密关联的生态系统功能。反过来,生物多样性变化是多维的,主要包括生物群落组成变化和生物多样性丧失,表现为物种多样性以及物种多度、物种分布和遗传多样性等方面的变化(Pereira et al, 2012)。生物多样性变化的多维性使得研究生物多样性对气候变化的反馈作用变得异常复杂。

基于以上背景,本文重点概述了近10年气候变化与生物多样性之间的复杂关系和反馈机制的研究进展,并展望了未来发展方向和需要解决的关键科学问题。

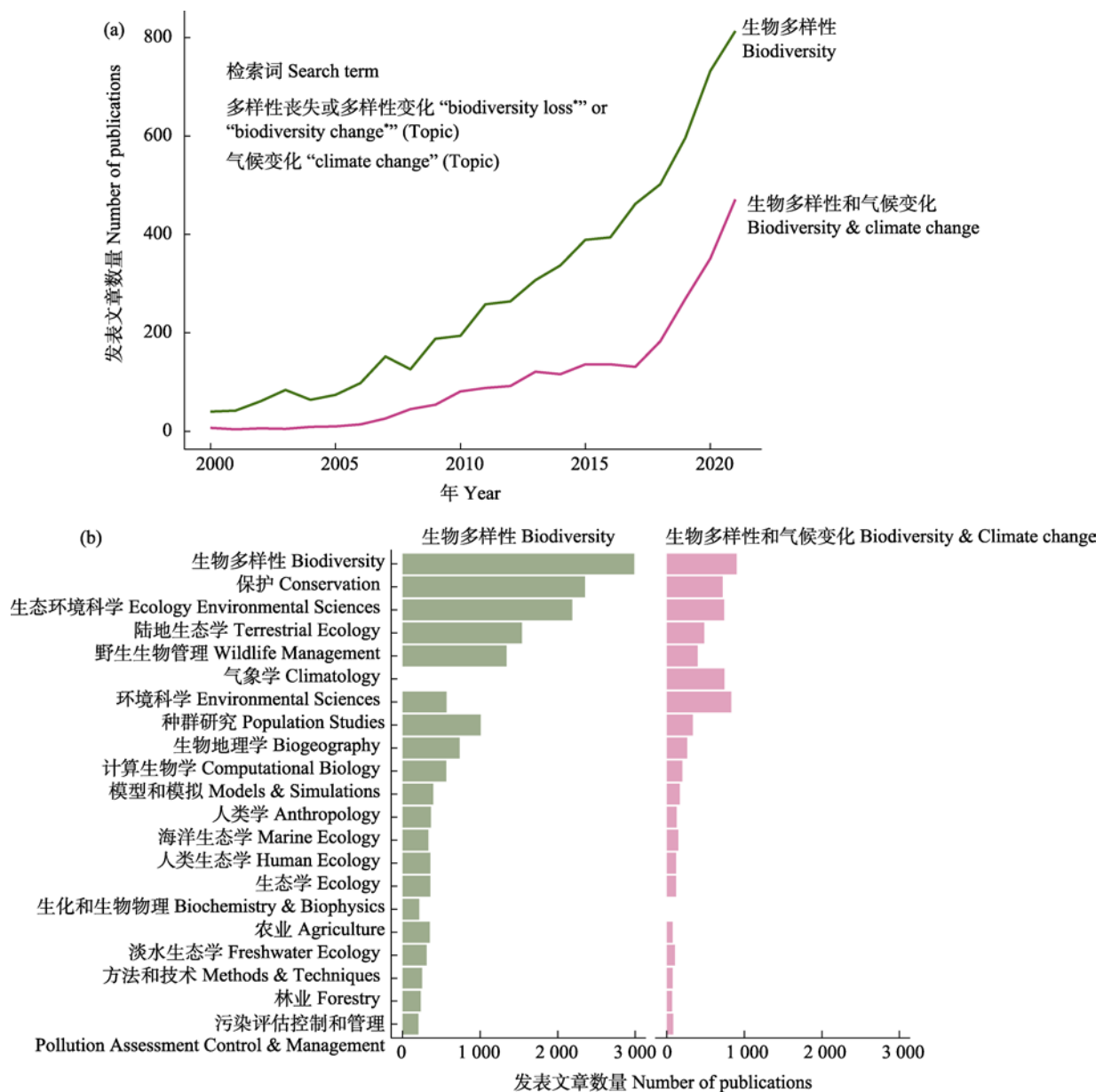


图2 生物多样性和气候变化领域发表文章趋势分析和主要研究方向。(a)近20年生物多样性和气候变化相关文章发表趋势(数据来源Web of Science, 最后一次访问2022年8月6日)。(b)生物多样性和气候变化主要研究方向发表文章数量。
Fig. 2 Analysis of publication trends and main research areas in the field of biodiversity and climate change. (a) Publication trends in biodiversity and climate change-related articles published over the last 20 years (data sources: Web of Science, last accessed August 6, 2022). (b) Number of articles published in the main research areas of biodiversity and climate change.

1 相关研究领域的现状和主要问题

针对气候变化和生物多样性之间的复杂关系和反馈机制,在这一部分我们着重综述了(1)气候变化对生物多样性的影响,包括直接和间接影响、对不同组织层次、维度和营养级生物多样性的影响,(2)生物多样性与生态系统功能的关系,以及(3)生物多样性对气候变化的贡献和反馈等相关研究领域的

现状和主要问题。

1.1 气候变化对生物多样性的直接和间接影响

近代以来,生境丧失、农业扩张、资源过度开发、外来物种入侵和土地利用变化一直是生物多样性丧失主要且直接的驱动因素(Hoffmann et al, 2010; 魏辅文等, 2014; Isbell et al, 2022),但目前越来越多的研究表明,气候变化很可能成为过去一个世纪物种消失甚至灭绝的主要原因(Jones et al, 2016)。

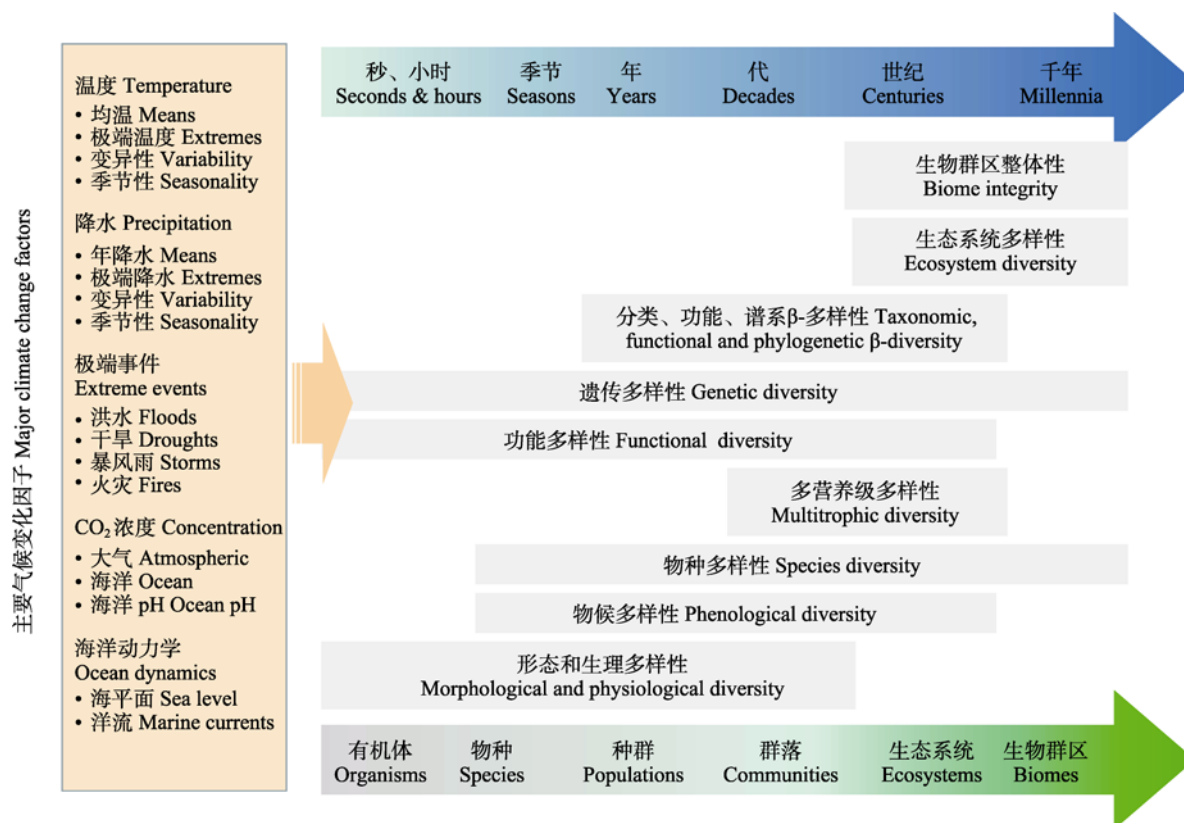


图3 主要气候变化因子对不同时空尺度和不同组织层次上生物多样性的影响

Fig. 3 Impacts of major climate change factors on biodiversity at different spatial and temporal scales and different levels of organization

气候变化对生物多样性的影响不仅表现在对生物体的生理、活性、生长和温度敏感性产生直接影响，还会通过改变非生物环境而间接影响物种的空间分布、群落组成以及物种相互作用。在受到气候变化影响后，生物一般有3种可能的反应：变化，迁移，灭绝(Rinawati et al, 2013)。例如，随着全球变暖，植物和动物向两极或更高海拔移动(Chen et al, 2011; Lenoir et al, 2020; 祖奎玲和王志恒, 2022)，也有些物种表现出开花提前等变化，甚至还有一些物种发生了快速进化以适应环境变化(Shen et al, 2022)。除了前两种反应，从一个地区灭绝的生物也不在少数。气候变化增加了极端气候的频率和强度，洪水、热浪、干旱和火灾的增加也深刻影响了生物多样性。有研究发现，如果全球大气温度超过工业化前水平的1.5°C，植物、动物和昆虫等的地理分布范围将下降50%，物种灭绝会明显加速(Warren et al, 2021)。除了直接影响，气候变化还可能通过物种相互作用影响生物多样性水平。例如，当一些关键物

种因为气候变化而灭绝，与之依赖的物种也必然会受到影(王晴晴等, 2021)，包括捕食者或猎物(Terraube et al, 2017)、寄生虫(Pardikes et al, 2022)以及对植物繁殖至关重要的物种，例如传粉昆虫(Vasiliev & Greenwood, 2021; Ganuza et al, 2022)。此外，气候变化可能影响特定物种的竞争者(Collins et al, 2022)、捕食者(Bestion et al, 2019)或病原体(Delgado-Baquerizo et al, 2020; Makiola et al, 2022)，从而影响生物多样性。另外，气候变化还可能导致相互依存的物种由于对环境变化响应的不同步，从而出现物候的不匹配(Kharouba et al, 2018; 刘安榕等, 2018; Visser & Gienapp, 2019)。目前气候变化对生物多样性直接影响的研究很多，但针对间接影响的研究仍然较少，而如何确定与量化气候变化对物种相互作用的方向以及程度仍面临挑战(Blanchet et al, 2020; Collins et al, 2022)。目前大部分研究仅仅关注单一或多种气候变化因子对有限的生物多样性维度、组织层次或时空尺度的直接或间接影响。因

此, 未来的实验设计与理论分析需要同时考虑多种气候变化因子在更大时空尺度上对多维度、多组织层次生物多样性的直接与间接影响, 以便全面地评估和量化气候变化对生物多样性的影响。

1.2 气候变化对不同组织层次生物多样性的影响

气候变化可在分子、个体、种群、群落、生态系统和生物群区等不同组织层次影响生物多样性。在分子水平上, 气候变化会影响生物体内相关基因的表达及代谢产物的生成, 这些变化有助于提高生物体对气候变化的适应(Scheffers et al, 2016)。如植物在干旱环境中会生产更多的脯氨酸、丙二醛、脱落酸等以提高自身的抗胁迫能力(Li et al, 2021)。在个体水平上, 生物体响应气候变化主要表现在生理形态特征(Bjorkman et al, 2018)和生长繁殖策略(Petry et al, 2016)这两方面, 但具体的响应模式还取决于其自身的生理特征和地理分布范围(Humphrey et al, 2018)。在种群水平上, 气候变化会引起物种微进化。微进化是指生物在基因组水平上通过基因突变与多基因交互作用, 改变表型或其他性状以适应新环境(Bonnet et al, 2022)。例如, 在沿美国加利福尼亚州海岸线的一项研究中发现, 因气候变化所引起的入海口水流变化(由急水流向缓水流变化)使得低骨板化的三刺鱼(*Gasterosteus aculeatus*)种群数量显著上升(Des Roches et al, 2020)。在群落水平, 气候变化主要通过非生物和生物因素两方面来影响生物多样性。一方面, 如在寒冷且潮湿的温带地区, 温度的升高可增加土壤有机质的分解, 提高土壤养分的可利用性(Hicks Pries et al, 2017)。这些变化为生物体提供更多生态位的同时, 也会带来新的植物物种间及植物-微生物间的竞争关系。在更大的生态系统水平上, 气候变化还会导致生态系统结构、功能以及多样性发生改变。如生态系统的退化将直接导致生物多样性的丧失。另一方面, 在生态系统响应气候变化的同时, 也会对气候变化产生一系列的反馈效应(详见1.6节), 正反馈效应将导致更程度的气候变化, 进而加剧气候变化对生态系统结构和功能的影响。在更大的生物群区水平, 以极端气候著称的生物群区, 如极地、山地、荒漠和北方森林等, 往往微小的温度或降水变化就会对物种组成和生物多样性产生较大的影响(Sala et al, 2000)。

值得注意的是, 不同组织层次的生物多样性对气候变化的响应可能不同, 且不同组织层次间也可能相互影响。因此未来研究必须综合考虑气候变化对不同组织层次生物多样性的影响。此外, 气候变化会在不同时间和空间尺度上影响生物多样性, 要准确地评估气候变化对生物多样性的影响需要长时间、多位点的研究, 在研究方法上也需要适当加入遥感等大数据集并耦合相关的统计和过程模型。

1.3 气候变化对不同维度生物多样性的影响

气候变化对生物多样性的影响因生物多样性的多维度性而变得复杂。首先, 在物种多样性层面的研究最为广泛, 但经常因研究区域、生态系统类型和生物类群的不同而得到不一致的结论(Gruner et al, 2017; Bastazini et al, 2021)。比如, 有的研究发现气候变暖导致物种丰富度下降, 但对群落均匀度影响很小; 也有研究发现气候变暖不影响物种丰富度, 但会影响物种的优势度。气候变化对功能多样性的影响, 目前关注最多的主要是以功能性状表征为主的功能多样性。功能性状是指那些影响个体或物种的生长、存活和繁殖等表现, 最终影响物种适合度的形态、生理、物候等性状(Violle et al, 2007)。物种性状选择、性状空间维度和空间结构的量化(Mouillot et al, 2021)是该领域主要关注的方向之一。在群落水平, 气候变化可能不会导致功能多样性的直接丧失, 一个可能的原因是物种功能冗余(一个或多个物种的丧失对生态系统功能的影响很小或可忽略)可能缓冲气候变化对功能多样性的影响(Gallagher et al, 2013)。但目前有关气候变化对功能多样性的影响研究主要来自于地上生物, 而对土壤生物功能多样性的影响尚缺乏系统性认识(Malik et al, 2020)。在进化水平, 假如因气候变化导致的物种丧失在进化树上不是随机分布的, 那么气候变化可能导致谱系多样性不成比例地丧失(Thuiller et al, 2011; Li et al, 2019)。有研究发现快速的气候变化是导致谱系多样性丧失的重要原因(Saladin et al, 2020)。尽管如此, 谱系多样性如何响应气候变化的选择压力仍缺少实证性研究(Lavergne et al, 2010; Li et al, 2019)。

气候变化对不同营养级生物多样性的影响也不尽相同, 这可能与不同营养级的物候对气候变化的响应存在差异有关。在过去的几十年间, 植物、

鸟类、昆虫、两栖动物、真菌等物候都发生了显著的改变(Thackeray et al, 2016; Roslin et al, 2021)。然而, 生物间物候的变化, 特别是不同营养级物种的物候, 对气候变化的响应并不同步, 这改变了物种间相互作用强度(Gilman et al, 2010), 导致高营养级物种多样性的下降(Potts et al, 2010), 甚至造成了局部地区动植物种群衰退。物候对气候变化的非同步性响应不但存在于不同营养级物种间(Roslin et al, 2021), 也会发生于同一生物的不同器官间(Blume-Werry, 2022)。最近的研究发现, 植物地上、地下部分的物候对气候变暖的响应存在差异(Liu et al, 2022a), 这势必会影响植物向地上绿色食物网和地下棕色食物网所提供资源的季节动态(Thakur, 2020)。由于棕色食物网对气候变化的响应具有更高的稳定性(Thakur, 2020), 因此, 植物地上、地下物候的非同步性响应引起的资源质量和数量输入的季节性改变可能会造成绿色和棕色食物网间物质和能量流动的失衡(Visser & Gienapp, 2019), 从而对物种多样性及生态系统功能造成严重威胁。目前为止, 在气候变化背景下, 人们对生物物候的非同步性变化如何影响多营养级生物多样性的认识尚不清晰, 极有可能成为未来研究热点。

1.4 生物多样性变化对生态系统功能的影响

生物多样性变化最直接的后果是生态系统功能的变化; 而生态系统功能的变化, 如初级生产力的变化, 反过来又影响气候变化。因此, 厘清生物多样性与生态系统功能之间的关系是理解生物多样性与气候变化复杂关系的关键(Mori et al, 2021)。过去30年, 生物多样性与生态系统功能关系研究得以快速发展, 是因为多样性的丧失会对生态系统功能造成直接负面的影响, 进而影响生态系统为人类提供的各类服务(Tilman et al, 2014; van der Plas, 2019)。长期以来, 该领域的研究主要以草地生态系统为主, 近些年因森林生物多样性在固碳方面的重要性(Díaz et al, 2009a; Liu et al, 2018; Feng et al, 2022; Hua et al, 2022), 其与生态系统功能的关系等方面的研究得以发展, 研究方法涉及到控制实验、野外观察、森林清查等(Verheyen et al, 2016)。生物多样性丧失对生态系统功能的影响主要有两大机理性的解释, 分别是取样效应(the sampling effect)和互补效应(the complementarity effect) (Loreau &

Hector, 2001)。其中, 取样效应是指优势物种的特定功能性状对生态系统功能的影响占优势, 而互补效应是指在高的生物多样性群落里面, 由于资源分异或正的种间关系使得生态系统整体资源利用效率增加, 进而提升生态系统功能。因草地和森林生态系统结构的差异, 所涉及的机理过程各有不同(详见Forrester & Bauhus, 2016)。已有的研究普遍发现, 取样和互补效应同时共存, 并且随着时间的推移, 生物多样性的互补效应逐渐增强(Tilman et al, 2001; Huang et al, 2018; Bongers et al, 2021)。尽管如此, 生物多样性对生态系统功能影响的环境依赖(Ratcliffe et al, 2017; Fei et al, 2018; Jing et al, 2022)、尺度推演(Craven et al, 2020; Gonzalez et al, 2020; Qiu & Cardinale, 2020)仍是当前研究面临的挑战。

传统的研究主要关注生物多样性丧失对单一生态系统功能的影响, 比如生态系统初级生产力。而一个健康的生态系统, 不仅能提供初级生产力, 还同时提供养分循环、有机质分解等多样的生态系统功能。也即, 生态系统具有同时提供多重生态系统功能的能力, 称作生态系统多功能性(Hector & Bagchi, 2007; Byrnes et al, 2014; 徐炜等, 2016; Manning et al, 2018)。虽然当前的研究主要以观测研究为主, 但研究者已达成一些共识。例如, 生态系统需要更多的物种才能支持更高的生态系统多功能性, 这是因为更多的物种往往有更高的功能多样性, 与此同时, 不同的物种支持的生态系统功能不尽相同。不仅如此, 更高的生态系统多功能性, 还需要不同营养级生物多样性来支撑(Schuldt et al, 2018; Luo et al, 2022)。生物多样性与生态系统多功能性研究已经有大量工作发表, 涉及到生物多样性的维度、空间依赖、全球变化因子的影响等方面的工作(井新和贺金生, 2021)。尽管如此, 该领域还面临诸多挑战。比如, 生物多样性丧失对生态系统多功能性、生态系统多服务性影响的机理还不清楚(van der Plas et al, 2016; 徐炜等, 2016; Gamfeldt & Roger, 2017; 井新和贺金生, 2021), 生态系统多功能性的量化方法及其数理统计原理等方面的研究需要加强(Jing et al, 2020)。

1.5 生物多样性对生态系统响应气候变化的贡献

生物多样性除对生态系统功能有直接的影响, 它对生态系统响应气候变化还具有重要的调控作

用。一方面,生物多样性丧失对生态系统功能的影响,与干旱、氮沉降、CO₂浓度增加等气候变化相关驱动因子同等重要,甚至远强于这些因子(Hooper et al, 2012; Tilman et al, 2014; Duffy et al, 2017)。另一方面,生物多样性对生态系统功能的影响不仅体现在对初级生产力的促进作用,同时还体现在对生态系统稳定性的影响,包括生态系统对气候变化的缓冲、抗性和恢复力等(李周园等, 2021)。也就是说,气候变化对生态系统功能的影响受生物多样性的调控。首先,高的生物多样性往往能形成与周围环境不同的微气候,从而有效缓冲因干旱、气候变暖等气候变化因子对生态系统结构和功能的负面影响(Zellweger et al, 2020)。其次,高的生物多样性往往有复杂的群落结构和高的资源获取能力和资源利用效率,比如在干旱环境下,对土壤水分的有效利用能帮助森林生态系统抵抗干旱胁迫(Grossiord, 2020)。再次,大量的研究表明,在干旱、火烧、热浪等干扰下,高的生物多样性也往往伴随有高的生态系统恢复力。反过来,气候也能调控生物多样性与生态系统功能之间的关系(Jing et al, 2015; Fei et al, 2018),甚至调控生物多样性与生态系统稳定性之间的关系(García-Palacios et al, 2018)。目前,生物多样性对生态系统响应气候变化的作用机制尚无统一的认识,这是因为生物多样性的作用机制涉及面很广,包括优势物种的功能性状、不同物种对气候变化响应的非同步性、多个物种对同一生态系统功能影响的功能冗余程度、时空保险效应以及对响应性状和效应性状的分类等(de Bello et al, 2021)。

1.6 生物多样性对气候变化的反馈作用

生物多样性对气候变化有正、负两方面的反馈作用(Mori et al, 2021)。气候变化可能会导致局域生物多样性格局的变化,如林线因气候变暖向高海拔或高纬度区域扩张,往往伴随着生态系统生产力的提升,进而增加生态系统的固碳量,这样大气中的CO₂通过植物的光合作用被固定在生态系统中,从而减缓或降低气候变暖,最终对气候变化有负反馈效应。与此相反,气候变化也会导致生物多样性的丧失,进而降低生态系统的生产力。由于输入生态系统的碳远远低于输出的碳,大量的CO₂通过分解作用释放到大气中,进一步加剧气候变暖,最终对

气候变化有正反馈效应。一般来说,生物多样性对气候变化的负反馈效应使得生态系统更加稳定,而正反馈效应使得生态系统加速改变,变得不稳定。因此,生物多样性对气候变化的正负反馈效应关乎生态系统的变化及其稳定性,涉及到气候变化、生物多样性和生态系统功能3个方面。

目前生物多样性对气候变化的正、负反馈效应是国内外研究的盲点,尤其是对其机理认识还不够深入,并且正负反馈效应还没有系统地纳入人类社会、政策制定等框架里面,亟需长期、跨学科研究(O'Connor et al, 2021)。尽管如此,从生物多样性与生态系统功能的关系出发是应对、减缓、适应气候变化的一种有效的、基于自然的解决方案(nature-based solution),而保护和恢复生物种的多样性和生境,将增强负反馈效应,以达到气候变化减缓的目的。虽然森林在生物多样性的正负反馈效应中有决定性作用,但在占全球面积40%的干旱、半干旱区的植树造林活动备受质疑,而如何调整次生林的分布和结构将是平衡碳固定与其他限制性资源竞争的有效途径(Liu et al, 2022b)。除此以外,未来的研究还面临诸多挑战,比如,由于生物多样性对气候变化的正负反馈效应会影响到未来种群、群落和生态系统的稳定性和变化轨迹,如何利用模型来模拟未来气候变化情景,以准确预测生物多样性变化对未来气候变化的正负反馈效应仍是一个极大的挑战(Mori et al, 2021)。未来的挑战还涉及到过去气候变化的滞后效应如何来影响当前时期生物多样性的地理分布格局,在多大程度和时间尺度上影响生物多样性及其功能。最后,极端气候事件,如干旱、热浪、极端降雨对生物多样性和生态系统功能的影响也不容忽视,尤其需要关注极端气候事件与其他全球变化因子(如土地利用变化、环境污染、荒漠化、土地退化)的相互作用。

2 未来发展方向和需要解决的关键科学问题

鉴于生物多样性对生态系统功能的重要影响以及生物多样性对气候变化的反馈作用,多因子气候变化对生物多样性的作用、生物多样性保护和气候变化减缓和适应的关系,生物多样性与生态系统功能的关系,以及生物多样性在实现碳中和目标中的作用,将仍是未来的研究重点,这些研究领域将

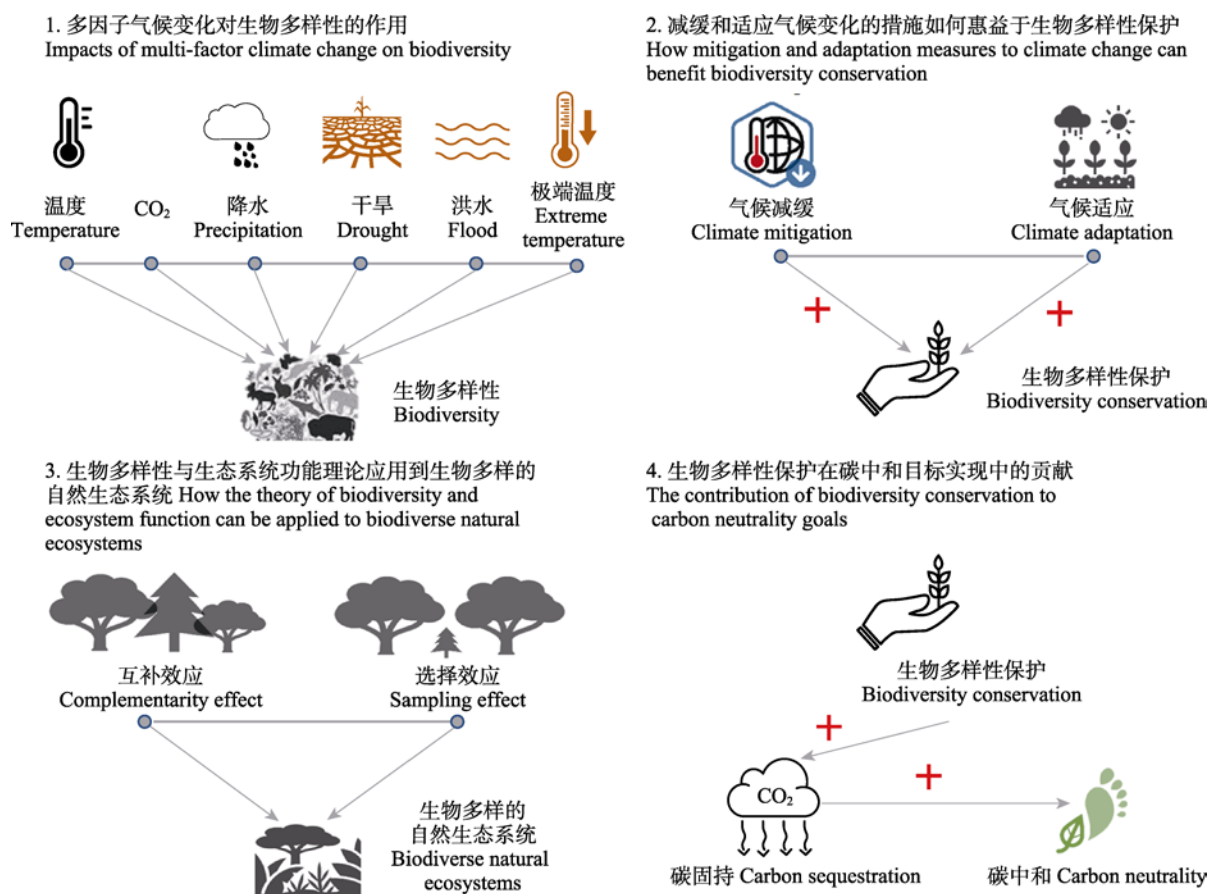


图4 未来发展方向和需要解决的关键科学问题

Fig. 4 Future directions and key scientific questions to be addressed

从不同层次进一步解析气候变化与生物多样性之间的复杂关系和反馈机制(图4)。

2.1 多因子气候变化对生物多样性的作用

不同的气候变化因子之间存在着复杂的作用(Komatsu et al, 2019; 牛书丽和陈卫楠, 2020), 深入理解这些因子之间的相互作用对探讨未来气候变化情景下生物多样性变化格局具有重要作用。先前的工作表明不同气候变化因子对生物多样性和生态过程的影响较为复杂, 表现为加和、协同和拮抗作用(Song et al, 2019; Isbell et al, 2022)。另外, 当前大多数研究仅关注降水、温度和CO₂这3个气候变化因子及其交互作用, 对干旱、洪水、低温等气候变化因子的关注不足。Rillig等(2019)指出增加全球变化因子的数量会增加土壤性质、土壤过程和微生物群落的方向性变化, 当超过8个全球变化因子组合时就会出现不可预测的非叠加性效应。因此未来的研究需纳入更多的气候变化因子, 并注重不同气候

变化因子间以及与其他全球变化因子的相互作用(Custer & Dini-Andreote, 2022; Yang et al, 2022)。其次, 与生物相关的气候变化要素还包括极端事件的发生(例如干旱、洪水、热浪、低温)。极端气候事件突发性强、难以预测, 却对全球生态系统的结构和功能有着不可忽视的影响。尽管目前针对极端气候事件进行了大量的研究, 得到了一些重要结论, 但极端气候事件对生物多样性的影响仍存在较大的不确定性。未来的研究需要进一步加强多源数据与模型模拟的结合、设计区域联网实验, 以更好地解析极端气候事件影响生物多样性的内在机制。最后, 历史上的气候变化问题可能还会对生物多样性产生遗留效应(Hawkes et al, 2017)。例如, 在严重干旱后的1-4年内, 树木会普遍出现生长缓慢、恢复不完全的现象(Anderegg et al, 2015)。因此预测未来气候变化对生物多样性的影响还需要了解历史气候变化造成的时间滞后问题。

2.2 减缓和适应气候变化的措施如何惠益于生物多样性保护

为了同时减缓气候变化和保护生物多样性, 我们必须保护和恢复现存的生物多样性与生态系统(Pettorelli et al, 2021)。目前已有多个研究提出有利于气候与生物多样性的3个主要措施, 即保护、恢复和管理(Pettorelli et al, 2021; Shin et al, 2022; Smith et al, 2022)。保护措施主要是指减少森林等富碳生态系统的破坏与退化。例如在63个国家中, 设立保护区可以使森林砍伐率降低41%, 有效阻止了生物多样性的丧失(Wolf et al, 2021)。有研究表明, 对地球上退化最严重地区的恢复, 结合生物多样性保护, 可以显著提高生态系统碳固存能力, 同时防止约70%的物种灭绝(Strassburg et al, 2020)。在保护与恢复之后, 为了能够可持续发展, 必须进行科学的管理(于贵瑞等, 2021)。比如采用集约化的农业经营方案, 提高单位农业面积生产力的同时, 释放更多土地用于生物多样性保护(Pretty et al, 2018)。此外, 还可以通过增加城市绿化增强碳吸收(De la Sota et al, 2019), 同时也为一些生物在城市定居提供了条件, 有利于生物多样性保护和维持。

总而言之, 大部分减缓或适应气候变化的措施都惠益于生物多样性保护, 但也有一些措施存在争议, 比如大面积的人工生态系统(如人工栽培单一树种或能源作物), 虽然有益于减缓气候变化, 但对生物多样性产生不利影响并可能与粮食生产竞争土地(Smith et al, 2022)。然而, 这些对生物多样性的潜在不利影响, 可以通过更加细化且具有针对性的方案, 来最小化甚至抵消负面影响。因此, 在实施相应措施时一定要注重因地制宜, 方可产生最佳的双赢解决方案(贺金生等, 2020)。

2.3 生物多样性与生态系统功能理论应用到自然生态系统

传统的生物多样性与生态系统功能研究多集中于受控的实验系统, 涵盖的空间尺度比较小, 与人类社会活动相对应的自然生态系统联系比较少(贺金生等, 2003)。未来发展方向之一是如何将小尺度的实验研究的理论和发现应用到生物多样的自然生态系统(Manning et al, 2019; van der Plas, 2019), 尤其是与气候变化相关政策的制定和生态系统管理等层面相匹配的尺度, 包括草地、森林和干旱生

态系统、农业生态系统和城市生态系统等。其中, 尺度推演(Craven et al, 2020; Gonzalez et al, 2020; Qiu & Cardinale, 2020)、营养级(Eisenhauer et al, 2019)、生物多样性维度(Le Bagousse-Pinguet et al, 2019)和地上和地下生态系统关联(Bardgett & Wardle, 2010)是理论应用扩展的基石, 但尚缺乏深刻的认识。首先, 尺度推演不仅涉及到时空尺度, 还涉及到研究对象从个体到生态系统, 甚至到景观、区域尺度的变化。随着尺度的扩展, 影响生物多样性格局的气候、土壤和植被等驱动因子也随之改变。其次, 传统研究为了简化问题, 常常只关注初级生产者, 而其他营养级对生态系统功能的影响研究不足。再次, 由于生物多样性维度的复杂性, 以及生物群落物种的多样性, 实验研究难以综合考虑这些因素, 因此需要借助野外观察、长期监测和遥感观测等方法来综合研究分类多样性、功能多样性和谱系多样性对生态系统功能的影响。最后, 近年随着高通量测序和宏基因组技术的发展, 生态系统地下部分生物多样性与生态系统功能的关系研究得以发展(褚海燕等, 2020; 高贵锋和褚海燕, 2020; 米湘成等, 2021), 但由于土壤物理化学属性的复杂性, 土壤生物种的鉴定难度和土壤生物间的复杂关系, 使得地上和地下部分关联的机理研究缺乏(Bardgett & van der Putten, 2014; Bardgett, 2018)。因此, 将生物多样性和生态系统功能理论应用到自然生态系统是未来需要解决的关键科学问题之一。

2.4 生物多样性保护在碳中和目标实现中的贡献

减少碳排放、增加碳吸收和固存是实现碳中和的有效途径(方精云, 2021; 朴世龙等, 2022; 杨元合等, 2022; 于贵瑞等, 2022)。碳中和措施的实施不仅有效减缓气候变化, 同时, 通过生物栖息地保护、退化土地恢复和生态系统管理等措施, 还将对生物多样性保护有深远影响。反过来, 作为生物多样性与生态系统功能理论应用到自然生态系统的案例, 生物多样性也将在碳中和目标实现中起到至关重要的作用。这是因为, 生态系统碳固持的功能, 包括碳固持量、固持速率、固持时间等也会随着生物多样性的提升而提升; 而对生物多样性的保护也是一种基于自然的气候变化减缓与调控的解决方案(Díaz et al, 2009b; Shin et al, 2022)。因此, 生物多样性保护在碳中和目标实现中的贡献是未来的研

究方向和需要解决的关键科学问题之一。尽管如此,我们也面临诸多挑战,比如,在不同生态系统类型、时空尺度和生态系统管理措施下,生物多样性通过哪些机理过程作用于生态系统碳排放和固持(Díaz et al, 2009b)。在实践中,如何实现最优的生态系统布局、最优的物种配置、最优的生态系统管理,来实现生物多样性保护和碳中和的双赢目标(方精云, 2021)。同时,如何通过生物多样性的保护和管理,以实现气候变化减缓与其他可持续发展的共同目标(Shin et al, 2022)。

3 具体可实施的措施建议

3.1 建立、健全生物多样性监测系统

传统的生物多样性监测系统常常以物种多样性、单一营养级、单一空间尺度为中心,但伴随着新技术的开发和应用,如高通量测序技术,为开展以多维度(分类多样性、功能多样性和谱系多样性)、多营养级(生产者、消费者、分解者)、跨尺度(生态系统、景观、生物群区)的生物多样性长期监测奠定了基础。因此,建议依托国家公园、自然保护区、定位研究站,建立统一的生物多样性监测指标和规范,以实现保护生物多样性、预测多样性变化、适应和减缓气候变化的目的。

3.2 构建基于自然的减缓和适应气候变化的解决方案

基于自然的解决方案往往是最快、成本最低的政策管理方案。当前构建基于自然的减缓和适应气候变化的解决方案,需要将生物多样性纳入可持续发展框架中,以解决人类社会面临的诸多环境问题。生境保护、生态系统可持续管理、退化生态系统恢复将是核心。因此,建议对适宜生物生存的原始生境进行保护,厘清驱动生物多样性变化的主要气候变化因子和极端气候事件,以实现生态系统的可持续管理和退化生态系统的恢复目标,最终为气候-自然-社会提供三赢解决方案。





3.3 加强对气候变化-生物多样性变化正、负反馈机制的认识

在全球尺度上生物多样性丧失是不争的事实,在生态系统尺度生物群落物种组成的变化也是不争的事实,而物种组成的变化涉及到物种的丧失或增加两个主要过程,与生态系统对气候变化的正、

负反馈机制息息相关。因此,需要明确不同生态系统导致生物多样性变化的主要驱动因子是什么,如何通过调控这些因子来阻止甚至扭转气候变化对生物多样性的负面影响,同时通过对生物多样性的保护,提升生态系统碳固持能力,以实现气候变化减缓和生物多样性保护的协同发展。

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