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•综述•　创刊30周年纪念专辑

昆虫多样性三十年研究进展

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摘要: 当前, 全球昆虫数量和多样性均处于下降趋势, 而导致这一趋势的原因主要包括人为干扰及气候变化。本文基于森林、草地、农业、水生和土壤生态系统, 以植食性、访花、捕食性、寄生性、食果以及食腐昆虫为重点功能昆虫群, 综述了近三十年来国内外昆虫多样性研究领域的主要进展, 并分析了发展趋势。近年来, 昆虫多样性的研究维度不断拓展, 形态多样性研究不断深入, 系统发生多样性、功能多样性和遗传多样性等研究也显著加强。此外, 昆虫多样性研究的空间尺度也逐步扩大, 大尺度区域性研究甚至全球范围的调查持续增长。昆虫进化历史也被引入多样性格局研究中, 并随着系统发生信息学方法的普及而被整合到生态系统建成和生物多样性形成机制研究中。未来需要加强关键昆虫类群整合分类学研究、功能性状多样性、林冠昆虫多样性、互作网络结构等方向的研究。

关键词: 功能昆虫群; 多维度多样性; 生态系统; 昆虫多样性丧失

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Research progress on insect diversity

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ABSTRACT

Background & Aims: We reviewed progress on insect biodiversity research over the past 30 years and further analyzed the trends, focusing on varied study systems (e.g. forest, grassland and agriculture etc.) and important functional insect groups, such as pollinators, herbivores and predators.

Progresses: Declines of insect abundance and diversity are being reported worldwide. Anthropogenic disturbance, climate change, and other factors contribute to this crisis.

Strategies & Prospects: Studies of insect biodiversity have expanded from early comparisons of species richness on composition to multiple dimensions of diversity. Current studies include both in-depth work on morphological diversity and much deeper consideration of genetic, phylogenetic, and functional diversity. Moreover, the studies' scale has expanded from local to global. The development of morphometrics and phylogenetic bioinformatics further contributes to understanding evolution and global patterns in diversity. We also need to pay more attention to topics on integrative taxonomy on functional insect groups, functional diversity, insect diversity within canopy, and species interaction networks.

Key words: functional insect groups; multiple diversity components; ecosystem; insect diversity loss

昆虫纲是动物界中最大的一类，占动物界已描述物种数的一半以上(Stork, 2018)，昆虫多样性对于生态系统功能至关重要。伴随气候变化和人类活动加剧，全球生物多样性呈现衰减趋势，昆虫数量和多样性也急剧下降(Deutsch et al, 2018; Eisenhauer et al, 2019; Outhwaite et al, 2022)，其下降速度达到脊椎动物的2倍(Wagner et al, 2021)。不同昆虫功能群在生态过程和服务中分别扮演着不同角色，因此研究不同类群的昆虫多样性具有重要意义。如，传粉昆虫通过访花授粉促进植物繁殖，提高粮食产量；植食者通过植食作用，反向作用于植物群落并间接影响生态系统物质循环；捕食者通过捕食过程调节猎物种群密度等。昆虫在地球上的分布极其广泛，基于不同生态系统的研究有助于全面了解其多样性和群落结构。例如，森林生态系统中的昆虫数量大、多样性高，包括了许多重要的生物防治资源和环境监测指示生物(Ridgway, 2013; Stork & Habel, 2014; Bryant et al, 2019)；农业生态系统中农作物的更替导致植物群落结构不断调整和变化，容易引发昆虫群落结构组成单一及不稳定(Landis et al, 2000; Beckmann et al, 2019; Chase et al, 2020)；水生态系统易受人类活动的影响，某些昆虫

的幼虫或者若虫营水生，对于水体变化尤为敏感，其多样性面临更大威胁(张澂波等, 2013; 刘海铃等, 2021)。同时，考虑到昆虫极高的多样性，加强其多样性监测、多手段研究昆虫多样性及其驱动机制也尤为重要，包括控制实验、系统发生信息学等。目前，研究昆虫的多维度多样性也是一个重要的发展态势，这包括物种多样性、系统发生多样性、功能多样性以及遗传多样性等。此外，当前研究多以局部地区或单一类群为研究对象，缺乏基于全球尺度的研究(Pilotto et al, 2020; Jähnig et al, 2021)。这要求我们在更大的尺度下跨生态系统研究不同功能昆虫群，并探索影响其多样性变化的一般规律和相应机制。

1 不同生态系统中的昆虫多样性

1.1 森林生态系统

1.1.1 林下昆虫多样性

森林作为陆地重要的生态系统之一，其物种多样性在陆生生态系统中占主导地位，且有大量昆虫物种有待描述(Stork & Habel, 2014)。此前研究表明，与纯林和人工林相比，植物物种丰富、具有相应草本植物和灌木层的森林有更高的昆虫多样性(Lucey & Hill, 2012)。不同的昆虫类群对生物和非生物条件变化的响应不同，一般难以得出森林生态系统中不同异质性或干扰程度与昆虫物种丰富度的一般关系(Ewers & Didham, 2007)。例如，森林中的林窗可能会对喜阴和喜阳的昆虫造成不同影响。此外，植食性昆虫可能从森林中的草本植物和灌木层中获益，而林中草本和灌木的过度生长可能会给喜阳昆虫带来不利影响(Hayes et al, 2009)。因此，一般认为: 虽然植被结构、空间位置和森林生境破碎化均会影响昆虫多样性和群落结构(da Silva et al, 2019)，但森林类型是决定昆虫多样性和群落结构更重要的因子(Habel et al, 2021)。

历史气候变暖和集约化农业土地利用可导致昆虫多样性下降近50% (Outhwaite et al, 2022)。相关研究表明，昆虫多样性的下降不仅出现在农业生态系统和其他相对开放的生境，在森林生态系统中亦是如此(Seibold et al, 2019)。目前人们发现森林中的一些甲虫濒临灭绝，蝴蝶数量也急剧下降(Wermeille et al, 2014)。研究发现，森林覆盖率的降低和生境同质化对昆虫均有负面影响(Solar et al, 2015; Toivonen et al, 2017)。森林对气候变化敏感，能对林下昆虫造成影响。例如: 干旱等极端气候会降低树木的抵抗力，使其更容易被小蠹等植食性昆虫取食; 温度和降水对树木有直接影响，进而导致林下昆虫种群发生变化(Huey et al, 1999)。

到目前为止，关于森林昆虫暴发的大多数研究仅限于温带的森林生态系统。关于气候变化所引发的森林和昆虫之间关系变化的研究近几年有所增加(Deutsch et al, 2018; Pureswaran et al, 2018; Outhwaite et al, 2022)。科研工作者通过研究不同海拔梯度分布的热带植食性昆虫(卷叶甲虫)发现: 位于中高海拔的物种对高温的耐受性相较于低海拔的物种更弱(Colwell et al, 2008)。该结果表明: 在当今全球变暖的大趋势下，某些昆虫灭绝的风险可能很大(García-Robledo et al, 2016)。但值得注意的是，气候变化虽然能显著影响某些类群，但有的昆虫类群并不受此影响(Bentz & Jönsson, 2015)。

1.1.2 林冠昆虫多样性

林冠被认为是“生物最后的边界” (Erwin, 1983)，仍有许多物种有待发现(Hamilton et al, 2010)。森林具有复杂的垂直结构，地上及地下微生境强的异质性使森林蕴含着极高的物种多样性(Dickie et al, 2002; Nakamura et al, 2017)。垂直分布在树上的附生植物和藤本植物为森林中的其他生物提供了筑巢、食物和小气候避难所，这进一步增强了地上微生境的异质性(Ellwood et al, 2002; Yanoviak, 2015; Odell et al, 2019)。树上的藤本植物还能作为高效的“廊道”，通过连接树冠进一步增加了森林结构的复杂性(Adams et al, 2017)。林冠通过阻挡阳光、雨水和风，致使下层植被栖息地形成的小气候被分隔(Scheffers et al, 2014; de Frenne et al, 2019)。森林小气候形成了一定的垂直分层结构，从地面到冠层，温度、水汽压匮乏程度等均在不断增加(Scheffers et al, 2013; Nakamura et al, 2017)。因此，森林生态系统的资源和小气候条件在水平方向和垂直方向上均具有异质性(Nakamura et al, 2022)。

林冠的植物叶片通常具有更高的多样性和生产力(Erwin, 1982)，并可能与林下叶片发生竞争(Kira et al, 1969; Ishii et al, 2004)。因此，人们认为冠层的昆虫多样性比林下更高(Wettlaufer et al, 2018;

Gámez & Harris, 2022)。近年来，的确有研究发现林冠层的昆虫多样性更高，如捕食蜂(Sobek et al, 2009)、蜜蜂(Ulyshen et al, 2010)、果蝇(Ishii et al, 2004)和蝴蝶(Devries et al, 2012)，但甲虫(Stork & Grimbacher, 2006)和蛾类(Ashton et al, 2016)除外。因此，对森林昆虫多样性和生态系统过程的研究应从不同维度加以考虑(Gámez & Harris, 2022)。

尽管不同类型的森林树冠中昆虫多样性的高低并不一致，但已有研究发现，森林树冠中特有的昆虫物种是形成昆虫多样性垂直分层群落结构的关键(Devries et al, 2012; Basset et al, 2015; Ashton et al, 2016)。此外，由昆虫引发的如捕食(Loiselle & Farji-Brener, 2002; van Bael et al, 2003)、寄生(Sobek et al, 2009)和植食(Neves et al, 2014)等生态过程在林冠比林下更明显，但也有研究发现了捕食(Aikens et al, 2013)和植食(Pontes & Basset, 2007; Thomas et al, 2010)的相反模式。为了更好地理解昆虫多样性的垂直分层格局、驱动因子及其生态过程，有必要适当改进研究方法，如对森林昆虫进行大范围的定量采集(Volf et al, 2019)以及开展控制实验等(Nakamura et al, 2017)。

森林昆虫多样性受到的人为干扰日益严重，包括跨时空尺度的污染、毁林、入侵物种、硝化作用和全球变暖等(Wagner et al, 2021)。受干扰的森林系统(如选择性砍伐的森林)冠层叶片分布稀疏，减弱了对林下层微气候的保护(Nakamura et al, 2022)。昼夜变化、季节性以及极端的气候渗透到林下层，减弱了小气候的垂直异质性，最终导致森林物种多样性下降(Basham & Scheffers, 2020)。此外，森林树冠对气候变化敏感(Ozanne, 2013, Sallé et al, 2021)，这能进一步导致昆虫多样性受气候变化等因素的影响。例如，雨林中树栖蚂蚁的温度上限与预测的未来温度非常接近，这意味着树栖昆虫可能面临着局部灭绝的风险(Leahy et al, 2022)。因此，我们迫切需要更多的研究来了解森林昆虫，以便能够量化并预测人为干扰对森林中昆虫多样性的影响(Nakamura et al, 2022)。

1.2 草地生态系统

草地覆盖了地球陆地面积的30%–40%，为大量物种提供了重要栖息地，对全球放牧经济发挥着重要作用(Coupland, 1979; Samson & Knopf, 1996)。虽然放牧以及气候变化是草地生态系统主要的驱动因素(Wang H et al, 2020)，但通过与昆虫物种间的相互作用，能为草地生态系统的群落结构和生态系统功能奠定基础(van Oijen et al, 2018)。

温带草原的植食性动物多以昆虫为主，热带草原则以大型有蹄类为主。昆虫在草地生态系统中发挥着重要作用，如草地系统的养分循环、维持土壤结构和肥力以及为其他类群提供主要的食物来源，并在一定程度上有助于草地生物量的增长(与一般草地相比，长期采用化学杀虫剂的草地年产量降低15%)。与森林相比，草地植被的结构更简单、异质性更弱，昆虫多样性也相对较低(Giweta, 2020; Bardgett et al, 2021)。

草地上的昆虫群落在很大程度上受到植物类型、气候、土壤类型和管理等因素的影响。在这些因素中，植物物种丰富度是昆虫多样性的主要决定因素，在集中管理和高肥料的草地上可能只有10–15种昆虫，而在广泛管理和低投入的温带草地上可能有50–70种(Andow, 1991)。热带草原可能有200多种。通过植物区系多样性或相关的植被结构特征，尤其是群落生物量和结构异质性，可以较好地预测草地生态系统昆虫多样性。蝴蝶、野生蜂、植食性甲虫等的物种丰富度与植物物种丰富度均呈正相关。草地捕食者和寄生蜂类群的比例随草地面积和年龄的增加而显著增加，但随植物物种丰富度的变化不大(Ebeling et al, 2012)。

1.3 农业生态系统

农业生态系统是一种相对不稳定的人工生态系统，主要由作物生境和多样化的非作物生境组成(Landis et al, 2000)。非作物生境包括景观尺度与斑块/田块尺度两方面。景观尺度的非作物生境包括农田周边的森林、草地、大面积的缓冲带等；田块尺度的非作物生境包括长有杂草与灌木的田埂、水渠、林带等。这些非作物生境是昆虫重要的越冬和庇护场所，提供了食物来源，对于维持农业生态系统中的昆虫种群繁衍和物种多样性非常关键(Tscharntke et al, 2005; Bianchi et al, 2006; Ramsden et al, 2015)。研究表明，非作物生境可显著影响作物生境中的昆虫多样性及其生态功能(Kruess & Tscharntke, 1994; Tscharntke et al, 2012; Vasseur et al, 2013)。在我国华北地区的研究发现，景观尺度下高

占比的非作物生境能显著提升作物生境中捕食性天敌昆虫的多样性和丰富度(Liu et al, 2018; Yang et al, 2019)，以及寄生性天敌的生物控蚜作用(Yang et al, 2021)。在我国南方丘陵地区的研究也发现，传粉昆虫多样性随着非作物生境比例的增加而增加(Zou et al, 2017)。但随着农业集约化进程的加快，全球范围内农业生态系统中非作物生境的面积和斑块数量显著减少(Beckmann et al, 2019)。这是导致近年来昆虫多样性降低(Chase et al, 2020)和个别物种灭绝的重要原因(Haddad et al, 2009)。

作物生境受人类活动干扰严重。随着现代农业的发展，作物种植结构不断调整和变化，大面积单一化种植、集约化生产程度明显提升，农药等化学投入品被大量使用(Meehan & Gratton, 2015)。这些因素均导致作物生境中的昆虫多样性明显下降(Zabel et al, 2019; Tooker & Pearsons, 2021)、昆虫群落结构严重受损(Douglas & Tooker, 2016)，特别是重要功能昆虫群的丧失(Main et al, 2018)，使作物害虫暴发成灾、自然授粉功能下降等生态风险加剧。为此，近年来农业生产中愈发重视管理和生态调控。例如，利用间作套种等合理种植方式增加植被多样性，为昆虫提供更稳定的食物和栖息地资源，有利于提升作物生境中的昆虫多样性(Tschumi et al, 2016; Wei et al, 2021)。有机农业种植方式能有效降低化肥和农药的使用(Larsen et al, 2021)，提升生物多样性(Tuck et al, 2014; Gong et al, 2022)和生态系统稳定性(Wittwer et al, 2021)，增强作物害虫的自然控制功能(Muneret et al, 2018; Tscharntke et al, 2021)。转基因抗虫作物的商业化种植能够大幅减少化学农药的使用，促进有益天敌保育及生物控害功能(Lu et al, 2012)。

1.4 水生生态系统

水生昆虫在水生生态系统中占据重要地位，常作为河湖健康评估中重要的指示物种。水生昆虫已记录10万余种(Balian et al, 2008)，并且仍有大量水生昆虫物种有待描述，预计将超过20万种。而对水生昆虫幼期的研究显得更加薄弱。相关研究表明，1928–2018年间水生昆虫多度以平均每十年11%的速率在增长(主要区域为温带地区)。这可能是由部分净水行动、气候变暖、营养输入增多导致的水体初级生产力增大而引起的(Van Klink et al, 2020)。由于水生昆虫对水质变化非常敏感，部分物种在栖息地受到人为活动干扰的情况下面临消失的风险。例如，由于人类活动的影响，一些河流水生态系统的河段生境发生改变，从而影响敏感水生昆虫的多样性(张溦波等, 2013; 刘海铃等, 2021)。

1.5 土壤生态系统

在有关土壤昆虫多样性的研究中，昆虫通常会和其他节肢动物一起被归为土壤中的大型无脊椎动物(包括蚯蚓、白蚁、蚂蚁以及一些昆虫幼虫)一并研究(Cifuentes-Croquevielle et al, 2020)。其中，有关蚂蚁的研究相对较多(Samson & Knopf, 1996; Fisher, 1999; Armbrecht et al, 2004)，它作为土壤昆虫的主要类群，具有成熟的采样策略和研究体系(King & Porter, 2005)。与土壤相关的环境因素会影响土壤中昆虫类群的多样性，这些因素包括湿度(Ramírez-Hernández et al, 2021)、含氮量(Ramírez-Hernández et al, 2021)、pH值(Strauss & Biedermann, 2006)以及土壤容重(Wang L et al, 2019)。例如，土壤昆虫多样性随着土壤湿度的增加而增加(Ramírez-Hernández et al, 2021)。此外，土壤中的污染物也会影响土壤昆虫的多样性(Belskaya et al, 2017)。在农业生产中，化肥的使用会对土壤中的昆虫群落造成影响(Lin et al, 2013)。有些研究发现，蚂蚁的多样性随着土壤重金属含量的增加而增加(Grześ, 2009)。

许多具有重要功能的昆虫幼虫期是生活在土壤之下的，比如葬甲(分解者)、地蜂和隧蜂(传粉者)(Cope et al, 2019)、步甲(捕食者) (Goulet, 2003)。由于直接采集这些昆虫的幼虫难度较大，目前调查时还是以采集成虫为主。采集土壤中昆虫类群的手段正日益丰富。比如陈云康等(2021)发明了一种避免被较大型动物侵入或破坏的昆虫诱捕器；Cope等(2019)使用羽化诱捕器(emergence trap)采集从土壤中羽化的膜翅目昆虫；莫畏等(2018)通过埋入一种深土层陷阱收集器研究了北京近郊土层下动物群落的结构组成。

2 重要功能昆虫群多样性

2.1 植食性昆虫

植食性昆虫一般取食各类植物组织，包括叶片、果实以及种子等，具有极高的物种多样性。许

多研究者认为: 植食性昆虫繁盛的主要驱动力是昆虫的植食性(Wiens et al, 2015)。由于它们取食范围的变化, 在进化过程中为物种的形成提供了机会, 从而引发了植食性昆虫多样化(Futuyma & Agrawal, 2009)。植食性昆虫和植物通过植食作用相互联系, 成为生态系统中一种重要的种间相互作用。这种相互作用能够通过植物群落的改变影响植食性昆虫群落。已有大量研究表明: 植食性昆虫的多度和多样性受植物多样性的正向作用(Borer et al, 2012; Wang MQ et al, 2019), 植食性昆虫群落在植物多样性高的群落中更稳定(McCann, 2000; Albrecht et al, 2007; Staab et al, 2015)。这些研究结果也支持了一些相关的经典假说, 如资源专化假说(resource specialization hypothesis)、更多个体假说(more individuals hypothesis)、资源集中假说(resource concentration hypothesis)以及天敌假说(enemy hypothesis)等。

植食性昆虫的多样性还能反向作用于植物并影响相应的生态系统功能, 例如, 植食性昆虫能通过植食作用增加植物叶片的营养浸出、代谢、病原体的传播和改变植物资源配置来影响生态系统过程(Maron & Simms, 1997; Finke, 2012; Bagchi et al, 2014)。近年来, 有关植食性昆虫多样性的研究已经从早先的以物种多样性研究为主逐渐过渡到更多维度的多样性研究, 包括系统发生多样性、功能多样性和遗传多样性等。例如, 最近的相关研究表明, 鳞翅目植食性昆虫的系统发生多样性能够直接或间接由植物物种多样性、系统发生多样性和功能多样性决定(Muiruri et al, 2019; Wang MQ et al, 2020)。关于功能多样性的研究, 则主要集中在植物功能性状和植物功能多样性对植食性昆虫的影响, 比如重要的植物功能性状和功能多样性能够决定植食者的取食范围和群落结构(Pellissier et al, 2013; Muiruri et al, 2019; Wang MQ et al, 2020)。

相关研究表明, 寄主植物的遗传多样性对植食性昆虫多样性和群落总体上影响较低, 但在更小的空间尺度上影响更显著(Tack & Roslin, 2011)。研究者普遍认为植物的化学组成和多样性是进一步理解植物对植食者多样性和群落影响的一项重要预测指标。定量研究植物化学成分多样性变化是理解植食性昆虫多样性变化和群落构建机制的重要手段(Richards et al, 2015)。另一方面, 由于植食性昆虫的扩散能力有限, 对寄主植物的空间分布非常敏感(Bernays, 1998)。因此, β多样性可能更有助于理解物种组成在不同时空尺度上的变化(Antão et al, 2019)。β多样性的分解能反映物种周转和物种丰富度的差异(Baselga, 2010), 利用β多样性分解能为理解不同生态系统中的植食性昆虫多样性和群落组成提供帮助(Banda et al, 2016)。

食果昆虫取食植物的繁殖器官, 常被作为植食性昆虫中特殊的一类, 但食果昆虫有其重要和特别之处(Janzen, 1971)。因为种子是种子植物特有的繁殖器官, 在被子植物中是植物生活史中重要的一环。广义的食果昆虫包括所有取食果实或种子任何部分的昆虫。它们移动种子并使其命运不确定, 可能起到一定的传播功能。狭义的食果昆虫主要是指种子捕食者, 一般会致使种子植物的繁殖器官死亡(Janzen, 1970)。食果昆虫的研究相对较少(Lewis & Gripenberg, 2008), 但它们与种子的存亡紧密相关。食果昆虫与植物的协同进化是负密度制约效应、捕食者饱和假说和大年结实现象等理论的基础, 影响着植物的种群动态和群落组成(Larios et al, 2017)。

食果昆虫在所有生境中均有发现, 对果实和种子的取食率在不同地区和不同植物类群中变化较大。取食率大部分时候较低, 但有时也可造成大量甚至当年全部的种子死亡(Chen et al, 2017)。通常可将食果昆虫分为种子传播前的取食者和种子传播后的取食者: 前者食性较专一, 例如取食橡果的象甲; 后者食性较广泛, 例如甲虫和蚂蚁(Crawley, 1992; Hulme, 1998)。需要注意的是, 有些传播前的食果昆虫更为人知的是它们传粉者的身份(McCall & Irwin, 2006; Johnson et al, 2015)。例如, 榕小蜂(Cook & Rasplus, 2003)、丝兰蛾(Pellmyr, 2003)。它们在传粉时把卵产在胚珠中, 幼虫以发育中的种子为食, 成为传播前的种子捕食者。同理, 有些传播后的食果昆虫的主要生态功能是种子传播者, 比如某些以种皁为食的蚂蚁(Giladi, 2006)。据Janzen (1971)的不完全统计, 食果昆虫主要分布在以下这些类群: 鞘翅目的象甲科、豆象科、小蠹科; 膜翅目的蚁科、长尾小蜂科、广肩小蜂科; 鳞翅目的螟蛾科、卷蛾科、小卷蛾科; 半翅目的缘蝽科、红蝽科、长蝽科; 双翅目的实蝇科、瘿蚊科、潜蝇科。

2.2 访花昆虫

传粉者包括昆虫、鸟类、蝙蝠、啮齿动物和蜥蜴等生物类群，可以为农作物和野生植物提供重要的传粉服务。传粉昆虫是传粉者中多样性最高的类群，存在于昆虫纲多个目中，其中鳞翅目(蝴蝶和蛾类)、膜翅目(如蜜蜂和胡蜂)、鞘翅目(如花萤和叶甲)和双翅目(包括食蚜蝇和蜂虻等)是多样性最高的四个目(Kevan & Baker, 1983; Ollerton, 2017)。

受到人类活动和气候变化的影响，传粉昆虫在世界范围内正经历持续的丧失(Potts et al, 2010; Cameron et al, 2011; Burkle et al, 2013)。但传粉者丧失仅在欧洲和美洲有广泛报道，且局限于膜翅目和鳞翅目的部分类群(Sánchez-Bayo & Wyckhuys, 2019)。例如，研究发现家养蜜蜂(*Apis mellifera*; Ellis, 2012)、熊蜂(Cameron et al, 2011; Dupont et al, 2011; Figueroa & Bergey, 2015)、独栖性蜜蜂(Biesmeijer et al, 2006; Gardner & Spivak, 2014; Ollerton et al, 2014; Powney et al, 2019)、访花胡蜂(Ollerton et al, 2014)、蝴蝶(van Dyck et al, 2009; van Swaay et al, 2010; Forister et al, 2016)和蛾类(Conrad et al, 2006; Fox, 2013)种群数量在多个地区均有不同程度的降低。传粉昆虫种群数量下降可能进一步导致分布区的缩减甚至物种灭绝，对生物多样性造成不可挽回的损失。

传粉昆虫丧失会削弱其对植物的传粉服务能力，对农作物产量和植物多样性均有不利影响(Thomann et al, 2013)。全球约75%的农作物依靠昆虫传粉(Klein et al, 2007)，传粉服务的降低威胁着全球粮食安全并加剧微量营养元素缺乏的隐性饥饿。被子植物中接近90%的物种依靠动物传粉(Ollerton et al, 2011)，传粉者缺乏会导致植物种子数目和质量的降低而影响种群更替。在群落内，如果传粉昆虫丧失达到阈值，将会引起不同传粉昆虫种群同时崩溃(Lever et al, 2014)。传粉者缺乏会进一步改变植物群落组成和生态系统复原能力，并可能破坏生态系统的稳定(Kevan & Viana, 2003; van der Sluijs, 2020)。

生境丧失和破碎化对传粉昆虫食物来源、筑巢位置和种群间基因交流均有不利影响，是导致传粉者缺失最主要的不利因素(Winfree et al, 2011; Sánchez-Bayo & Wyckhuys, 2019)。化学污染(如杀虫剂和除草剂)和光污染直接影响传粉昆虫的生理和行为，也对传粉昆虫多样性和多度有负面影响(Henry et al, 2012; Whitehorn et al, 2012; Owens et al, 2020)。另外，传粉昆虫的入侵(如家养蜜蜂和熊蜂)通过竞争食物资源和筑巢位置，同样可引起本土传粉昆虫的局域丧失(Russo, 2016)。气候变化直接影响传粉昆虫和其访问植物的地理分布和物候，物种间时空错配会引起传粉昆虫食源缺乏而种群减小(Memmott et al, 2007; Harrison & Winfree, 2015)。上述导致传粉昆虫丧失的不利因素通常存在叠加影响，对传粉昆虫产生更大的威胁。

已有研究发现，不同群落中的物种组成虽然有很大差异，但传粉网络结构常呈现一致的特征(如物种互作的不对称性和嵌套结构)，可以作为判断传粉网络健康水平的指标(Bascompte & Jordano, 2007)。传粉网络分析还可以用于甄别影响群落稳定性的关键物种，这在实践中可用于保护和修复生态系统。

2.3 捕食性昆虫

捕食性昆虫是指以活体动物为食的昆虫类群，是生态系统中重要的组成部分，承担了重要的生态系统服务与功能，如生物防治和能量传递等。最常见的捕食性昆虫包括蜻蜓、螳螂、猎蝽、瓢虫、捕食性甲虫和胡蜂等，相近的还包括蜘蛛和捕食性螨类。环境和土地利用的变化导致了日益严重的生物多样性丧失(van Klink et al, 2020; Millard et al, 2021)。有研究认为，捕食者对环境变化的忍耐力比其猎物更差，因为捕食者不仅会直接受到非生物因素(温度、湿度、纬度等)的影响(Logan et al, 2006; Thakur et al, 2017)，还会间接受到因环境导致的生物因素变化(食物和栖息地资源缺乏)的影响(Voigt et al, 2003; Vasseur & McCann, 2005)。例如，纬度梯度对捕食者的多样性具有显著影响，在环境条件适宜和食物资源更丰富的低海拔地区捕食者的物种丰富度更高(Franzén & Dieker, 2014; Tiede et al, 2017)。

生物因素的直接作用也能对捕食者的多样性产生重要影响。Root (1973)提出经典的天敌假说后，捕食性昆虫作为重要的天敌在农业和草地生态系统中得到了大量的研究与应用。该假说认为：增加植物多样性能够提高猎物资源多样性和庇护所复

杂性，进而维持较高的捕食性昆虫多样性，降低集团内捕食的发生，最终提高捕食性昆虫的生物防治作用(Crowder et al, 2010; Sarthou et al, 2014; Dassou & Tixier, 2016)。相较于植被种类和结构相对简单的农业生态系统，天敌假说是否适用于更为复杂的森林生态系统尚不明确(Staab & Schuldt, 2020)。有研究表明，森林中植物多样性与捕食性蚂蚁的多样性相关(Staab et al, 2014)，而在人工林(Schuldt et al, 2015)和亚热带森林(Schuldt et al, 2011)中，植物丰富度并没有促进捕食者多样性及其捕食作用。

不同捕食者功能团对环境与猎物响应和效应作用的强度与方向不同。通过捕食者功能性状的视角，如体型大小、捕猎模式、食谱范围、扩散能力等，为解释在不同生境下的捕食者–猎物相互作用机制和强度的多样性提供了理论基础(Schmitz, 2008, 2017; Kuile et al, 2022)。Schmitz (2008)发现不同捕猎模式的蜘蛛(游猎型和结网型)对植物物种多样性的作用相反。此外，广食性捕食者也会攻击捕食同种猎物的其他天敌，或是同类相食，这通常被称为集团内捕食(Gagnon et al, 2011)。集团内捕食增加了生态系统内物种互作网络的复杂性，但是目前对于集团内捕食如何影响捕食者及其下层营养级多样性仍然没有一致的结论(Martin et al, 2013)。个体水平的种内变异是理解种群生态学的核心。研究表明，不同特性的捕食者(例如，水蚤、蜘蛛等)对下层营养级以及对同类的捕食强度不同(Start & Gilbert, 2017)，揭示了捕食者的种内变异是决定猎物多样性和群落组成的重要因素。

捕食者与猎物之间的相互作用是重要的生态系统功能之一(Joern & Laws, 2012)。衡量广食性捕食者的捕食范围有助于进一步了解捕食者类群(或功能群)对下层营养级的调控路径。传统的方法是观察捕食者肠道和粪便中的残渣与碎屑来构建捕食者–猎物关系。该方法存在一些缺陷：不适用于研究吸食猎物体液的捕食者，对研究人员专业技能要求高。近年来，快速发展的DNA宏条形码技术能够有效地对捕食者肠道或粪便进行检测并分析出捕食者食谱信息，构建捕食者–猎物网络，进一步预测捕食者在生态系统中的作用(Pompanon et al, 2012)。目前，DNA宏条形码技术已经成功应用于构建多种捕食者–猎物互作网络(Zhong et al, 2019)，发现了捕食者耦合地上和地下的能量流动网络(Toju & Baba, 2018)。但是目前关于捕食者–猎物互作网络与环境因子、生产者多样性等因素之间相互作用的研究仍相对较少(Eitzinger et al, 2019)。

2.4　寄生性昆虫

寄生性昆虫是指那些把卵产在寄主(主要是昆虫，也包括少量其他节肢动物和软体动物)的体表或体内，幼虫以寄主为食完成自身发育并最终杀死寄主的一类昆虫(Godfray, 1994)。寄生性昆虫出现在多个全变态的昆虫类群中，包括膜翅目、双翅目、鞘翅目、脉翅目、鳞翅目、捻翅目和毛翅目。其中，寄生蜂多样性研究得最全面(Eggleton & Belshaw, 1992; Godfray, 1994)。寄生性昆虫是物种多样性最高的昆虫类群之一，约占目前已知的100万余种昆虫的10% (Eggleton & Belshaw, 1992; Godfray, 1994; Huber, 2017)。越来越多的学者认为，寄生性昆虫尤其是寄生蜂的种类至少在100万种以上(Bebber et al, 2014; Forbes et al, 2018)。寄生性昆虫的寄主繁多，包括很多农业林业和卫生害虫，很多种类在生物防治中有着广泛的运用(Eggleton & Belshaw, 1992; Heraty, 2017; Miller et al, 2021)。寄生性昆虫在授粉服务中的作用也越来越受到关注(Zemenick et al, 2019)，而且已成功地被用作生态系统健康的指标(Anderson et al, 2011)。

营寄生生活的方式大大提升了该类昆虫的多样性。寄生性昆虫与其寄主之间的密切联系促进了它们的专化性和共同进化的互作，进而促进物种的形成和多样化(Forbes et al, 2018; Stireman et al, 2021)，即类似于植食性昆虫里发现的“多样性产生多样性”。寄生性昆虫的多样性、多度、对寄主的寄生率会受到其生境中各种生物和非生物因素的影响。研究发现，在各类生态系统中植物物种丰富度(Sperber et al, 2004; Guo et al, 2021)、植物系统发生多样性(Staab et al, 2016)、避难所(Hawkins, 1993)、生境异质化(Burks & Philpott, 2017)等都与寄生性昆虫的多样性正相关。

物种丰富度向赤道地区增加是最普遍的生物地理分布模式之一。然而一些研究表明，寄生蜂的多样性分布格局是个例外。寄生蜂物种丰富度分布呈双峰模式，即在中纬度地区达到峰值，向赤道地区减少(Owen & Owen, 1974; Janzen & Pond, 1975;

Skillen et al, 2000; Jones et al, 2012; Quicke, 2012)。虽然一些学者推测这种非典型的分布格局可能在寄生性昆虫中普遍存在，但越来越多的研究发现，包括寄生蜂在内，寄生性昆虫的多样性分布符合典型的分布模式(Sääksjärvi et al, 2004; Veijalainen et al, 2012; Timms et al, 2016; Burington et al, 2020)。由于仍有大量的寄生性昆虫缺乏分类学研究，也有一些学者认为，寄生蜂多样性的数据通常太有限，目前还无法得出关于纬度分布模式的结论(Quicke, 2012; Veijalainen et al, 2012; Gómez et al, 2018)。

2.5　食腐昆虫

分解者是一类专以粪便、动植物遗骸等为食的生物(Barton et al, 2013)。分解者分解有机物是生态系统的一个关键过程(Mico, 2018)。腐食性昆虫是分解者中最多样化和最丰富的类群之一(Baz et al, 2014)。独特的进化特征(Mico, 2018)、对不同资源的利用以及对相同资源不同的利用方式(Baz et al, 2014)造就了腐食性昆虫巨大的多样性。

根据腐殖质类型的不同，可将腐食性昆虫分为三大类，即：粪食性、腐木食性(半腐木材和腐烂植物)和尸食性(王运兵等, 2007; 吴殿鹏等, 2008; Putchkov et al, 2017)。各类型腐食性昆虫的详细研究如下：

(1)粪食性昆虫。粪食性昆虫以动物粪便作为主要营养来源，主要包括鞘翅目和双翅目昆虫(Serrão et al, 2022)。其中，受关注度最高的当属鞘翅目金龟科的蜣螂亚科。蜣螂是世界范围内分解粪便的关键生物(Nichols et al, 2008)，超过5,000种蜣螂使用动物的粪便作为成虫和幼虫的食物资源。蜣螂与动物之间的这种联系最早可追溯到白垩纪中期(Gunter et al, 2016)。蜣螂有着“生态系统工程师”的美誉，在大多数陆地生境中发挥着重要作用(Howison et al, 2016; Johnson et al, 2016)，对养分循环、植物生长、种子二次传播和寄生虫控制等均有重要贡献(Nichols et al, 2008; 白明和杨星科, 2010; Beynon et al, 2015)。研究表明，蜣螂群落的多样性可能与放牧强度(Lobo et al, 2006; Verdú et al, 2007)等因素有关。例如，Lobo等(1998)发现与最近使用的牧场相比，在连续放牧且牲畜数量恒定的牧场中，蜣螂的多样性和多度更高。在长期停止放牧和/或放牧空间分布不规则而放弃牲畜活动的地区，蜣螂多样性可能会下降(Lobo et al, 2006)。另外，蜣螂的多样性可能还受到降水量的影响，Abot等(2012)发现，蜣螂的丰富度和数量随着降水量增加而增加。

(2)腐木昆虫。从功能的角度来看，腐木昆虫是指在森林生态系统中对木质材料分解过程起关键作用的一类昆虫(Quinto et al, 2012)。在泥盆纪早期的森林中，随着枯木的出现，腐木昆虫开始变得多样化。研究表明，在北欧等地区的森林中，约20%–30%的森林昆虫为腐木昆虫(Mico, 2018)。全球的腐木昆虫估计为280,000–990,000种(Siitonen & Jonsson, 2012)。腐木昆虫的多样性主要与取食的木材种类、木材位置(站立/悬挂或倒下)、木材直径、环境条件(阳光照射、温度和湿度)等因素有关(Mico, 2018)。鞘翅目是腐木昆虫中多样性最高的一个类群，在所有现存的鞘翅目科级阶元中，约有65%的科中含有腐木昆虫(Gimmel & Ferro, 2018)。除此之外，双翅目和膜翅目中也有大量的腐木昆虫(Hilszczanski, 2018; Ulyshen, 2018)。

(3)尸食性昆虫。昆虫是自然界中腐肉分解的主要驱动力(Payne, 1965; Grassberger & Frank, 2004)。腐肉对于尸食性昆虫来说是一种庇护所或食物来源(Barton et al, 2013)，通常会增加尸食性昆虫的多度和多样性。研究表明，在尸体腐烂过程中，尸食性昆虫的多度、物种丰富度和Shannon多样性指数都会增加；随着尸体水分减少，这些昆虫的多样性则会随之减少(Sawyer & Bloch, 2020)。在尸体腐烂与分解的不同阶段出现的昆虫会依一定的次序侵袭尸体。在人类尸体上出现的昆虫对尸体死亡时间、地点、原因等方面的推测具有重要意义。因此有关尸体上昆虫群落演替规律的研究是法医昆虫学的重要内容之一(吴殿鹏等, 2008)。此外，尸食性昆虫的多样性还受尸体大小、季节、尸体所在地等因素的影响。分解腐肉，除了会增加尸食性昆虫自身的物种多样性，也会促进腐肉周围非尸食性生物的增加，对其周围的生态群落具有重要影响(Sawyer & Bloch, 2020)。

作为生态系统的分解者之一，腐食性昆虫对于生态系统持续稳定发展的重要性不言而喻。但截至目前，世界范围内腐食性昆虫的物种总数仍然未知(Siitonen, 2012)。尽管分子工具已广泛运用到生物多样性监测中来，但由于分类学者群体减少导致分

类学知识的短缺(Hong et al, 2022; Zhu et al, 2022), 这一进展仍旧受到限制(Garrick & Bouget, 2018)。另外, 受城市化(Foster et al, 2020)、工业污染(Vorobeichik et al, 2012)、森林砍伐、放牧、土地利用变化等因素影响(Quinto et al, 2012), 腐食性昆虫的多样性面临巨大威胁。

3 昆虫多样性研究发展态势

3.1 昆虫多维度多样性

传统意义上, 多样性指物种多样性, 是物种数量多少最直接的体现。描述生物多样性对于理解和保护生物多样性至关重要, 并主要通过物种丰富度来表征。除此之外, 系统发生多样性和功能多样性等能够从不同的角度帮助我们全面理解昆虫多样性的分布格局。

3.1.1 系统发生多样性

通过研究具体生态系统的群落结构、营养级互作、食物网络等, 我们可以验证各种生态假说如环境过滤(environmental filtering)和竞争排斥(competitive exclusion)等。但是, 演化过程同样作用于具体的群落结构。比如, 按物种分类阶元的目或纲为单位, 物种多度可随纬度增高而降低, 但按属级水平为参考, 则规律不明显(Buckley et al, 2010)。因此, 群落生态学研究也需要在系统发生尺度(phylogenetic scale)上考虑物种或类群的演化历史, 从而深入理解群落物种组成(如区分由生物地理事件导致的物种形成和中性理论下的物种扩散、物种形成等) (Hubbell, 2001; Cavender-Bares et al, 2009), 或预测外来物种的潜在成功入侵能力(Thuiller et al, 2010), 或以此为依据制定物种保护优先级别(Redding et al, 2014)。

在系统发生尺度, 系统发生多样性(phylogenetic diversity, PD)用于度量群落物种组成的相关程度, 现已广泛应用于生态学和保护生物学。Faith (1992)提出了基于系统发生树枝长的系统发生多样性量化指标, 统计物种从树根到支端所有枝长的总和。同时, 进化区别度(evolutionary distinctiveness, ED)、两两系统发生平均距离(mean phylogenetic pairwise distance, MPD)、最近物种系统发生平均距离(mean nearest taxon distance, MNTD)等指标也可用于量化系统发生多样性, 且结合具体的物种库(species pool)在实际研究中得到广泛应用。此外, 系统发生多样性也可用于比较不同群落的物种组成, 即系统发生beta多样性(phylogenetic beta diversity, PBD), 采用系统发生树枝长来反映群落之间的物种周转(species turnover)和物种嵌套(species nestedness)程度。R包picante (Kembel et al, 2010)目前多用于系统发生多样性指标计算。依据系统发生多样性, Hu等(2021)研究了中国陆生脊椎动物且发现其在华南及西南地区系统发生多样性最高; Wang MQ等(2019)则很大程度上解释了树木多样性对鳞翅目幼虫物种多度的作用和影响。

3.1.2 功能多样性

功能多样性为“某一群落内物种间功能性状变化的范围” (Tilman, 2001; Petchey & Gaston, 2002)。此类多样性不仅是物种多样性作用的结果, 还涉及个体性状以及与系统发生关系相关的组分(Bello et al, 2017)。目前, 能够反映群落内功能性状分布的指数主要包括功能丰富度(functional richness)、功能均匀度(functional evenness)和功能分化度(functional divergence) (Mason et al, 2005)。其中, 不同参数从不同角度反映了群落内性状的分布情况, 如, 功能丰富度反映的是群落中物种所占据的功能空间, 而功能均匀度强调的是功能性状在生态位空间中分布的均匀程度。

目前, 功能性状研究领域主要涉及3个方面。

(1)评估群落构建。为满足自身生存和繁殖所需, 物种的生态位取决于其对非生物和生物环境的响应以及其对两者的影响所决定, 而此类相互作用关系又与性状息息相关(McGill et al, 2006)。因此, 近年来生态学家尝试基于功能性状了解生物群落的组成及结构变化(Díaz et al, 2013)。此领域目前所关注的热点问题可简要概括为不同环境梯度, 前者如海拔(Nunes et al, 2017)、后者如栖息地类型(Castro et al, 2020)等, 或人类活动干扰(生物入侵(Wong et al, 2020)、城镇化(Gimenez & Higuti, 2017)及农业集约化(Flynn et al, 2009))如何影响昆虫群落结构和组成? 例如, Fontanilla等(2019)调查了中国云南省热带、亚热带和亚高山海拔样带上蚂蚁群落的功能多样性, 结果发现功能多样性随海拔的升高线性下降; Banaszak-Cibicka和Dylewski (2021)的研究结果显示, 城镇化程度不同的地区间的蜜蜂功能多样性存

在显著差异。

(2)评估种间互作。在互作网络中，性状的匹配性将决定物种间的互作强度及有效性(Vázquez et al, 2009)。因而，功能多样性将有利于揭示物种间的相互作用机制(Albrecht et al, 2018; Psomas et al, 2018)。目前，关于功能多样性如何影响互作网络，进而促进生态系统功能的假说主要有两种。其一，某一营养水平功能多样性的增加将会为更高营养级提供更多的生态位。这种“生态位构建”是基于食物网的构建顺序提出的假设，其中上行控制效应(资源控制)占主导地位。如，植物多样性对传粉者功能多样性具有积极作用(Papanikolaou et al, 2017)。另一种假说强调了下行控制效应(营养调节)的重要性，即高营养级的功能多样性对低营养级的多样性具有消极作用。如，捕食者性状的多样化将会导致植食者多样性的降低(Greenop et al, 2018)。

(3)评估生物多样性–生态系统功能关系(biodiversity–ecosystem function relationships, BEF)。昆虫在生态系统中往往能够提供多种生态系统服务功能，如传粉(Woodcock et al, 2019)、养分循环(Cheli et al, 2022)、能量流动(Barnes et al, 2016)等，但其所能提供的生态系统服务却因生物多样性丧失而受到威胁(Dainese et al, 2019; Grab et al, 2019)。Díaz和Cabido (2001)提出，面对持续的全球环境变化，仅提高生态系统中的物种丰富度将无法维持一些至关重要的生态系统服务功能。因此，生态学家们提出利用功能性状的研究方法来探究生态系统中重要服务功能的动态变化。目前，关于群落性状结构如何影响生态系统服务功能的假说主要包括3种：零假说、功能互补性假说及功能同一性假说。这3种主流假说分别强调了物种多度、性状的互补性及性状的一致性在生态系统功能中的作用(Wong et al, 2019)，皆已在不同类群中获得了论证，但并未达成一致结论(Fründ et al, 2013; Gagic et al, 2015; Barnes et al, 2016)。如，Fründ等(2013)认为一些新增的物种通过占据与原有物种不同的功能生态位，增强了功能性状的互补性，从而有效提高了作物的传粉。然而，Gagic等(2015)验证了功能同一性的重要性，认为将生物多样性与天然生物群落中的生态系统功能联系起来的关键因素是功能性状组成的同一性。

3.2 昆虫多样性研究方法

3.2.1 定量形态学

形态多样性是生物多样性的重要表现形式。生物体在形态上呈现的万千差异，是人们认识自然和探究生命的原始动力(国春策等, 2014)。特化的外部形态使得昆虫种群的数量更加庞大、分布范围更广(张萌娜等, 2015)。形态比较是人们了解世界的重要方式，其中以主观性较强的比较形态学作为代表，被分类学家用于生物学及其相关领域的研究(白明和杨星科, 2014)，该方法因其易用性使其在分类领域发挥着重要作用。然而，传统的分类学方法很大程度上包含了定性的判别概念，对于物种形态趋同问题，不少生物类群很难找到好用或易用的形态特征(Bouchard et al, 2011)，缺乏客观定量分类技术的介入，导致形成了同一类群有多个分类系统，也造成一些分类单元的系统地位频繁发生变动。直到20世纪初，生物研究中对特征分析方式从描述性的定性手段开始转向定量手段。几何形态学作为一种定量的分析方法，可以通过叠印法(superimposition method)消除样本大小、方位和物理属性的影响(Bookstein, 1991; Rohlf & Marcus, 1993)。

在分类学中，间断性形态特征通常是分类的重要依据。然而，很难发现足够多的间断性形态特征去解决分类中的难题。基于此种情况，几何形态学分析方法的出现不失为一种解决的方法(Villemant et al, 2007; Hájek & Fikáček, 2010; Xu et al, 2013; Bai et al, 2014; Zúñiga-Reinoso & Benítez, 2015)。近年有研究基于几何形态学的方法，对甲虫连续性特征的形态学信息进行测试，证实了甲虫的连续性特征具有重要的分类学信息(张萌娜等, 2015; 佟一杰等, 2016)，前胸背板和鞘翅的连续形态信息适用于高阶元分类(佟一杰, 2021)。有研究发现，鞘翅目拟步甲科中漠甲亚科和窄甲亚科的属、种丰富度与形态多样性呈正相关，鞘翅形态多样性与类群丰富度的相关性从族级水平到种级水平是逐级降低的，揭示了物种丰富度和形态多样性的关联度在不同阶元中并不总是一致的(Cheng et al, 2022)。连续性特征受到协同进化的影响很大，其蕴含的形态学信息与生活习性有着紧密的联系，有研究通过解读形态信息，推断出金龟挖掘能力的演变(Bai et al, 2013)。为了充分挖掘连续性形态特征所承载的分类学信

息、理解形态多样性和物种丰富度之间的关系、阐明形态多样性和生物演化的关系，未来需要针对不同的类群选取更多的形态特征、进行更全面的分析，从而能得出更详细的生物学结论(Tong et al, 2021)。

3.2.2　智能多样性监测

目前有多项研究表明，全球昆虫的多样性和数量正在急剧下降(Hallmann et al, 2017; Seibold et al, 2019)，亟需对昆虫进行有效监测，以期为其多样性保护提供科学参考。然而，由于现有的研究和监测物种及其种群变化趋势的方法大多为依赖人工计数的劳动密集型工作(Sun et al, 2018; Hong et al, 2021)，导致目前关于物种多样性和数量变化的数据在时间和空间上存在很大偏差(Dornelas et al, 2018; Blowes et al, 2019)。因此，我们需要更高效且可靠的方法来监测和研究昆虫多样性(Montgomery et al, 2020)。

随着物联网(internet of things, IOT)、大数据、云计算的不断发展，人工智能监测为这一全球挑战提供了潜在的新的解决方案。国外在昆虫智能监测方面的研究起步较早，提出了用于昆虫种群自动监测的电子陷阱(Holguin et al, 2010)。目前，自动监测已成为农作物病虫害监测、农业资源管理和优化的重要手段之一(Li et al, 2019)。例如，基于物联网(IOT)的智能陷阱监测系统可以实时采集地区内的作物害虫种群信息以及GPS位置信息，并将收集到的数据传送至害虫管理系统，有助于及时控制农田的有害生物数量(Potamitis et al, 2017)。此外，我国学者设计了一种基于物联网与安卓系统的昆虫生境移动监测系统。该系统通过采集温度、湿度、光照、土壤pH值等各种昆虫生境因子，并借助云服务实现了生境数据的在线传输、存储、处理和显示等功能，为昆虫与生态保护研究提供现代化信息手段(罗桂兰等, 2018)。

近几年来，由于深度学习(deep learning, DL)领域的不断发展，尤其是卷积神经网络(convolutional neural networks, CNNs)的应用，使得目标监测技术日益成熟，因此，基于计算机视觉的昆虫监测也受到了越来越多的关注(Goodfellow et al, 2016)。果蝇的自动监测系统通过利用CNN，可以监测到特定种类的果蝇，并能够成功区分果蝇的性别(Roosjen et al, 2020)。与此同时，将深度学习应用于昆虫研究也将带来新的技术挑战。随着深度学习与昆虫学研究结合得越来越紧密，在未来有望实现对昆虫行为的实时监测、追踪。这将有助于科研人员采取有效的措施来减少甚至恢复生物多样性下降造成的损失(Høye et al, 2021)，也将有助于进一步了解昆虫种群的动态，从而预测生物演化、虫害发生风险及未来爆发的可能性(Potamitis et al, 2017)。

3.2.3　系统发生信息学

分子数据经过几十年的积累，促进了分子分类学的发展，同时衍生出系统发生信息学。该学科的研究方法与系统信息学一致(Page, 2005)，其目的是全面建立系统发生数据库，并基于相关数据集构建实用的信息系统。迄今为止，大多数物种丰富的昆虫系统学研究都以包括DNA条形码在内的分子标记为核心(Hao et al, 2020a, b; Kennedy & Krehenwinkel, 2020)。

目前在构建昆虫的系统发生关系方面，对鞘翅目的研究最为全面。迄今为止最大的鞘翅目系统发生树包括8,441种物种(Bocak et al, 2014)，该系统发生树基于4个分子标记(18S、28S rRNA、线粒体*rrnL*和*COI*)构建而成。其中，用于构建系统发生树的大部分序列都来自NCBI数据库。对于该类系统发生树的构建，RaxML软件用于生成主要拓扑结构，生物信息学分析(bioinformatics analysis)基于Bash/Perl环境完成(Hunt & Vogler, 2008)，例如基于NCBI分层信息构建的简要分类字符串，大大简化了大型系统发生关系的人工核查和注释工作；此外，主要工具还包括Blast和BlastAlign，它们能分别对同源序列进行比对和提取，修改和对齐长度多变的RNA序列，以及完成在物种水平上基于注释结果的过滤。

对于膜翅目昆虫, Peters等人在2011年就利用系统信息学流程构建了超过1,100种、80,000个位点的序列矩阵。该研究表明，相较于个别数据的研究结果，整合数据库中序列所能揭示的结果将更为全面(Peters et al, 2011)。利用Ruby和Perl语言可以实现一套完整的分析流程；步骤包括：同源推断和提取，翻译对齐，模糊信息检测以及异质性检验。对于鳞翅目昆虫而言，目前应用较为广泛的系统发生树包括115科483种，该树基于19个蛋白编码基因构建(Regier et al, 2013)。例如，Kawahara等(2018)在研究鳞翅目活动节律等关键特征时，将其作为主干树并

与其他系统发生树相结合。在毛翅目研究中，研究人员从BOLD挖掘数据并构建了5,569个“BINs” (3,280个命名物种和MOTU)的系统发生关系，并通过“锚定类群” (anchor taxa)改进主干树结构(Zhou et al, 2016)。锚定类群是主干树的系统发生关系和DNA条形码序列重叠的物种，通过固定拓扑结构，并结合序列差异排列。

目前，少有研究对昆虫物种水平进行全面的系统发生研究，这可能是因为标准的系统发生方法不能很好地扩展，数万或数十万种物种的系统发生构建需要新的信息学方法。由于昆虫的系统发生树多基于分类水平构建所得，迄今为止最全面的生命之树在很大程度上仍不完善(Hinchliff et al, 2015)。昆虫作为物种最丰富的动物类群，其全面的系统发生关系需要基于特定的信息学流程进行构建(Chesters, 2020)；这套流程最早起源于对鞘翅目(Hunt & Vogler, 2008)的分析，结合了Bash和Perl，并主要依赖Blast完成。

为昆虫系统发生提供信息的分子数据类型主要包括DNA条形码、多物种整合的系统发生标记(phylomarkers)、基因组和多组学技术。但仅基于DNA条形码的系统发生学，其系统发生信息内容仍不够充分(DeSalle & Goldstein, 2019)。近年来，随着基因组学的飞速发展(Lewin et al, 2018)，包括昆虫在内的所有生物的组学数据快速增加(Feron & Waterhouse, 2022)。通过整合这些数据，如利用宏条形码和组学数据，并结合鸟枪测序技术，可应用于物种丰富度极高的昆虫类群的研究，并提高所构建系统发生树的分辨率。目前，研究人员已经启动了旨在提高昆虫生命之树覆盖度的全球项目，有望借此进一步实现全球系统发生多样性的完整性(Bian et al, 2022)。

近年来高通量DNA宏条形码技术的发展为研究昆虫的遗传多样性奠定了基础，这也促使了昆虫遗传多样性的研究逐步兴起(Beng et al, 2016; Elbrecht et al, 2018, 2019)。目前而言，较多的研究关注更低营养级(如植物)的遗传多样性对昆虫的影响(Castagneyrol et al, 2012)，最近一项全球尺度的研究表明，昆虫遗传多样性与纬度高度相关，并且呈现出双峰模式(French et al, 2022)。类似的结果能为深入了解生态进化的潜在机制提供新的视角。尤其对于进化系统学研究而言，通过研究种群中现存的遗传多样性，同时将多功能群和环境变化纳入研究，有望发现新的进化模式。

4 中国昆虫多样性综合性实验

结合目前全球昆虫多样性下降的趋势，加之目前生态文明建设的迫切需求，有必要针对昆虫多样性开展一系列野外实验和长期监测工作。因此，国内学者目前也正在致力于这些方面的工作，涉及全球合作、野外控制实验和昆虫监测网的布局。

4.1 “SITE-100”国际大科学计划

为揭示全球昆虫多样性下降的格局和机制，“SITE-100” (Site-based, Insects, Taxonomy, Environment, 100)国际大科学计划拟覆盖全球生物多样性热点地区和典型区域，选取100个大样地(中国至少10个大样地)，通过被动式采集方式(飞行阻隔器法、马来氏网法、罐诱法等)定量收集昆虫样本(滕备等, 2021)，从物种、形态和遗传3个维度探究全球昆虫多样性格局，定量绘制全球昆虫多样性模式和时空动态(Bian et al, 2022)。目前，该项目已在中国设立了6个大样地，在国外建立了30余个大样地(李盼盼等, 2021; Zhao et al, 2022)。

4.2 BEF-China控制实验

在全球生物多样性丧失备受关注的当下，生物多样性与生态系统功能控制实验是验证生物多样性与生态系统功能(biodiversity–ecosystem functioning, BEF)关系的良好手段(贺金生等, 2003; 马克平, 2013; Jochum et al, 2020)。BEF研究的系统性为研究昆虫多样性与相关营养级的关系提供了契机。以目前世界上最大的树种多样性实验基地BEF-China为例，研究人员通过设置一系列的树种丰富度梯度以模拟植物多样性丧失情景(Bruelheide et al, 2014)，开展了一系列包括植食者、传粉者以及寄生者在内的重要功能昆虫群多样性和互作的研究工作(Zhang et al, 2017; Schuldt et al, 2019; Wang MQ et al, 2019, 2020, 2022; Guo et al, 2021)。

4.3 昆虫多样性监测网

有研究表明，目前超过40%的昆虫种类在下降，其中1/3是濒危物种。近40年来，地面上的昆虫数量急剧下降了98% (Sánchez-Bayo & Wyckhuys, 2019)。鉴于昆虫数量的急剧下降，全球范围内也掀

起了建立昆虫多样性监测网的行动(Pereira & David Cooper, 2006)，通过国际合作也取得一定的进展(Basset et al, 2012)。中国科学院在生物多样性监测网络(Sino-BON)框架下建立了中国昆虫多样性监测专项网，研究地点涉及东北地区和俄罗斯远东毗邻地区、新疆、江西新岗山、云南西双版纳及高黎贡山地区、海南岛及南沙群岛，监测对象包括了传粉功能昆虫群(刘海铃等, 2021; 易浪等, 2021; Miao et al, 2022)、植食性昆虫群(Wang MQ et al, 2019, 2020)、捕食功能群(Schuldt et al, 2011, 2019)等。

这些多样性监测措施将增进我们对于昆虫多尺度和多维度多样性、内在维持机制及其生态系统服务功能变化和驱动因素的理解。

5 展望

5.1 功能性状多样性

虽然基于功能性状的研究方法已在昆虫生态学中得到了广泛应用，但无论在理论基础(Loreau et al, 2001)还是实验验证(Cardinale et al, 2012)方面，都远不及其在植物生态研究中的发展与应用。相关研究仍存在许多空白亟待生态学家们共同努力去填补。如目前关于功能多样性的研究多局限于局部区域内，缺乏大尺度如不同景观梯度下的研究。另外，关于功能多样性如何通过互作网络影响生态系统功能的认识仍停留在初步的理论模型，而缺乏实验数据的验证，尚未获取一个完整的因果关系网络(Gravel et al, 2016)，复杂互作网络研究也鲜有报道。

5.2 林冠昆虫多样性

树冠的昆虫多样性一直是生物学家关注的重点区域之一，然而，靠近林冠的采集具有一定挑战，这使得全面开展林冠研究受到一定阻碍(Cannon et al, 2021)。通过悬挂在林冠树枝上的绳索连接的收集装置(如诱饵陷阱、定时灯光陷阱、林冠马来氏网(SLAM陷阱)和飞行阻隔器)能够采集到树上的昆虫(Lowman et al, 2012)。然而，这些装置也有一定的局限性：物种间的相互作用难以衡量，也不能对采样进行有效控制。塔吊为林冠采集提供了一种安全可行的方法，从而能够直接观察物种间的相互作用并进行实验操作(Nakamura et al, 2017)。塔吊的建造成本较高，但中国目前已在不同纬度地区建立了8座森林塔吊(Nakamura et al, 2017)，这必将推动林冠昆虫多样性监测及林冠昆虫实验科学的发展。

5.3 传粉昆虫多样性

我国是传粉昆虫最丰富的国家之一。鉴于传粉昆虫对植物传粉的重要性及其丧失将造成的严重后果，建议在以下几个方面加强对传粉昆虫的监测和研究：(1)建立较为详尽的传粉昆虫本底数据库，包括全国普查虫媒农作物和野生植物的传粉昆虫的多样性。(2)选择关键区域代表性群落进行长期监测，包括传粉昆虫多样性、多度、季节动态、食物报酬来源等方面(Breeze et al, 2021)。(3)建立完备的传粉昆虫鉴定体系，包括编制易于使用的地区性检索表，以及利用新技术(如传粉昆虫图像识别和基因汤测序)加速传粉昆虫鉴定。(4)利用人工巢管在不同生态环境监测独栖性蜜蜂的生活史和生物学特性，调查其传粉植物信息，以便有助于进一步对当地植物的授粉利用。(5)将传粉网络作为一个核心监测和研究对象：传粉网络包含群落内所有传粉者、虫媒植物和传粉者–植物种间互作信息，具备生态系统的关键特征。

5.4 其他昆虫多样性

除上述重要昆虫类群，各生态系统中的其他昆虫多样性亦不容忽视。

(1)草地昆虫多样性。采伐、放牧和焚烧是典型的草地管理方式。随着管理对植物生长和植被结构的深刻改变(Geruo et al, 2020)，伴生昆虫群落也随之发生变化。昆虫对环境变化的响应在不同的功能类群和分类类群之间有很大的差异，因此很难确定哪种管理策略在保护整体多样性方面是最好的。因此，草地生态系统中昆虫多样性及其生态服务功能在不同草地管理方式、植被组成调整以及气候变化等众多因素的共同影响下如何响应，仍需长期监测和评价研究。

(2)农业昆虫多样性。农业生态系统中昆虫多样性及其生态服务功能受到全球气候变化、种植结构调整、耕作制度变革等众多因素的共同影响，亟需长期监测和评价研究。同时，应大力发展生态调控对策与方法，有效提升农业生态系统中的昆虫群落多样性与稳定性，及其授粉、生物控害等重要生态服务功能，保障农业的可持续发展。

(3)水生昆虫多样性。为更高效地开展水生态系

统中水生昆虫生物多样性的监测与保护，需响应生态环境部《重点流域水生态环境保护规划(2021–2025)》和《“十四五”生态环境监测规划》中的推动环境DNA宏条形码技术监测试点的相关要求，同时组织分类学者共同构建水生昆虫物种DNA条形码参考数据库(Weigand et al, 2019; Lin et al, 2021; Li et al, 2022)。

(4)土壤昆虫多样性。在之后的研究中，针对重要的土壤昆虫群组的幼虫做针对性研究。除此之外，当讨论土壤中的昆虫类群时，人们更多倾向于调查土壤昆虫(通常是害虫)对农业生产的影响(Johnson et al, 2006)，而不是侧重于昆虫多样性及其保护的部分。需要更多地侧重土壤中的昆虫多样性的调查，以及一些环境因素的影响。

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