

传粉动物多样性的保护与农业景观传粉服务的提升

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摘要: 传粉动物为许多植物尤其是作物提供了重要的传粉服务, 在保障全球粮食安全和人类福祉、缓冲气候变化对作物产量的影响等方面都发挥着重要的作用。然而来自全球土地利用变化、化学农药使用、外来物种入侵及气候变化等的威胁, 导致传粉动物的多样性下降并造成了依赖动物传粉的作物产量和品质的下降。针对这一情况, 作者提出了农业景观传粉动物多样性保护和利用的3种主要途径: (1)改善生产管理, 例如减少化学农药的使用、适当当地采取有机种植; (2)促进景观多样性, 包括创建适宜野生传粉者的半自然生境、保护高价值的自然生境、作物多样化、合理配置资源和生境的空间分布; (3)加强对本土传粉动物的保护和开发利用。文章最后提出, 为进一步提升传粉服务, 还需加强对传粉者的生物学特征、传粉服务的需求与供给现状、影响传粉动物多样性和传粉服务的农作措施和景观因素等方面的研究。

关键词: 生物多样性, 生态服务, 野生传粉者, 景观管理

Conserving pollinator diversity and improving pollination services in agricultural landscapes

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Abstract: Pollinators provide the vital process of pollination to plants. Maintaining diverse pollinators in ecosystems is essential to global food security, human welfare, and to buffer the negative ecological impacts of climate change. Globally, pollinators are experiencing serious threats from land use change, chemical pesticide use, the introduction of alien invasive species and climate change, leading to a decline in pollinator diversity. This decline can cause decreases in the yield and quality of animal-pollinated crops. Here we propose following three approaches to conserve pollinator diversity and improve pollination services in agricultural landscapes: (1) wildlife-friendly farm practices, such as reduced application of pesticides or conversion to organic farming; (2) promotion of landscape diversity, including conserving and establishing suitable semi-natural habitats, maintaining residual natural habitats, improving crop diversity and optimizing resources or habitats; (3) the use of local pollinator species in industrial applications. Further research is needed examining biological characteristics of pollinator, demand and provision of pollination services, as well as the effects of management practices on pollinator diversity and pollination services.

Key words: biodiversity, ecological services, wild pollinators, landscape management

传粉服务是人类社会持续存在与发展所依赖的重要生态系统服务之一(Millennium Ecosystem Assessment, 2005)。许多被子植物需要通过动物传粉进行有性生殖(Kearns *et al.*, 1998; Ashman *et al.*,

2004), 其中包括人类食用或生产所需的植物也直接或间接地依赖动物传粉。因此, 传粉动物在陆地生态系统中为栽培作物和野生植物提供的传粉服务, 不仅有助于维持野生植物的遗传多样性, 也关

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系着作物的产量、食物安全与人类福利。然而, 近些年来在欧洲和北美地区的研究显示传粉动物的多样性呈现降低的趋势(Kremen *et al.*, 2002; Biesmeijer *et al.*, 2006; Potts *et al.*, 2010a), 由此所导致的传粉服务减退和作物产量降低问题也成为了研究和关注的热点(Steffan-Dewenter *et al.*, 2005; Klein *et al.*, 2007)。然而, 目前国内有关传粉的研究主要集中在传粉昆虫生物学、行为学方面(黄双全和郭友好, 2000; 安建东等, 2007; 刘红平等, 2008), 对传粉动物带来的生态服务及经济影响方面的研究还不够系统和全面(安建东和陈文锋, 2011)。本文将在介绍传粉动物多样性及其提供的传粉服务的基础上, 重点回顾导致传粉动物多样性降低和传粉服务下降的驱动原因, 探讨提升农业景观传粉动物多样性和传粉服务的管理途径。

1 传粉动物的多样性及其生态服务

在自然界中有报道的能起到传粉作用的动物种类繁多, 比如无脊椎动物中的昆虫(Kevan & Baker, 1983)、脊椎动物中的蝙蝠和鸟类等(Winfree *et al.*, 2011), 以及一些非飞行哺乳动物如啮齿类的睡鼠(*Graphiurus ocularis*)、有袋类的负鼠(*Cercartetus nanus*)、灵长类的狐猴(*Varecia variegata*)等(Carthew & Goldingay, 1997)。其中昆虫是传粉动物的主体, 包括膜翅目(占全部传粉昆虫的43.7%)、双翅目(28.4%)、鞘翅目(14.1%), 其余的还有鳞翅目、缨翅目、半翅目、直翅目, 但所占比例很小(郭柏寿等, 2001)。膜翅目蜜蜂总科(Hymenoptera: Apoidea)是种类和数量最多的一类传粉昆虫(李捷等, 2007), 全球有记录的已超过17,500种(Michener, 2007), 我国已被命名的传粉蜂也有1,000多种(徐环李等, 2009), 大多数都是有效的传粉者, 例如利用零星蜜源的本土中华蜜蜂(*Apis cerana*)、全球广泛饲养的西方蜜蜂(*A. mellifera*)、为豆科牧草授粉的切叶蜂(*Megachile*)、为温室作物授粉的熊蜂(*Bombus*)、为果树授粉的壁蜂(*Osmia*)等(吴杰, 2003)。这些蜂类由于对特定作物的访花专一性和访花频率高、花粉沉降量和接触柱头次数多、花粉携带量大, 已被商业开发利用(Bosch & Kemp, 2002; Moisan-Desserres *et al.*, 2014)。

多种多样的传粉动物在给作物和野生植物授粉的同时, 也为人类提供了重要的生态服务, 主要

体现在以下几个方面:

(1)传粉动物多样性是全球粮食安全和人类福祉的保障。维持传粉动物的物种多样性或功能群多样性, 可以提高作物授粉的成功率(Klein *et al.*, 2003a; Hoehn *et al.*, 2008), 直接关系着作物的产量、产品的质量和经济价值。研究分析显示, 全球约70%的主要作物(产量占全球作物总产量的35%)可通过动物传粉增产(Klein *et al.*, 2007); 在我国主要种植的44种水果和蔬菜中约57%为虫媒作物, 其产值占了蔬果总产值的25.5%(安建东和陈文锋, 2011)。然而这些较为依赖动物传粉的作物, 它们的相对产量以及产量的增幅和稳定性较低, 容易受到花粉的限制, 传粉动物多样性的增加有助于稳定和增加授粉作物的产量(Garibaldi *et al.*, 2011)。动物传粉不仅能使作物增产, 还可以提升食物的营养价值和商业价值, 例如传粉能提高杏仁中油酸和亚油酸的含量(Brittain *et al.*, 2014)、改善草莓的质量和保鲜期(Klatt *et al.*, 2014)、增加油菜籽的含油量(Bommarco *et al.*, 2012)。经过动物授粉后, 食物中的维生素、抗氧化物、脂类、微量元素等营养物质的含量也会增加, 使得人类的膳食更健康(Eilers *et al.*, 2011; Wang & Ding, 2012)。如果没有传粉动物, 全球农业总产量预计会下降3–8%, 若要弥补这部分损失, 全球需要将2/3的陆地变为耕地(Aizen *et al.*, 2009), 这在人口不断增加的当今社会将难以实现。此外, 随着人类生活水平的提高, 对高经济价值的、依赖动物传粉的作物(主要是温带和热带的水果和坚果)的需求量在过去50年里增长了3倍多(Aizen & Harder, 2009)。因此, 传粉动物的多样性及传粉服务的提供直接关系着粮食安全、经济贸易以及人类的膳食均衡和生活质量。

(2)传粉动物多样性是维持植物遗传多样性的保障。传粉是许多植物进行有性生殖以及形成大量种子和果实的一个必要过程(Abrol, 2012), 超过90%的被子植物需要借助动物特别是昆虫来传送花粉(Kearns *et al.*, 1998)。以动物为媒介的异花授粉方式能给植物有性繁殖的子代带来更大的遗传变异以更好地适应环境变化, 子代产生的杂种优势或杂交效应也会使其经济学和生物学性状在质量和数量上发生显著改变, 因而动物传粉有助于增加作物的产量和产品的质量, 自交亲和的作物也可借助异花传粉来改善种质(Shrestha, 2008)。异花授粉也是

维持植物的基因流、减少植物的基因漂移和近交衰退的一个必要过程(Trant *et al.*, 2010)。多数植物与传粉动物之间是多对多的广泛互惠关系,且随时间和空间变化而异(Kearns *et al.*, 1998),不同的植物需要不止一种传粉者,因此传粉动物的多样性有助于维持植物的遗传多样性,其功能多样性也有利于增加植物群落的稳定性(Fontaine *et al.*, 2006)。

(3)传粉动物多样性是应对气候变化的保障。不同传粉者的活动时间有差异,气候变化导致植物的花期提前或延后(Fitter & Fitter, 2002),植物的有效传粉者也会发生改变(Wall *et al.*, 2003)。较高的传粉动物多样性可以使植物与传粉者的物候期保持更好的同步,提供更充足的传粉服务(Bartomeus *et al.*, 2013)。不仅如此,不同的传粉动物类群间还可以起到互补的作用(Parsche *et al.*, 2011),提升传粉者的多样性,尤其是保护与植物关系紧密的传粉者,可以减少环境变化对植物授粉结实的影响以及对植物与传粉者关系的冲击(Winfree *et al.*, 2014)。例如,气候变暖会抑制家养蜜蜂传粉,但会促进本土野生传粉者提供传粉服务,因此维持传粉动物的多样性有利于在变化的气候和环境中为作物提供总体比较稳定的传粉服务(Rader *et al.*, 2013)。又如极端的气候变化会导致可可树的产量降低,通过保护传粉昆虫,即使传粉服务仅提升10%,可可的产量也会翻倍(Wanger, 2014),弥补了极端气候对产量的不利影响。

2 传粉动物多样性和传粉服务的丧失及其驱动因素

传粉动物正面临着大范围的生物多样性丧失的危险(Potts *et al.*, 2010a)。对全球不同地区尤其是欧洲和北美国家的调查显示,传粉动物的多样性均呈现下降的趋势。例如美国在1947–2005年间蜜蜂蜂群减少了59% (NRC, 2007),而中欧在1985–2005年间蜂群减少了25%(Potts *et al.*, 2010b)。英国与荷兰的蜜蜂多样性在半数以上的景观中出现了下降,尤其是生境或食性相对专一、喙较长、迁移性差以及繁殖速度慢的物种丰度降幅更大(Biesmeijer *et al.*, 2006);英国89%的蝴蝶出现了分布范围缩小、数量下降的趋势,而一些迁移能力强和生境广布的蝴蝶物种逐渐在群落占据优势(Warren *et al.*, 2001)。为天南星科和兰花蕉科里具有腐败气味的开花植

物提供传粉服务的蜣螂(*Onthophagus spp.*)亦在全球范围内数量减少,甚至在局部地域消失(Nichols *et al.*, 2008)。其他地区如马达加斯加以及作为蜜蜂的发源地并拥有一些独特蜂类的非洲地区,也面临着蜂类多样性下降的问题(Eardley *et al.*, 2009)。

2.1 传粉动物多样性和传粉服务丧失的后果

随着传粉动物多样性的降低,传粉服务的提供会受到限制,进而影响相关作物的产量和品质。在印尼的咖啡种植园中,当访花蜂类的物种数超过20种时,咖啡的挂果率可高达95%;而当蜂的种类减少为6种时,咖啡的挂果率则降为70%(Klein *et al.*, 2003b)。爱尔兰的冬油菜(*Brassica napus*)结籽数量在完全隔离传粉者后减少了27%,每个荚果的种子重量减少了30%(Stanley *et al.*, 2013)。假设世界上所有传粉者全部消失,那么基于2005年的全球消费水平,水果和蔬菜的产量分别会出现-12%和-6%的供应不足(Gallai *et al.*, 2009)。美国直接依靠昆虫传粉的作物产值在1996–2001年间减少了36亿美元,间接依靠昆虫传粉(所结的籽粒作为种子播种)的作物产值在1996–2004年间减少了34.5亿美元(Calderone, 2012)。

传粉动物多样性的丧失也带来了植物遗传多样性降低的问题。例如,英国与荷兰的一些本土传粉动物多样性的下降导致了依靠它们授粉的植物物种的减少,在局部地区消失(Biesmeijer *et al.*, 2006);在新西兰北岛,由于鸟类数量的减少引发功能性灭绝,提供的传粉服务减退,导致灌木 *Rhabdothamnus solandri*的种群密度变小,种子产量降低了84%,幼苗减少了55%(Anderson *et al.*, 2011)。而大多数泛化的传粉者(generalized pollinators,如熊蜂和一些独居蜂)的消失,与一些特化的传粉者(specialized pollinators)相比,会使植物物种多样性减少得更快(Memmott *et al.*, 2004)。

多样化的传粉动物能够在一定气候变化范围内调节和保障作物的产量(Wanger, 2014),但随着干扰的加剧、物种的锐减,起缓冲作用的植物与传粉者动态网络结构也会达到临界点而崩溃(Hegland *et al.*, 2009)。

2.2 传粉动物多样性丧失的驱动原因

传粉动物多样性及传粉服务降低的现象几乎遍及全球,究其原因主要包括以下几个方面:

(1)土地利用变化所导致的农业景观结构的改

变。土地利用变化包括农田扩张、森林砍伐等,首先会改变景观要素的组成,导致自然和半自然生境大量减少或退化、生境多样性下降、传粉动物所依赖的资源匮乏(Steffan-Dewenter & Westphal, 2008; Winfree *et al.*, 2009)。个体大、功能有效性高的传粉昆虫更容易受到生境丧失的影响,从而加速传粉服务的丧失(Larsen *et al.*, 2005)。另外,景观要素的空间格局也会发生变化,影响传粉动物的多样性及其提供的传粉服务。例如在集约化的农业景观中,随隔离度的增加,距离物种丰富的生境越来越远,蜜蜂的多度、植物的籽粒数也渐渐下降(Steffan-Dewenter & Tscharntke, 1999)。与野外重要的蜜粉食源和筑巢地的隔离也会导致本土蜜蜂数量和种类的减少及其传粉服务的丧失(Kremen *et al.*, 2002)。再如森林砍伐造成生境面积缩小、边缘效应和斑块内孔隙度增加,降低了动物为林内植物传粉的成功率(Magrach *et al.*, 2012);同时森林生境碎片面积越小,本地传粉者出现的频率和物种数也越少(Aizen & Feinsinger, 1994)。

(2)农药的使用。农药在农业中的大量使用,也会对非靶标昆虫造成伤害。蜜蜂经常暴露在充满各种化学药剂的农业景观中,会因为取食了受污染的花粉和花蜜,接触了空气里、水滴中或植物上的农药等而发生急性或慢性中毒(Riscu & Bura, 2013)。曾在蜜蜂采集的花粉中检测到35种不同的杀虫剂和高浓度的杀菌剂,有的样品中杀虫剂高氟戊菊酯和亚胺硫磷浓度高达半数致死剂量,而杀菌剂虽然对蜜蜂没有直接的毒害作用,但会令蜜蜂容易被微孢子虫(*Nosema ceranae*)寄生而得病(Pettis *et al.*, 2013)。烟碱类农药占据超过1/4的全球市场份额,是近年来使用最广泛的一类杀虫剂,在目前的大田剂量下能引发诸多亚致死效应,造成蜜蜂神经中枢损伤、易得病、幼蜂发育不良、觅食困难等(van der Sluijs *et al.*, 2013)。暴露在多种农药环境中,不仅会影响蜂类个体的行为,在集群水平上也会制约幼虫孵化和新集群的建立(Gill *et al.*, 2012)。

(3)外来驯养蜂的引入、寄生虫和病害。外来驯养蜂的引入会对本土传粉者造成不利的影响。以我国为例,自1896年西蜂(*Apis mellifera*)被引入后,由于西蜂人工饲养数量增加、竞争性强、易传播疾病等原因,导致本地种中华蜜蜂的分布区域缩小75%以上,种群数量减少80%以上(杨冠煌, 2005)。不仅

国内如此,国外也存在类似的现象。由于养蜂业的发展,蜂王被远距离迁移,又因为蜂群的交配体系混乱,使得本土蜜蜂可能因杂交而丧失经长期自然选择而形成的有价值的性状组合(De la Rua *et al.*, 2009),还容易被外来的病原体感染(Jaffe *et al.*, 2010)。如外寄生性的狄斯瓦螨(*Varroa destructor*)入侵美国后,在蜜蜂蜂群中的传播速度极快,几乎造成了毁灭性的大规模死亡(Kraus & Page, 1995)。狄斯瓦螨的寄生率高,还会伴随发生翅膀致畸病毒(DWV)、蜜蜂急性麻痹病毒(ABPV)的侵染,是导致德国的蜜蜂蜂群冬天大量死亡的主因(Genersch *et al.*, 2010)。以色列急性麻痹病毒(IAPV)则与美国蜂群崩坏症(CCD)的发生有很大关系(Cox-Foster *et al.*, 2007)。另外,细菌和真菌等也都可以引起蜂群的消失(Genersch, 2010)。

(4)气候变化的影响。气候变化(包括CO₂浓度升高、气温上升、干旱等)可以在不同尺度上影响传粉者的多样性:在个体水平上可以引起其体温和飞行能力的改变(Stone & Willmer, 1989),在物种水平上导致其物候(活动时间)的改变(Hegland *et al.*, 2009)、物种气候生态位的改变及其分布范围的改变、缩小甚至在局部地区灭绝(Parmesan *et al.*, 1999; Williams *et al.*, 2007; Giannini *et al.*, 2012),在群落水平上可以改变传粉动物的群落结构和功能组成(Minckley *et al.*, 2013)。除了直接作用外,气候变化也可以通过改变物种间的相互作用而间接影响传粉动物的多样性及其功能。例如,由于植物和传粉动物对气候变化的响应不同,可能使得它们在时间、空间、形态和生理方面出现不匹配,从而破坏了植物和传粉者之间的关系,降低了传粉的成功率(Memmmott *et al.*, 2007; Hegland *et al.*, 2009; Rafferty & Ives, 2012; Polce *et al.*, 2014)

引起传粉动物多样性下降的主要原因各地有所不同,也可能是多因素共同作用的结果,需要辨析主次、影响尺度及其协同效应(Potts *et al.*, 2010a)。

3 农业景观传粉动物多样性及传粉服务管理途径

作为占据地球陆地面积37.8%以上(FAOSTAT, 2012)的重要景观类型,农业景观在维持生物多样性包括传粉动物多样性的过程中扮演着重要的角色(Pimentel *et al.*, 1992; Tscharntke *et al.*, 2005;

Scherr & McNeely, 2008), 传粉动物也为农业景观提供了重要的生态服务。但是, 传粉动物多样性的降低直接或间接地受到农业生产管理的影响, 并反作用于农业的可持续发展。因此, 农业景观传粉动物多样性的保护和传粉服务的管理是农业可持续发展需要考虑的重要内容。

农业景观中主要的传粉动物为家养蜂和野生传粉昆虫(Kremen *et al.*, 2002; Goulson, 2003; Klein *et al.*, 2007), 尽管家养蜂的数量占优势, 但野生传粉者往往能够提供更有效的传粉服务, 两者可以起到互补的作用(Garibaldi *et al.*, 2013)。传粉昆虫的生存与繁衍需要在其觅食范围内具备适宜的筑巢点、筑巢材料以及充足的食物如植物的花粉和花蜜等资源, 这些资源可能分散在农业景观不同生境类型的镶嵌斑块中(包括自然生境、半自然生境及农田等)(Westrich, 1996)。农业景观中资源的空间异质性和时间动态性会造成生物多样性的时空动态变化(Williams & Kremen, 2007)。传粉者的多样性会受到非作物生境的面积比例、农业管理措施(如农药的使用)、种植方式(如作物与草地轮作)以及虫媒作物(如油菜)花期的影响(Le Feon *et al.*, 2013)。传粉者的觅食距离不同(Gathmann & Tscharntke, 2002; Greenleaf *et al.*, 2007), 受到农业景观结构变化(如生境面积比例等)影响的尺度也不同(Steffan-Dewenter *et al.*, 2002)。

农业景观生物多样性的保护和管理经历了一个从重视局部尺度生产管理方式的改善, 到强调栖息地和景观尺度管理的过程。最近的研究也显示, 生产管理及景观结构存在交互作用, 要实现农业景观传粉动物多样性及生态服务的有效管理, 需要依据所在景观的结构状况, 制定适宜的生产管理和景观管理策略(Batary *et al.*, 2011; Concepcion *et al.*, 2012)。

从局部尺度来说, 首先必须要改善农事措施, 例如减少化肥和农药的使用(Kovacs-Hostyanszki *et al.*, 2011; Otieno *et al.*, 2011)、实行有机种植方式(Holzschuh *et al.*, 2007), 以降低人类生产活动对传粉者的不利影响。根据法国对54种全国主要作物在过去20年的生产数据分析显示, 农业的集约化并没有让依赖动物传粉的作物增产, 反而随着时间的推移还降低了其产量的稳定性, 集约化的收益被传粉服务的减退所抵消(Deguines *et al.*, 2014)。

由于传粉者容易迁移、对空间尺度上的生态因子较为敏感, 故传粉服务深受周边景观中资源的时间和空间分布、生物种间关系(传粉者间的资源竞争、植物间的传粉者竞争)等的影响(Kremen *et al.*, 2007), 农业景观中传粉昆虫多样性的保护还需要在景观尺度上对景观结构进行调整和改善。具体的途径主要有:

(1)利用农田边界、田间地头的边角地创建和维护适宜的非作物生境(如多花带、树篱、草带), 增加田间本土植物的多样性和高质量生境, 为传粉者提供食物来源(Pywell *et al.*, 2005)和筑巢生境(Holzschuh *et al.*, 2012), 作为附近农田作物的本土传粉者种库(Ockinger & Smith, 2007)和避难所(Nicholls & Altieri, 2013), 从而提高本地野生传粉动物的多样性(Carvell *et al.*, 2007; Carvalheiro *et al.*, 2012; Rollin *et al.*, 2013), 为周边的农田作物提供传粉服务(Albrecht *et al.*, 2007; Morandin & Kremen, 2013a)。即使在交通繁忙的马路边的狭窄地带, 也能通过种植多种本土开花植物为蜂类提供生境, 增加其物种数(Hopwood, 2008)。

(2)对残留自然生境的保护与休耕地的利用。残留的自然生境如森林斑块是野生传粉者的生境之一, 对森林的保护有助于增加传粉者的多样性(De Marco & Coelho, 2004; Ricketts, 2004)。休耕地可与自然生境和农田共同为本地传粉者提供物候期互补以及种类丰富的植物花粉和花蜜资源, 让它们能够在不同类型的生境间迁移觅食, 并能在不断变化的农业景观中长期生存(Mandelik *et al.*, 2012)。

(3)农作物的搭配和变换。农业景观中作物种类的多样化可以增加传粉者的数量, 例如较大面积地种植虫媒传粉的作物如油菜, 可有效增加熊蜂的密度(Westphal *et al.*, 2003)。

(4)改善景观要素的空间配置, 使资源的空间分布合理化。例如, 在农业景观中, 除了保留较大面积的自然生境以维持传粉者种群的持续发展外, 还可在景观中分散点缀一些吸引传粉动物的小生境, 使提供的传粉服务具有空间连续性, 从而提升作物的产量(Brosi *et al.*, 2008; Winfree *et al.*, 2008)。为了应对气候变化的影响, 在景观尺度上建设合理的生态网络或绿色廊道也是必要的措施(Mawdsley *et al.*, 2009)。

除了改善局部和景观尺度的管理, 还需要研究

和开发利用野生传粉蜂类。随着农作物的种植面积增加, 农业对传粉服务的需求也相应增大(Aizen *et al.*, 2008), 全球人工饲养和管理的家养蜂数量在过去50年中快速增长(Aizen & Harder, 2009)。但是, 为了避免不恰当地引入外来物种, 应当限制向本土蜜蜂已占据的生境内再引入高繁殖率的亚种, 以维护本土蜜蜂种群的遗传多样性(De la Rua *et al.*, 2009)。野生蜂具有比家养蜂更高的遗传多样性(Moritz *et al.*, 2007)和更高的访花率(Winfree *et al.*, 2008)。从全球来看, 目前对传粉动物的开发利用是不足的, 以蜂类为例, 全世界有记录的超过17,500种(Michener, 2007), 仅有少数几个物种被商业开发和利用(Bosch & Kemp, 2002; Cane, 2008), 包括群居的西蜂和熊蜂、洞穴筑巢独居的苜蓿切叶蜂(*Megachile rotundata*)和几种壁蜂、地面筑巢的黑彩带蜂(*Nomia melanderi*)和灰头苜蓿蜂(*Rhophitoides canus*)。因此, 迫切需要对本土传粉动物多样性进行调查, 筛选传粉效率高的传粉者, 了解其取食、筑巢、生活史等生活习性, 研究其饲养、释放、病虫害控制、规模化生产和利用等技术(Bosch & Kemp, 2002)。

4 结论与展望

传粉动物多样性及其所提供的传粉服务是人类福祉的重要保障。仅依靠少数几种家养蜂传粉的高度集约化和单一化种植的农业, 已经无法应对全球气候变化以及人类活动对植物与传粉者关系网络的冲击, 因此创建传粉动物高度多样性的农业景观, 尤其是增加传粉者功能组的多样性或者主要功能组内的物种数(Albrecht *et al.*, 2012), 是稳定和提高作物产量、保障粮食安全、恢复生态系统服务与功能、推动农业可持续发展的需要。应分别从小尺度的生产管理与较大尺度的景观管理共同着手, 一方面降低不利于传粉者的人为管理强度; 另一方面在农业景观中保护和构建适宣传粉者的生境、合理分配资源。

然而, 目前对于传粉动物多样性及传粉服务影响因素的研究还不全面(Kremen *et al.*, 2002; 谢正华等, 2011; Brittain *et al.*, 2013)。为了更有效地落实管理措施, 将来需要进一步开展以下几个方面的研究(Allen-Wardell *et al.*, 1998; Klein *et al.*, 2007; Dicks *et al.*, 2013): (1)深入认识传粉者的生物学特

征, 尤其是野生传粉者的食物需求、筑巢需求、对干扰的敏感性等(李捷等, 2007); (2)深入认识作物对传粉服务的需求, 尤其是不同作物品种对传粉服务需求的差异; (3)深入评估传粉动物尤其是野生传粉者对作物生产的贡献, 评估生产区内特定传粉者丧失的潜在影响; (4)研究化学农药对传粉者的影响程度及改善措施; (5)建立并完善对昆虫传粉者的监测网络, 了解花蜜和花粉资源在景观中的供应与分布, 在此基础上利用详细的传粉者分布数据和农业景观数据, 绘制出传粉服务需求与供给地图, 根据两者的匹配度为不同地区的政策制定、景观规划提供指导(Lautenbach *et al.*, 2012; Schulp *et al.*, 2014); (6)深入认识植被组成(Gotlieb *et al.*, 2011; Morandin & Kremen, 2013b)、生境特征(开花植物的多样性和覆盖度、生境面积等)(Holzschuh *et al.*, 2007; Fruend *et al.*, 2010; Bommarco *et al.*, 2014)、景观结构和景观配置(觅食范围内半自然生境的比例、所处位置即与景观中自然或半自然生境的距离、生境间的连通性等等)(Steffan-Dewenter *et al.*, 2002; Ricketts *et al.*, 2008; Benjamin *et al.*, 2014; Bommarco *et al.*, 2014)对传粉动物的丰富度、群落组成和种间关系造成的影响, 通过景观设计和管理来加强传粉者的保护和服务功能。

近些年来, 农业景观传粉动物多样性及其对生态服务的影响机制已经成为国际上新的研究热点, 例如在欧盟第七框架下, 由欧洲研究区网(Europe Research Area-Net) BiodivERsA^①资助, 德国、法国、西班牙、美国、加拿大、阿根廷的科学家共同就世界不同地区改变作物组成和配置的异质性能否促进生物多样性保护及传粉等生态服务展开了研究(<http://www.farmland-biodiversity.org>)。而欧盟的共同农业政策要求各成员国通过鼓励、补贴采取野生动物友好型生产(如有机农业)和乡村景观管理(建立多花带、草带、树篱等)来促进农业景观生物多样性和生态服务保护。作为一个幅员辽阔、生物多样性资源丰富, 但各种生态问题不断出现的农业大国, 我国目前在农业景观生物多样性和生态服务保护和利用方面的研究还相当不足, 迫切需要加强对传粉动物多样性资源调查、传粉者生物学和生态学

^① BiodivERsA 是欧盟 15 个国家的 21 个研究基金部门的联合机构, 负责协调欧盟国家间生物多样性研究, 并协调组织这一领域的研究项目的国际基金(<http://www.eugrism.info/DisplayFunding.asp?f=136>)

方面的研究(郭柏寿等, 2001; 李捷等, 2007; 谢正华等, 2011), 在充分认识传粉动物多样性现状、变化趋势以及时空、地理分布特征和传粉动物多样性对生态服务影响机制的基础上, 研究制定不同地理和景观特征下对传粉动物尤其是本土传粉者这一宝贵的自然资源进行保护以及合理利用的措施, 以满足日益增长的农业可持续发展和生态环境保护的需求。

除此之外, 将这些理论真正应用于实践, 还需要科研人员、政府部门和农民等相关利益群体的共同参与和协作。科学研究提供的相关数据, 例如农业景观中维持传粉者种群的最小生境面积、提升传粉服务的有效范围大小、资源斑块的最大间隔距离、非作物生境在景观中合适的面积比例等(Ricketts, 2004), 应该更好地应用于指导政府的规划决策。而政府的管理决策中也需要加强多方利益的权衡(Kremen *et al.*, 2002; Garibaldi *et al.*, 2011), 例如生产用地与生态用地之间数量的平衡, 化学农药的减少、传粉动物多样性、传粉服务与作物产量之间的平衡, 养蜂业的发展与外来蜂种的引入以及本土传粉者的利用。只有科学合理地抉择与取舍, 奖罚分明, 才可能很好地实现农业生产和人类社会的可持续发展。

参考文献

- Abrol DP (2012) Pollination—basic concepts. In: *Pollination Biology* (ed. Abrol DP), pp. 37–54. Springer, Dordrecht.
- Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine ‘Chaco serrano’. *Ecological Applications*, **4**, 378–392.
- Aizen MA, Garibaldi LA, Cunningham SA, Klein AM (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current Biology*, **18**, 1572–1575.
- Aizen MA, Garibaldi LA, Cunningham SA, Klein AM (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, **103**, 1579–1588.
- Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Current Biology*, **19**, 915–918.
- Albrecht M, Duelli P, Mueller C, Kleijn D, Schmid B (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, **44**, 813–822.
- Albrecht M, Schmid B, Hautier Y, Mueller CB (2012) Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4845–4852.
- Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox PA, Dalton V, Feinsinger P, Ingram M, Inouye D, Jones CE, Kennedy K, Kevan P, Koopowitz H, Medellin R, Medellin-Morales S, Nabhan GP, Pavlik B, Tepedino V, Torchio P, Walker S (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12**, 8–17.
- An JD (安建东), Chen WF (陈文锋) (2011) Economic value of insect pollination for fruits and vegetables in China. *Acta Entomologica Sinica* (昆虫学报), **54**, 443–450. (in Chinese with English abstract)
- An JD (安建东), Wu J (吴杰), Peng WJ (彭文君), Tong YM (童越敏), Guo ZB (国占宝), Li JL (李继莲) (2007) Foraging behavior and pollination ecology of *Bombus lucorum* L. and *Apis mellifera* L. in greenhouse peach garden. *Chinese Journal of Applied Ecology* (应用生态学报), **18**, 1071–1076. (in Chinese with English abstract)
- Anderson SH, Kelly D, Ladley JJ, Molloy S, Terry J (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068–1071.
- Ashman TL, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT, Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology*, **85**, 2408–2421.
- Bartomeus I, Park MG, Gibbs J, Danforth BN, Lakso AN, Winfree R (2013) Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters*, **16**, 1331–1338.
- Batary P, Andras B, Kleijn D, Tscharntke T (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1894–1902.
- Benjamin FE, Reilly JR, Winfree R (2014) Pollinator body size mediates the scale at which land use drives crop pollination services. *Journal of Applied Ecology*, **51**, 440–449.
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.
- Bommarco R, Lindborg R, Marini L, Öckinger E (2014) Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Diversity and Distributions*, **20**, 591–599.
- Bommarco R, Marini L, Vaissiere BE (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, **169**, 1025–1032.
- Bosch J, Kemp WP (2002) Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research*, **92**, 3–16.
- Brittain C, Kremen C, Garber A, Klein AM (2014) Pollination

- and plant resources change the nutritional quality of almonds for human health. *PLoS ONE*, **9**, e90082.
- Brittain C, Williams N, Kremen C, Klein AM (2013) Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122767.
- Brosi BJ, Armsworth PR, Daily GC (2008) Optimal design of agricultural landscapes for pollination services. *Conservation Letters*, **1**, 27–36.
- Calderone NW (2012) Insect pollinated crops, insect pollinators and US agriculture: trend analysis of aggregate data for the period 1992–2009. *PLoS ONE*, **7**, e37235.
- Cane JH (2008) A native ground-nesting bee (*Nomia melanderi*) sustainably managed to pollinate alfalfa across an intensively agricultural landscape. *Apidologie*, **39**, 315–323.
- Carthew SM, Goldingay RL (1997) Non-flying mammals as pollinators. *Trends in Ecology and Evolution*, **12**, 104–108.
- Carvalheiro LG, Seymour CL, Nicolson SW, Veldtman R (2012) Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. *Journal of Applied Ecology*, **49**, 1373–1383.
- Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29–40.
- Concepcion ED, Diaz M, Kleijn D, Baldi A, Batary P, Clough Y, Gabriel D, Herzog F, Holzschuh A, Knop E, Marshall EJP, Tscharntke T, Verhulst J (2012) Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, **49**, 695–705.
- Cox-Foster DL, Conlan S, Holmes EC, Palacios G, Evans JD, Moran NA, Quan P, Briese T, Hornig M, Geiser DM, Martinson V, Vanengelsdorp D, Kalkstein AL, Drysdale A, Hui J, Zhai J, Cui L, Hutchison SK, Simons JF, Egholm M, Pettis JS, Lipkin WI (2007) A metagenomic survey of microbes in honey bee colony collapse disorder. *Science*, **318**, 283–287.
- De la Rua P, Jaffe R, Dall’Olio R, Munoz I, Serrano J (2009) Biodiversity, conservation and current threats to European honeybees. *Apidologie*, **40**, 263–284.
- De Marco P, Coelho FM (2004) Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. *Biodiversity and Conservation*, **13**, 1245–1255.
- Deguines N, Jono C, Baude M, Henry M, Julliard R, Fontaine C (2014) Large-scale trade-off between agricultural intensification and crop pollination services. *Frontiers in Ecology and the Environment*, **12**, 212–217.
- Dicks LV, Abrahams A, Atkinson J, Biesmeijer J, Bourn N, Brown C, Brown MJF, Carvell C, Connolly C, Cresswell JE, Croft P, Darvill B, De Zylva P, Effingham P, Fountain M, Goggin A, Harding D, Harding T, Hartfield C, Heard MS, Heathcote R, Heaver D, Holland J, Howe M, Hughes B, Huxley T, Kunin WE, Little J, Mason C, Memmott J, Osborne J, Pankhurst T, Paxton RJ, Pocock MJO, Potts SG, Power EF, Raine NE, Ranelagh E, Roberts S, Saunders R, Smith K, Smith RM, Sutton P, Tilley LAN, Tinsley A, Tonhasca A, Vanbergen AJ, Webster S, Wilson A, Sutherland WJ (2013) Identifying key knowledge needs for evidence-based conservation of wild insect pollinators: a collaborative cross-sectoral exercise. *Insect Conservation and Diversity*, **6**, 435–446.
- Eardley CD, Gikungu M, Schwarz MP (2009) Bee conservation in sub-Saharan Africa and Madagascar: diversity, status and threats. *Apidologie*, **40**, 355–366.
- Eilers EJ, Kremen C, Greenleaf SS, Garber AK, Klein AM (2011) Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS ONE*, **6**, e21363.
- FAOSTAT (2012) Download Data/Inputs/Land. <http://faostat3.fao.org/download/R/RL/E> (2015-03-10)
- Fitter AH, Fitter R (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.
- Fontaine C, Dajoz I, Meriguet J, Loreau M (2006) Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, **4**, 129–135.
- Fruend J, Linsenmair KE, Bluethgen N (2010) Pollinator diversity and specialization in relation to flower diversity. *Oikos*, **119**, 1581–1590.
- Gallai N, Salles J, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, **68**, 810–821.
- Garibaldi LA, Aizen MA, Klein AM, Cunningham SA, Harder LD (2011) Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences, USA*, **108**, 5909–5914.
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhoffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipolito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlof M, Seymour CL, Schuepp C, Szentgyorgyi H, Taki H, Tscharntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608–1611.
- Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764.
- Genersch E (2010) Honey bee pathology: current threats to honey bees and beekeeping. *Applied Microbiology and Biotechnology*, **87**, 87–97.
- Genersch E, von der Ohe W, Kaatz H, Schroeder A, Otten C, Buechler R, Berg S, Ritter W, Muehlen W, Gisder S, Meixner M, Liebig G, Rosenkranz P (2010) The German bee monitoring project: a long term study to understand periodically high winter losses of honey bee colonies. *Apidologie*, **41**, 332–352.
- Giannini TC, Acosta AL, Garofalo CA, Saraiva AM, Alves-

- dos-Santos I, Imperatriz-Fonseca VL (2012) Pollination services at risk: bee habitats will decrease owing to climate change in Brazil. *Ecological Modelling*, **244**, 127–131.
- Gill RJ, Ramos-Rodriguez O, Raine NE (2012) Combined pesticide exposure severely affects individual- and colony-level traits in bees. *Nature*, **491**, 105–119.
- Gotlieb A, Hollender Y, Mandelik Y (2011) Gardening in the desert changes bee communities and pollination network characteristics. *Basic and Applied Ecology*, **12**, 310–320.
- Goulson D (2003) Conserving wild bees for crop pollination. *Journal of Food Agriculture and Environment*, **1**, 142–144.
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.
- Guo BS (郭柏寿), Yang JM (杨继民), Xu YB (许育彬) (2001) Problems and research advance of the pollination insects. *Southwest China Journal of Agricultural Sciences* (西南农业学报), **14**, 102–108. (in Chinese with English abstract)
- Hegland SJ, Nielsen A, Lázaro A, Bjerknes A, Totland Ø (2009) How does climate warming affect plant–pollinator interactions? *Ecology Letters*, **12**, 184–195.
- Hoehn P, Tscharntke T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2283–2291.
- Holzschuh A, Dudenhoeffer J, Tscharntke T (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation*, **153**, 101–107.
- Holzschuh A, Steffan-Dewenter I, Kleijn D, Tscharntke T (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, **44**, 41–49.
- Hopwood JL (2008) The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*, **141**, 2632–2640.
- Huang SQ (黄双全), Guo YH (郭友好) (2000) Advances in the pollination biology. *Chinese Science Bulletin* (科学通报), **45**, 225–237. (in Chinese)
- Jaffe R, Dietemann V, Allsopp MH, Costa C, Crewe RM, Dall’Olio R, De la Rua P, El-Niweiiri MAA, Fries I, Kezic N, Meusel MS, Paxton RJ, Shaibi T, Stolle E, Moritz RFA (2010) Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. *Conservation Biology*, **24**, 583–593.
- Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics*, **29**, 83–112.
- Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. *Annual Review of Entomology*, **28**, 407–453.
- Klatt BK, Holzschuh A, Westphal C, Clough Y, Smit I, Pawelzik E, Tscharntke T (2014) Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132440.
- Klein AM, Steffan-Dewenter I, Tscharntke T (2003a) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 955–961.
- Klein AM, Steffan-Dewenter I, Tscharntke T (2003b) Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology*, **40**, 837–845.
- Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.
- Kovacs-Hostynszki A, Batáry P, Baldi A (2011) Local and landscape effects on bee communities of Hungarian winter cereal fields. *Agricultural and Forest Entomology*, **13**, 59–66.
- Kraus B, Page RE (1995) Effect of *Varroa jacobsoni* (Mesostigmata: Varroidae) on feral *Apis mellifera* (Hymenoptera: Apidae) in California. *Environmental Entomology*, **24**, 1473–1480.
- Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, Lebuhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vazquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein AM, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.
- Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences, USA*, **99**, 16812–16816.
- Larsen TH, Williams NM, Kremen C (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, **8**, 538–547.
- Lautenbach S, Seppelt R, Liebscher J, Dormann CF (2012) Spatial and temporal trends of global pollination benefit. *PLOS ONE*, **7**, e35954.
- Le Feon V, Burel F, Chifflet R, Henry M, Ricroch A, Vaissiere BE, Baudry J (2013) Solitary bee abundance and species richness in dynamic agricultural landscapes. *Agriculture Ecosystems and Environment*, **166**, 94–101.
- Li J (李捷), Zhu CD (朱朝东), Wang FH (王凤鹤), Huang DY (黄敦元), Zhang YZ (张彦周), Ding L (丁亮), Huang HR (黄海荣) (2007) Current research on the status of wild bees and their pollination roles. *Biodiversity Science* (生物多样性), **15**, 687–692. (in Chinese with English abstract)
- Liu HP (刘红平), Li XX (李晓霞), Wang XJ (王晓娟) (2008) Pollinating insect species and their foraging behaviors on *Medicago sativa*. *Chinese Journal of Ecology* (生态学杂志), **27**, 780–784. (in Chinese with English abstract)
- Millennium Ecosystem Assessment (MA) (2005) *Ecosystems and Human Well-being: Synthesis*. <http://www.millennium-assessment.org/documents/document.356.aspx.pdf> (2014-08-07)
- Magrach A, Santamaría L, Larrinaga AR (2012) Differential effects of anthropogenic edges and gaps on the reproduction of a forest-dwelling plant: the role of plant reproductive ef-

- fort and nectar robbing by bumblebees. *Austral Ecology*, **37**, 600–609.
- Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, **22**, 1535–1546.
- Mawdsley JR, O'Malley R, Ojima DS (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology*, **23**, 1080–1089.
- Memmott J, Craze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, **10**, 710–717.
- Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, 2605–2611.
- Michener CD (2007) *The Bees of the World*, 2nd edn. The Johns Hopkins University Press, Baltimore, USA.
- Minckley RL, Roulston TH, Williams NM (2013) Resource assurance predicts specialist and generalist bee activity in drought. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122703.
- Moisan-Deserres J, Girard M, Chagnon M, Fournier V (2014) Pollen loads and specificity of native pollinators of lowbush blueberry. *Journal of Economic Entomology*, **107**, 1156–1162.
- Morandin LA, Kremen C (2013a) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, **23**, 829–839.
- Morandin LA, Kremen C (2013b) Bee preference for native versus exotic plants in restored agricultural hedgerows. *Restoration Ecology*, **21**, 26–32.
- Moritz RFA, Kraus FB, Kryger P, Crewe RM (2007) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees. *Journal of Insect Conservation*, **11**, 391–397.
- Nicholls CI, Altieri MA (2013) Plant biodiversity enhances bees and other insect pollinators in agroecosystems: a review. *Agronomy for Sustainable Development*, **33**, 257–274.
- Nichols E, Spector S, Louzada J, Larsen T, Amezcua S, Favila ME (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, **141**, 1461–1474.
- National Research Council (NRC) (2007) *Status of Pollinators in North America*. http://www.nap.edu/openbook.php?record_id=11761&page=40 (2014-08-13)
- Ockinger E, Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44**, 50–59.
- Otieno M, Woodcock BA, Wilby A, Vogiatzakis IN, Mauchline AL, Gikungu MW, Potts SG (2011) Local management and landscape drivers of pollination and biological control services in a Kenyan agro-ecosystem. *Biological Conservation*, **144**, 2424–2431.
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Parsche S, Fruend J, Tscharntke T (2011) Experimental environmental change and mutualistic vs. antagonistic plant flower–visitor interactions. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 27–35.
- Pettis JS, Lichtenberg EM, Andree M, Stitzinger J, Rose R, Vanengelsdorp D (2013) Crop pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen *Nosema ceranae*. *PLoS ONE*, **8**, e70182.
- Pimentel D, Stachow U, Takacs DA, Brubaker HW, Dumas AR, Meaney JJ, O'Neil JAS, Onsi DE, Corzilius DB (1992) Conserving biological diversity in agricultural/forestry systems. *BioScience*, **42**, 354–362.
- Polce C, Garratt MP, Termansen M, Ramirez-Villegas J, Chal-linor AJ, Lappage MG, Boatman ND, Crowe A, Endalew AM, Potts SG, Somerwill KE, Biesmeijer JC (2014) Climate-driven spatial mismatches between British orchards and their pollinators: increased risks of pollination deficits. *Global Change Biology*, **20**, 2815–2828.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010a) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution*, **25**, 345–353.
- Potts SG, Roberts SPM, Dean R, Marrs G, Brown MA, Jones R, Neumann P, Settele J (2010b) Declines of managed honey bees and beekeepers in Europe. *Journal of Apicultural Research*, **49**, 15–22.
- Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, Bennett D, Wright A, Critchley C, Sherwood A (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, **121**, 479–494.
- Rader R, Reilly J, Bartomeus I, Winfree R (2013) Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, **19**, 3103–3110.
- Rafferty NE, Ives AR (2012) Pollinator effectiveness varies with experimental shifts in flowering time. *Ecology*, **93**, 803–814.
- Ricketts TH (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, **18**, 1262–1271.
- Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA, Ochieng A, Viana BF (2008) Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, **11**, 499–515.
- Riscu A, Bura M (2013) The impact of pesticides on honey bees and hence on humans. *Scientific Papers: Animal Science and Biotechnologies*, **46**, 272–277.
- Rollin O, Bretagnolle V, Decourtey A, Aptel J, Michel N, Vaissiere BE, Henry M (2013) Differences of floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture, Ecosystems and Environment*, **179**, 78–86.
- Scherr SJ, McNeely JA (2008) Biodiversity conservation and agricultural sustainability: towards a new paradigm of ‘eco-

- agriculture' landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 477–494.
- Schulp CJ, Lautenbach S, Verburg PH (2014) Quantifying and mapping ecosystem services: demand and supply of pollination in the European Union. *Ecological Indicators*, **36**, 131–141.
- Shrestha JB (2008) Honeybees: the pollinator sustaining crop diversity. *Journal of Agriculture and Environment*, **9**, 90–92.
- Stanley DA, Gunning D, Stout JC (2013) Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: ecological and economic incentives for pollinator conservation. *Journal of Insect Conservation*, **17**, 1181–1189.
- Steffan-Dewenter I, Munzenberg U, Burger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421–1432.
- Steffan-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution*, **20**, 651–652.
- Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, **121**, 432–440.
- Steffan-Dewenter I, Westphal C (2008) The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology*, **45**, 737–741.
- Stone GN, Willmer PG (1989) Warm-up rates and body temperatures in bees: the importance of body size, thermal regime and phylogeny. *Journal of Experimental Biology*, **147**, 303–328.
- Trant AJ, Herman TB, Good-Avila SV (2010) Effects of anthropogenic disturbance on the reproductive ecology and pollination service of Plymouth gentian (*Sabatia kennedyana* Fern.), a lakeshore plant species at risk. *Plant Ecology*, **210**, 241–252.
- 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**, 857–874.
- van der Sluijs JP, Simon-Delso N, Goulson D, Maxim L, Bonmatin J, Belzunces LP (2013) Neonicotinoids, bee disorders and the sustainability of pollinator services. *Current Opinion in Environmental Sustainability*, **5**, 293–305.
- Wall MA, Timmerman-Erskine M, Boyd RS (2003) Conservation impact of climatic variability on pollination of the federally endangered plant, *Clematis socialis* (Ranunculaceae). *Southeastern Naturalist*, **2**, 11–24.
- Wang XH, Ding SY (2012) Pollinator-dependent production of food nutrients by fruits and vegetables in China. *African Journal of Agricultural Research*, **7**, 6136–6142.
- Wanger TC (2014) Cocoa shortfall: pollination curbs climate risk to cocoa. *Nature*, **511**, 155.
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, **6**, 961–965.
- Westrich P (1996) Habitat requirements of central European bees and the problems of partial habitats. In: *The Conservation of Bees* (eds Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH), pp. 1–16. Academic Press, London.
- Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, **17**, 910–921.
- Williams PH, Araujo MB, Rasmont P (2007) Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation*, **138**, 493–505.
- Winfree R, Aguilar R, Vazquez DP, Lebuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, **90**, 2068–2076.
- Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 1–22.
- Winfree R, Williams NM, Dushoff J, Kremen C (2014) Species abundance, not diet breadth, drives the persistence of the most linked pollinators as plant-pollinator networks disassemble. *The American Naturalist*, **183**, 600–611.
- Winfree R, Williams NM, Gaines H, Ascher JS, Kremen C (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, **45**, 793–802.
- Wu J (吴杰) (2003) The characteristics and application of several important pollinating bees. *Apiculture of China* (中国养蜂), **54**(5), 24–25. (in Chinese)
- Xie ZH (谢正华), Xu HL (徐环李), Yang P (杨璞) (2011) Notes on monitoring, assessing and conserving pollinator biodiversity. *Chinese Journal of Applied Entomology* (应用昆虫学报), **48**, 746–752. (in Chinese with English abstract)
- Xu HL (徐环李), Yang JW (杨俊伟), Sun JR (孙洁茹) (2009) Current status on the study of wild bee-pollinators and conservation strategies in China. *Acta Phytophylacica Sinica* (植物保护学报), **36**, 371–376. (in Chinese with English abstract)
- Yang GH (杨冠煌) (2005) Harm of introducing the western honeybee *Apis mellifera* L. to the Chinese honeybee *Apis cerana* F. and its ecological impact. *Acta Entomologica Sinica* (昆虫学报), **48**, 401–406. (in Chinese with English abstract)