•综述•

传粉昆虫下降背景下的授粉生态弹性：内涵、机制和展望

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摘要: 全球传粉昆虫多样性正在下降, 如何保障农林生态系统传粉功能是当前研究的热点。理论上说, 传粉功能不仅与生态系统的传粉昆虫多样性相关, 还与生态系统的调节能力有关。近年来, 学者们逐渐认识到授粉生态弹性对传粉功能的影响。本文在回顾已有研究的基础之上, 总结传粉昆虫授粉生态弹性的内涵, 厘清授粉生态弹性与工程弹性、稳定性和抗性的异同。目前, 学者对授粉生态弹性形成机制开展广泛探讨, 提出功能冗余假说、密度补偿假说、响应多样性假说、连接周转假说和跨尺度弹性假说, 但这5个假说间的关系仍不清楚, 存在一词多义、词意混淆等现象。我们依次阐述功能冗余假说、密度补偿假说、响应多样性假说、连接周转假说和跨尺度弹性假说, 介绍不同假说中授粉生态弹性形成过程、研究热点和发展动态。通过解析授粉生态弹性的形成机制可知, 5个假说在内涵上存在紧密联系, 它们从不同空间尺度和研究对象下解释传粉昆虫授粉生态弹性的形成机制。未来授粉生态弹性研究将整合传粉昆虫群落动态和传粉功能动态的量化方法, 通过实验验证5个假说的合理性, 并揭示不同假说间的联系, 由此阐明授粉生态弹性的发生条件、形成阈值和动态规律。随着研究的深入, 授粉生态弹性理论有望用于指导农林生态系统传粉功能的经营管理。

关键词: 传粉昆虫下降; 传粉服务; 生态弹性; 工程弹性; 人类干扰

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Ecological resilience of pollination in the face of pollinator decline: Content, mechanism and perspective

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ABSTRACT

Background & Aims: Pollinators are declining worldwide and there is a global concern about how to conserve pollination services of agroforestry ecosystems. In theory, the pollination services are determined not only by the level of pollinator diversity but also by the adaptive capability of pollinator communities against disturbances. Recently, researchers have realized the importance of ecological resilience of pollination; nevertheless, the concept of ecological resilience of pollination is not clear and it is often misapplied to other ecological processes, like engineering resilience, resistance, and stability.

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Objectives: This study explains the concept and content of ecological resilience of pollination and discusses the differences from other similar ecological processes. Moreover, the underlying mechanisms driving the ecological resilience of pollination are reviewed and the hypotheses explaining ecological resilience of pollination are summarized. The ecological importance of ecological resilience of pollination is addressed in terms of managing pollination functioning of agricultural ecosystems.

Progresses: Ecosystems under outer disturbances can absorb the disturbances by reorganizing the inner structures or components to let the ecosystem functioning remain unchanged or at an acceptable level. Reorganization of the pollinator communities under disturbances drives the occurrence of ecological resilience of pollination. Functional redundancy, density compensation, response diversity, interaction turnover, and cross-scale resilience are the five hypotheses explaining the ecological resilience of pollination, but they are often used imprecisely and incorrectly. We state that the five hypotheses are different but internally interlinked, explaining the ecological resilience of pollination at different spatial scales. From functional redundancy, density compensation, response diversity, interaction turnover to cross-scale resilience, the five hypotheses explain the ecological resilience of pollination ranging from small to large scales and from simple to complex ecosystems. Moreover, the hypothesis running at a relatively large spatial scale (e.g. cross-scale resilience) can be applied to explain the hypothesis at a relatively small scale (e.g. functional redundancy and density compensation). For each hypothesis, a conceptual diagram is presented to illustrate how pollinators reorganize their communities to enhance the ecological resilience of pollination. The experimental evidences to support the five hypotheses are still in shortage, particularly for interaction turnover hypothesis and the cross-scale resilience hypothesis. Nowadays, few studies have explored the pollination functioning of ecosystems by methods integrating the five hypotheses. Moreover, the relationships among the five hypotheses are not tested empirically by field study, either. Therefore, more field evidences are expected to support those hypotheses.

Perspectives: The ecological resilience of pollination is always measured using biodiversity indexes, such as species richness and Simpson diversity. Since ecological resilience of pollination is a measurement of ecosystem functioning, we suggest that its indicator need to integrate pollination functioning, such as pollen grains deposited on stigma surfaces, initial fruit sets and final fruit sets. Future research also should examine how the disturbance intensification influences the ecological resilience of pollination and when the ecological resilience of pollination occurs. Moreover, the five hypotheses should be tested empirically and their relationships need to be explored. With the development of knowledge on ecological resilience of pollination, researchers can apply those theories to manage the agricultural ecosystems. For example, the ecological resilience of pollination can guide the researchers to determine when and how to provide the managed pollinators (e.g. honey bees) to safeguard the pollination functioning of ecosystems.

Key words: pollinator decline; pollination service; ecological resilience; engineering resilience; anthropogenic disturbance

在全球传粉昆虫下降背景下, 如何保障生态系统传粉服务功能和农林作物授粉需求是当前重要的科学议题(Vanbergen & The Insect Pollinators Initiative, 2013)。近40年来, 全球传粉昆虫依赖作物(pollinator-dependent crop)的种植面积持续增长, 传粉昆虫下降的负面影响将逐渐凸显(Aizen & Harder, 2009)。保障和维持生态系统传粉服务功能已成为众多农林经营措施的重要内容(Potts et al, 2016)。例如, 部分欧洲国家实行的传粉昆虫友好性经营措施(如英国的农业环境计划 Agriculture Environmental Schedule)有望调节生态系统传粉昆虫群落, 保障生态系统传粉服务功能。

从理论上说, 维持传粉昆虫物种多样性或多度将在一定程度上保障农林生态系统的传粉服务功能。值得注意的是, 生态系统传粉服务功能不仅与

传粉昆虫多样性相关, 还与环境压力下生态系统的调节能力有关。近年来, 传粉昆虫授粉生态弹性引起了学者的广泛关注, 并在内涵和机制方面开展了大量理论探讨工作(Dicks et al, 2012)。伴随生态弹性研究从理论探讨走向运用实践, 授粉生态弹性逐渐被学者、农田经营者和政策制定者重视(Dudney et al, 2018)。从保障生态系统传粉功能的角度看, 认识授粉生态弹性具有重要的生产意义。在全球传粉昆虫下降和农林作物传粉需求日益增长的双重压力下, 了解授粉生态弹性规律显得尤为重要, 这有助于生产经营者掌握农田生态系统的传粉功能, 并依此做出正确的管理决策(Aizen & Harder, 2009; Potts et al, 2016)。本文综述传粉昆虫下降背景下生态系统授粉生态弹性的内涵、形成机制、研究热点和发展动态, 为农林生产中科学利用传粉昆虫奠定

理论基础。

1 弹性的定义

20世纪70年代, Holling总结生态系统非线性动态规律时首次提出弹性概念(Holling, 1973), 之后学者们一直在探讨弹性的定义和内涵, 但目前学界仍未就此达成一致(Brand & Jax, 2007)。早期研究多集中于讨论弹性(resilience)与稳定性(stability)(Holling, 1973; Mori, 2016)、抗性(resistance)(Shade et al, 2012; Lake, 2013; Nimmo et al, 2015)和持续性(persistence)(Holling, 1973; Astegiano et al, 2015)等词汇的异同, 这些工作为厘清弹性内涵奠定了理论基础(表1)。稳定性指生态系统功能在时间或空间过程中保持不变(Holling, 1973)。通常情况下, 生态系统稳定性由系统抗性和弹性共同决定(Shade et al, 2012; Connell & Ghedini, 2015)。抗性是指生态系统受到外界干扰或压力时对外界做出的抵抗能力(Oliver et al, 2015; Connell et al, 2016)。系统发生抗性时, 系统内部结构和组分可能并不发生变化(Shade et al, 2012; Connell & Ghedini, 2015)。当外界干扰或压力较弱时, 生态系统才呈现抗性(Connell & Ghedini, 2015)。

弹性可简单分为生态弹性(ecological resilience)和工程弹性(engineering resilience)(表1)。生态弹性指干扰条件下生态系统通过调节系统结构和组分来吸收外部干扰, 使系统功能保持不变或维持在可接受水平(Holling, 1973; Mori, 2016)。当外界变化超过一定阈值时, 系统才转换到另一状态。而工程弹性则指生态系统受到干扰时恢复到平衡点的时间或能力(Pimm, 1984; Gunderson, 2000)。由于授粉工程弹性研究较少, 因而本文主要关注授粉生态弹性。

2 授粉生态弹性

授粉生态弹性指外界干扰和压力作用下传粉昆虫群落通过调节结构或组分, 使生态系统传粉功能保持不变或维持在可接受的水平(图1)。由此可见, 授粉生态弹性以传粉昆虫群落结构为对象, 关注传粉昆虫的传粉功能动态, 探讨传粉昆虫多样性和传粉功能的关系。已有研究证实, 在土地类型变化、高强度农业耕作、气候变化、生境丧失和破碎化以及生物入侵等作用下, 生态系统传粉昆虫多样性下降, 传粉昆虫群落结构变化(Kremen et al, 2007)。传粉昆虫群落在多种作用机制下保障生态系统传粉

表1 生态弹性内涵及其与相似生态过程的异同

Table 1 The content of ecological resilience and its difference with other ecological processes

生态现象/过程 Ecological phenomenon/process	不同术语(参考文献) Glossary (references)
生态系统受到一定程度的外界干扰/压力时, 系统通过吸收干扰和重组系统内部结构或组分, 使生态系统功能保持不变或维持在可接受的水平。 Ecosystems under outer disturbances/pressures absorb the disturbances by reorganizing the inner structures or components to let the ecosystem functioning remain unchanged or at an acceptable level.	主流术语: 生态弹性 其他术语: 抗性; 生态系统弹性; 补偿性 Main terms: ecological resilience (Holling, 1973; Gunderson, 2000; Baho et al, 2017) Other terms: resistance (Isbell et al, 2015; Walker, 2020); ecosystem resilience (Brand & Jax, 2007); compensation (Connell & Ghedini, 2015)
生态系统在干扰和压力后恢复到平衡点的能力, 或生态系统恢复到平衡点所需要的时间。 The capability for ecosystems to return to an equilibrium point following a disturbance or pressure event, or the time for ecosystems to return to an equilibrium point after disturbance or pressure event.	主流术语: 工程弹性 其他术语: 弹性; 系统性弹性; 稳定性; 伸缩性 Main terms: engineering resilience (Folke et al, 2004; Brand & Jax, 2007; Mori, 2016) Other terms: resilience (Isbell et al, 2015); systemic resilience (Scheffer et al, 2018); stability (Holling, 1973); elasticity (Grimm & Wissel, 1997)
生态系统维持生态功能不变的现象, 对生态系统运行状态的一种表现性描述。通常不涉及生态系统功能的维持机制。 A description for the status of ecosystems which has a stable and invariable function. Generally, the underlying mechanisms for ecosystem functioning are not concerned.	主流术语: 稳定性 其他术语: 持续性 Main terms: stability (Isbell et al, 2015; Angeler & Allen, 2016) Other terms: persistence (Astegiano et al, 2015)
生态系统结构或组成在外界干扰和压力发生时未发生变化的现象 No change in ecosystem structures and components under outer disturbances/pressures	主流术语: 抗性 其他术语: 补偿性 Main terms: resistance (Shade et al, 2012; Angeler & Allen, 2016; Connell et al, 2016) Other terms: compensation (Connell & Ghedini, 2015)

功能, 形成授粉生态弹性(图1)。值得注意的是, 生态系统传粉功能存在多种保障机制, 如传粉昆虫群落结构对环境胁迫具抗性(Karp et al, 2011; Kühnel & Blüthgen, 2015), 植物生殖特性(如自花授粉)能缓解花粉限制压力(Chacoff et al, 2008)。然而这些保障机制并非由传粉昆虫多样性下降引起, 因此不在传粉昆虫授粉生态弹性研究范畴内, 本文不阐述相应的作用机制。

针对生态系统授粉生态弹性形成机制, 目前学者已提出以下5个假说: 功能冗余假说(functional redundancy)、密度补偿假说(density compensation)、响应多样性假说(response diversity)、连接周转假说(interaction turnover)、跨尺度弹性假说(cross-scale resilience) (图1) (Martin et al, 2019; Weise et al, 2020)。虽然学者对上述各假说开展了广泛的探讨, 但是不同假说间的关系仍未厘清, 存在一词多义、词意混淆等现象。各假说内涵存在紧密联系, 它们从不同空间尺度下解释传粉昆虫授粉生态弹性形

成机制(图1) (Oliver et al, 2015; Baho et al, 2017)。从功能冗余假说至跨尺度弹性假说, 研究尺度由小到大, 研究对象由少至多, 研究内容由简至繁。功能冗余假说探讨小尺度上(如植株尺度)功能团间的互作关系, 而跨尺度弹性假说探讨大尺度上(如生态系统尺度)传粉功能团间的关系(Astegiano et al, 2015)。根据由简至繁的顺序, 我们依次对图1中的5个假说进行说明。

3 授粉生态弹性形成机制

3.1 功能冗余假说

为开花植物授粉的不同传粉功能团(或物种)存在生态位的重叠, 不同功能团间形成传粉功能冗余(Gitay et al, 1996; Rosenfeld, 2002)。例如, 假设由传粉功能团a、功能团b、功能团c组成的传粉昆虫群落, 当传粉功能团a和功能团c降低传粉服务时, 传粉功能团b提高传粉服务, 填补功能团a和c减少的传粉功能(图2)。由于传粉功能团间的功能冗余作用, 生

图1 传粉昆虫下降背景下授粉生态弹性不同机制示意图。以土地类型变化为代表的全球变化引起传粉昆虫群落结构变化。在①功能冗余、②密度补偿、③响应多样性、④连接周转、⑤跨尺度弹性机制作用下, 传粉功能团保障传粉功能(如植物柱头上沉降花粉数量)在可接受的水平, 形成授粉生态弹性。

Fig. 1 The framework showing the different mechanisms of ecological resilience of pollination in the face of pollinator decline. The global changes, such as land use change, invoke the variations in pollinator community. Under the mechanisms of ①functional redundancy, ②density compensation, ③response diversity, ④interaction turnover; ⑤cross-scale resilience, pollinator communities are able to deliver an acceptable level of pollination functioning (e.g. pollen grains on stigma surface), forming the ecological resilience of pollination.

态系统传粉功能并不下降,生态位的重叠引起生态弹性(Blüthgen & Klein, 2011; Tschamntke et al, 2012)。

功能冗余假说从生态系统传粉功能角度阐述传粉昆虫的授粉生态弹性。在多个传粉功能团同时存在的生态系统中,不同功能团形成传粉功能补偿(functional compensation)作用,某功能团的传粉服务下降时,其他功能团的传粉功能得以加强(Naeem, 1998; Mori, 2016)。虽然功能冗余假说并未直接强调传粉昆虫群落结构变化,但从功能冗余假说可知,传粉功能团越丰富的生态系统越容易得到其他功能团的传粉补偿,具有更高的授粉生态弹性(e.g. Nash et al, 2014)。功能冗余假说能直观地解释授粉生态弹性形成机制,但因授粉生态弹性缺乏有效的量化方法,目前研究并未揭示功能冗余与授粉生态弹性的关系模型。已有研究表明功能冗余可以提高生态系统传粉稳定性(Klein et al, 2003; Garibaldi et al, 2011),但由于传粉稳定性与授粉生态弹性两者存在差异(表1),因此研究功能冗余与授粉生态弹性的关系具有重要的科学意义。

功能冗余假说中不同传粉功能团对环境变化的响应尺度和方向不一致,因而对环境变化存在不同的响应规律(Williams et al, 2010; Mori et al, 2013)。值得注意的是,功能冗余假说在小尺度上(如图2植株尺度)解释授粉生态弹性的形成机制,而传粉功能团对环境变化的响应发生在更大的空间尺度上(如景观尺度)。对生态系统来说,功能冗余机制与授粉生态弹性的其他形成机制往往同时发生,且功能冗余机制是其他机制的基石,即其他机制均可在小尺度上转换成功能冗余作用进行解释(图1)。

3.2 密度补偿假说

密度补偿是指干扰作用下传粉昆虫群落中部分传粉功能团(或物种)访花密度下降而其他传粉功能团(或物种)访花密度增长的现象(图3) (Gonzalez & Loreau, 2009)。在蜜粉源资源恒定的条件下,不同传粉功能团对蜜粉源资源形成竞争关系,其访花密度在数值上呈现“一增一减”的变化动态(Winfree, 2013)。虽然部分传粉功能团访花密度下降,其提供的传粉功能下降,但其他传粉功能团访花密度增长,补偿了生态系统的传粉功能(图3)。从结果来看,生态系统传粉功能并不因某一功能团访花密度的下降而下降,传粉功能团间的密度补偿引起授粉生态

弹性(Gonzalez & Loreau, 2009; Staver et al, 2018)。密度补偿假说关注传粉功能团访花密度的动态变化,其生态作用表现为不同功能团间的传粉功能冗余,因此密度补偿是功能冗余在访花密度上的一种表现,功能冗余是密度补偿在生态功能上的一种结果。

密度补偿作用主要研究空间小尺度上传粉功能团间访花密度的互作关系。例如,室内控制环境下,人造花上熊蜂访花频率增长时,蜜蜂访花密度下降(Rogers et al, 2013)。田间样地中,开花植物上熊蜂访花频率下降时,蜜蜂访花频率增长(Thomson, 2016)。已有的研究证实自然界中小尺度下传粉功能团间存在密度补偿作用。值得注意的是,不同传粉功能团访花密度出现“增减”变化后,生态系统传粉功能还同时受昆虫传粉效率(pollination efficiency)的影响(Hallett et al, 2017)。如果变化后的传粉昆虫保持较高的传粉效率,则生态系统传粉功能并不因某一传粉功能团访花密度的下降而下降。例如,当人为阻隔开花植物马利筋(*Asclepias verticillata*)上的熊蜂时,传粉效率相似的马蜂提高访花频率,因此马利筋接收的花粉数量并不下降,传粉昆虫群落呈现授粉生态弹性(Hallett et al, 2017)。

密度补偿作用的研究多以植物、哺乳动物和鸟类为对象,对传粉昆虫的研究相对较少(Houlahan et al, 2007; Jiang, 2007)。由密度补偿作用形成机制可知,传粉功能团对蜜粉源资源的竞争是密度补偿的诱因,因而研究时需固定环境中蜜粉源资源数量,使传粉功能团的访花密度动态变化。然而,此类研究在自然生态系统中难以实现,尤其是空间大尺度下不同传粉功能团同时受环境因子的影响时(Winfree & Kremen, 2009; Winfree, 2013),传粉功能团间的密度补偿作用可能被传粉昆虫与环境因子间的协同动态(synchronous dynamics)所掩盖(Gonzalez & Loreau, 2009; Lasky et al, 2016)。同时,传粉功能团访花密度下降后,剩余传粉功能团的传粉效率和访花行为同样对传粉功能具有重要的影响(Brosi & Briggs, 2013; Hallett et al, 2017),然而目前学者对相关的变化规律知之甚少。由于上述两方面的原因,密度补偿作用对授粉生态弹性的影响仍需要深入研究。

3.3 响应多样性假说

响应多样性是指不同传粉功能团(或物种)对干

图2 不同传粉功能团间功能冗余引起授粉生态弹性的机制示意图。假设生态系统中3个传粉功能团(a、b和c)均为开花植物授粉(A), 当传粉功能团a沉降的花粉(黄色)数量和传粉功能团c沉降的花粉(橙色)数量下降时, 传粉功能团b沉降的花粉(蓝色)数量增加(B)。柱头花粉数总量保持不变, 传粉昆虫群落形成授粉生态弹性。

Fig. 2 Conceptual diagram showing the mechanical effect of functional redundancy among functional groups of pollinators on ecological resilience of pollination. Three functional groups (a, b and c) are supposed to pollinate the flowering plants in the ecosystems (A). When the amount of pollens delivered by functional group a (yellow) and functional group c (orange) decreases, the amount of pollens delivered by functional group b (blue) increases (B). The number of pollens deposited on stigma surfaces does not change. The pollinator communities have the ecological resilience of pollination.

图3 密度补偿作用引起授粉生态弹性的机制示意图。假设生态系统存在传粉功能团a和传粉功能团b (A), 全球变化下生态系统由功能团a的4个个体和功能团b的5个个体的传粉昆虫群落(A)转变为功能团a的2个个体和功能团b的9个个体的传粉昆虫群落(B)。当生态系统内传粉功能团a访花频率下降时, 传粉功能团b访花频率上升, 反之亦然(B)。虽然不同传粉功能团传粉效率(如单次访花花粉沉降量)存在差异, 但沉降花粉数量保持不变, 形成授粉生态弹性。

Fig. 3 Conceptual diagram illustrating the mechanical effect of density compensation on ecological resilience of pollination. Two functional groups of pollinators (a and b) are supposed to deliver pollens on stigma surfaces (A). In the face of global changes, the pollinator communities with 4 individuals of functional group a and 5 individuals of functional group b (A) is transformed to a different pollinator communities with 2 individuals of functional group a and 9 individuals of functional group b (B). The visit density of functional group a decreases, but the visit density of functional group b increase, and vice versa (B). Due to the differences in pollination efficiency (e.g. pollen deposition per visit), the overall pollen numbers delivered by different pollinator communities are the same. The pollinator communities have the ecological resilience of pollination.

扰的差异性响应现象(Elmqvist et al, 2003; Mori et al, 2013) (图4)。受传粉昆虫个体大小、巢穴位置、食性专性、社会性和生活史等因素影响, 传粉昆虫对

环境变化的响应并非完全一致(Öckinger et al, 2010; Williams et al, 2010)。例如, 不同个体大小的传粉功能团对自然生境的空间响应尺度存在差异(图4A),

个体大的传粉昆虫具更大的空间搜索范围,对自然生境的空间响应尺度大于个体小的传粉昆虫(图4B)(Miguet et al, 2016)。又如,巢穴位置的差异引起传粉昆虫对自然生境变化的差异性响应(图4C)。通常情况下,当自然生境数量下降时,树栖性传粉昆虫多度随自然生境数量的减少而下降,但土栖性传粉昆虫多度可能保持不变,而砖栖性传粉昆虫多度随自然生境数量的减少而增加(图4D)(Williams et al, 2010; Xie et al, 2020)。已有的研究表明,传粉昆虫对干扰表现出多样的响应规律(Winfree & Kremen, 2009; Cariveau et al, 2013)。响应多样性假说认为传粉功能团的响应多样性引起传粉昆虫的授粉生态弹性(图4E)(Biggs et al, 2012; García et al, 2018)。

早期的研究通过统计模型对传粉昆虫多样性进行检测,定性地证实了传粉昆虫对环境变化的响应多样性现象,并且认为响应多样性与传粉昆虫的

性状相关(Williams et al, 2010; Cariveau et al, 2013)。近年来,结合“功能多样性”研究方法,学者们开始以传粉昆虫个体大小、食性、生活史、搜索行为等性状为内容来量化传粉昆虫的响应多样性,从而将响应多样性研究由定性研究阶段拓展到定量研究阶段(Bartomeus et al, 2018; Wong et al, 2019)。已有的研究表明,定量研究方法比定性研究方法能更准确地解释环境变化对传粉昆虫多样性的影响(Wong et al, 2019)。但令人不解的是,以传粉昆虫个体大小、食性、生活史等为内容的性状多样性却不能较好地解释生态系统传粉功能(如结实率)(Garibaldi et al, 2015),传粉昆虫响应多样性如何影响授粉生态弹性的作用机制仍不清楚。

伴随“基于响应性状-效应性状框架”(trait-based response-and-effect framework)理论的推广,学者们逐渐认识到传粉昆虫响应性状和效应性

图4 响应多样性引起授粉生态弹性的机制示意图。假设传粉功能团在个体大小和巢穴位置等响应性状方面表现出多样性,不同个体大小的传粉昆虫(A)对自然生境的空间响应尺度存在差异,个体大的传粉昆虫响应尺度大于个体小的传粉昆虫(B)。同时,不同巢穴位置的传粉昆虫(C)种群数量对自然生境呈现不同的响应规律,部分传粉昆虫种群数量随自然生境百分率的下降而下降,但其他传粉昆虫种群数量保持不变甚至增长(D)。传粉功能团的响应多样性可能通过效应多样性调节传粉功能,使植物柱头花粉沉降数量保持不变,形成授粉生态弹性(E)。

Fig. 4 Conceptual diagram showing the mechanical effect of response diversity on ecological resilience of pollination. Pollinators are supposed to be different in body size and nesting site. The pollinators with different body sizes (A) respond to natural habitats at different spatial scales, with a relatively large scale of effect for the large pollinators compared to a relatively small scale of effect for the smaller pollinators (B). Meanwhile, the pollinators with different nesting sites (C) respond differently to the natural habitats, with a decrease of populations for most pollinators along the loss of semi-natural habitats but an increase or stability of populations for other pollinators (D). Response diversity can affect ecosystem pollination functioning through effect diversity. The overall pollen numbers delivered by pollinators keep the same. The pollinator communities have the ecological resilience of pollination (E).

状的差异, 并将传粉昆虫功能多样性划分为响应性状多样性和效应性状多样性(Suding et al, 2008; Bartomeus et al, 2018)。同时认为, 前期研究中的功能性状(如个体大小、食性等)应归于传粉昆虫的响应性状, 而传粉昆虫的访花频率和单次访花花粉沉降数等性状才是效应性状(Bartomeus et al, 2018)。环境变化影响传粉昆虫响应性状多样性, 而效应性状多样性决定生态系统传粉功能。因此该理论框架搭建起传粉昆虫响应多样性同传粉功能的桥梁, 并揭示了响应多样性不能直接解释传粉功能的原因。由此可见, 探索传粉昆虫响应多样性同效应多样性的关系将是未来研究的重点。传粉昆虫响应多样性

可能通过调节效应性状多样性的途径来影响生态系统传粉功能, 使传粉昆虫群落呈现授粉生态弹性, 但响应多样性影响授粉生态弹性的机制仍需深入研究。

3.4 连接周转假说

传粉网络的连接周转(或连接替换)是指干扰作用下传粉昆虫和开花植物的部分连接消失但同时建立新连接的现象(图5)(Poisot et al, 2012; Simanonok & Burkle, 2014)。传粉昆虫和开花植物间的连接重连(interaction rewiring)和物种周转(species turnover)均可引起传粉网络的连接周转(Poisot et al, 2012; CaraDonna et al, 2017)。连接重连指群落组成

图5 连接周转引起授粉生态弹性的机制示意图。在生态系统中, 假设原传粉网络存在3种传粉昆虫(a_1 , a_2 , a_3)和3种开花植物(p_1 , p_2 , p_3) (A)。干扰作用下, 传粉昆虫和开花植物间部分连接消失但新的连接形成, 网络连接发生重连(B); 或者传粉昆虫下降, 对应的连接消失, 或新的传粉昆虫(a_4)进入网络, 建立新连接, 传粉昆虫发生物种周转(C)。在传粉网络重连和物种周转的共同作用下, 传粉昆虫和开花植物形成传粉网络连接周转(D)。对开花植物来说, 连接周转前后传粉昆虫群落组成存在差异, 但原传粉网络中的传粉昆虫和连接周转后的传粉昆虫传播等量花粉, 形成授粉生态弹性(E)。黑线示意周转前传粉昆虫同开花植物间的联系, 红线示意形成的新连接。

Fig. 5 Conceptual diagram illustrating the mechanical effect of interaction turnover on ecological resilience of pollination. The ecosystem is hypothesized to have an original pollination network with three pollinators (a_1 , a_2 , a_3) and three plants (p_1 , p_2 , p_3) (A). Under disturbances, some interactions are lost but new interactions occur, forming interaction rewiring (B). Interactions are also lost as a result of pollinators decline, but new interactions is built as new pollinators (a_4) enter the pollination network, resulting from species turnover of pollinators (C). The combined effect of interaction rewiring and species turnover explains an interaction turnover of the pollination network (D). For plants, their pollinator assemblages are different before and after interaction turnover, however, the amount of pollens delivered by the pollinator assemblages is the same. The pollinator communities have the ecological resilience of pollination (E). Black lines indicate the original interactions before interaction turnover and red lines indicate newly-built interactions after interaction turnover.

不变的情况下传粉昆虫和开花植物部分连接消失但同时建立新连接(图5B) (Kaiser-Bunbury et al, 2010; Simanonok & Burkle, 2014)。物种周转指部分物种消失或新物种进入网络后传粉昆虫或开花植物因物种组成变化而形成新连接(图5C) (CaraDonna et al, 2017)。网络重连和物种更替往往同时发生,但在不同的生态系统中二者对网络变化的相对贡献存在差异(图5D) (Simanonok & Burkle, 2014; Robroek et al, 2021)。从开花植物的角度来看,网络变化后部分连接和传粉昆虫消失,对应的传粉功能下降,但新连接的传粉昆虫同样可以为开花植物授粉,在传粉功能上表现为补偿作用(图5E)。由此可见,网络变化后传粉昆虫群落组成和多度维持在原网络相似水平时,传粉昆虫群落形成授粉生态弹性。

前期研究多假设传粉网络为静止状态,主要描述传粉网络的物种组成和拓扑结构的特征(Memmott et al, 2004; Bascompte & Jordano, 2007)。近年来,学者们普遍认为自然界中传粉网络是动态变化的,传粉昆虫和开花植物的连接周转是常见的生态现象(Tylianakis & Morris, 2017)。在干扰作用下,传粉昆虫与开花植物的平行下降(parallel decline)和传粉昆虫提升对开花植物的相遇概率(encounter probability)都可以引起传粉昆虫和开花植物的新连接(图5) (Biesmeijer, 2006; Tylianakis & Morris, 2017)。例如,在气候变化和生物入侵等作用下,生态系统传粉网络可以形成新的连接(Burkle & Alarcón, 2011; Burkle et al, 2013; Kaiser-Bunbury et al, 2017)。

普遍的观点认为连接周转可以使传粉昆虫形成授粉生态弹性(Kaiser-Bunbury et al, 2017; Fantinato et al, 2019)。从网络水平来看,网络变化后传粉网络拓扑结构稳固性(robustness)并不下降(Kaiser-Bunbury et al, 2010; Vizentin-Bugoni et al, 2020)。从群落水平来看,网络变化后开花植物的传粉昆虫泛化度(generality)保持不变(Fantinato et al, 2019)。在物种水平上来看,网络变化后开花植物连接的传粉昆虫多样性(partner diversity)保持不变(Fantinato et al, 2019)。不同水平的指标表明,连接周转后虽然传粉昆虫群落结构和组成发生变化,但变化后的传粉昆虫同样为开花植物授粉,传粉昆虫群落形成授粉生态弹性(图5D)。然而,网络变化后

传粉功能受昆虫的传粉效率和访花频率的影响,而访花频率又受开花植物和传粉昆虫间物候性状的匹配性、开花植物的特化程度以及它们之间互作关系的影响(Garibaldi et al, 2015; CaraDonna et al, 2017; Kaiser-Bunbury et al, 2017)。因而,传粉昆虫是否形成授粉生态弹性还取决于网络变化后开花植物的传粉昆虫群落结构。例如,传粉昆虫物种或多度下降后,传粉昆虫间的竞争作用降低,增加了传粉昆虫访问其他开花植物的概率。传粉昆虫对开花植物的忠诚度(floral fidelity)下降,同一开花植物间的花粉传播数量下降(Brosi & Briggs, 2013)。又如,网络变化后春美草(*Claytonia virginica*)的传粉昆虫访花频率大幅下降,传粉功能冗余度降低,为开花植物提供的传粉功能降低(Burkle et al, 2013)。在此条件下,网络变化后传粉昆虫未能使生态系统的传粉功能保持不变或维持在可接受的水平,传粉昆虫群落未形成授粉生态弹性。因此,传粉昆虫是否形成授粉生态弹性还取决于网络变化后传粉昆虫群落结构。

3.5 跨尺度弹性假说

跨尺度弹性是指不同空间或时间尺度下传粉的功能团为开花植物授粉而引起传粉功能弹性的生态现象(图6) (Peterson et al, 1998; Nash et al, 2014)。以空间尺度为例,不同传粉功能团空间传粉范围可能存在交叉或重叠(图6A)。在空间尺度内(within-scale),不同功能团提供多样性的传粉服务;在空间尺度间(cross-scale),不同功能团重复传粉加强传粉功能(Peterson et al, 1998)。尺度内多样性的传粉功能和尺度间增强的传粉功能共同促使形成授粉生态弹性(Allen et al, 2005)。当干扰作用下部分传粉功能团多度下降时,不同搜索范围的、功能冗余的其他传粉功能团补偿传粉功能,形成跨尺度的传粉功能冗余(cross-scale redundancy) (Allen et al, 2005)。理论假设认为,授粉生态弹性与跨尺度传粉功能冗余相关,跨尺度传粉功能冗余越高,授粉生态弹性越强(图6C, D)。对开花植物来说,虽然干扰后传粉昆虫群落组成发生变化,但传粉功能保持不变或维持在一定水平,传粉昆虫形成授粉生态弹性(图6C, D) (如: Sundstrom et al, 2018)。由此可见,跨尺度弹性假说在生态系统水平上解释传粉昆虫的授粉生态弹性,其内涵整合了功能冗余假说、密度补偿假说和响应多样性假说。

图6 跨尺度弹性引起授粉生态弹性的机制示意图。在生态系统中, 假设空间分布的开花植物a、b、c、d、e和f存在大、中、小3种传粉功能团, 传粉功能团空间传粉尺度(或空间搜索范围)分别约为300 m、1,000 m和1,500 m, 个体大的传粉昆虫空间跨尺度为开花植物传粉(A)。3种传粉功能团在个体大小(body size)轴上形成不连续性的分布(B)。开花植物a接收3个传粉功能团传粉, b、d和f接收2个传粉功能团传粉, c和e仅接收1个传粉功能团传粉, 因此开花植物a的传粉功能团跨尺度传粉功能冗余程度高于其他开花植物(C)。以开花植物a为对象, 当某搜索范围(如300 m)的传粉功能团访花密度下降时, 其他尺度(如1,500 m)的传粉功能团增加访花密度, 传播等量花粉, 形成授粉生态弹性(D)。在(C)和(D)中, 线条长度示意对应的传粉昆虫空间传粉范围, 线条宽度示意传粉昆虫空间传粉功能。

Fig. 6 Conceptual diagram showing the mechanical effect of cross-scale resilience on ecological resilience of pollination. The ecosystems are hypothesized to have three functional groups with large (1,500 m), medium (1,000 m) and small (300 m) spatial scales (i.e., foraging ranges), respectively, and they pollinate flowering plants a, b, c, d, e and f spatially distributed in ecosystems. The large-sized functional groups pollinate plants across scale (A). The three functional groups of pollinators are distributed discontinuously along the x-axis of body size (B). Flowering plant a is pollinated by three functional groups, flowering plant b, d and f are pollinated by two functional groups, and flowering plant c and e are pollinated by just one functional groups. Therefore, the level of cross-scale redundancy of pollinator assemblages for plant a is higher than that of other plants (C). If the visit density of a certain functional group of pollinators with a specific foraging range (e.g. 300 m) declines (e.g. plant a), other functional groups of pollinators with a large spatial foraging range (e.g. 1,500 m) increase their visit densities. The amount of pollens delivered by the pollinator assemblages on the stigma surface of plant a is similar. The pollinator communities have the ecological resilience of pollination (D). In (C) and (D), the lengths of lines corresponding to the pollinators indicate the foraging ranges of pollinators and the widths of lines quantify their pollination functioning.

已有的研究并没有系统完整地验证跨尺度弹性假说的合理性, 相关工作仅证实跨尺度弹性模型

的部分内容, 主要体现在传粉功能团的个体大小分布、空间传粉范围和跨尺度授粉功能三个方面。(1)

生态系统中传粉功能团的个体大小在异质生境中形成多尺度的、非连续性的分布(multi-scaled and discontinuous distributions) (Holling, 1992; Allen et al, 2005)。野外数据表明, 生态系统中哺乳动物、鸟类和鱼类不同功能团的个体大小在资源轴上并非连续性分布, 而呈现聚集特征(Allen et al, 2005; Wardwell et al, 2008; Nash et al, 2014)。虽然理论认为传粉昆虫在个体大小轴上同样会呈现非连续分布现象(图6B), 但以传粉昆虫为对象的研究却少见报道。(2)通常情况下, 个体大的传粉功能团有更大的空间传粉范围(Greenleaf et al, 2007), 不同的传粉昆虫空间传粉范围形成交叉或重叠, 具跨尺度授粉现象(图6C)。雷达追踪实验表明, 不同熊蜂空间搜索范围存在交错区域, 因而可在多个空间尺度上为开花植物授粉(Hagen et al, 2011)。(3)传粉昆虫跨尺度授粉保障开花植物传粉需求(图6C, D) (Peterson et al, 1998; Sundstrom et al, 2018)。已有的研究利用传粉功能团空间飞行距离不同的特点, 发现了生态系统中传粉昆虫跨尺度授粉现象, 并因此保障开花植物传粉需求(Klaus et al, 2021)。然而, 跨尺度授粉的生态功能研究目前仍十分缺乏(Williams et al, 2019)。

Winfree等试图探讨跨尺度弹性对生态系统传粉功能的影响, 但其研究仅揭示传粉昆虫对自然生境的响应多样性现象, 并未探讨跨尺度弹性的形成机制(Winfree & Kremen, 2009)。Klaus等(2021)发现, 自然生境中的独栖性传粉昆虫为近处的蓝翅草(*Phacelia tanacetifolia*)授粉, 而自然生境中的熊蜂和蝇类却能为远处的蓝翅草授粉, 熊蜂和蝇类的跨尺度授粉行为保障了远处蓝翅草的传粉需求。但Klaus等(2021)的工作仅证实了不同距离下传粉功能团的传粉行为, 未量化授粉生态弹性, 也未探讨个体大小的非连续分布现象, 因而同样未能探讨跨尺度弹性的形成机制。就目前的结论来看, 跨尺度弹性机制的研究多停留在理论探讨阶段, 验证工作十分有限(Winfree, 2013; Williams et al, 2019)。

4 展望

研究传粉昆虫的授粉生态弹性首先需要量化授粉生态弹性。因为理论假说认为生态弹性受物种多样性的影响, 所以目前学者多以物种多样性指数

(如物种丰富度或Simpson指数)来量化生态弹性(Fischer et al, 2007; Karp et al, 2011; Martin et al, 2019)。但是传粉昆虫授粉生态弹性量化方法和标准并未得到统一认可。已有的生态弹性量化方法仅考虑到授粉生态弹性的部分内涵, 如生态系统中传粉昆虫群落动态, 并未综合考虑授粉生态弹性的生态意义, 未将传粉功能纳入量化内容, 因而这些量化方法不能完整揭示授粉生态弹性的形成机制(如: Karp et al, 2011; Martin et al, 2019)。由于授粉生态弹性关注传粉昆虫群落与传粉功能的关系(图1), 因此授粉生态弹性的量化方法应该包含传粉昆虫群落动态和传粉功能动态两部分内容。传粉功能动态的量化指标, 如柱头花粉沉降数量、结实率和结果率的变化等, 将是量化授粉生态弹性的重要内容。传粉昆虫授粉生态弹性的量化方法中纳入传粉功能等指标将更符合Holling (1973)对弹性的定义, 如何整合传粉昆虫群落指标和传粉功能指标将是量化授粉生态弹性的重要研究内容。

理论假说认为, 外界干扰下生态系统传粉昆虫群落组成发生变化, 传粉昆虫授粉生态弹性在一定程度上保障传粉功能。田间实验表明, 在干扰强度持续增大的条件下, 生态系统传粉服务功能将不能满足开花植物的传粉需求(Kremen et al, 2007)。然而, 传粉昆虫的授粉生态弹性随干扰强度的动态变化规律目前还不清楚。在干扰强度持续增大的情况下, 授粉生态弹性是线性增长, 还是与干扰强度成幂函数关系? 在不能满足开花植物传粉需求的临界点, 干扰强度是多大? 此时授粉生态弹性引起的传粉功能占全部传粉功能的比率是多少? 此外, 不同类型的干扰(如土地类型变化、气候变化)对授粉生态弹性存在协同作用吗? 弄清楚这些科学问题有助于判定授粉生态弹性的发生条件、形成阈值和动态规律。以密度补偿为例, 研究干扰强度梯度变化下(如土地类型变化)不同传粉功能团间的密度补偿动态及其引起的传粉功能动态, 有望揭示授粉生态弹性的形成条件及其对干扰的响应规律。

已有的工作多以水生生态系统的鱼类、陆地生态系统的爬行动物和鸟类为研究对象, 探讨生态系统内生态弹性动态规律(Forys & Allen, 2002; Fischer et al, 2007; Nash et al, 2016)。授粉生态弹性的研究目前多处于理论探讨阶段(e.g. Dicks et al,

2012; Tschamntke et al, 2012), 还没有研究系统证实功能冗余机制、密度补偿机制、响应多样性机制、连接周转机制和跨尺度弹性机制对授粉生态弹性的影响, 更缺乏同一生态系统中不同尺度上授粉生态弹性的研究。同时, 理论研究多关注生态系统水平上(如连接周转)的作用机制, 而对小尺度上的作用机制(如功能冗余和密度补偿作用)的关注相对较少。随着研究的深入, 不仅有望证实不同假说的合理性, 而且有望阐明不同假说间的联系。

授粉生态弹性对管理农林生态系统传粉功能具有重要的指导意义。农林生态经营者可以根据授粉生态弹性理论来判断在何种情况下干预生态系统的传粉功能, 同时判断干预方向和干预强度。例如, 传粉昆虫多样性下降时, 群落结构的变化可以使农林生态系统传粉功能保持在一定水平。仅从维持传粉功能的角度来说, 并不因传粉昆虫种群数量的下降而直接干预生态系统传粉。随着授粉生态弹性理论的发展和成熟, 人们将对生态系统传粉昆虫群落结构和传粉功能有更深入的了解, 在授粉生态弹性理论上判定传粉功能管理的临界点。在此基础上, 授粉生态弹性理论有望纳入农林生态系统综合管理的技术体系。

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