

利用生物多样性控制作物害虫的理论与实践*

尤士骏^{1, 2, 3**} 张 杰^{1, 2, 3} 李金玉^{1, 2, 3} 陈燕婷^{1, 2, 3}
刘天生^{1, 2, 3} 牛东升^{1, 2, 3} 尤民生^{1, 2, 3***}

(1. 闽台作物有害生物生态防控国家重点实验室, 福建农林大学应用生态研究所, 福州 350002; 2. 教育部害虫生态防控国际合作联合实验室, 福建农林大学, 福州 350002; 3. 农业部闽台作物有害生物综合治理重点实验室, 福建农林大学, 福州 350002)

摘 要 生物多样性是人类可持续发展的重要基础, 保护和利用生物多样性是国际社会普遍关注的问题。近年来, 通过改善农田生物多样性和强化农田生态系统保益控害的服务功能, 实现作物病虫害生态调控已成为国内外研究的热点。本文在总结分析国内外利用生物多样性控制害虫理论研究和实际应用的基础上, 综述了该领域的研究进展、实践成果和发展前景。文中介绍了生物多样性的基本概念及其与害虫综合治理的关系, 系统概述了利用农田生物多样性控制作物害虫的各种理论假说, 包括天敌假说、资源集中假说、联合抗性假说、“推-拉”假说、中度复杂假说、景观缓冲假说等; 从提高天敌多样性、作物多样性、非作物多样性和景观多样性等方面综合评述了利用农田生物多样性控制作物害虫的应用实践, 重点介绍了我国的一些典型的实际应用案例, 旨在充分展示中国昆虫学科技工作者在该领域做出的贡献; 针对现代农业集约化经营导致农田生态系统结构简单、农田生物多样性不断下降等特点, 对如何以农田景观为单元进一步做好利用生物多样性控制作物害虫的理论研究和应用实践进行了讨论和展望。

关键词 生物多样性; 生态系统服务; 生境管理; 害虫生态防控

Theory and practice of utilizing biodiversity to enhance pest control in agroecosystems

YOU Shi-Jun^{1, 2, 3**} ZHANG Jie^{1, 2, 3} LI Jin-Yu^{1, 2, 3} CHEN Yan-Ting^{1, 2, 3}
LIU Tian-Sheng^{1, 2, 3} NIU Dong-Sheng^{1, 2, 3} YOU Min-Sheng^{1, 2, 3***}

(1. State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, Institute of Applied Ecology, Fujian Agriculture and Forestry University, Fuzhou 350002, China; 2. Joint International Research Laboratory of Ecological Pest Control, Ministry of Education, Fuzhou 350002, China; 3. Key Laboratory of Integrated Pest Management for Fujian-Taiwan Crops, Ministry of Agriculture, Fuzhou 350002, China)

Abstract The effective utilization of biodiversity for sustainable development and conservation is a universal concern. In recent years, ecological pest management has become a hot topic at home and abroad because it can improve biodiversity and enhance ecosystem services through biological control in agroecosystems. This paper presents an overview of the progress and practice of rational utilization of biodiversity to enhance pest control, and future prospects for this approach, based on achievements in China and other countries. We first describe the basic concept of biodiversity and its association with integrated pest management, then introduce theoretical hypotheses on utilizing biodiversity to control crop pests (including the natural enemy, resource concentration, associational resistance, “push-pull”, moderate complexity and landscape buffer, hypotheses. Finally, we provide an overview of the practical application of improving biodiversity to support pest control, focusing on some previously reported examples in China to reflect contributions made by Chinese entomologists. Given that modern agricultural intensification has increasingly led to the simplification of agroecosystems and a decline in biodiversity, we discuss in some detail the potential for facilitating both theoretical research and the practical application of biodiversity to

*资助项目 Supported projects: 海峡博士后交流资助计划项目 (201806); 国家自然科学基金项目 (31230061; 31320103922); 福建省科技重大专项/专题 (2018NZ0002-1)

**第一作者 First author, E-mail: sjyou@fafu.edu.cn

***通讯作者 Corresponding author, E-mail: msyou@fafu.edu.cn

收稿日期 Received: 2019-09-24; 接受日期 Accepted: 2019-10-12

further improve landscape level pest control.

Key words biodiversity; ecosystem service; habitat management; ecological pest control

1 引言

人类与害虫的斗争已经走过了漫长的历史。在与害虫斗争的实践中,人类不断提高认识,改变策略,并采用新的手段,积累了大量害虫防控的理论和实践经验,总体防控水平也不断提高。从早期的人工防治、耕作防治到 20 世纪中后期逐步开始实施的化学防治、生物防治、有害生物综合治理(Integrated pest management, IPM),以及近些年得到普遍认可和重视的害虫生态防控、害虫绿色防控等新对策和新方法,反映了人类对害虫防治的重视和曲折历程(尤民生等, 2004b; 彭露等, 2015)。

在现代农田生态系统中,人类为了满足人口增长对食物的需求,通常把自然植物群落改造成大面积种植单种特定的作物,同时配套使用大量的化学农药(杀虫剂)等高产栽培措施。化学农药的大量不合理使用,不仅给人类自身的健康造成威胁,而且使得很多害虫产生了严重的抗药性(Resistance),引发害虫的再增猖獗(Resurgence),导致农药越用越多、虫害愈演愈烈的恶性循环不断频繁出现;同时,农药残留(Residue)引起了污染土壤和水资源(尤民生等, 2004b; Arias-Estévez *et al.*, 2008; Pimentel and Burgess, 2014; 彭露等, 2015),破坏农田生物多样性等一系列的生态、环境和社会问题(Tscharntke *et al.*, 2005; Fritch *et al.*, 2017)。因此,寻求可持续的害虫综合治理策略,不仅可以降低化学农药的用量,而且有利于提高农产品的质量,促进农业生产的持续、稳定和健康发展。“转方式、调结构”和“到 2020 年农药使用量零增长行动”战略的实施表明,农业害虫综合治理事关国家粮食安全,农产品质量安全和农村生态环境安全(陆宴辉等, 2017)。

许多研究都表明,在农田生态系统中,人们可以利用生物多样性来提高对病虫害的防控水平(Andow, 1991)。例如,通过合理的农事操

作可以调控田间植被(包括作物种类布局、作物栽培模式、杂草防除等),使之朝着有利于天敌种群繁衍的方向发展,达到保持农田生态系统中生物群落稳定性和控制害虫种群数量的目的,从而起到发挥农田生态系统保益控害服务功能的作用(李正跃等, 2009; Cardinale *et al.*, 2012)。利用生物多样性控制作物害虫是近 40 年来的研究热点,在 Web of Science 上可以发现超过 8 600 篇的研究报道(图 1),且发表论文的数量呈现逐渐上升的趋势,尤其是进入 21 世纪以来,发表论文的递增速度更快。由此可见,充分利用农田生态系统及其生物多样性的功能,更加安全、有效和持续地开展作物害虫的综合治理,应该作为广大植物保护领域的科研人员、相关行政管理部门的管理人员和从事病虫害防控的技术人员的重要理念和行动指南。

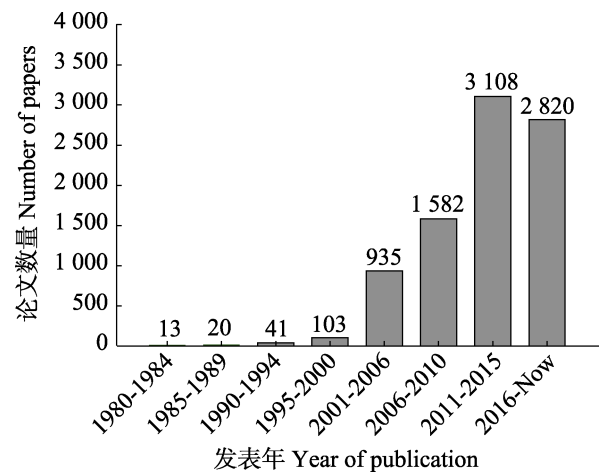


图 1 生物多样性与害虫综合治理相关研究论文的发表动态

Fig. 1 Historical trend in the research publications on biodiversity and integrated pest management (IPM)

2 利用生物多样性控制作物害虫的理论

农田生态系统中的多样性主要取决于作物的多样性、周围植被的多样性、农事操作的强度和景观的复杂度。根据农田生态系统的多样性组

成, 可将其分为计划多样性 (Planned diversity) 和关联多样性 (Associated diversity) (Altieri, 1999; Altieri and Nicholls, 2018) (图 2)。计划多样性指的是人们有计划地进行作物品种的多样性选择、作物的空间和时间布局 (如间作和轮作)、非作物生境植物的管理 (Altieri, 1999; Wood *et al.*, 2015) 以及天敌的释放 (Cardinale *et al.*, 2003; Van Lenteren, 2012)。合理的耕作制度不仅可以保护和提高农田生物多样性, 同时也有利于恢复农田生态系统的动态平衡, 促进农业害虫的生态控制和综合治理 (尤民生等, 2004a, 2004b)。大量的研究报道表明, 植被多样性的增加可通过直接的上行效应 (Bottom-up effects) 减少害虫的爆发 (Denno *et al.*, 2002; Scherber *et al.*, 2010; Letourneau *et al.*, 2011), 以及通过下行效应 (Top-down effects) 提高自然天敌对害虫的防控效率 (Wang *et al.*, 2009; Haddad *et al.*, 2011; Han *et al.*, 2014)。多样化种植的方式包括间作和轮作, 可通过改变植物的气味场, 干扰害虫 (尤其是专食性害虫) 找到最适寄主以及改变害虫在田间的分布 (Finch and Collier, 2000; Poveda *et al.*, 2008; Letourneau *et al.*, 2011), 从而减少作物害虫的数量 (Letourneau *et al.*, 2011; Lopes *et al.*, 2016; Baillod *et al.*, 2017; Rusch *et al.*, 2017)。“推-拉”策略 (Push-pull) 的应用也是基于作物的间作以及在作物田

周围种植其他植被而实现对害虫的防控 (Khan *et al.*, 2016; Xu *et al.*, 2018)。在“推-拉”策略中, 对害虫具有趋避作用或者干扰害虫对寄主的识别定位的非主栽作物/植物起到“推”的作用, 而对害虫具有吸引作用的非主栽作物/植物起到“拉”的作用 (Cook *et al.*, 2007a; Khan *et al.*, 2010)。种植在主栽作物之间或者周围的非主栽伴生作物/植物 (companion plants), 需要通过对害虫行为影响进行筛选, 如视觉、嗅觉、味觉或者产卵刺激等 (Eigenbrode *et al.*, 2016)。非作物生境管理主要包括杂草的管理和蜜源植物等的配置。增加农田周围非作物生境的植被多样性, 如蜜源植物、避难场所, 使得自然天敌种群增加, 从而通过增加上行效应对害虫进行更好的控制 (Landis *et al.*, 2000; Gurr *et al.*, 2017)。通过田间的管理起到保护天敌种群多样性, 从而对害虫起到防控效果, 属于保护性生物防治 (Conservation biological control) 的范畴 (Landis *et al.*, 2000; Gurr *et al.*, 2017)。此外, 人们还可通过强化生物防治 (Augmentative biological control) 的手段对害虫进行控制, 即大量地释放某类自然天敌对目标害虫起到直接的控制作用 (Cardinale *et al.*, 2003; Van Lenteren, 2012), 从而减少化学农药的使用 (van Lenteren and Bueno, 2003), 维持物种多样性以及生态系统服务功能 (Cock *et al.*, 2010)。

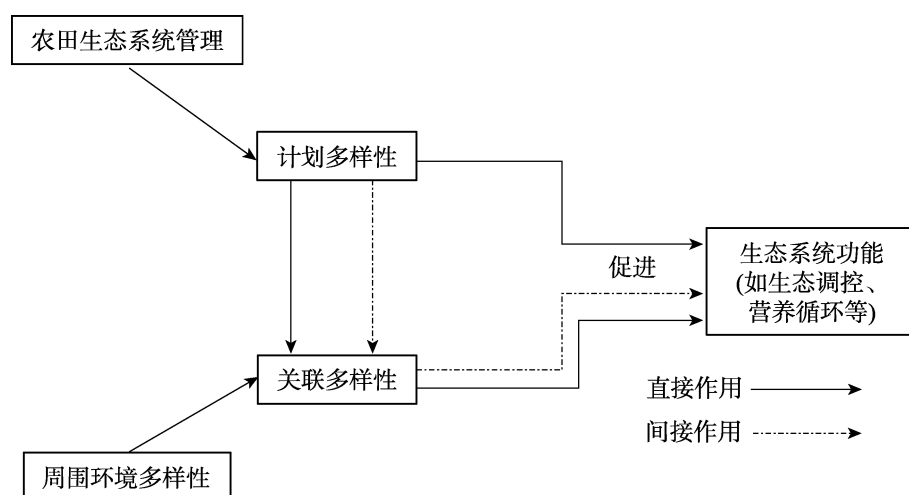


图 2 农田生态系统生物多样性组成 (改自 Altieri and Nicholls, 2018)

Fig. 2 Two distinct components of diversity in agroecosystems (adapt from Altieri and Nicholls, 2018)

关联多样性指的是由于农田作物及周边植物配置的多样性(计划多样性)所调控的其他物种多样性,如自然天敌多样性、土壤微生物多样性等(Altieri, 1999; Wood *et al.*, 2015)。复杂多样的生境能够为天敌提供替代食物或者猎物,这对于发挥天敌控害功能具有促进作用,如蜜源植物能够显著提高自然天敌的寿命、繁殖力、搜寻寄主能力、寄生率或者捕食率以及增加雌性比(Berndt and Wratten, 2005; Araj *et al.*, 2011; Zhu *et al.*, 2015; Pandey *et al.*, 2018),甚至提高了天敌昆虫后代的捕食能力(Amorós-Jiménez *et al.*, 2014; Zhu *et al.*, 2014)。农田周围的非作物生境除了为自然天敌提供食物,还可以为其提供越冬或夏眠场所,改善生存的微气候,为天敌在遭受外界干扰时段提供庇护所,有利于天敌种群的增长(Landis *et al.*, 2000; Hof and Bright, 2010; Morandin *et al.*, 2014; Gurr *et al.*, 2017)。“推-拉”策略主要直接作用于害虫,而针对天敌可以采用“吸引和奖赏”(Attract and reward)的策略(Khan *et al.*, 2008; Simpson *et al.*, 2011a, 2011b),利用人工合成的虫害诱导植物挥发物(Herbivore-induced plant volatiles, HIPVs)将周边的自然天敌吸引过来(James, 2005; James and Grasswitz, 2005; Mallinger *et al.*, 2011),并以蜜源植物作为“奖赏”,提高作物生境中天敌丰富度以增强生物防治效果(Simpson *et al.*, 2011b; Gordon *et al.*, 2013)。

从景观尺度来看,把农田生态系统理解为一个大的景观区域,包含作物生境和非作物生境,其中作物生境即为田间不同的作物类型,非作物生境包括林地、休耕地、草地、道路、田块边缘区和河流等(郑云开和尤民生, 2009)。这些不同斑块要素的有无以及他们之间的配置格局、连通状况、尺度空间和变化过程被认为会深刻影响其中害虫及其天敌昆虫的多样性组成和结构、种群的时空分布和迁移动态以及他们之间直接或间接的相互作用(Kareiva and Wennergren, 1995; 郑云开和尤民生, 2009; Martin *et al.*, 2013, 2016),进而势必影响作物害虫的生态防控功能(Gurr, 2012; Martin *et al.*, 2013, 2016;

Gurr *et al.*, 2017)。

近年来,在利用生物多样性控制害虫的理论方面开展了大量研究,众多学者进行了多层次,多方面的理论总结。下面我们重点介绍一些主流学说。

2.1 天敌假说, 种库理论及 β 多样性支配假说

天敌假说(Enemy hypothesis)认为,相比于单一作物集约化种植的简单农业生态系统,在镶嵌大量非作物生境的复杂农业生态系统中,多样化的生境能为天敌提供一系列的替代猎物或寄主,可以确保系统中存在更多更为丰富的害虫天敌种群(Root, 1973, 1975; Altieri and Letourneau, 1982; Andow, 1991; 刘雨芳等, 2000),而多样化的天敌群落比单一化的天敌群落能更有效地调控作物害虫的种群(Clough *et al.*, 2011)。因此,认为复杂多样的生态系统具有更强的控害能力。

种库理论(Species pool or species reservoir)认为,与作物生境相比,农田周围的非作物生境(如田埂、水渠、杂草地、林地、休耕地等)较少受到干扰,植被类型多样,覆盖时间也较长,是更稳定的异质化环境,有利于害虫天敌种群的栖息和繁衍(刘雨芳等, 2000)。因此,这些非作物生境通常贮存着丰富多样的天敌资源,被认为是农田潜在的天敌资源种库,可以促进和调节邻近农田生境中天敌群落多样性的建立与发展,进而对其中害虫种群起到明显的调节和控制作用(郑云开和尤民生, 2009; Tschamntke *et al.*, 2012; Zhao and Reddy, 2019)。特别是当农田生境遭受破坏时(如作物收获、农药施用等),种库生境对作物生境中天敌群落多样性的这种补充、促进和调节作用更是显得重要,它们可以为寄生性和捕食性天敌种群提供适宜的越冬(Collins *et al.*, 2003a, 2003b)和避难场所(Cardarelli and Bogliani, 2014),补充替代猎物和寄主(Parolin *et al.*, 2012; Andorno and López, 2014)以及花粉(Araj and Wratten, 2015)和花蜜(Araj *et al.*, 2011)等营养资源。通常认为,天敌种库容量及天敌自身运动迁移能力会决定作物生境中天敌

种群的丰富度和群落重建的速度,而种库生境的天敌资源容量与其生境结构的复杂性和植被多样性密切相关(刘雨芳等,2000)。

如果把整个农田景观尺度上的所有天敌群落理解为一个完整的资源库,沿着生境梯度,对不同生境天敌群落之间物种组成的相异性进行度量,即形成 β 多样性的概念(Clough *et al.*, 2007; Hendrickx *et al.*, 2007; Flohre *et al.*, 2011),也被称为生境间的多样性(Kessler *et al.*, 2009)。 β 多样性的提出可以让我们进一步理解景观异质性对农田天敌群落多样性的促进作用(Hendrickx *et al.*, 2007)。不同的生物物种具有不同的生活需求和生存对策(郑云开和尤民生,2009;张鑫等,2015),异质性高的农田景观中不同生境和植被类型可以更好满足天敌群落不同物种的生存需要(Duelli and Obrist, 2003; Bianchi *et al.*, 2006)。因此异质性、多样化的农业景观可以让更多的天敌物种存活和繁殖(Balzan *et al.*, 2016; Martin *et al.*, 2016; Gurr *et al.*, 2017; Zhao and Reddy, 2019),进而维系和促进大尺度农田景观背景中天敌群落资源库的多样性(Bianchi *et al.*, 2006; Holland *et al.*, 2016),也会进一步影响其对作物害虫的防治功能(Gurr, 2012; Liere *et al.*, 2015; Gurr *et al.*, 2017; Soti *et al.*, 2019)。该假说同时还提出,不同类型生境斑块间保持足够的隔离度,可以减少斑块间天敌种群的基因交流,避免大尺度景观区域内天敌资源库的同质化,最大限度的维系和促进其多样化(Tscharntke *et al.*, 2012)。

2.2 联合抗性假说、资源集中假说与植物显著性假说

联合抗性(Associational resistance)假说,其核心是在多样化的复杂农田生态系统,除寄主植物本身的抗性外,它们与周围邻近其他物种和生境会耦合形成相对复杂的群落结构、化学环境以及相关的小气候,从而整体上表现出对植食性害虫的“联合抗性”(Root, 1975; Litsinger and Moody, 1976; Uvah and Coaker, 1984; Barbosa *et al.*, 2009)。因此,认为相比于单一化种植的

系统,在复杂的农田生态系统中,植食性害虫数量会减少,作物受其进攻的机会也会减少。

资源集中(Resource concentration)假说试图解释植食性害虫搜寻、发现和定居寄主作物生境斑块的能力和趋向性。他们强调资源相对集中的农田生态系统,如在大面积、高密度单一化种植作物生境中,寄主作物能让植食性特别是狭食性和单食性的害虫更容易发现和停留,从而吸引更多的害虫前来取食为害,进而影响寄主作物的生长和造成作物产量的降低(Altieri and Letourneau, 1982)。而在多种作物或作物与非作物混作的生态系统中,多样化的植物可能干扰植食性害虫搜索和刺探靶标寄主作物的视觉和嗅觉刺激,导致其“迷失方向”,从而影响害虫对寄主作物的侵袭和为害。特定的植物组合还可能改变生境内的微环境和小气候,调节害虫的取食选择和运动行为(如在作物田周围布置对害虫具有引诱或拒避作用的其他植物),致使害虫从寄主作物中迁出,从而大大降低寄主作物上害虫的种群密度,减轻为害(刘雨芳等,2000)。

植物显著性(Plant apparency)假说认为,对于害虫而言,单一种植模式使现有作物比其祖先更加显眼。在农业生产中,农田周围相关的植物会使作物更加突出(Burn *et al.*, 1987; Feeny, 1976),大面积的单作系统使作物更明显的暴露给植食者。而植食者对寄主的选择受植物的颜色和高度的影响,植食者倾向于降落在绿色和高大的植物上。

2.3 适宜/不适宜降落假说与“推-拉”理论

适宜/不适宜降落(Appropriate/inappropriate landings)假说认为,植食性昆虫降落主要受视觉刺激,而不是化学信号。植食性昆虫会避免降落在如土壤颜色的棕色表面,而会不加区分地降落在绿色的表面。因此,寄主植物种植在裸露的土地上,会吸引更多的植食性昆虫定殖其上,而寄主植物种植在非寄主植物中间,则定殖在寄主植物上的植食性昆虫会减少(Finch and Collier, 2000)。

“推-拉”(Push-pull)理论是指通过筛选对

害虫具有趋避(如拒食剂、抗聚集信息素、报警信息素、产卵趋避物或产卵趋避信息素)或干扰害虫对寄主植物进行识别定位的植物和化学合成物质驱使害虫逃离需要保护的主栽作物,同时筛选对害虫具有视觉、嗅觉、味觉和产卵刺激作用的植物和化学合成物质吸引害虫到非主栽作物上(Cook *et al.*, 2007a)。更为普遍的现象是仅具有推或只有拉的作用。通过种植具有刺激性气味的植物,驱赶害虫逃离多作系统,即“推”(Uvah and Coaker, 1984)。种植害虫更喜欢的引诱植物,可以使害虫聚集在引诱植物上,从而减少对作物的取食,即“拉”(Cook *et al.*, 2007a)。当然,推或拉的对象不局限于害虫,如果能将天敌吸引到需要保护的主栽作物上,害虫将得到更为有效的控制(Cook *et al.*, 2007a)。

2.4 生物溢出效应、边缘效应、岛屿生物地理学和复合种群理论

如上所述,在异质化的农田景观格局中,生物体在其生命周期中往往需要一种以上的斑块生境,他们在不同生境斑块间迁移和扩散,以获取和满足其在不同生命阶段所需要不同资源,如食物、空间条件等(郑云开和尤民生, 2009; 张鑫等, 2015)。因此,作物害虫及其天敌种群在不同生境斑块间的移动是十分常见的,这种移动可能发生在各种不同的生境界面,既有从农田生境到自然生境的扩散,也有从自然生境向农田生境的移动,进而形成了独特的源-汇动态(郑云开和尤民生, 2009)和时间或空间上的溢出效应(Rand *et al.*, 2006)。研究结果显示,这样的一个动态溢出过程会对景观范围内的群落结构和相关生物的种群动态产生深远的影响(Rand *et al.*, 2006; Tschamntke *et al.*, 2012)。从农业景观管理的角度来看,强化天敌种群从自然生境到农田生境源源不断的溢出或跨边界的移动可以在很大程度上提升对农田生境中害虫的调控和防治作用(MacFadyen *et al.*, 2011; 赵紫华等, 2012)。当然,促进天敌种群从农田迁出补充替代猎物和花粉、花蜜等营养资源,或者当农田生境受到干扰如作物采收或农药施用,让更多天敌

种群可以向周围非作物生境迁出寻求越冬和避难场所,也是保护天敌群落多样性和加强害虫生态防控很重要的一个内容(Holzschuh *et al.*, 2008; Parolin *et al.*, 2012)。此外,使害虫种群更多从作物生境迁出也是减少其对农田作物为害的一种策略(Cook *et al.*, 2007a)。众多研究表明,农田景观尺度上作物与非作物生境斑块之间空间分布格局及相邻性质对害虫和天敌种群的溢出移动有决定性的调节作用,进而会影响它们在作物生境中的组成、分布、活动及所起的作用(Flohre *et al.*, 2011; Tschamntke *et al.*, 2012; Martin *et al.*, 2016; Gurr *et al.*, 2017)。

首先,根据岛屿生物地理学和复合种群理论,作物与非作物生境之间的连通状况是最重要的一个方面(Dieckotter *et al.*, 2008),这里就涉及农田景观范围内不同生境斑块间的排列方式和廊道建设的问题(Berggren *et al.*, 2002)。当农田与周围非作物生境的排列结构或廊道设计使其有足够的连通性或可接近性时,更大尺度景观区域的天敌资源库可以向农田生境输入和补充,使其在作物田中建立有效的种群(Nicholls *et al.*, 2001; Dieckotter *et al.*, 2008; Holzschuh *et al.*, 2009; Fahrig *et al.*, 2011);当农田生境缺乏资源或受到干扰时,生活其中的天敌种群才能实现向周围非作物生境迁出寻求补充资源或避难场所,以保住和维持种群增长,避免面临灭绝的可能性(Berggren *et al.*, 2002; Fahrig *et al.*, 2011);也同时才能实现害虫种群从作物田中的源源迁出(Cook *et al.*, 2007a)。

其次,邻近非作物生境斑块质量、数量及其界面大小和植物类型也是重要的调节因子。对于天敌种群来说,这些因子直接决定了景观范围内天敌种库的“容量”(Schmidt *et al.*, 2008; Tschamntke *et al.*, 2012)以及作物和非作物生境间“溢出量”的大小(郑云开和尤民生, 2009; Tschamntke *et al.*, 2012)。资源生境数量、大小、质量及其植物类型对天敌种库多样性(“容量”)的影响作用已在上一节描述。而对“溢出量”的调节方面,通常认为跨越生境的迁移和溢出随着边缘密度(即周长-面积比)的增加而增加

(Tscharnkte *et al.*, 2012)。因此,当资源生境以镶嵌化的小斑块散布在作物生境周围时,边缘密度可以得到提升,其中生境斑块间的功能连通性也会得到增强(Perovic *et al.*, 2010),这种功能连通性可以使天敌种群从资源库向农田生境源源不断的溢出并建立种群,也可以使其从作物生境快速迁出补充资源和寻求越冬或避难场所以维持种群的过程(Fahrig *et al.*, 2011)。对于作物害虫来说,当在农田周围存在其更喜好的植物类型和生境条件时,为了生存,害虫种群会倾向于选择从农田生境中迁出到这类生境斑块中(Khan *et al.*, 2000; Cook *et al.*, 2007a)。

其三,非作物生境斑块合理布局的调节作用还要取决于天敌种群跨生境界面的迁移扩散能力。对于一些扩散能力极其有限的天敌物种如拟寄生生物,农田周围的自然生境斑块虽然可以提供花蜜和避难所资源,但却可能阻碍了它们向作物生境的迁移扩散(Tscharnkte *et al.*, 2007)。大面积的自然生境可以维持更多的天敌种类及个体,但对于扩散能力较弱的天敌种群来说,对这类资源斑块的利用效率是有限的,从非作物生境到作物生境之间的距离会限制他们进入作物生境的数量和空间范围(Mouquet *et al.*, 2005)。这种限制作用最直接的表现就是边缘效应,也即田块边缘地带的天敌群落种类、数量和寄生率会明显高于田块中间(Mouquet *et al.*, 2001; Tscharnkte *et al.*, 2012)。相反,在农田周围散布大量小自然生境斑块的景观中,这类景观的边缘密度大,接触界面也比较大,迁移扩散能力的限制作用会被弱化,即使是移动能力有限的天敌,也比较容易进入作物生境(Tscharnkte *et al.*, 2002)。迁移扩散能力限制作用的影响也表现在天敌种群迁出作物生境补充资源和寻求避难的过程中,如果富含可利用资源的非作物生境斑块与农田的距离大于它们的移动能力,那么将导致这些物种在农业景观区域内变得稀少或缺失(Rand *et al.*, 2006; Jha and Dick, 2010; Blitzer *et al.*, 2012)。相比于迁移能力受限的种类,扩散力强的天敌物种跨生境界面的迁移扩散过程通常不受限制,不会表现边缘效应,它们的高活

动性有助于其在作物生境中的扩散和定居过程,也有利于其迁出作物生境补充资源和寻求庇护的过程(Holland *et al.*, 2004; Schmidt *et al.*, 2004),但是仍然还会在一定程度上受到大尺度景观背景如斑块排列方式及其廊道连通性的影响(Tylianakis *et al.*, 2004; Clough *et al.*, 2005; Holzschuh *et al.*, 2010)。

最后,农业景观调节作用还要考虑作物属性,已有的研究表明,在多年生作物景观中,大面积资源生境斑块的存在和其中多样化的天敌群落有利于天敌向作物生境的持续移动和补充;而短周期的一年生作物则更需要广泛分布的小资源生境斑块,以实现天敌向作物生境斑块的快速移动(Bianchi *et al.*, 2006)。

2.5 景观缓冲假说

如上所述,在具有较高非作物生境比例和多样化的复杂景观中,天敌群落的多样性和功能连通性可以得到维持和加强。景观缓冲假说认为,在这样的农业景观中,天敌功能群多样性的冗余和资源补充的能力可以提供一种缓冲机制,在环境变化时,当一些物种发生灭绝或种群出现空间或时间上波动时,这些物种的功能作用可以被其他物种替代而防止生态系统功能的下降(Loreau *et al.*, 2003; Winfree *et al.*, 2007; Tscharnkte *et al.*, 2012)。因此,多样化的景观在应对环境变化时,生态过程和功能通常表现出具有更高的稳定性和可塑性。农田景观是一类动态景观,环境变化频繁(如农作物收割和农药喷洒),功能冗余和缓冲在这类景观中显得尤为重要(Winfree and Kremen, 2009; Bluthgen and Klein, 2011)。正因为具备这样的功能缓冲作用,多样化的农业景观通常表现出较好的天敌控害效能和更低的作物危害程度。

2.6 中度复杂假说和空间尺度效应

基于异质化景观对天敌群落多样性和生态防控功能的促进调节作用,在人类主导的农田景观中,非作物生境的保护及其在农田生态系统中的合理规划、布局和利用(生境管理)成为害虫

防治过程(即保护性生物防治)中的首要原则(Fiedler *et al.*, 2008; Letourneau *et al.*, 2011; Holland *et al.*, 2012, 2016)。研究表明生物多样性在景观与农田两个不同尺度之间相互交流(Chase and Bengtsson, 2010),而且对害虫防控发挥重要的作用(Kareiva and Wennergren, 1995; Clough *et al.*, 2005),人类主导的生境管理和保护性生物防治实施的效果受到农田景观复杂程度的影响(Tscharntke *et al.*, 2012; Woltz *et al.*, 2012; Happe *et al.*, 2019)。景观中度复杂性假说认为,相比于高度复杂和结构极其简单或均匀的景观,保护性生物防治在中等复杂的农田景观中发挥的作用最高(Tscharntke *et al.*, 2005, 2012; Batary *et al.*, 2010; Concepción *et al.*, 2008; Smith *et al.*, 2010)。在自然或半自然栖境比例很高(>20%)的复杂景观中,本身区域内生物多样性和害虫生态防控功能已经很高,因此在这种区域实施生境管理和保护性生物防治措施往往不能产生非常明显的管理效果(Tscharntke *et al.*, 2012)。而在非作物生境比例很低(<1%)的简单景观中,则是种库资源的匮乏限制了农田保护性生物防治效果的发挥(Tscharntke *et al.*, 2012)。因此,相比于高度复杂和简单的农田景观,在中等复杂的农田景观(自然和半自然栖境比例为1%-20%)中实施保护性生物防治,如在农田周围规划和布局有机作物田、田块边缘区、灌木篱墙和休耕区等生境管理措施,可以更好地提升作物田天敌群落的多样性及其生态防控效能(Thies and Tscharntke, 1999; Roschewitz *et al.*, 2005; Tscharntke *et al.*, 2005; Holzschuh *et al.*, 2007; Batary *et al.*, 2010; Tscharntke *et al.*, 2012)。

此外,在农田景观中,为了更加有效地保护和管理非作物生境,尺度效应也是需要考 虑的一方面(Gabriel *et al.*, 2010)。天敌和害虫对于不同生境类型响应的空间尺度也是不同的(Steffan-Dewenter *et al.*, 2002; Grand and Cushman, 2003; Wasserman *et al.*, 2010; Rusch *et al.*, 2011; Dominik *et al.*, 2018),研究表明不同空间尺度上对天敌和害虫种群有影响的生境类型是不同的(Schmidt *et al.*, 2008; Sivakoff *et al.*, 2013;

Motzke *et al.*, 2016)。当然,不同种类的害虫与天敌受到生境空间尺度的影响也是不同的(Gabriel *et al.*, 2010)。研究表明专食性天敌和多食性天敌对半自然生境有同等依赖性,但是多食性天敌可以利用更大的空间范围(Chaplin-Kramer *et al.*, 2011)。另外,受扩散能力的限制,寄生性天敌对景观格局响应的空间尺度则较小,而扩散能力较强的捕食性天敌通常对景观格局响应的空间尺度较大,并发现通过景观格局设计来提高寄生蜂种群数量的最优空间尺度为0.5-1 km(Thies *et al.*, 2011)。因此,不同天敌类群表现出明显的“空间尺度效应”。理解不同空间尺度下的生境如何影响害虫和天敌的分布、丰富度和适合度,有助于在多尺度空间下进行不同大小生境斑块和生境类型的空间组合排列,最终达到害虫种群的生态治理。

3 利用生物多样性控制作物害虫的实践

通过提高农田生态系统的物种多样性,充分保护和利用自然天敌,可以直接抑制害虫爆发成灾。同时通过提高作物种植多样化(如间作、套作和轮作)及非作物生境多样化,有助于维持和提高农田生态系统的天敌多样性,间接提高对害虫的控制效力。

3.1 提高天敌多样性

关于充分利用天敌对害虫进行有效控制,目前的主要方法有三种:经典生物防治(Classical biological control),淹没性生物防治(Augmentative biological control),保护性生物防治(Conservation biological control)。

经典生物防治指从外地或者害虫原产地引入天敌,将害虫控制在经济阈值以下,起到防治害虫的作用。例如,美国农业部在20世纪90年代从欧洲引入盲蝽寄生蜂 *Peristenus digoneutis* 来防治美国牧草盲蝽 *Lygus lineolari*, 成功控制了牧区绿盲蝽的数量(Day, 1996, 2005; Day and Hoelmer, 2012);中国自2001年从比利时引入大喙腊甲 *Rhizophagus grandis* 来控制红脂大小

蠹 *Dendroctonus valens*, 取得了良好的防治效果 (赵建兴, 2006)。尽管自 20 世纪 70 年代以来全世界对天敌的引入案例不断减少, 但得益于防治成功率的升高, 应用经典生物防治措施的国家数量反而在增加 (Cock *et al.*, 2016)。

淹没性生物防治指大量释放天敌以消灭害虫, 如在大棚蔬菜种植中通过释放捕食螨或者真菌来控制害虫。利用捕食螨防治粉虱和蓟马则在温室蔬菜和观赏植物中得到广泛应用就(余德亿等, 2008; 黄建华等, 2016), 利用斯氏钝绥螨 *Amblyseius swirskii* 和巴氏钝绥螨 *Amblyseius barkeri* 防治西花蓟马 *Frankliniella occidentalis* (王恩东等, 2010), 都取得了较好的效果。

保护性生物防治指为本地天敌提供合适的栖息地和食物资源, 使其种群得到保持甚至扩大, 从而长期有效防治害虫 (Fiedler *et al.*, 2008)。半自然生境在保护性生物防治中具有十分重要的作用, 因为其可以提供天敌需要的花蜜、花粉、猎物 and 越冬场所 (Landis *et al.*, 2000; Duelli and Obrist, 2003; Gurr *et al.*, 2017)。一方面, 在半自然生境中多样性的植物可以分泌多种花蜜和花粉, 有助于提高寄生蜂和部分捕食者的寿命和繁殖力, 如荞麦 *Fagopyrum sagittatum* 和茴蒿香 *Agastache foeniculum* 花蜜能够增加红足侧沟茧蜂 *Microplitis croceipes* 的寿命 (Nafziger and Fadamiro, 2011); 二斑瓢虫 *Adalia bipunctata* 成虫在取食以花粉为食的地中海斑螟 *Ephesia kuehniella* 时, 其繁殖力达到取食豆蚜 *Acyrtosiphon pisum* 时的两倍 (De Clercq *et al.*, 2005); 细扁食蚜蝇 *Episyrphus balteatus* 和大灰优蚜蝇 *Eupeodes corollae* 在花蜜开放型的野花中丰富度更高 (Hatt *et al.*, 2019)。另一方面, 保护作物周围的半自然生境可为捕食性天敌提供更多猎物和避难所, 有利于捕食性天敌的生存与繁殖。例如, 在丛生草地中由于有稳定的环境, 越冬后其节肢动物的存活率要高于其他植物类群 (D'Hulster and Desender, 1982)。田地周围的树篱通过为步甲科、隐翅虫科天敌和蜘蛛提供越冬的微环境, 比田地边缘地区表现出更高的物种多样性和丰富度 (Pywell *et al.*, 2005; Griffiths

et al., 2007)。

尽管提高天敌多样性有助于降低害虫丰富度、提高作物产量和增加农民的经济利益, 但并不是所有案例均能够实现这一目标 (Rosenheim, 1998; Chaplin-Kramer *et al.*, 2011; Letourneau *et al.*, 2011; Martin *et al.*, 2013), 这可能由天敌间复杂的相互关系导致的。当多种天敌生态位重叠时, 功能团内部的出现互相取食 (Intraguild predation) 时可导致天敌数量减少而产生消极影响, 不同天敌的生态位互补 (Niche complementarity) 时可产生积极影响, 而天敌间出现功能冗余 (Functional redundancy) 时则对控制害虫没有作用 (Straub *et al.*, 2008; Jonsson *et al.*, 2008; Martin *et al.*, 2013)。因此, 在利用天敌多样性进行害虫防治时应该充分考虑天敌间相互关系。

3.2 提高作物植被多样性

间套作 (Intercropping) 一般指在一块地上, 同时期按照一定的行、株距和占地的宽窄比例间隔种植两种以上的作物, 因而增加了作物植被多样性。在作物中间作趋避害虫/引诱天敌的作物, 可通过趋避害虫或吸引天敌来达到控制害虫的目的。在非洲, 通过在玉米和高粱田间作螟虫类害虫的非寄主植物糖蜜草 *Melinis minutiflora*, 田间大螟绒茧蜂 *Cotesia sesamiae* 寄生率显著升高, 且害虫的危害显著降低, 就是由于糖蜜草释放出的挥发性物质驱走害虫并吸引寄生蜂的结果 (Khan *et al.*, 1997)。高泽正等 (2004) 研究发现白菜与葱、菜心与茄子间作, 能显著降低黄曲条跳甲对白菜和菜心的为害。另外一项实验也表明通过在小白菜田间套作大蒜, 可提高寄生性天敌寄生蜂的丰富度、丰盛度和多样性指数, 这都说明通过合理的间套作, 有助于增强天敌对害虫的生态调控作用 (蔡鸿娇和尤民生, 2007)。在棉花和大豆的整个生长期, 苘麻 *Abutilon theophrasti* 对 B 型烟粉虱 *Bemisia tabaci* 有极显著诱集作用, 可通过间作提高防治效果 (林克剑等, 2006)。在蚕豆 *Vicia faba* 地中间作罗勒 *Ocimum basilicum* 或夏香薄荷 *Satureja hortensis*, 均可显著降低黑豆蚜 *Aphis fabae* 的数量, 表明可通过

间作罗勒或夏香薄荷来趋避黑豆蚜,从而降低害虫危害 (Basedow *et al.*, 2006)。此外,在烟田套种大蒜,田间捕食性和寄生性天敌的物种丰富度和数量都有提高,显著推迟烟田中烟蚜种群的始发期并降低其个体数量,表明间套作大蒜可对烟蚜种群有明显的控制作用 (赖荣泉, 2011)。在茶园中间作百喜草 *Paspalum notatum* 和间作圆叶决明 *Cassia rotundifolia*, 其茶冠层和凋落层的捕食螨有效多样性指数、个体数和绝对丰盛度均有提高,表明通过茶园间作可提高茶园天敌的生物控制功能 (陈李林等, 2011)。对非洲地区的间作措施影响收入和产量进行综合分析发现,间作作为一种可持续性农业措施,确实可以提高作物产量和农民收入 (Himmelstein *et al.*, 2016)。

轮作 (Crop rotation) 是指在在同一块土地上按照一定时间顺序 (如季节或年份), 种植不同作物的种植方式,也是提高农田生物多样性一种有效措施。轮作不仅有利于提高土壤质量和肥力,控制杂草和土传病害,还可以通过切断农田中害虫的生活史及改变其生存环境,从而抑制农田中害虫的种群发展,达到明显的控制害虫作用 (Mohler and Johnson, 2009)。尤其在控制玉米根虫 *Diabrotica virgifera*、马铃薯甲虫 *Leptinotarsa decemlineata*、金针虫 *Melanotus communi*、蛱蛄 *Phyllophaga* spp 等一些重要害虫的效果尤其明显 (Mohler and Johnson, 2009)。在农业生产中,种植非寄主植物或抗虫、趋避害虫的寄主植物进行轮作,可以降低目标害虫的虫口密度。在新西兰,通过轮作白三叶 *Trifolium repens* 或黑麦草 *Lolium perenne* 可以降低新西兰草地蛱蛄的虫体体重和繁殖率,提高害虫死亡率,降低害虫种群密度 (Farrell and Sweney, 1974; Farrell, 1975)。在美国,高粱、向日葵、大豆和绿豆种植区更容易受到金针虫危害,而轮作冬麦 *Triticum aestivum* 可显著降低其危害 (Robertson, 1993)。水稻和棉花轮作则可以推迟红蜘蛛进入棉田时间,从而减轻害虫为害 (柯道秀等, 1995)。在广州地区,对稻菜轮作地中的褐飞虱和蜘蛛数量进行调查,发现轮作稻田中的褐飞虱数量要显著低于连作稻田,说明稻菜轮作模式可减少害虫数量 (蔡尤

俊等, 2015)。在昆明对连作、轮作和间作模式下种植的当归 *Angelica sinensis* 中根结线虫 *Meloidogyne* sp. 调查,结果表明间作和轮作都是控制当归中根结线虫的有效措施,且轮作控制效率最高 (Xie *et al.*, 2016)。另外,轮作可以在时间尺度上增加农业生态系统的生物多样性,如在轮作苜蓿的玉米大豆田中的步甲的活动要显著高于传统玉米农田 (O'Rourke *et al.*, 2008),这有助于充分发挥天敌对害虫的控制作用。

3.3 提高非作物植被多样性

3.3.1 对天敌的影响 目前在应用最多的 4 类非作物功能植物为荞麦 *Fagopyrum esculentum*、钟穗花 *Phacelia tanacetifolia*、香雪球 *Lobularia maritima* 和香菜 *Coriandrum sativum*, 它们对天敌有很好的吸引作用,能够有效地增加控制害虫作用 (Landis *et al.*, 2000; Kleijin *et al.*, 2006; Fiedler *et al.*, 2008)。实验表明,荞麦花蜜能显著延长多种寄生蜂的寿命,如中红侧沟茧蜂 *Microplitis mediator*、弯尾姬蜂 *Diadegma fenestrata* (Géneau *et al.*, 2012)、粉蝶盘绒茧蜂 *Cotesia glomerata* (Lee and Heimpel, 2005) 等。香雪球 *L. maritima* 花蜜能够延长小花螯 *Orius majusculus*、寄生蜂 *Cotesia marginiventris* 和岛弯尾姬蜂 *Diadegma insulare* 的寿命和提高其繁殖力,在包菜周围种植香雪球可以提高寄生蜂的防治效果 (Johanowicz and Mitchell, 2000; Pumariño and Alomar, 2012)。在水稻田周边种植芝麻 *Sesamum indicum* 可以显著增加天敌稻螟赤眼蜂 *Trichogramma japonicum* 的数量,提高其寄生和扩散能力,降低害虫造成的危害 (田俊策等, 2018; Zhu *et al.*, 2018)。此外, Silveira 等 (2009) 在巴西圣保罗州在有机洋葱田边种植显花植物万寿菊,结果表明,自然天敌的丰富度和多样性都有提高,有效地降低害虫的数量。伞形花科植物对食蚜蝇科 (Van Rijn *et al.*, 2013)、花螯科 (Sigsgaard and Kollmann, 2007)、脉翅目 (Van Rijn, 2012) 和瓢甲科 (Burgio *et al.*, 2004) 昆虫有积极影响。在间作罗勒、猫薄荷 *Nepeta cataria*、矢车菊 *Centaurea cyanus* 的梨园中,由

于花期增加,其主要天敌类群的数量显著增加,提高了对害虫的控制作用 (Song *et al.*, 2010)。作物周边种植向日葵 *Helianthus* spp. 也被证明可作为吸引多种天敌昆虫的有效途径 (Jones and Gillett, 2005)。多项研究表明,由于蜈蚣花 *Phacelia tanacetifolia* 可以提供食蚜蝇所需营养,在作物周围种植蜈蚣花可以显著提高作物中食蚜蝇的数量 (Klinger, 1987; White *et al.*, 1995)。在甘蓝 *Brassica oleracea* 菜田中种植矢车菊 *Centaurea cyanus* 显著提高了田间害虫卵和幼虫的寄生率,从而提高作物产量 (Balmer *et al.*, 2014)。在瑞士,通过在马铃薯田周围设置花带,主要为菊科、十字花科和蓼科野花,结果表明食蚜蝇、草蛉和瓢虫等天敌的丰富度显著增加,马铃薯田中蚜虫的数量减少了 75% (Tschumi *et al.*, 2016)。

3.3.2 对害虫的影响 尤民生等 (2004a) 认为可以通过改变农田周边环境植被的组成、结构和覆盖度等,来营造不利于害虫过渡生存的环境或有利于集中杀灭害虫的条件,达到对作物害虫的持续控制。十字花科野草中的野生油菜 *Brassica campestris* 可引诱羽衣甘蓝 *Brassica oleracea* 上的芜菁黄条跳甲 *Phyllotreta cruciferae* (Altieri and Gliessman, 1983)。在肯尼亚,研究表明蔬菜地周围多种十字花科野草是小菜蛾重要的繁殖场所,如 *Brassica juncera*、*Raphanus raphanistrum*、*Rorippa nudiuscula* 等,且相比于包菜和甘蓝,小菜蛾更喜欢在此类十字花科野草上产卵 (Kahuthia-Gathu, 2007)。欧洲山芥 *Barbarea vulgaris* 可作为小菜蛾 *Plutella xylostella* 的致死性诱集植物 (Badenes-Perez *et al.*, 2004, 2005)。与单作棉花 *Gossypium barbadense* 相比,间作罗勒的棉田可显著降低害虫的为害率,减少 50% 的棉红铃虫 *Pectinophora gossypiella* 种群数量 (Schader *et al.*, 2005)。在间作罗勒、猫薄荷、矢车菊的梨园中,因为推迟了害虫发生期,害虫为害期缩短,从而降低了害虫危害 (Song *et al.*, 2010)。在水稻田埂和沟渠边常见的水莎草 *Cyperus serotinus* 可作为大螟 *Sesamia inferens* 的致死性诱集植物 (Liu *et al.*, 2011)。

3.4 提高农业景观多样性

3.4.1 景观结构对天敌和害虫的影响 景观结构包括多样性、斑块面积和破碎化,直接影响到害虫和天敌的扩散能力和死亡率 (Martin *et al.*, 2016)。研究发现不断增加的生境多样性通常与捕食性和寄生性天敌的丰富度和多样性存在密切联系。Elliott 等 (1999) 等调查了麦田景观对蚜虫天敌的影响,结果表明增加半自然生境有利于提高捕食性天敌的丰富度,而破碎化的生境会导致天敌对害虫的控制效能降低。Thies 和 Steffan (2003) 研究发现,当景观中的非作物生境比例增加时,油菜花粉甲 *Meligethes aeneus* 幼虫的寄生致死率上升,害虫取食植物的损失降低。大量国外研究都表明,增加作物生境类型和非作物生境多样性能够提高天敌的种类和数量,从而抑制害虫种群发展 (Agnew and Smith, 1989; Cai *et al.*, 2007; Concepción *et al.*, 2008; Chaplin-Kramer *et al.*, 2011; Liere *et al.*, 2015; Balzan *et al.*, 2016; Holland *et al.*, 2016)。在国内,赵紫华等 (2010) 研究了不同麦田结构对麦蚜种群的影响,结果表明多样化的麦田生境能够迟滞麦蚜的迁入,降低其迁入量。杨龙等 (2016) 对华北地区不同麦田生境下瓢虫种群进行监测发现,农田景观系统中非作物生境有利于麦田早期瓢虫种群的发生。

3.4.2 景观类型对天敌和害虫的影响 农业景观由不同的生境类型构成,包括林地、休耕地、草地、道路、田块边缘区和河流等,适当提高景观构成多样性,有利于增加天敌的多样性和丰富度。了解不同生境类型对于害虫和天敌群落的影响对于制定有效的生境管理策略来控制害虫是十分重要的。

一项在英国的研究发现,灌木类树篱可支持更多种类的天敌 (Baudry *et al.*, 2000; Maudsley, 2000)。例如,伞形花科植物对食蚜蝇科 (van Rijn *et al.*, 2013)、花蝽科 (Sigsgaard and Kollmann, 2007)、脉翅目 (Van Rijn, 2012) 和瓢甲科 (Burgio *et al.*, 2004) 昆虫有正面的影响,增加树篱的面积也有助于寄生类昆虫的繁殖和生存。

(MacFadyen *et al.*, 2011)。在树篱面积达到 9% 至 16% 时,瓢甲科天敌就可对蚜虫进行有效控制 (Bianchi and Van der Werf, 2003)。同时,研究也表明树篱可能会对害虫防治产生不利影响,如在作物生长季节为蚜虫的生长提供资源 (Leather, 1993),或者阻碍捕食性天敌昆虫的迁入 (Thomas *et al.*, 1998; Holland *et al.*, 2004)。对森林生境的研究发现,阔叶林中的寄生蜂种类最为丰富,而松柏科树林也可以支持多种寄生蜂 (Fraser *et al.*, 2007)。森林生境对食蚜蝇也有很大的支持作用 (Bennewicz, 2011),却会对多种天敌产生负面影响 (Sarhou *et al.*, 2014)。在瑞士的研究发现,靠近森林的果园中蜘蛛的丰富度更高 (Bailey *et al.*, 2010), Schüepp 等 (2014) 在樱桃园中也获得了相似的结果。但是 Rusch 等 (2012) 的研究表明增加森林的比例虽然提高了对花粉甲的寄生率,但其危害却增加了。对于草地生境,包括田边带、甲虫堤、绿化道等,可为捕食性天敌提供越冬场所和食物,是十分有利于捕食性天敌生存的。在秋天和春天,耕种及新生的草间带可以支持捕食性甲虫,如步甲科,花萤科,瓢甲科和隐翅虫科天敌,以及蜘蛛类天敌 (Lagerlöf and Wallin, 1993; Thomas and Marshall, 1999; Meek *et al.*, 2002)。在冬天,草地中的捕食性天敌的存活率要高于田地中的,包含隐翅虫科,狼蛛科,皿蛛科等 (Pywell *et al.*, 2005; van Alebeek *et al.*, 2006; Griffiths *et al.*, 2007)。也有研究发现,草地对某些天敌没有影响,这可能与不同昆虫对生境的反应方式不同有关 (Cook *et al.*, 2007b)。对于害虫, Van Alebeek 等 (2006) 发现增加田间草地的比例可以提高对蚜虫的控制效果,主要是因为捕食性天敌增多了。赵紫华等 (2012) 的研究也表明草地对蚜虫寄生蜂种群的增长有促进作用。但是, Holland 等 (2012) 的研究发现草地面积反而会导致危害加重。这些研究说明草地生境可以支持更多捕食性天敌来加大对害虫的压力,但是,也可能会支持害虫而导致更严重危害。Sivakoff 等 (2013) 研究了棉田周围不同作物斑块对草盲蝽 *Lygus hesperus* 种群动态的影响,发现不同作物对于草盲蝽的作用

是有差异的 (支持、抑制或者无影响)。

3.4.3 景观尺度对害虫和天敌的影响 近年来,北美和欧洲等地区用农田生境管理实施多尺度空间下害虫生态调控,旨在利用大区域景观设计和农田作物布局与农事操作的有机结合,通过生境管理措施、调节种植模式或者改变农业景观格局的空间配置等以切断害虫种群的生活史,建立和恢复天敌种库与转移通道,从而最大程度地提高农业生态系统自身的控害功能 (Parolin *et al.*, 2012; Tschardt *et al.*, 2012)。为了适应当地生境条件,不同生物都进化出适应性的行为,使其栖境及活动空间最大化并能够在变化的环境中生存下来 (Holt, 2003),为了更加有效的管理和保护其生境,就需要了解害虫和天敌与生境间联系如何变化。天敌和害虫对于不同生境类型响应的空间尺度是不同的 (Steffan-Dewenter *et al.*, 2002; Grand and Cushman, 2003; Wasserman *et al.*, 2010; Rusch *et al.*, 2011),而不同的害虫与天敌受到生境影响的空间尺度也是不同的。Thies 和 Steffan (2003) 研究了不同空间尺度下半自然生境对花粉甲幼虫寄生率的影响,结果表明半自然生境有助于提高田间花粉甲幼虫寄生率,且在空间尺度为 1.5 km 时,两者相关性最高。Rusch 等 (2011) 调查了不同空间尺度下花粉甲幼虫寄生率,结果表明不同寄生蜂响应的空间尺度是不一样的。Chaplin-Kramer 等 (2011) 总结前人研究发现专食性天敌和广食性天敌对半自然生境的同等依赖性,但是,多食性天敌可以利用更大的空间范围。Mutzke 等 (2016) 研究了在不同空间尺度上与蜜蜂丰富度响应的生境类型,结果说明不同空间尺度上对蜜蜂有影响的生境类型是不同的,这与 Sivakoff 等 (2013) 对草盲蝽的研究得到的结论相一致。Thies 等 (2011) 对蚜虫及其天敌的研究表明,扩散能力更强的广食性的捕食性天敌由于可以利用更大空间尺度范围内的资源,因而比扩散能力较弱的寄生性天敌对景观格局响应的空间尺度更大。综上所述,不同种类的害虫和天敌都表现出一定的“空间尺度效应”。因此,理解不同空间尺度下的生境如何影响害虫和天敌的分布、丰富度和适

合度,有助于在多尺度空间下进行不同大小生境斑块和生境类型的空间组合排列,最终达到害虫种群的生态治理。

4 小结与讨论

生物多样性是一个描述自然界生物有机体变异的基本概念,它是指单生态系统中所有生物(包括植物、动物和微生物等)及其相互作用的群体(Mcneely *et al.*, 1990)。在自然生态系统中,所有的生物是一个和谐的整体,不同的物种占据着特定的时间、空间、营养生态位,发挥着各自的生态功能,维系着系统的连续性和稳定性。在农田生态系统中,由于受到人类的控制和不断干扰,如使用大量化学物质和采用有机机械化耕种等措施,导致农田生态系统中的生物多样性的减少,物种之间的相互作用趋于弱化,破坏了生态系统的连续性和稳定性(李正跃等, 2009)。

作为农田生态系统的重要组成成分,只有保证生物群落的稳定与健康,才能维持整个农田生态系统功能的稳定和持久,从而实现农业生产的可持续性发展(丁岩钦, 1993)。尽管大量研究表明,提高农田生物群落多样性有利于对害虫进行生态控制,但也有研究表明生物群落多样性的提高(如天敌种类增多)反而不利于进行生态控制。例如,Finke 和 Denno (2004)的研究就表明复杂的天敌群落削弱了天敌对植食性害虫的控制,甚至要低于简单天敌群落对害虫的控制作用。然而,更多的研究表明提高天敌群落多样性能够比单一化的天敌群落提供更为有效的害虫控制效果(Losey and Denno, 1998; Cardinale *et al.*, 2003; Schmidt *et al.*, 2003; Snyder and Ives, 2003; Gurr *et al.*, 2017)。当然,也有研究表明提高天敌多样性并不会增强或减弱对害虫的控制作用(Wilby *et al.*, 2005)。Straub 等(2008)及 Letourneau 等(2009)也都认为提高天敌多样性并不一定会提高生态系统的生物防控功能,因为天敌间相互关系决定了最终控制效果。当天敌生态位互补时,明显有利于控制害虫;当天敌表现为功能冗余时,对控制害虫没有帮助;而当天敌间出现竞争关系时,则对控制害虫表现出消极

作用。因此,利用天敌进行害虫控制时,必须考虑天敌群落的相互关系。在利用田间植被管理及周围非作物生境调节进行害虫防治时,必须考虑其对天敌间相互关系的影响,否则会导致防治失败(Tscharntke *et al.*, 2016)。

现代农业集约化经营的一个显著特征是农业土地利用面积和范围的扩展以及大面积种植单一作物,导致农田生态系统趋向简单化。这种简单化的系统及其生物多样性的丧失,必然引起生态系统服务功能的退化,尤其是与农业生产息息相关的害虫生态控制功能(Ives *et al.*, 2000; Wilby and Thomas, 2002; Gurr *et al.*, 2003)。保护和利用农田生物多样性,不仅有利于强化农田生态系统保益控害的服务功能,而且有利于减少化学农药的使用、提高作物的产量和品质以及促进农业的持续、稳定和健康发展。

农田生态系统是一个开放型的系统,因此,对于同类作物的害虫种群的数量控制,以景观为单元要比以田块为单元更加合适,可避免以保护较小空间尺度下的某一种作物为目的而开展害虫防治的局限性(尤民生等, 2004a)。提高农业景观多样性有利于在农田生态系统中维持多样化的生物群落,增加景观中非作物生境的比,可以为天敌昆虫提供更多补充食物以及越冬和避难所,有利于天敌在作物生境与非作物生境间迁移扩散,从而提高对害虫控制作用。越来越多的研究开始关注于不同景观背景(组成和结构)如何影响“作物-害虫-天敌”之间的相互作用,多样化的农业景观如何调节生物多样性,以及景观生态学在保护性害虫生物防治上的应用。这些研究对于利用景观管理,通过优化农业景观格局、尺度和过程,从而促进害虫生态控制,实现农业生产的可持续发展具有重要的意义。

展望未来,对于从事害虫生态防控及综合治理的科研工作者及相关从业人员,以下几个方面的问题值得更多的思考和探索:

1. 进行基于关键天敌群落功能的多样性保护,以期从事作物栽培及管理的一线人员提供更有针对性和更明确的建议,将有利于提高害虫控制的效率;

2. 加强对本地功能植物的筛选, 不仅有利于降低成本, 同时也可以规避由于引进外来物种所带来的适应性和潜在的生态风险;

3. 在利用寄生性天敌和捕食性天敌昆虫进行害虫防治的同时, 也可以充分考虑将更多其他功能性群体纳入综合防治体系, 比如鸟类和哺乳动物等, 目前还缺乏针对此方面的深入调查研究;

4. 害虫防治方案的制定, 应充分考虑方案对农田生态系统食物网动态的潜在影响, 尤其是对天敌物种相互作用的影响。

尽管多年的理论积累与实践经验证明利用生物多样性控制害虫是一条行之有效的途径, 但当今世界的害虫治理工作仍然面临着各种问题和挑战, 尤其是将针对不同时空尺度的防治方案进行协同整合, 以期实现生态系统服务功能及种植者利益之间的平衡。

参考文献 (References)

- Agnew CW, Smith JW, 1989. Ecology of spiders (Araneae) in a peanut agroecosystem. *Environmental Entomology*, 18(1): 30–42.
- Altieri M, Nicholls C, 2018. Biodiversity and Pest Management in Agroecosystems. Boca Raton: CRC Press. 11.
- Altieri MA, 1999. The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment*, 74(1/3): 19–31.
- Altieri MA, Gliessman SR, 1983. Effects of plant diversity on the density and herbivory of the flea beetle, *Phyllotreta cruciferae* Goeze, in California collard (*Brassica oleracea*) cropping systems. *Crop Protection*, 2(4): 497–501.
- Amorós-Jiménez R, Pineda A, Fereres A, Marcos-García MÁ, 2014. Feeding preferences of the aphidophagous hoverfly *Sphaerophoria rueppellii* affect the performance of its offspring. *BioControl*, 59(4): 427–435.
- Andorno AV, López SN, 2014. Biological control of *Myzus persicae* (Hemiptera: Aphididae) through banker plant system in protected crops. *Biological Control*, 78: 9–14.
- Andow DA, 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.*, 36: 561–586.
- Araj SE, Wratten S, Lister A, Buckley H, Ghabesh I, 2011. Searching behavior of an aphid parasitoid and its hyperparasitoid with and without floral nectar. *Biological Control*, 57: 79–84.
- Araj SE, Wratten SD, 2015. Comparing existing weeds and commonly used insectary plants as floral resources for a parasitoid. *Biological Control*, 81: 15–20.
- Arias-Estévez M, López PE, Martínez CE, Simal GJ, Mejuto JC, García RL, 2008. The mobility and degradation of pesticides in soils and the pollution of groundwater resources. *Agriculture, Ecosystems & Environment*, 123(4): 247–260.
- Badenes-Perez FR, Nault BA, Shelton AM, 2005. Manipulating the attractiveness and suitability of hosts for diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*, 98(3): 836–844.
- Bailey D, Schmidt-Entling MH, Eberhart P, Herrmann JD, Hofer G, Kormann U, Herzog F, 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology*, 47(5): 1003–1013.
- Baillod AB, Tschamtké T, Clough Y, Batáry P, 2017. Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of Applied Ecology*, 54(6): 1804–1813.
- Balmer O, Géneau CE, Belz E, Weishaupt B, Förderer G, Moos S, Ditenner N, Juric I, Luka H, 2014. Wildflower companion plants increase pest parasitism and yield in cabbage fields: Experimental demonstration and call for caution. *Biological Control*, 76: 19–27.
- Balzan MV, Bocci G, Moonen AC, 2016. Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. *BioControl*, 61(2): 141–154.
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z, 2009. Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics*, 40(1): 1–20.
- Basedow T, Hua L, Aggarwal N, 2006. The infestation of *Vicia faba* L. (Fabaceae) by *Aphis fabae* (Scop.) (Homoptera: Aphididae) under the influence of Lamiaceae (*Ocimum basilicum* L. and *Satureja hortensis* L.). *Journal of Pest Science*, 79(3), 149.
- Batary P, Matthiesen T, Tschamtké T, 2010. Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. *Biological Conservation*, 143(9): 2020–2027.
- Baudry J, Bunce RGH, Burel F, McCollin D, 2000. Hedgerows: an international perspective on their origin, function and management. *Journal of Environmental Management*, 60(1): 7–22.
- Bennewicz J, 2011. Aphidivorous hoverflies (Diptera: Syrphidae) at field boundaries and woodland edges in an agricultural landscape. *Polish Journal of Entomology/Polish Pismo Entomologiczne*, 80(1): 129–149.
- Berggren A, Birath B, Kindvall O, 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's Bush-Cricket (*Metrioptera roeseli*). *Conservation*

- Biology*, 16(6): 1562–1569.
- Berndt LA, Wratten SD, 2005. Effects of alyssum flowers on the longevity, fecundity, and sex ratio of the leafroller parasitoid *Dolichogenidea tasmanica*. *Biological Control*, 32(1): 65–69.
- Bianchi FJ, Booij CJH, Tschamtkke T, 2006. Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society. B-Biological Sciences*, 273(1595): 1715–1727.
- Bianchi FJJA, Van der Werf W, 2003. The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: a simulation study. *Environental Entomology*, 32(6): 1290–1304.
- Blitzer EJ, Dormann C, Holzschuh A, Klein AM, Rand T, Tschamtkke T, 2012. Functionally important spillover of organisms across the managed system-natural habitat interface-a review. *Agriculture, Ecosystems & Environment*, 146: 34–43.
- Bluthgen N, Klein AM, 2011. Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic Applied Ecology*, 12(4): 282–291.
- Burgio G, Ferrari R, Pozzati M, Boriani L, 2004. The role of ecological compensation areas on predator populations: An analysis on biodiversity and phenology of Coccinellidae (Coleoptera) on non-crop plants within hedgerows in Northern Italy. *Bulletion of Insectology*, 57(1): 1–10.
- Burn AJ, Coaker TH, Jepson PC, 1987. Integrated Pest Management. London: Academic Press. 27–68.
- Cai HJ, Li ZS, You MS, 2007. Impact of habitat diversification on arthropod communities: A study in the fields of Chinese cabbage, *Brassica chinensis*. *Insect Science*, 14(3): 241–249.
- Cai HJ, You MS, 2007. Effects of garlic-Chinese cabbage intercropping systems on the guilds of arthropod communities in vegetable fields. *Entomological Journal of East China*, 16(1): 1–7. [蔡鸿娇, 尤民生, 2007. 大蒜-小白菜间作套种对菜田节肢动物功能团的影响. 华东昆虫学报, 16(1): 1–7.]
- Cai YJ, Shen JW, Diao SX, Liu ZC, Zhang WQ, 2015. The effect of rice-vegetable rotation cultivation on density of the brown planthopper and spiders in the fields. *Journal of Environmental Entomology*, 37(3): 548–550. [蔡尤俊, 沈嘉伟, 刁石新, 刘志超, 张文庆, 2015. 稻菜轮作对稻田褐飞虱和蜘蛛数量的影响. 环境昆虫学报, 37(3): 548–550.]
- Cardarelli E, Bogliani G, 2014. Effects of grass management intensity on ground beetle assemblages in rice field banks. *Agriculture, Ecosystems & Environment*, 195: 120–126.
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, 2012. Biodiversity loss and its impact on humanity. *Nature*, 486: 59.
- Cardinale BJ, Harvey CT, Gross K, Ives AR, 2003. Biodiversity and biocontrol: Emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, 6: 857–865.
- Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C, 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, 14(9): 922–932.
- Chase JM, Bengtsson J, 2010. Increasing spatio-temporal scales: metacommunity ecology//Verhoef HA, Morin PJ (eds.). *Community Ecology*. Oxford: Oxford University Press. 57–68.
- Chen LL, Lin S, You MS, Chen SB, Liette V, Ye SC, 2011. Effects of cover crops on mite communities in tea plantations. *Biodiversity Science*, 19(3): 353–362. [陈李林, 林胜, 尤民生, 陈少波, Liette Vasseur, 叶树纯, 2011. 间作牧草对茶园螨类群落多样性的影响. 生物多样性, 19(3): 353–362.]
- Clough Y, Barkmann J, Juhrendt J, Kessler M, Wanger TC, Anshary A, Buchori D, Cicuzza D, Darras D, Dwi Putra D, Erasmi S, Pitopang R, Schmidt C, Schulze CH, Seidel D, Steffan-Dewenter I, Stenchly K, Vidal S, Weist M, Wielgoss AC, Tschamtkke T, 2011. Combining high biodiversity with high yields in tropical agroforests. *PNAS*, 108(20): 8311–8316.
- Clough Y, Holzschuh A, Gabriel D, Purtauf T, Kruess A, Steffan Dewenter I, Kleijn D, Tschamtkke T, 2007. Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology*, 44(4): 804–812.
- Clough Y, Kruess A, Kleijn D, Tschamtkke T, 2005. Spider diversity in cereal fields: Comparing factors at local, landscape and regional scales. *Journal of Biogeography*, 32(11): 2007–2014.
- Cock MJ, Van Lenteren JC, Brodeur J, Barratt BI, Bigler F, Bolckmans K, Cónsoli FL, Haas F, Mason PG, Parra JRP, 2010. Do new access and benefit sharing procedures under the convention on biological diversity threaten the future of biological control? *BioControl*, 55(2): 199–218.
- Cock MW, Murphy ST, Kairo MK, Thompson E, Murphy RJ, Francis AW, 2016. Trends in the classical biological control of insect pests by insects: An update of the BIOCAT database. *BioControl*, 61(4): 349–363.
- Collins K, Boatman N, Wilcox A, Holland J, 2003a. A 5-year comparison of overwintering polyphagous predator densities within a beetle bank and two conventional hedgebanks. *Annals of Applied Biology*, 143(1): 63–71.
- Collins K, Boatman N, Wilcox A, Holland J, 2003b. Effects of

- different grass treatments used to create overwintering habitat for predatory arthropods on arable farmland. *Agriculture, Ecosystems & Environment*, 96(1/3): 59–67.
- Concepción ED, Díaz M, Baquero RA, 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landscape Ecology*, 23(2): 135–148.
- Cook SK, Morris AJ, Henderson I, Jones NE, Bradbury A, 2007b. Experiment 3: Assessing the Integrated Effects of Crop and Margin Management. The SAFFIE Project Report. 524–635.
- Cook SM, Khan ZR, Pickett JA, 2007a. The use of push-pull strategies in integrated pest management. *Annual Review of Entomology*, 52: 375–400.
- Day WH, 1996. Evaluation of biological control of the tarnished plant bug (Hemiptera: Miridae) in Alfalfa by the introduced parasite *Peristenus digoneutis* (Hymenoptera: Braconidae). *Environmental Entomology*, 25(2): 512–518.
- Day WH, 2005. Changes in abundance of native and introduced parasites (Hymenoptera: Braconidae), and of the target and non-target plant bug species (Hemiptera: Miridae), during two classical biological control programs in alfalfa. *Biological Control*, 33(3): 368–374.
- Day WH, Hoelmer KA, 2012. Impact of the introduced parasitoid (Hymenoptera: Braconidae) on tarnished plant bug (Hemiptera: Miridae) infesting strawberries in northwestern New Jersey, USA. *Biocontrol Science and Technology*, 22(8): 975–979.
- De Clercq P, Bonte M, Van Speybroeck K, Bolckmans K, Deforce K, 2005. Development and reproduction of *Adalia bipunctata* (Coleoptera: Coccinellidae) on eggs of *Ephestia kuehniella* (Lepidoptera: Phycitidae) and pollen. *Pest Management Science*, 61(11): 1129–1132.
- Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF, 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, 83: 1443–1458.
- D'hulster M, Desender K, 1982. Ecological and faunal studies on Coleoptera in agricultural land. . Seasonal abundance and hibernation of Staphylinidae in the grassy edge of a pasture. *Pedobiologia*, 23(6): 403–414.
- Diekötter T, Billeter R, Crist TO, 2008. Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. *Basic and Applied Ecology*, 9(3): 298–307.
- Ding YK, 1993. Ecologically based pest management. *Acta Ecologica Sinica*, 13(2): 99–106. [丁岩钦, 1993. 论害虫种群的生态控制. 生态学报, 13(2): 99–106.]
- Dominik C, Seppelt R, Horgan FG, Settele J, Václavík T, 2018. Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. *Journal of Applied Ecology*, 55(5): 2461–2472.
- Duelli P, Obrist MK, 2003. Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic and Applied Ecology*, 4(2): 129–138.
- Eigenbrode SD, Birch ANE, Lindzey S, Meadow R, Snyder WE, 2016. A mechanistic framework to improve understanding and applications of push-pull systems in pest management. *Journal of Applied Ecology*, 53(1): 202–212.
- Elliott NC, Kieckhefer RW, Lee JH, French BW, 1999. Influence of within-field and landscape factors on aphid predator populations in wheat. *Landscape Ecology*, 14(3): 239–252.
- Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL, 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14(2): 101–112.
- Farrell JK, 1975. Effects of food plant species on the weight loss, survival, and fecundity of adult *Costelytra zealandica* (Coleoptera: Scarabaeidae). *New Zealand Journal of Agriculture Research*, 18(3): 303–305.
- Farrell JAK, Sweney WJ, 1974. Plant resistance to the grass grub *Costelytra zealandica* (Coleoptera: Scarabaeidae) . Resistance in Lotus and Lupinus. *New Zealand Journal of Agricultural Research*, 17(1): 69–72.
- Feeny P, 1976. Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, 10(1): 1–40.
- Fiedler AK, Landis DA, Wratten SD, 2008. Maximizing ecosystem services from conservation biological control: The role of habitat management. *Biological Control*, 45(2): 254–271.
- Finch S, Collier RH, 2010. Host-plant selection by insects—a theory based on arriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata*, 96: 91–102.
- Finke DL, Denno RF, 2004. Predator diversity dampens trophic cascades. *Nature*, 429(6990): 407.
- Flohre A, Fischer C, Aavik T, Bengtsson J, Berendse F, Bommarco R, Ceryngier P, Clement LW, Dennis C, Eggers S, Emmerson M, Geiger F, Guerrero I, Hawro V, Inchausti P, Liira J, Morales MB, Onate JJ, Pärt T, Weisser WW, Winqvist C, Thies C, Tschamtké T, 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications*, 21(5): 1772–1781.
- Fraser SEM, Dytham C, Mayhew PJ, 2007. Determinants of parasitoid abundance and diversity in woodland habitats. *Journal of Applied Ecology*, 44(2): 352–361.
- Fritch RA, Sheridan H, Finn JA, McCormack S, Oacute, Huallacháin

- D, 2017. Enhancing the diversity of breeding invertebrates within field margins of intensively managed grassland: Effects of alternative management practices. *Ecology and Evolution*, 7(22): 9763–9774.
- Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG, 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, 13(7): 858–869.
- Gao ZZ, Wu WJ, Cui ZX, 2004. The effect of intercrop on the densities of *Phyllotreta striolata* (L.). *Chinese Agriculture Science Bulletin*, 20(5): 214–216. [高泽正, 吴伟坚, 崔志新, 2004. 间种对黄曲条跳甲种群数量的影响. 中国农学通报, 20(5): 214–216.]
- Géneau CE, Wäckers FL, Luka H, Daniel C, Balmer O, 2012. Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic and Applied Ecology*, 13(1): 85–93.
- Gordon GUSO, Wratten SD, Jonsson M, Simpson M, Hale R, 2013. ‘Attract and reward’: Combining a herbivore-induced plant volatile with floral resource supplementation – multi-trophic level effects. *Biological Control*, 64(2): 106–115.
- Grand J, Cushman SA, 2003. A multi-scale analysis of species-environment relationships: Breeding birds in a pitch pine–scrub oak (*Pinus rigida*–*Quercus ilicifolia*) community. *Biological Conservation*, 112(3): 307–317.
- Griffiths GJK, Winder L, Holland JM, Thomas CFG, Williams E, 2007. The representation and functional composition of carabid and staphylinid beetles in different field boundary types at a farm-scale. *Biological Conservation*, 135(1): 145–152.
- Gurr GM, 2012. An introduction to ecological engineering for pest management// Zhu ZR (eds.). *Ecological Engineering for Pest Management in Rice*. China: Agriculture Press. 9–20.
- Gurr GM, Wratten SD, Snyder WE, 2012. *Biodiversity and Insect Pests: Key Issues for Sustainable Management*. Chichester: John Wiley & Sons. 214–219.
- Gurr GM, Wratten SD, Landis DA, You M, 2017. Habitat management to suppress pest populations: progress and prospects. *Annual Review of Entomology*, 62: 91–109.
- Gurr GM, Wratten SD, Tylianakis J, Kean JM, Keller M, 2003. Providing plant foods for insect natural enemies in farming systems: balancing practicalities and theory// Wäckers FL, Rijn PCJ, Bruin J (eds.). *Plant-Derived Food and Plant-Carnivore Mutualism*. UK: Cambridge University Press, Cambridge. 107–116.
- Haddad NM, Crutsinger GM, Kevin G, John H, David T, 2011. Plant diversity and the stability of foodwebs. *Ecology Letters*, 14(1): 42–46.
- Han P, Niu CY, Desneux N, 2014. Identification of top-down forces regulating cotton aphid population growth in transgenic Bt cotton in central China. *PLoS ONE*, 9: e102980.
- Happe AK, Alins G, Blüthgen N, Boreux V, Bosch J, Garcia D, Hambäck P, Klein A, Martínez Sastre R, Miñarro M, Müller AK, Porcel M, Rodrigo A, Roquer-Beni L, Samnegård U, Tasin M, Mody K, 2019. Predatory arthropods in apple orchards across Europe: Responses to agricultural management, adjacent habitat, landscape composition and country. *Agriculture, Ecosystems & Environment*, 273: 141–150.
- Hatt S, Uytendroek R, Lopes T, Mouchon P, Osawa N, Piqueray J, Monty A, Francis F, 2019. Identification of flower functional traits affecting abundance of generalist predators in perennial multiple species wildflower strips. *Arthropod-Plant Interactions*, 13(1): 127–137.
- Hendrickx F, Maelfait J, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R, Bailey D, Bukacek R, Burel F, Diekötter T, Dirksen J, Herzog F, Liira J, Roubalova M, Vandomme V, Bugster R, 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, 44(2): 340–351.
- Himmelstein J, Ares A, Gallagher D, Myers J, 2016. A meta-analysis of intercropping in Africa: Impacts on crop yield, farmer income, and integrated pest management effects. *International Journal of Agricultural Sustainability*, 15(1): 1–12.
- Hof AR, Bright PW, 2010. The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields. *Agriculture, Ecosystems & Environment*, 139(1/2): 280–283.
- Holland JM, Begbie M, Birkett T, Southway S, Thomas SR, Alexander CJ, Thomas CG, 2004. The spatial dynamics and movement of *Pterostichus melanarius* and *P. madidus* (Carabidae) between and within arable fields in the UK. *International Journal of Ecology and Environmental Sciences*, 30: 35–50.
- Holland JM, Bianchi FJ, Entling MH, Moonen AC, Smith BM, Jeanneret P, 2016. Structure, function and management of semi-natural habitats for conservation biological control: A review of European studies. *Pest Management Science*, 72(9): 1638–1651.
- Holland JM, Oaten H, Moreby S, Birkett TC, Simper J, Southway S, Smith B, 2012. Agri-environment scheme enhancing ecosystem services: A demonstration of improved biological control in cereal crops. *Agriculture, Ecosystems & Environment*, 155: 147–152.
- Holt RD, 2003. On the evolutionary ecology of species’ ranges. *Evolutionary Ecology Research*, 5(2): 159–178.
- Holzschuh A, Steffan-Dewenter I, Kleijn D, Tschamtker T, 2007. Diversity of flower-visiting bees in cereal fields: Effects of farming system, landscape composition and regional context.

- Journal of Applied Ecology*, 44(1): 41–49.
- Holzschuh A, Steffan-Dewenter I, Tschamtkke T, 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, 117(3): 354–361.
- Holzschuh A, Steffan-Dewenter I, Tschamtkke T, 2009. Grass strip corridors in agricultural landscapes enhance nest-site colonization by solitary wasps. *Ecological Applications*, 19(1): 123–132.
- Holzschuh A, Steffan-Dewenter I, Tschamtkke T, 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, 79(2): 491–500.
- Huang JH, Chen HF, Wang LS, Liu AF, Shen HX, 2016. Advances in controlling thrips using predatory mites. *Chinese Journal of Biological Control*, (1): 119–124. [黄建华, 陈洪凡, 王丽思, 柳岸峰, 沈华喜, 2016. 应用捕食螨防治蓟马研究进展. 中国生物防治学报, (1): 119–124.]
- Ives AR, Klug JL, Gross K, 2000. Stability and species richness in complex communities. *Ecology Letters*, 3(5): 399–411.
- James DG, 2005. Further field evaluation of synthetic herbivore-induced plant volatiles as attractants for beneficial insects. *Journal of Chemical Ecology*, 31(3): 481.
- James DG, Grasswitz TR, 2005. Synthetic herbivore-induced plant volatiles increase field captures of parasitic wasps. *BioControl*, 50(6): 871–880.
- Jha S, Dick CW, 2010. Native bees mediate long-distance pollen dispersal in a shade coffee landscape mosaic. *PNAS*, 107: 13760–13764.
- Johanowicz DL, Mitchell ER, 2000. Effects of sweet alyssum flowers on the longevity of the parasitoid wasps *Cotesia marginiventris* (Hymenoptera: Braconidae) and *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Florida Entomologist*, 83(1): 41.
- Jones GA, Gillett JL, 2005. Intercropping with sunflowers to attract beneficial insects in organic agriculture. *Florida Entomologist*, 88(1): 91–97.
- Jonsson M, Wratten SD, Landis DA, Gurr GM, 2008. Recent advances in conservation biological control of arthropods by arthropods. *Biological Control*, 45(2): 172–175.
- Kahuthia-Gathu R, 2007. The importance of wild crucifers for diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) and its parasitoids in Kenya. Doctoral dissertation. Hannover: Gottfried Wilhelm Leibniz Universität.
- Kareiva P, Wennergren U, 1995. Connecting landscape patterns to ecosystem and population processes. *Nature*, 373(6512): 299–302.
- Ke DX, He HJ, Huang SM, Xiong YQ, 1995. Functions of field rotation of cotton and paddy rice in controlling *Tetranychus cinnabarinus* (Boisduval). *Plant Protection*, 21(5): 2–4. [柯道秀, 何洪俊, 黄明松, 熊映清, 1995. 稻棉轮作对棉红蜘蛛控制作用的研究. 植物保护, 21(5): 2–4.]
- Kessler M, Abrahamczyk S, Bos M, Buchori D, Putra DD, Gradstein SR, Hohn P, Kluge J, Orend F, Pitopang R, Shahabuddin S, Schulze CH, Sporn SG, Steffan-Dewenter I, Tjitrosoedirdjo SS, Tschamtkke T, 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. *Ecological Applications*, 19(8): 2142–2156.
- Khan ZR, Ampomnyarko K, Chiliswa P, Hassanali A, Kimani S, Lwande W, Overholt WA, Overholt WA, Pickett JA, Smart LE, 1997. Intercropping increases parasitism of pests. *Nature*, 388(6643): 631–632.
- Khan ZR, James DG, Midega CAO, Pickett JA, 2008. Chemical ecology and conservation biological control. *Biological Control*, 45(2): 210–224.
- Khan ZR, Midega CAO, Bruce TJA, Hooper AM, Pickett JA, 2010. Exploiting phytochemicals for developing a 'push-pull' crop protection strategy for cereal farmers in Africa. *Journal of Experimental Botany*, 61(15): 4185.
- Khan ZR, Midega CAO, Hooper A, Pickett J, 2016. Push-Pull: Chemical ecology-based integrated pest management technology. *Journal of Chemical Ecology*, 42: 689–697.
- Khan ZR, Pickett J, Den Berg JV, Wadhams LJ, Woodcock CM, 2000. Exploiting chemical ecology and species diversity: Stem borer and striga control for maize and sorghum in Africa. *Pest Management Science*, 56(11): 957–962.
- Kleijn D, Baquero RA, Clough Y, Díaz M, Esteban JD, Fernández F, Gabriel D, Herzog F, Holzschuh A, Jöhl R, Knop E, Krüess A, Marshall EP, Dewenter ID, Tschamtkke T, Verhulst J, West TM, Yela JL, 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, 9(3): 243–254.
- Klinger K, 1987. Effects of margin-strips along a winter wheat field on predatory arthropods and the infestation by cereal aphids. *Journal of Applied Entomology*, 104(1): 47–58.
- Lagerlöf J, Wallin H, 1993. The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. *Agriculture Ecosystems & Environment*, 43(2): 141–154.
- Lai RQ, 2011. Effects of garlic intercropping on bio-communities in tobacco fields. Doctoral dissertation Fuzhou: Fujian Agriculture and Forestry University. [赖荣泉, 2011. 套种大蒜对烟田生物群落的影响. 博士学位论文. 福州: 福建农林大学.]
- Landis DA, Wratten SD, Gurr GM, 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45: 175–201.

- Leather SR, 1993. Overwintering in six arable aphid pests: A review with particular relevance to pest management. *Journal of Applied Entomology*, 116(1/5): 217–233.
- Lee JC, Heimpel GE, 2005. Impact of flowering buckwheat on Lepidopteran cabbage pests and their parasitoids at two spatial scales. *Biological Control*, 34(3): 290–301.
- Letourneau DK, Armbrrecht I, Rovera BS, Lerma JM, Carmona EJ, Daza MC, Escobar S, Galindo V, Gutiérrez C, López SD, Mejía JL, Rangel AMA, Rangel JH, Rivera L, Saavedra CA, Torres AM, Trujillo AR, 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, 21(1): 9–21.
- Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR, 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 40(1): 573–592.
- Li ZY, Altieri MA, Zhu YY, 2009a. Biodiversity and Integrated Pest Management. Beijing: Science Press. 3–7. [李正跃, Altieri MA, 朱有勇, 2009a. 生物多样性与害虫综合治理. 北京: 科学出版社. 3–7.]
- Liere H, Kim TN, Werling BP, Meehan TD, Landis DA, Gratton C, 2015. Trophic cascades in agricultural landscapes: Indirect effects of landscape composition on crop yield. *Ecological Applications*, 25(3): 652–661.
- Lin KJ, Wu KM, Zhang YJ, Guo YY, 2006. Evaluation of piemarker abutilon theophrasti medic as a trap plant in the integrated management of *Bemisia tabaci* (biotype b) in cotton and soybean crops. *Scientia Agriculture Sinica*, 39(7): 1379–1386. [林克剑, 吴孔明, 张永军, 郭予元, 2006. 利用诱集寄主苘麻防治 b 型烟粉虱的研究. 中国农业科学, 39(7): 1379–1386.]
- Litsinger JA, Moody K, 1976. Integrated pest management in multiple cropping systems//Stelly M (ed.). Multiple Cropping: Madison, Wisconsin: ASA Special Publication. 293–316.
- Liu YF, Zhang GR, Gu DX, 2000. The influence of habitat and vegetation diversity on arthropod community and its mechanism in farmland ecosystem. *Journal of Xiangtan Normal University*, (6): 74–78. [刘雨芳, 张古忍, 古德祥, 2000. 农田生态系统中生境与植被多样性对节肢动物群落的影响及其作用机制探讨. 湘潭师范学院学报(社会科学版), (6): 74–78.]
- Liu ZR, Gao YL, Luo J, Lai FX, Li YH, Fu Q, Peng YF, 2011. Evaluating the non-rice host plant species of *Sesamia inferens* (Lepidoptera: Noctuidae) as natural refuges: Resistance management of Bt rice. *Environmental Entomology*, 40(3): 749.
- Lopes T, Hatt S, Xu Q, Chen J, Liu Y, Francis F, 2016. Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control: A review. *Pest Management Science*, 72(12): 2193–2202.
- Loreau M, Mouquet N, Gonzalez A, 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *PNAS*, 100(22): 12765–12770.
- Losey JE, Denno RF, 1998. Positive predator-predator interactions: Enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79(6): 2143–2152.
- Lu YH, Zhao ZH, Cai XM, Cui L, Zhang HN, Xiao HJ, Li ZY, Zhang LS, Zeng J, 2017. Progresses on integrated pest management (IPM) of agricultural insect pests in China. *Chinese Journal of Applied Entomology*, 54(3): 349–363. [陆宴辉, 赵紫华, 蔡晓明, 崔丽, 张浩男, 肖海军, 李振宇, 张礼生, 曾娟, 2017. 我国农业害虫综合防治研究进展. 应用昆虫学报, 53(3): 349–363.]
- Macfadyen S, Gibson R, Symondson WO, Memmott J, 2011. Landscape structure influences modularity patterns in farm food webs: Consequences for pest control. *Ecological Applications*, 21(2): 516–524.
- Mallinger RE, Hogg DB, Gratton C, 2011. Methyl salicylate attracts natural enemies and reduces populations of soybean aphids (Hemiptera: Aphididae) in soybean agroecosystems. *Journal of Economic Entomology*, 104(1): 115–124.
- Martin EA, Reineking B, Seo B, Steffan-Dewenter I, 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. *PNAS*, 110(14): 5534–5539.
- Martin EA, Seo B, Park CR, Reineking B, Steffan-Dewenter I, 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, 26(2): 448–462.
- Maudsley MJ, 2000. A review of the ecology and conservation of hedgerow invertebrates in Britain. *Journal of Environmental Management*, 60(1): 65–76.
- Mcneely JA, Miller KR, Reid WV, Mittermeier RA, Werner TB, 1990. Conserving the world's biological diversity. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland; World Resources Institute, Conservation International, World Wildlife Fund-US and the World Bank, Washington, DC. 193.
- Meek B, Loxton D, Sparks T, Pywell R, Pickett H, Nowakowski M, 2002. The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, 106(2): 259–271.
- Mohler CL, Jonson SE, 2009. Crop rotation on organic farms: A planning manual. USA: Natural Resource, Agriculture, and Engineering Service (NRAES). 41–43.
- Morandin LA, Long RF, Kremen C, 2014. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive

- agricultural landscape. *Agriculture, Ecosystems & Environment*, 189: 164–170.
- Motzke I, Klein AM, Saleh S, Wanger TC, Tschamtk T, 2016. Habitat management on multiple spatial scales can enhance bee pollination and crop yield in tropical homegardens. *Agriculture, Ecosystems & Environment*, 223: 144–151.
- Mouquet N, Hoopes MF, Amarasekare P, 2005. The world is patchy and heterogeneous. Trade-off and source-sink dynamics in competitive metacommunities// Holyoak M, Leibold MA, Holt RD (eds.). *Metacommunities: Spatial Dynamics and Ecological Communities*. Chicago and London: The University of Chicago Press. 237–262.
- Mouquet N, Mulder GE, Jansen VA, Loreau M, 2001. *The Properties of Competitive Communities with Coupled Local and Regional Dynamics*. Oxford, UK: Oxford University Press. 311.
- Nafziger Jr TD, Fadamiro HY, 2011. Suitability of some farmscaping plants as nectar sources for the parasitoid wasp, *Microplitis croceipes* (Hymenoptera: Braconidae): Effects on longevity and body nutrients. *Biological Control*, 56(3): 225–229.
- Nicholls CI, Parrella MP, Altieri MA, 2001. The effect of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. *Landscape Ecology*, 16(2): 133–146.
- O'Rourke ME, Liebman M, Rice ME, 2014. Ground beetle (Coleoptera: Carabidae) assemblages in conventional and diversified crop rotation systems. *Environmental Entomology*, 37(1): 121–130.
- Pandey S, Rahman A, Gurr GM, 2018. Australian native flowering plants enhance the longevity of three parasitoids of brassica pests. *Entomologia Experimentalis Applicata*, 166(4): 265–276.
- Parolin P, Bresch C, Desneux N, Brun R, Bout A, Boll R, Poncet C, 2012. Secondary plants used in biological control: A review. *International Journal of Pest Management*, 58(2): 91–100.
- Peng L, He WY, Xia XF, Xie M, Ke FS, You SJ, Huang YP, You MS, 2015. Prospects for the management of insect pests in the genomic era. *Chinese Journal of Applied Entomology*, 52(1): 1–22. [彭露, 何玮毅, 夏晓峰, 谢苗, 柯富士, 尤士骏, 黄宇萍, 尤民生, 2015. 基因组学时代害虫治理的研究进展及前景. *应用昆虫学报*, 52(1): 1–22.]
- Perez FR, Shelton AM, Nault BA, 2004. Evaluating trap crops for diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Economic Entomology*, 97(4): 1365–1372.
- Perovic DJ, Gurr GM, Raman A, Nicol HI, 2010. Effect of landscape composition and arrangement on biological control agents in a simplified agricultural system: a cost-distance approach. *Biological Control*, 52(3): 263–270.
- Pimentel D, Burgess M, 2014. *Integrated Pest Management*. Dordrecht: Springer. 47–71.
- Poveda K, Gómez MI, Martínez E, 2008. Diversification practices: Their effect on pest regulation and production. *Revista Colombiana de Entomología*, 34(2): 131–144.
- Pumariño L, Alomar O, 2012. The role of omnivory in the conservation of predators: *Orius majusculus* (Heteroptera: Anthocoridae) on sweet alyssum. *Biological Control*, 62(1): 24–28.
- Pywell RF, James KL, Herbert I, Meek WR, Carvell C, Bell D, Sparks TH, 2005. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biological Conservation*, 123(1): 79–90.
- Pywell RF, James KL, Herbert I, Meek WR, Carvell C, Bell D, Sparks TH, 2005. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biological Conservation*, 123(1): 79–90.
- Rand TA, Tylianakis JM, Tschamtk T, 2006. Spillover edge effects: The dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters*, 9(5): 603–614.
- Robertson LN, 1993. Population dynamics of false wireworms (*Gonocephalum macleayi*, *Pterohelaus alternatus*, *P. darlingensis*) and development of an integrated pest management program in central Queensland field crops: A review. *Australian Journal of Experimental Agriculture*, 33(7): 953–962.
- Root RB, 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, 43(1): 95–124.
- Root RB, 1975. Some consequences of ecosystem texture// Levin SA, (ed.). *Ecosystem Analysis and Prediction*: SIAM, Philadelphia. 83–97.
- Roschewitz I, Gabriel D, Tschamtk T, Thies C, 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology*, 42(5): 873–882.
- Rosenheim JA, 1998. Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology*, 43(1): 421–447.
- Rusch A, Bommarco R, Ekbom B, 2017. Conservation biological control in agricultural landscapes. *Advances in Botanical Research*, 81: 333–360.
- Rusch A, Valantin-Morison M, Roger-Estrade J, Sarthou JP, 2012. Using landscape indicators to predict high pest infestations and successful natural pest control at the regional scale. *Landscape and Urban Planning*, 105(1): 62–73.
- Rusch A, Valantin-Morison M, Sarthou JP, Roger-Estrade J, 2011. Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landscape Ecology*, 26(4): 873–882.

- 473–486.
- Sarthou JP, Badoz A, Vaissiere B, Chevallier A, Rusch A, 2014. Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. *Agriculture, Ecosystems & Environment*, 194: 17–28.
- Schader C, Zaller JG, Köpke U, 2005. Cotton-basil intercropping: effects on pests, yields and economical parameters in an organic field in Fayoum, Egypt. *Biological Agriculture & Horticulture*, 23(1): 59–72.
- Scherber C, Eisenhauer N, Weisser WW, Bernhard S, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E, Beßler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein AM, Koller R, König S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Müller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharnkte T, 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468(7323): 553–556.
- Schmidt MH, Lauer A, Purtauf T, Thies C, Schaefer M, Tscharnkte T, 2003. Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society B-Biological Sciences*, 270(1527): 1905–1909.
- Schmidt MH, Thies C, Nentwig W, Tscharnkte T, 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, 35(1): 157–166.
- Schmidt MH, Thies C, Tscharnkte T, 2004. Landscape context of arthropod biological control// Gurr GM, Wratten SD, Altieri MA (eds.). *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. Australia: CSIRO Publishing. 55–63.
- Schüepp C, Uzman D, Herzog F, Entling MH, 2014. Habitat isolation affects plant-herbivore-enemy interactions on cherry trees. *Biological Control*, 71:56–64.
- Sigsgaard L, Kollmann J, 2007. Beneficial effects of hedgerow plants for insect predators in adjacent orchards-the value of pollen and nectar to *Anthocoris nemorum* (L.). *IOBC/ WPRS Bulletin*, 30: 9.
- Silveira LC, Filho EB, Pierre LS, Peres FS, Louzada J, 2009. Marigold (*Tagetes erecta* L.) as an attractive crop to natural enemies in onion fields. *Scientia Agricola*, 66(6): 780–787.
- Simpson M, Gurr GM, Simmons AT, Wratten SD, James DG, Leeson G, Nicol HI, Orre-Gordon GUS, 2011a. Attract and reward: Combining chemical ecology and habitat manipulation to enhance biological control in field crops. *Journal of Applied Ecology*, 48(3): 580–590.
- Simpson M, Gurr GM, Simmons AT, Wratten SD, James DG, Leeson G, Nicol HI, Orre GUS, 2011b. Field evaluation of the 'attract and reward' biological control approach in vineyards. *Annals of Applied Biology*, 159(1): 69–78.
- Sivakoff FS, Rosenheim JA, Dutilleul P, Carrière Y, 2013. Influence of the surrounding landscape on crop colonization by a polyphagous insect pest. *Entomologia Experimentalis et Applicata*, 149(1): 11–21.
- Smith HG, Danhardt J, Lindstrom A, Rundlof M, 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia*, 162(4): 1071–1079.
- Snyder WE, Ives AR, 2003. Interactions between specialist and generalist natural enemies: Parasitoids, predators, and pea aphid biocontrol. *Ecology*, 84(1): 91–107.
- Song BZ, Wu HY, Kong Y, Zhang J, Du YL, Hu JH, Yao YC, 2010. Effects of intercropping with aromatic plants on the diversity and structure of an arthropod community in a pear orchard. *BioControl*, 55(6): 741–751.
- Soti V, Thiaw I, Debaly ZM, Sow A, Diaw M, Fofana S, Diakhate M, Thiaw C, Brevault T, 2019. Effect of landscape diversity and crop management on the control of the millet head miner, *Heliocheilus albipunctella* (Lepidoptera: Noctuidae) by natural enemies. *Biological Control*, 129: 115–122.
- Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharnkte T, 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83(5): 1421–1432.
- Straub CS, Finke DL, Snyder WE, 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biology Control*, 45(2): 225–237.
- Thies C, Haenke S, Scherber C, Bengtsson J, Bommarco R, Clement LW, Tscharnkte T, 2011. The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecological Applications*, 21(6): 2187–2196.
- Thies C, Steffan IT, 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, 101(1): 18–25.
- Thies C, Tscharnkte T, 1999. Landscape structure and biological control in agroecosystems. *Science*, 285(5429): 893–895.
- Thomas CFG, Parkinson L, Marshall EJP, 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia*, 116(1): 103–112.
- Thomas CG, Marshall EP, 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems & Environment*, 72(2): 131–144.
- Tian JC, Wang GR, Zheng XS, Lu SX, 2018. The effect of sesame flowers on the fecundity and dispersal ability of *Trichogramma*

- japonicum. *Chinese Journal of Biological Control*, 34(6): 4–9.
[田俊策, 王国荣, 郑许松, 吕仲贤, 2018. 芝麻花对稻螟赤眼蜂寄生和扩散能力的影响. *中国生物防治学报*, 34(6): 4–9.]
- Tscharntke T, Bommarco R, Clough Y, Clough Y, Crist TO, Kleijn D, Rand TA, Tylianakis JM, van Nouhuys S, Vidal S, 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, 43: 294–309 (reprint in *Biological Control*, 45(2): 238–253).
- Tscharntke T, Clough Y, Wanger TC, Jackson L, Motzke I, Perfecto I, Vandermeer J, Whitbread A, 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151(1): 53–59.
- Tscharntke T, Karp DS, Chaplin-Kramer R, Batáry P, De Clerck F, Gratton C, Hunt L, Ives A, Jonsson M, Larsen A, Martin EA, Martínez-Salinas A, Meehan TD, O'Rourke M, Poveda K, Rosenheim JA, Rusch A, Schellhorn N, Wanger TC, Wratten S, Zhang W, 2016. When natural habitat fails to enhance biological pest control-five hypotheses. *Biological Conservation*, 204: 449–458.
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C, 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters*, 8(8): 857–874.
- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C, 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, 12(2): 354–363.
- Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Dewenter IS, Thie C, van der Putten WH, Westphal C, 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological Reviews*, 87(3): 661–685.
- Tschumi M, Albrecht M, Collatz J, Dubsy V, Entling MH, Najar-Rodriguez AJ, Jacot K, 2016. Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *Journal of Applied Ecology*, 53(4): 1169–1176.
- Tylianakis J, Veddeler D, Lozada T, Lopez RM, Benítez P, Klein AM, Koning GHJ, Olschewski R, Veldkamp E, Navarrete H, Onore G, Tscharntke T, 2004. Biodiversity of land-use systems in coastal Ecuador and bioindication using trap-nesting bees, wasps, and their natural enemies. *Lyonia*, 6(2): 7–15.
- Uvah I, Coaker TH, 1984. Effect of mixed cropping on some insect pests of carrots and onions. *Entomologia Experimentalis et Applicata*, 36(2): 159–167.
- Van Alebeek FAN, Kamstra JH, van Kruistum G, Visser AJ, 2006. Improving natural pest suppression in arable farming: Field margins and the importance of ground dwelling predators. *IOBC/WPRS Bulletin*, 29(6): 137–140.
- Van Lenteren JC, 2012. The state of commercial augmentative biological control: Plenty of natural enemies, but a frustrating lack of uptake. *BioControl*, 57(1): 1–20.
- Van Lenteren JC, Bueno VHP, 2003. Augmentative biological control of arthropods in Latin America. *BioControl*, 48(2): 123–139.
- Van Rijn PCJ, 2012. The suitability of field margin flowers as food source for *Chrysoperla lacewings*. *IOBC/WPRS Bulletin*, 75: 213–216.
- Van Rijn PCJ, Kooijman J, Wäckers FL, 2013. The contribution of floral resources and honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). *Biological Control*, 67(1): 32–38.
- Wang ED, Xu XN, Wu SY, 2010. Control effects of *Amblyseius barkeri* on *Frankliniella occidentalis* on the eggplants and their natural enemy *Orius sauteri* in the greenhouse. *Plant Protection*, 36(5): 101–104. [王恩东, 徐学农, 吴圣勇, 2010. 释放巴氏钝绥螨对温室大棚茄子上西花蓟马及东亚小花蝽数量的影响. *植物保护*, 36(5): 101–104.]
- Wang W, Liu Y, Chen J, Ji X, Zhou H, Wang G, 2009. Impact of intercropping aphid-resistant wheat cultivars with oilseed rape on wheat aphid (*Sitobion avenae*) and its natural enemies. *Acta Ecologica Sinica*, 29(3): 186–191.
- Wasserman TN, Cushman SA, Schwartz MK, Wallin DO, 2010. Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology*, 25(10): 1601–1612.
- White AJ, Wratten SD, Berry NA, Weigmann U, 1995. Habitat manipulation to enhance biological control of *Brassica* pests by hover flies (Diptera: Syrphidae). *Journal of Economic Entomology*, 88(5): 1171–1176.
- Wilby A, Thomas MB, 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters*, 5(3): 353–360.
- Wilby A, Villareal SC, Lan LP, Heong KL, Thomas MB, 2005. Functional benefits of predator species diversity depend on prey identity. *Ecological Entomology*, 30(5): 497–501.
- Wilson LJ, Whitehouse ME, Herron GA, 2018. The management of insect pests in Australian cotton: an evolving story. *Annual Review of Entomology*, 63: 215–237.
- Winfrey R, Kremen C, 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B-Biological Sciences*, 276: 229–237.

- Winfree R, Williams NM, Dushoff J, Kremen C, 2007. Wild bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10(11): 1105–1113.
- Woltz JM, Isaacs R, Landis DA, 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 152: 40–49.
- Wood SA, Karp DS, Fabrice DC, Claire K, Shahid N, Palm CA, 2015. Functional traits in agriculture: Agrobiodiversity and ecosystem services. *Trends in Ecology & Evolution*, 30(9): 531–539.
- Xie GH, Cui HD, Dong Y, Wang XQ, Li XF, Deng RK, Wang Y, Xie Y, 2016. Crop rotation and intercropping with marigold are effective for root-knot nematode (*Meloidogyne* sp.) control in angelica (*Angelica sinensis*) cultivation. *Canadian Journal of Plant Science*, 97(1): 26–31.
- Xu Q, Hatt S, Lopes T, Zhang Y, Bodson B, Chen J, Francis F, 2018. A push-pull strategy to control aphids combines intercropping with semiochemical releases. *Journal of Pest Science*, 91(1): 93–103.
- Yang L, Xu L, Liu B, Lu YH, 2016. Effects of landscape pattern on the occurrence of ladybeetles in wheat fields in northern China. *Chinese Journal of Applied Entomology*, 53(3): 612–620. [杨龙, 徐磊, 刘冰, 陆宴辉, 2016. 农田景观格局对华北地区麦田早期瓢虫种群发生的影响. *应用昆虫学报*, 53(3): 612–620.]
- You MS, Hou YM, Liu YF, Yang G, Li ZS, Cai HJ, 2004a. Non-crop habitat manipulation and integrated pest management in agroecosystems. *Acta Entomologica Sinica*, 47(2): 260–268. [尤民生, 侯有明, 刘雨芳, 杨广, 李志胜, 蔡鸿娇, 2004a. 农田非作物生境调控与害虫综合治理. *昆虫学报*, 47(2): 260–268.]
- You MS, Liu YF, Hou YM, 2004b. Biodiversity and integrated pest management in agroecosystems. *Acta Ecologica Sinica*, 24(1): 117–122. [尤民生, 刘雨芳, 侯有明, 2004b. 农田生物多样性与害虫综合治理. *生态学报*, 24(1): 117–122.]
- Yu DY, Zhang YX, Tang JY, Ji J, 2008. The application of predatory mites in biological control of agro-forest spider mites in China. *Chinese Bulletin of Entomology*, 45(4): 537–541. [余德亿, 张艳璇, 唐建阳, 季洁, 2008. 捕食螨在我国农林害螨生物防治中的应用. *昆虫知识*, 45(4): 537–541.]
- Zhang X, Wang YH, Liu YH, Dai PP, Dong J, Yu ZR, 2015. Approaches biological control of pests through landscape regulation: theory and practice. *Journal of Ecology and Rural Environment*, 31(5): 617–624. [张鑫, 王艳辉, 刘云慧, 戴飘飘, 董杰, 宇振荣, 2015. 害虫生物防治的景观调节途径: 原理与方法. *生态与农村环境学报*, 31(5): 617–624.]
- Zhao JX, 2006. Study on biological control of red turpentine beetle *Dendroctonus valens* (Coleoptera: Scolytidae) in China. Doctoral dissertation. Beijing: Chinese Academy of Forestry Sciences. [赵建兴, 2006. 红脂大小蠹生物防治研究. 博士学位论文. 北京: 中国林业科学研究院.]
- Zhao Z, Reddy GV, 2019. Semi-natural habitats mediate influence of inter-annual landscape variation on cereal aphid-parasitic wasp system in an agricultural landscape. *Biological Control*, 128: 17–23.
- Zhao ZH, Shi Y, He DH, Hang J, Zhao YS, Wang Y, 2010. Population dynamics of wheat aphids in different agricultural landscapes. *Acta Ecologica Sinica*, 30(23): 6380–6388. [赵紫华, 石云, 贺达汉, 杭佳, 赵映书, 王颖, 2010. 不同农业景观结构对麦蚜种群动态的影响. *生态学报*, 30(23): 6380–6388.]
- Zhao ZH, Wang Y, He HD, Guan XQ, Xin M, 2012. Effects of landscape structure and key landscape factors on aphids-parasitoid hyper parasitoids populations in wheat fields. *Acta Ecologica Sinica*, 32(2): 472–482. [赵紫华, 王颖, 贺达汉, 关晓庆, 辛明, 2012. 麦蚜及寄生蜂对农业景观格局的响应及关键景观因子. *生态学报*, 32(2): 472–482.]
- Zheng YK, You MS, 2009. Biological diversity in support of ecologically-based pest management at landscape level. *Acta Ecologica Sinica*, 29(3): 1508–1518. [郑云开, 尤民生, 2009. 农业景观多样性与害虫生态控制. *生态学报*, 29(3): 1508–1518.]
- Zhu P, Lu Z, Heong K, Chen G, Zheng X, Xu H, Yang Y, Nicol HI, Gurr GM, 2014. Selection of nectar plants for use in ecological engineering to promote biological control of rice pests by the predatory bug, *Cyrtorhinus lividipennis*, (Heteroptera: Miridae). *PLoS ONE*, 9(9): e108669.
- Zhu P, Wang G, Zheng X, Tian J, Lu Z, Kong LH, Xu H, Chen G, Yang Y, Gurr GM, 2015. Selective enhancement of parasitoids of rice Lepidoptera pests by sesame (*Sesamum indicum*) flowers. *BioControl*, 60(2): 157–167.
- Zhu P, Zheng X, Zhang F, Xu H, Yang Y, Chen G, Lu Z, Johnson AC, Gurr GM, 2018. Quantifying the respective and additive effects of nectar plant crop borders and withholding insecticides on biological control of pests in subtropical rice. *Journal of Pest Science*, 91(2): 575–584.