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PII: S2214-5745(16)30116-X
DOI: http://dx.doi.org/doi:10.1016/j.cois.2017.05.012
Reference: COIS 335

To appear in:

Received date: 17-1-2017
Revised date: 8-5-2017
Accepted date: 10-5-2017

Please cite this article as: Bryony K. WillcoxMarcelo A. AizenSaul A. CunninghamMargaret M. MayfieldRomina Rader Deconstructing pollinator community effectiveness (2017), http://dx.doi.org/10.1016/j.cois.2017.05.012

Highlights

- We propose a new, additional community level property of pollination effectiveness
- This will facilitate connections among pollinators, plants and the environment
- This will require multiple methods and greater integration among research fields

Deconstructing pollinator community effectiveness

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ABSTRACT

Effective pollination is a complex phenomenon determined by both species-level and community-level factors. While pollinator communities are constituted by interacting organisms in a shared environment, these factors are often simplified or overlooked when quantifying species-level pollinator effectiveness alone. Here, we review the recent literature on pollinator effectiveness to identify the pros and cons of existing methods and outline three important areas for future research: plant-pollinator interactions, heterospecific pollen transfer and the variation in pollination outcomes. We conclude that there is a need to

acknowledge a new, additional community level property of pollination effectiveness (i.e. pollinator community effectiveness) in order to account for the suite of plant, pollinator and environmental factors known to influence different stages of successful pollination.

Introduction

Pollinator communities include native and introduced bees, flies, beetles, moths, butterflies, and birds among other taxa. These taxa provide pollination services for between 78 and 94% of all wild flowering plants and about 75% of the leading global food crops [1-3]. While pollinator communities are constituted by interacting organisms in a shared environment, these factors are often simplified or overlooked when quantifying species-level pollinator effectiveness alone.

Effective pollination is a complex phenomenon determined by both species-level and community-level factors. The effectiveness of a given pollinator species is influenced by species-level (e.g. pollinator density, morphology and behaviour; flower morphology and display size) as well as community-level factors (e.g. pollinator species diversity and species interactions; plant competition for pollinators; Fig. 1). Pollination failure can result from problems at any or all of these stages of pollination [4].

Here, we review the recent literature on plant and pollinator factors that impact pollinator effectiveness at species and community levels. Given the breadth of pollination studies across a range of natural and modified ecosystems, we attempt to derive general patterns and provide future research directions by focusing on well-studied crop systems. We identify the pros and cons of existing methods to determine pollinator species–level effectiveness, discuss the need to adapt existing methods and develop new methods, and outline three important research areas: plant and pollinator community interactions, the importance of heterospecific pollen transfer and the need to account for the variation in pollination outcomes. We conclude that there is a need to acknowledge a new, additional community level property of pollination effectiveness (i.e. pollinator-level community effectiveness; Fig. 1) in order to account for the suite of plant, pollinator and environmental factors known to influence different stages of successful pollination.

Factors known to influence successful pollination

It is well established that pollinators play a significant role in the provision of crop pollination ecosystem services worldwide [5]. However, there is less widespread appreciation that pollinator communities are not all equally effective at pollinating all plant species. Effective pollination results from a complex assortment of factors that influence different stages of the pollination process, operate at different spatial scales and stem from life history features of pollinators, plants and the complex interplay of these mutualisms.

Plants and pollinators directly affect the timing, amount and quality of pollen deposited and ultimately, plant population dynamics over time [6-11]. While pollinator constancy to one plant species is thought to be common among bees and some non-bee taxa [12-13], different taxa, and even individuals within a given species, may switch from visiting one (specialists) to many plant species (become generalists) in response to flower availability, floral preferences, flower characteristics and reward quantity and quality [7, 14-16]. At broader landscape and regional scales, pollinators respond to their surrounding environment and the availability of floral and nesting resources, especially the presence (or lack) of specific landscapes elements and nesting and foraging habitat [17-19].

After pollen deposition has occurred, pollen-pistil and pollen-pollen interactions on the stigma and in the style can have major impacts on final reproductive outputs [20-22]. Pollen grains deposited on stigmas represent populations of male gametophytes subjected to different density-independent and -dependent mortality processes that will determine ovule fertilization success and seed output [23]. Critical factors affecting these postzygotic processes are the amount and timing of pollen deposition as well as the genetic composition of the stigmatic pollen load.

Pros and cons of the visitation-based pollinator performance method

Despite the complex set of factors known to impact pollinator performance, pollination efficiency and effectiveness, it is rare for studies to incorporate even a small number of these factors. The most common approach currently employed to study pollination effectiveness is the visitation-based pollinator performance method [24]. This method focuses on pollinator performance and relies on documenting relative differences in pollinator foraging behaviour, visit frequency and per-visit pollen deposition. Visit frequency is often reported as one of the most important variables for determining plant reproductive success on a per-interaction basis. Per-visit pollen deposition is a commonly used method to assess relative differences in the performance of individual pollinator taxa [24-27]. This involves allowing an animal pollinator to visit a flower once and counting the number of conspecific pollen grains deposited on the visited flower's stigma(s) (i.e. per-visit pollen deposition).

There are, however, several shortcomings with these approaches. First, per-visit methods are laborious and time-consuming to carry out. It can be challenging to coax pollinators to visit test flowers, and there is potential for pollinators to behave differently (timid and cryptic) in the presence of researchers. Second, increasing visitor frequency or the amount of pollen transferred does not always improve pollination. High visitation frequencies can fail to benefit plant reproduction when, for example, a single pollinator visit is sufficient for a given plant to set fruit [28], when the transfer of large amounts of pollen results in high rates of pollen tube abortion due to scramble competition (e.g. competition between pollen tubes growing toward an ovary) [23], and/or when the transfer of low quality pollen results in reduced seed set [e.g. 6]. Finally, the benefits of increased visitation are dependent on the identities of the taxa involved [29] and can also be detrimental if visits increase the risk of pollen theft [6], nectar robbery [30], and flower damage [31-32].

While per-visit pollen deposition and visit frequency are valuable to compare the relative contributions of different pollinator taxa visiting common plant species [reviewed in 26], these approaches are not well suited to broader questions about pollinator performance and pollination success. First, visit frequency and per-visit pollen deposition alone are insufficient to ascertain whether the pollen transferred is of sufficient quality or quantity to result in plant reproduction. At the scale of individual plants, developing fruits may be aborted for reasons unrelated to pollen limitation [e.g. 22, 33-34]. In these cases, plants may re-allocate limiting resources and selectively mature fruits from flowers in which there has been greater pollen deposition and hence more pollen competition for access to ovules [35-36]. At broader scales, surrounding environmental and landscape conditions (e.g. drought, limiting nutrients) can also drive variation in fruit quality or quantity [22, 37-38; Fig 1].

Comparing per-visit fruit set among taxa is effective only for those plants and pollinator taxa for which a single visit is sufficient to result in fruit set. Some plant taxa need a minimum number of pollen grains (and hence multiple visits by some pollinators or many grains deposited in a single visit) in order to set fully formed fruits. In such cases, multiple visit comparisons (whereby fruit set is measured per number of visits for each taxon) are required if the aim is to determine the most efficient taxa at a given time and place as measured by fruit/seed production.

Important research directions

The standard approach to assessing pollinator effectiveness has many advantages and will undoubtedly remain a key component of pollination efficiency studies in the future. That said, the shortcomings with this method, detailed above, show that we lack knowledge about when and under what circumstances this method provides reasonable estimates of pollination efficiency and when alternative or modified approaches are needed. To improve upon the standard approach of assessing pollinator effectiveness we suggest three important research directions to fill gaps in our understanding of the factors affecting effective pollen transfer and to build a broader foundation of protocols for assessing pollination effectiveness across systems and taxa.

1. Incorporating pollinator and plant community interactions into assessments of pollinator effectiveness

Across whole communities, competitive or facilitative interactions among pollinators can increase or decrease fruit set in plants [39-40]. This is because pollinators interact in a variety of ways while pollinating. Simple encounters between pollinators before visiting a specific flower can alter visitation sequence, or prevent a pollinator from visiting at all [39-41]. For example, other bees can cause honey bees to move more often between rows of sunflower (*Helianthus annuus L.*), increasing the number of seeds produced per visit [41]. Furthermore, several correlative studies at the community level suggest that the diversity of pollinator functional groups accounts for more of the variance in seed set than species richness or abundance [42-44].

The acknowledged importance of pollinator interactions has resulted in an increasing number of studies on pollination interaction networks [e.g. 17, 45-46]. Most plant-pollinator network studies however, focus on visitation rates or pollen transfer alone in the absence of how these factors relate to plant reproduction per plant, or unit area [but see 17]. Incorporating functionality measures into networks, such as average pollen deposition on stigmas [47], is a promising step forward. However, given the current limitations of pollen deposition studies, an additional approach may be to focus on per-visit or multiple visit fruit or seed set measures in plant-pollinator network studies and relate plant pollinator interactions directly to pollination success.

2. Heterospecific pollen transfer

In many cases, individual flowers are visited by more than a single pollinator during their receptive period. When this occurs, the identity of pollinators, their foraging behaviour and the sequence of different pollinators determines the quantity and composition of stigmatic pollen loads [7, 16, 48-50]. Pollinator sharing, which is the primary way that heterospecific pollen is transferred, can be beneficial to plant reproduction when the presence of other flowering plants attracts more pollinators to a plant community [51-55]. Pollinator sharing can also be detrimental when, for instance, heterospecific pollen transfer is extensive [20-21]. As the number of visited plant species increases [e.g. >8 species; 56] so does the probability that heterospecific pollen will negatively impact plant reproduction [57].

Owing to the challenges of studying plant-pollinator interactions, pollination research has traditionally focused on specific stages of the pollination process or plant reproduction as a whole. For example, crop pollination studies have largely focused on the link between pollinator visitation rates and per-visit deposition on fruit set and quality [29, 58] and have overlooked the role of post-pollination processes, such as heterospecific pollen transfer on fruit quantity and quality [20-21]. Plant evolutionary ecology studies of pollination, on the other hand, tend to focus on post-pollination processes, such as selective seed abortion, but pay less attention to pre-pollination processes of visitation and per visit pollen transfer rates [e.g. 20-21]. Several studies have investigated the effects of heterospecific pollen transfer on plant reproduction, but these have relied on hand pollination, an approach that fails to advance knowledge on impacts of pollinator behaviour [57]. Finally, many studies have looked at foraging behaviour but few of these have also examined resulting pollen deposition on stigmas [9]. In order to advance our understanding of the mechanisms governing pollination-mediated variation in fruit quantity and quality, studies are needed that combine studies of pre- and post-pollination processes along with pollinator foraging behaviour.

Meta-barcoding pollen is one emerging technology that may provide a pathway for studying pre- and post-pollination within the same study system. Unlike traditional manual pollen identification methods [24], meta-barcoding can facilitate the faster identification of heterospecific pollen by allowing numerous samples to be run simultaneously. This method has recently been successfully used to quantify pollen loads on honey bees and wild bees [59-60], but is yet to be used to identify heterospecific pollen on stigmas [61]. Meta-barcoding is still hampered by a number of limitations in that it cannot yet be used to identify or quantify amounts of conspecific pollen on floral stigmas of the same plant species, quantify abundances of heterospecific species and large reference collections are required. Thus, a combination of traditional light microscopy methods and meta-barcoding technology may be the best approach for detailed studies of pollen deposition in natural systems.

3. Accounting for variation in pollination outcomes

The importance of pollinators in shaping patterns of plant reproduction could diminish when fruit and seed production is strongly limited by plant resources. However, understanding the interaction between plant reproduction and resource limitation is challenging due to the diversity of reproductive strategies represented across plant species as well as the variability in the reproductive responses of plants to environmental stress [22, 62-64]. Depending on the life history strategies of a species, plants can alter resource allocations to fruits and seeds [e.g., 65], depending on environmental conditions and regardless of pollination.

Nutrient deficiencies [38] and pest damage [22, 66] are broadly recognised to result in fruit abortion in some species. In some horticultural crops, notably kiwi, blueberry and oilseed rape, these factors have been successfully countered with fruit thinning, increased pest and disease management and the application of Nitrogen fertilizers [63, 67-68]. These solutions are largely crop species dependent, however, with the same approaches failing to reduce fruit loss in other crop species [64, 69].

One way forward could include conducting a greater number of experimental studies that investigate the relative contribution of pollination-related factors versus environmental factors (soil nutrients and water availability; see Fig 1). In combination with experimental work, the use of more sophisticated statistical tools such as structural equation modelling could facilitate identification of the major factors impacting variation in fruit production [70-71].

Conclusions

In conclusion, a more holistic understanding of community ecology is required to understand the connections among pollinators, plants and the surrounding environment. This will require the use of multiple methods simultaneously and greater integration among research fields. Future studies are required to quantify the variability in the study system to better understand the underlying mechanisms by which environmental conditions, and plant/pollinator species and community factors impact pollen transfer and ultimately, plant reproductive success.

Acknowledgements

B.K.W. was supported by a PhD scholarship from the University of New England and funded by RnD4Profit-14-01-008 “Multi-scale monitoring tools for managing Australian Tree Crops:

Industry meets innovation". R.R. was supported by the Ian Potter Foundation (ref:20160225), a Rural Industries Research and Development Corporation grant for the project "Secure Pollination for More Productive Agriculture (RnD4Profit-15-02-035)" and an Australian Research Council Discovery Early Career Researcher Award DE170101349. M.A.A. was supported by a grant from the National Fund for Research of Argentina (PICT 2015-2333).

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Box 1: Glossary of terms

Pollination: Pollination in angiosperms involves the release of pollen from the male parts of a flower, transport from the pollen source to the pollen recipient and deposition of the pollen on a floral stigma

Pollination success: Pollination is successful when pollen deposition on the stigma is followed by germination of the pollen grain and then by fertilization of the ovule/s. Pollination success is often measured as pollen germination, seed set or fruit set

Pollinator species-level effectiveness: This is a pollinator species-level trait used to compare the relative performance of individual pollinators to a given plant species. It describes the amount of pollen transferred to a floral stigma in a single visit and is usually measured either as the amount of pollen transferred or the fruit /seed set resulting after a single visit to a virgin floral stigma. This term is sometimes synonymous with pollinator efficiency, although pollinator efficiency considers the total contribution of a given pollinator species to pollination by multiplying pollinator effectiveness times visitation frequency.

Pollinator community-level effectiveness: This term defines a pollinator community level trait that describes the effectiveness of an entire pollinator community at a given space and time for one plant species. A given pollinator community may be effective for some plants and not for others in the same area given not only to the matching of the average pollinator traits and the plant trait, but also to all the indirect interspecific effects that can modify pollinator behaviour and plant attraction. This definition could be extended to the overall effectiveness of a given pollinator community to the whole plant community in the context of a plant-pollinator network and be taken as an overall measure of pollination efficiency.

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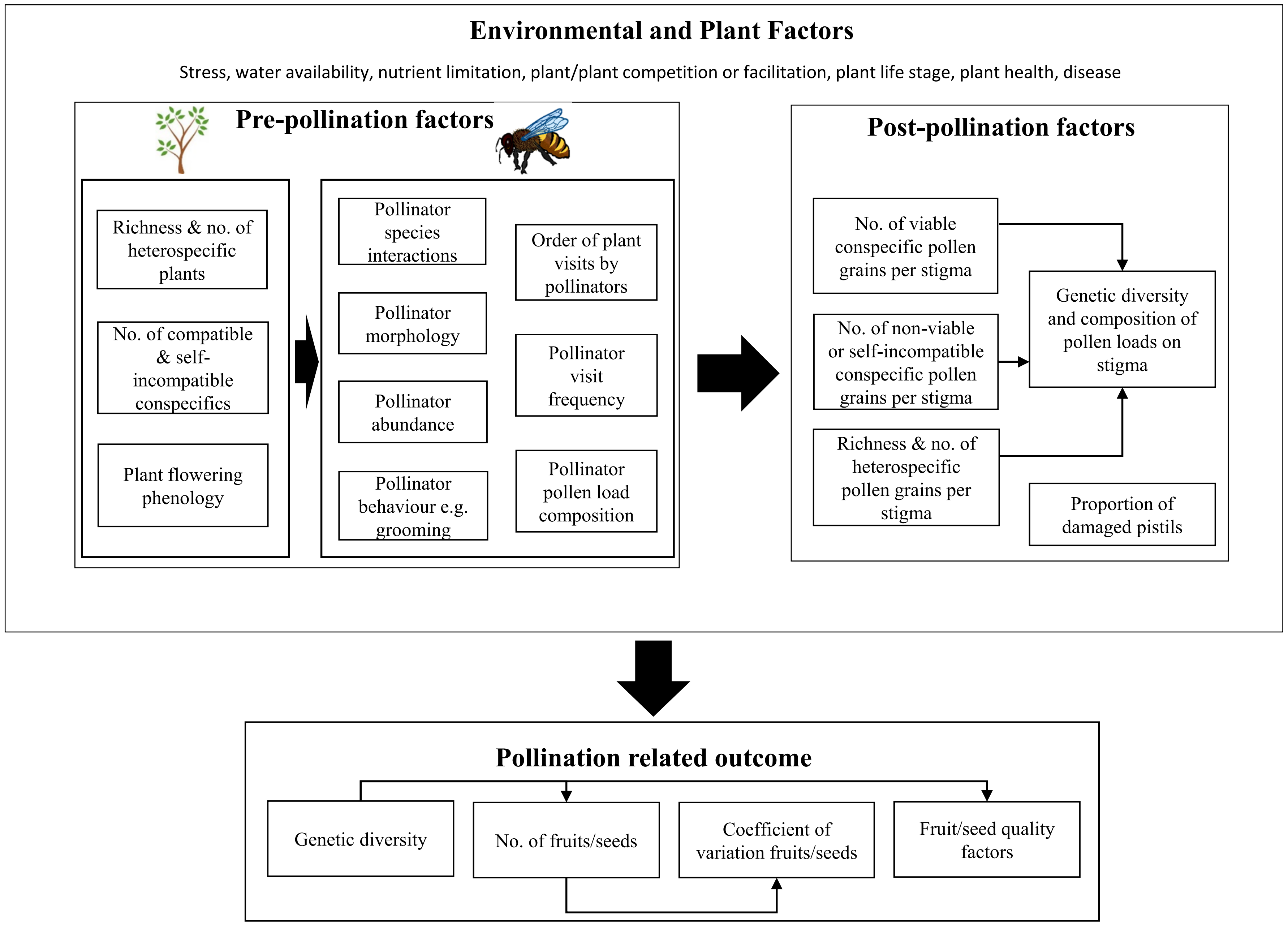
Environmental and Plant Factors
Stress, water availability, nutrient limitation, plant/plant competition or facilitation, plant life stage, plant health, disease
Pre-pollination factors
Richness & no. of heterospecific plants
No. of compatible & self-incompatible conspecifics
Plant flowering phenology
Pollinator species interactions
Pollinator morphology
Pollinator abundance
Pollinator behaviour e.g. grooming
Order of plant visits by pollinators
Pollinator visit frequency
Pollinator pollen load composition
Post-pollination factors
No. of viable conspecific pollen grains per stigma
No. of non-viable or self-incompatible conspecific pollen grains per stigma
Richness & no. of heterospecific pollen grains per stigma
Genetic diversity and composition of pollen loads on stigma
Proportion of damaged pistils
Pollination related outcome
Genetic diversity
No. of fruits/seeds
Coefficient of variation fruits/seeds
Fruit/seed quality factors