Floral evolution: Beyond traditional viewpoint of pollinator mediated floral design

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Abstract Pollination biology provides new insight for understanding the evolutionary mechanism and process of the existing diversity in floral design of angiosperms. Evolutionary biologists have established some rules and models to try to explain the ubiquitous relationship between pollination system and floral evolution. However, as new techniques have been applied and more and more new pollination events found in recent years, the relationship between pollination system and floral evolution becomes less clear. Researchers realized that floral evolution is more complicated and idiosyncratic than simple adaptive models. The traditional viewpoints on pollinator mediated floral design urgently need a reevaluation. This paper attempts to make a brief review of such main opinions and introduce their new insights according to recent studies. Finally, we also give some suggestions for future study by reviewing several new viewpoints about floral evolution.

Keywords: floral evolution, pollination, review.

DOI: 10.1360/982005-1084

High diversity of floral design in angiosperms provides ideal materials for studying adaptive evolution. This is clearly demonstrated by the fact that Darwin supported his new hypothesis of natural selection by focusing on floral design and function in the flowers of orchids[1] and other angiosperm species[2]. Nowadays, the adaptive analysis of floral evolution has become an active area of evolutionary research[3]. The rise and development of pollination biology is a process that continuously provides new insight into floral evolution[4-7]. Analyses based on interaction of floral evolution and pollination usually explain well the rationality and significance of the surprisingly high diversity in floral design. However, pollination biology is encountering a period with rapid development and renovation because of the infiltration of new techniques and findings into this area. More and more studies show that besides pollination, floral evolution has undergone a conflicting selection pressures[8], at the same time, the pressure of pollination system shows significantly different results among different taxa[9]. Thus, it is important to reevaluate the objective role of pollination system in influencing the direction of floral evolution. This paper attempts to make a brief review of traditional viewpoints and introduce the new developments and reevaluations in these viewpoints brought about by results of recent studies. We thereafter proceed to offer some suggestions for future study by reviewing several new progresses in research on floral evolution.

1 Traditional viewpoint of relationship between floral evolution and pollination

A classical topic of floral evolution is pollinator-shaped floral design[10,11]. Pollination biologists have obtained sufficient data to indicate that the type and behavior of pollination media influence significantly the evolution of flower structure, mating system and reproductive success[12-14]. Pollination is a prezygotic process, the evolutionary results of reproductive system due to selection pressure of pollination mainly concentrated on the flower architecture. The intensity and rapidity of such selection pressure are more obvious for the taxa with specialized pollination systems[15,16]. In one of the most influential studies, Grant and Grant[17] concluded that “a lock and key relation between flowers and pollinators is widespread and probably universal in the phlox family”. Traditional opinion pursued the argument that there should exist phenotypically co-adaptive traits between floral design and pollination system.

Another unfading viewpoint about pollination and floral evolution is that flower should evolve toward a certain pollination mechanism and tend to form a specialization pollination system[18-20]. This view mainly came from studies on the tropics and the species-rich temperate floras of the Southern hemisphere in which plants are documented with pollination systems that are remarkably specialized, often involving a single pollinator species[21]. Even for plants with generalization pollination systems, Stebbins[22] established the “most effective pollinator principle (MEPP)”, which suggested that the most effective pollinator shaped the evolutionary direction of floral evolution. Those hypotheses argued that the natural selection pressure of pollinator is the most important factor influencing floral evolution, and there should be a stable and specialized system between plants and their pollinators. Such selection pressure must be the main driving force behind plant speciation.

2 The development and reevaluation of several traditional viewpoints

However, as more and more new pollination events have been reported, it has become clear that the “one-to-one” pollination systems are much less common in nature than were originally thought to be. The traditional viewpoint of pollination biology is thus encountering strong challenge; some mainstream ideas such as the evolutionary direction and mode of pollination system, the pressure the pollinator imposes on floral evolution, and the role of...
pollination system in plant speciation must be reevaluated\(^{[12,14,16–23]}.\)

2.1 Specialization and generalization pollination systems

Although earlier studies tend to suggest that greater degrees of specialization existed in the pollination system in plant-pollinator interaction, actually, it has now been realized that the pollination event in nature is really a continuum between plants pollinated by literal hundreds of pollinator species and those pollinated by just one pollinator species\(^{[14]}.\) Plants with different life form, dispersal pattern and habitat own their relatively adaptive pollination system, but are not entirely evolved towards specialization pollination systems\(^{[16,18–29]}\).

A generalized pollination system also has its obvious evolutionary significance even though a specialized pollination system was regarded as a mechanism enhancing reproductive output. Plants with specialization pollination systems will undoubtedly stand a higher risk in the event of loss of the single pollinator species, while plants with relatively generalized pollination systems might be resilient to the alteration of some pollinator species\(^{[24]}\). For example, it is hard to imagine that the loss of any one of the 26 moth species that pollinate *Silene vulgaris* would be of much ecological consequence for the plant population\(^{[25]}\). But then, the collapse of a mutualism does not mean that the plant will not go through the lurch. Bond\(^{[24]}\) pointed out that many plants with highly specialized pollination systems have evolved compensatory mechanisms such as clonality, longevity and facultative self-pollination when loss of the pollinator occurs\(^{[26]}\).

According to the divarication of floral evolution response to generalization or specialization in the pollination system, Fenster et al.\(^{[27]}\) suggested that we must distinguish the two concepts of "ecological specialization" and "evolutionary specialization" with regard to floral evolution. The former indicates that the flower is responsive to the current pollinator fauna, while the latter concept implies that it is responsive to all the potential pollinators in the evolutionary history of the species. Exceptional events found in the current population do not indicate that selection pressure of pollinators has no influence on floral evolution. Herrera\(^{[28]}\) also pointed out that pollinator composition of plants with generalization pollination systems is a character closely related to spatio-temporal traits, but not a stable phenomenon at the level of species. Fenster et al.\(^{[27]}\) also brought about the concept of "pollinator functional group" for species with many pollinators. Floral specialization is adapted to a group of pollinators with similar selection function, but not in response to a single pollinator species. From different levels (intraspecific, interspecific, and at the levels of high taxa), they deduced that the selection pressure of floral specialization must come from pollination system.

2.2 Most effective pollinator principle (MEPP)

Ollerton\(^{[18]}\) discussed a contradiction in nature that flowers with obvious characteristics adapted to specialized pollination are usually pollinated by many kinds of animals. Such floral specialization is always ascribed to the “most effective pollinator principle". However, studies have shown that the difference in pollination efficiency is neither sufficient nor necessary for floral specialization\(^{[29]}\). The formation of specialization pollination systems due to differences in various pollinators has been reported in taxa in certain environments, but it is not sufficient to deduce from these cases that MEPP plays a primary role in floral evolution\(^{[29]}\). For example, if plants pay out less resource investment but receive similar reproductive success when adapting to less effective pollinators, the direction of floral evolution will not be influenced by most effective pollinators. Another obvious fault of MEPP is that it actually cannot form a stable selection pressure because such most effective or sufficient pollinators will vary significantly among different spatio-temporal populations\(^{[29]}\). The actual reasons behind the couple of contradictions might be that (i) only a small part of the pollinator fauna is effective\(^{[29,31]}\); (ii) all the pollinators have a similar pollination function and a coincident selection pressure\(^{[24]}\); and (iii) such pollinators just do not have strong pollination function and selection pressure\(^{[23]}\).

2.3 Pollinator shaped the evolution of flower

Floral specialization due to pollinator selection has been reported in some taxa\(^{[12,13]}\). However, trying to generalize this pattern to floral evolution of angiosperms will be inaccurate to some extent for many taxa\(^{[14,18]}\). Firstly, the interaction of plant and pollinator will be intrinsic and indirect. Secondly, floral form also responds to many other selection factors.

Many “irregular cases” have been reported in floral evolution and pollination in recent years\(^{[16,17,20,22,23]}\). For example, plants (*Viola cazorlensis*) with spur flowers are pollinated exclusively by a day-active hawkmoth. Experiment on pollinator choice did not influence significantly the spur length; the selection by pollinator should potentially affect the male function, but not the phenotypic traits\(^{[16]}\). Working on lavender (*Lavandula latifolia*), Herrera\(^{[17]}\) found that pollinators frequently ignore the artificially misshapen lavender flowers and pollinate them as successfully as the normal flowers. He then concluded that the entire mint family had likely developed the current corolla before they met up with these modern pollinators. In another study, Herrera and his colleagues indicated that the flower variation between populations of *Helleborus foetidus* could not be attributed to the difference in pollination system, but should be explained as a consequence of random genetic sampling in the characteristically small and ephemeral populations of this species,
rather than the result of the selective action of current pollinators. In an innovative study, Armbruster failed to find a tight evolutionary link between pollinators and bract color in Dalechampia. Instead, he concluded that new Dalechampia bract colors likely evolved simply as a byproduct of the protective vegetative pigments, not in response to the pressure of major pollinators, which remained unchanged at that time in the historical record.

Moreover, floral evolution not only responded to pollination function, but also underwent more complicated and idiosyncratic selection factors than previously thought. Many parts of a flower can be involved in more than one function. For example, showy petals might attract pollinators during the day but might protect other floral organs from rain or herbivores at night. If selection pressures on flower with multiple functions are in conflict, floral form will evolve as an adaptive compromise to reflect the net effect of different selection pressures.

2.4 Pollination system and plant speciation

Traditional opinion always tends to explain specialization pollination system as a isolation mechanism, then indicate that pollination selection is one of the main original driving forces of plant speciation. However, people can hardly explain how animal pollinators play their role in plant speciation and maintain the species boundaries for lack of convincing evidence. At the same time, more and more findings in generalization pollination system strongly challenged the theory of pollinator-mediated speciation. Although the existence of the relationship between animal pollinators and rapid plant speciation is undisputed, the origin of reproductive isolation and plant speciation seem not to associate tightly. Isolation mechanism always originates from the adaptive divergence among plants with different distribution areas, while plant speciation is ascribed to a accumulation of genetic variation. Floral adaptation may not be tightly coupled with the formation of biological species in angiosperms. To evaluate the role of pollination system in plant speciation, Waser suggested that “it is time to renew our efforts to explore the manifestation and mechanisms of reproductive barriers at all scales of spatial and phylogenetic separation, to see how directly these barriers map onto discontinuities in floral traits, and thus to consider whether and how tightly the evolution of floral adaptation and speciation are linked, and how animal pollinators are implicated in each”.

3 Integration of new technique and opinion

Up to now, most studies on floral evolution are focusing on the adaptive mechanism of pollination; however, floral function is tightly linked with many other relative factors. According to several recent innovative studies on floral evolution, three aspects of research shown below should be taken into account when floral design shows no obvious linkage with pollination system. Such studies provide new techniques and insights into floral evolution in angiosperms.

3.1 Floral display influence pollination adaptation during floral evolution

Usually, the single flower is the essential unit in studying floral evolution; however, reproductive success is an aggregate process that depends on the reproductive outcomes of all of a plant’s flowers. These reproductive outcomes need not be independent, so that the floral display, rather than the individual flower, should be the fundamental unit of plant mating. Therefore, floral display must be taken into account in studying pollination and floral evolution. Floral display traits significantly affect attraction and the incidence and consequences of joint visitation of flowers; thus they can influence mating outcomes and be subject to natural and sexual selection. Studies on floral display can effectively integrate the evolution of plant pollination and mating system which can account for the evolutionary significance of different architectures and sizes of inflorescence in nature. Moreover, it can provide a more rational understanding of some hitherto perplexing floral traits, such as dichogamy and flower longevity. It is time to go beyond “floricentrism” in studying floral evolution and pollination adaptation in angiosperms.

3.2 The influence of nonpollinating animals on pollination and floral evolution

Studies show that pollination and herbivory rarely operate independently of each other. The ecological consequence of pollinators and herbivores may be linked when they affect the same floral traits. More and more studies have demonstrated that herbivores can affect phenotypic traits related to pollination such as flowering phenology, flower display, floral morphology, flower color, quantity and quality of floral nectar, pollen production per flower, pollen performance, and even the mating system. By affecting these traits, herbivores can shape the interaction between the plants and their pollination mutualists. Therefore attention must be paid to selection due to herbivores in studying the interaction between pollination and floral evolution. On reviewing such kinds of studies, Brown pointed out that the flower is a compromise structure when it falls into a junction of conflicting selection factors.

3.3 Influence of electrostatic pollination on floral evolution

Researchers noticed that electrostatic forces might influence the pickup and deposition of pollen by pollinators and conducted theoretical analysis. It was expected that
when a pollinator approaches a flower, the flower develops an opposite charge to that of the animal, potentially making animal-borne pollen attractive to floral structures and vice versa. This process may significantly enhance deposition of pollen on pollinators and on stigmas. But how floral size and shape affect the electrostatic properties of flowers and how the electrostatic properties affect the delivery of pollen by pollinators was not studied until recently. Using apple pollen and metal models of apple flowers of varying size and shape, Vaknin et al. demonstrated that the size and shape of flowers influence their electrostatic properties and hence the rate of arrival of pollinator-borne pollen on their stigmas. These new data indicate that floral electrostatic properties might influence the floral evolution. Vaknin et al. also showed that electrostatic enhancement of pollination may tend to favor wider, more-open corollas, while selection of pollinators and nonpollinating insects may favor other corolla characteristics. Thus the process of adaptive compromise in flowers may be more complex than we previously thought. Armbruster pointed out that “new investigations into the effects of floral shape and size on the electrostatic properties of flowers and electrostatically ‘assisted’ pollination complement previous and ongoing studies of the effect of floral form on plant mate choice, attraction of animals, and the placement of pollen on, and capture of pollen from, pollinators”.

Acknowledgements  The authors are grateful to Dr. Robert W. Gituru for helpful suggestions and linguistic improvement. This work was supported by the State Key Basic Research and Development Plan (Grant No. G2000046804) and the National Natural Science Foundation of China (Grant No. 30500032).

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(Received July 8, 2005; accepted October 10, 2005)