Review Article

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Plant Attractants and Rewards for Pollinators: Their Significance to Successful Crop Pollination

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ABSTRACT

Plant and pollination have a mutualistic relationship where both parties offer and gain benefits for each other. The plant-pollinator interactions resulted in successful crop pollination in which the plant received pollination services by animal pollinator to increase food production that eventually increase crop economic value. Overall, ecosystem is highly dependent on pollinator thus there is a need to review potential valuation method of crop production and analyse the current understanding of the value of pollination service towards the ecosystem as well as the traits plant offer and benefits that pollinator gain from the relationship. The attractant and rewards highly depending on each other. Plant often able to attract pollinators through traits like the shape, size and colours of flower, deception, scents as well as location. In the meantime, plant would provide a reward for pollinators that visited the flower which includes food from pollen and nectar that contains high nutritional value, energetic rewards to reduce energy cost of survival, protection and shelter against predator and not to forget breeding, oviposition and mating sites inside the flower plant. This review emphasizes the ecological relationship of plant and pollinator that resulting in effective crop pollination if the attractant and incentives are significantly reliant on one another. However, there could be flaws, such as modifications to plant or environmental factors, would affect the rewards supplied and resulting in decrease crop output. With this review and current technological advancements, optimistically deeper investigations in the interaction of pollinator and flowering plant can be conducted and best pollinator management approaches can be established to secure sustainable crops production.

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Introduction

Pollination is the main ecosystem service that responsible for the transfer of genetic information between plants through pollen that is important to support the sexual reproduction of a wide range of crops [1]. The pollination activities usually performed by two types of agents which is biotic and abiotic such as birds, insects, water, wind and gravity that transport these pollens to stigma from anther. Pollination biology is often associated with mutualistic interactions among plants and their animal pollen vectors

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[2]. Plant-pollinator interactions work when pollinators transferring pollen to facilitate plant reproduction while they forage on flower for resources and rewards [3,4]. The relationship between plant and pollinations depends on the quantity of rewards they will receive and these usually correlates with floral trait or display [5]. The plant-pollinator communications include the display of reward attractants such as nectar, pollen, fragrances, oils, shelter, heat or reproduction [6,7] through the signalling of floral attractants with their visual, olfactory, gustatory and tactile signals to enable detection and discrimination by pollinators [8]. Plants have evolved variety of colours, shapes and sizes of flowers or inflorescences to attract animal pollinators [9]. As for the flower visitors, they developed numerous sensory capabilities to handle the floral signalling [10]. Through specific signals, innate and learnt preferences of flower visitors and sensory manipulation [11] in the selective attraction of pollinators and limitation of flower antagonists make communication between flowers and possible pollinators a highly complex and diversified relations [10]. Nevertheless, pollination is needed for the production of a variety of crops for food manufacture and human livelihoods and pollination by animals, especially insects which is a key element of the food chain. This short review highlights certain aspects involved in pollination contributions to food production and rewards gained by pollinators form the service.

Economic Value of Pollination Services

Globally, animal pollination is a major ecosystem service since crops plants representing 35% of the world's food crops production profit from animal-mediated pollination [12]. This mutualistic interaction between plants and animals is necessary by providing welfares to humans mainly in acquiring varied seed and fruit resources, supporting the population of plant diversity and assisting other cultural values [13]. Pollinator-dependent crops are also the core source of numerous micronutrients such as vitamin A and C, calcium, folic acid and fluoride [14]. Meanwhile, pollinators benefit from this interaction by gaining essential foods such as pollen and nectar. Insects mainly bees, flies, butterflies, beetles, wasps, moths, and midges play an important role to provide pollination services worldwide [15]. Among these pollinators, pollination activities primarily provided by Apidae bee species such as honey bees (*Apis mellifera*), some bumblebee species (e.g., *Bombus terrestris* L., *Bombus ignitus* Smith) and stingless bees [16]. In Europe, some beetles pollinate oilseeds and cucurbits, butterflies pollinate blackberry and clovers while certain flies are commercially used to pollinate sheltered crops such as chive, onion, strawberry, carrot and blackberry [17]. The existing information on this pollinator's contribution to pollination services are often inconsistent and inconclusive, as pollination requirements for fruit crops vary depending on the breeding method used. Certain crops are highly self-incompatible, while others may bear fruit with their own pollen. Despite that, there are varieties of fruits crops that depend or profit from animal pollination listed such as kiwifruit, grapefruit, blueberry, cashew, cherry, apple, pear, orange, plum, litchi and tangerine [18]. For tropical fruit, the most common crops that used pollination include citrus, starfruits, papaya, watermelon, guava, coconut, durian and mango [19].

Animal pollination of crop production is provided by both managed and wild pollinators, although most studies have highly valued the services offered by honey bee (*A. mellifera)*. A few studies have attempted to assess wild pollinators despite their ability to assist pollination with honeybees in the event of pollination shortage. Moreover, the service of pollination provided by wild and managed insects is dependent on their numbers and could be improved by diverse pollinator communities. Compared to managed pollinators, native animal species or wild pollinators and insects in certain areas capable of effectively assisting pollination in both agricultural and wild plants, where a variety of pollinators could contribute to sustainable pollination of crops and provide an insurance service to reduce the projected costs of crop failure [20]. However, in the recent years, the delivery of pollination service by wild and managed pollinators has declined progressively but steadily. Studies have shown that with the continuous decreasing in species distributions it is possible that pollination services to crops and wild plants have also reduced [21]. Although studies on pollinator decline are still inadequate, some researcher have highlighted the causes for this decline such as agricultural intensification [22], climate change [23], pesticide and viruses [24], risk from invasive alien species [25], and habitat fragmentation [26], although some of the factors may vary depending upon the type of crops and environmental conditions in the regions.

Pollination service provided from animal pollination hugely benefit crops because there is a significant surge in fruit production, improvement in fruit quality and economic value. In addition, certain fruits require insect-mediated pollination for fruit production itself, but for other fruits, although pollination with insects is not a strict requirement for fruit production, it greatly increases yields [1]. For example, in Eastern Amazon where crops with higher dependent on animal pollinators such as cocoa, watermelon, palm and soybean provide higher crop production value [27]. They added that most crop-producing areas account for more than 10% of the gross domestic product (GDP) associated with pollination services and it is said that it depends more on pollination of crops for its economic stability. Moreover, strawberry crop that is highly cross-pollinated and fully depending on insect for fruit production shows a higher percentage of fruit set and with less malformed fruits compared to control crops [28]. In Asia, most crops depend to a large extent on pollination services provided by pollinators who naturally live in the ecosystem, as they are rich in various animal pollinators such as stingless bees, honey bees, other solitary bees, beetles and even bats. Moreover, around 70% of tropical crops appear to have at least one variation for which animal pollinators improve production [19]. For example, crop studies conducted at Gunung Tebu Forest Reserves in Besut, Terengganu, such as rambutan, durian, melon and watermelon, showed that the commercial value of the wild pollinator constructed on the pollinator dependency ratio was around RM 6,588,630.91, representing approximately 56% of the region total production values [19]. This proved that pollination services could improves certain agriculture crops economic values.

However, the assessment of pollination services has been a subject of debate because of the complexity of the system and the lack of sources to properly evaluate the services provided to the crops economic value. Besides, the idea of studies in evaluating pollination services is to apprehend the significance that will be misplaced as a result of the loss of some pollinators in a given area include at the regional, national and global levels [29]. Moreover, to support the maintenance of pollination service in agriculture, it is necessary to better understand the economic value generated by the pollination services. In most agricultural areas, pollination is provided by a combination of managed honeybees and wild insects. Many publications have tried to value the pollination of honeybees, while fewer studies have attempted to value wild pollinators. Although honeybees are widely known as economically most valuable pollinators, studies have shown that wild pollinators are often plentiful as bees on crop inflorescences [30]. Other than bee pollinators, the non-bee pollinators such as flies, wasps, beetles, birds, butterflies executed around 25 to 50% of total number of visits of flowers. Even though non-bees were less effectual pollinators than bees per flower visit, they visit flowers more often; therefore, these two aspects compensate each other, ensuing in pollination services provided by non-bees which are the same as those offered by bees [31].

There is variety of method which has been proposed to access the economic value of pollination services in crops. The most common method used to evaluate the value of the pollination service includes the production value method that focus on the value of crop production attributable toward pollination and replacement value method which means to estimate the cost of using alternative technology or organism to attain the same function [29]. Other method used to evaluate economic value includes measuring the crop price, managed pollinator prices, dependence ratio, partial and generalised equilibrium models and stated preferences [32]. For example, the economic value of the pollination service is on the basis of three different levels using the production function method [1]. The author concluded that the value of the service varies greatly depending on the crop and market conditions at the local level. While nationally, the estimated value of the pollination service ranges from 1% to 16% of the market value of agricultural production and currently no reliable estimated value of the pollination service on a wide scale.

Nevertheless, estimates aimed at the economic value of the pollination services vary widely and there is no generally acknowledged evaluation method. Despite various doubts and differences, the present body of works mainly illustrates that pollination services are economically significant, and their forfeiture will have consequences for people around the biosphere. Moreover, even studies on the extent to which pollination services is limiting the current production of crops are still scarce, the results obtained showed that the decline of the pollinator could result directly in a decrease in yields or production for most crops [30]. A loss of pollinators might influence the manufacture of a pollinator-dependent crop by reducing yield and/or increasing producers' costs. Once pollinators are lost, the fruit set may decrease and, as a result, overall yield decreases. However, it is unclear to what extant agriculture crops could be impacted by pollinator deficits.

Not to mention, producing crops in a sustainable manner improves the system's ability to maintain long-term steady levels of food supply and quality. One of the methods to sustain crop production in a long-term includes, conservation agricultures that emphasises the preservation of a permanent soil cover, little soil disturbance, and plant diversity. This approach benefits agriculture in terms of reducing erosion, increasing water infiltration, increases soil surface aggregates, reduces soil compactness, promotes biological tilling methods, levels of surface soil organic matter as well as carbon content [33]. Moreover, Nanoremediation also able to sustain crop production by using nanoparticles for environmental remediations. The application of nanotechnology to the remediation of pollutants has yielded encouraging results that able to purify soil, air and water resources using nanoparticles as a catalyst and/or sensing systems [34]. By managing pollution as a priority, crop productions are able to sustains in a suitable environment. Similarly, biofertilizers can also increase crop productivity on a bigger scale while also saving the environment and contributing to soil sustainability [35]. Biofertilizer is an organically produced product containing specific living microorganism that provides nutrient supplies.

Plant Attractants

As mentioned earlier, the mutualistic plant-pollinator interaction is of central importance since it results in seed and fruit production and therefore key contributors to biodiversity, ecosystem maintenance and essential to economic services. Pollination is a coexistence process between flowering plants and pollinators that involves the display of primary attractants, such as nectar, pollen, or other types of floral rewards, that essential to its survival and also secondary attractants of flowers to enable acknowledgement and discrimination by pollinators [7,10]. Some features that contribute to the attraction of pollinators are called secondary attractants, which, with their visual, olfactory, or tactile signals, constitute the signalling apparatus or advertisement directed at potential pollinators [36]. Plants attractants are able to deliver information concerning the existence, location and quality of the reward. Plants have evolved specific structures to interact with pollinators which are the flowers. Flowers send signals to particular type of pollinators that are facilitated by floral characteristics or traits known as “pollination syndrome” [37,38]. Flower traits such as shape, size, colour, scent production, electric fields and movement have been measured and recognized to play roles in the recognition and attraction of pollinators to flowers [39–43]. Pollinator especially bees and other insects are impressively influenced by shape, outline form, length of flowers, odour, colour, pollen, nectar and other flower rewards of flowers. The biodiversity of angiosperms is largely based on a variety of traits that serve to attract pollinators [44] while repelling herbivores and excluding nectar and pollen thieves [10].

Visual attractants

Visual signals are the utmost studied in the context of flower trait evolution in shaping plant-animal interactions [45] where these signals aid in flower recognition and learning by pollinators [46]. Flower colour is a very essential feature that constrains the specific pollinators that visit flowmers and influences overall pollinator behaviour [47]. Insects perceived flower colour differently compared to humans which may influence the types of insects visiting flowers and the rates of visitation [48]. The colour of the flower varies between flowering plants and as well changes with the life of the flower. These colour differences do not refer to the darkening or fading of the flower, but to becomes fully bloomed and desirable flowers. The colours would provide signals toward pollinators to obtain flower and pollen location, species selection, sweetest nectar reward and ripeness [37,49]. However, colour itself is not the only factor considered in studying the attractiveness of flowers to pollinators of different plant species. In order to form a complete understanding of stimuli to pollinators based on “colour”, the intensity, wavelength content, brightness, and contrast could be deliberated in coincidence with colour vision. For certain flowering plants species, the contrast of dark spots on light background is an ordinary characteristics [50].

Changes in colour of flowers with age affects pollination behaviour and to be well pollinated, flowers must stand out from their background, as flowers developing in shady parts and against dim backgrounds be likely to be pale, whereas those flowering in open areas and against light backgrounds are darker [47]. For example, *Quisqualis indica* tend to change their flowers colour from white to pink to red, which might be referred with a change from moth to butterfly pollination. Firstly, the hawkmoths pollinated the flowers blossomed in white and when the flowers turn to pink and toward red, they droop and are pollinated by bees, flies and other possible insects [51]. Flower colour changes during development and function as visual cues for pollinators, pollination state, and even time of the day [52] to evade old flowers and surge pollination competence. In flowers, the flower parts such as the anthers, filaments, ovary, flower bracts and pollen can also be visually eye-catching even the petals and sepals are usually the main coloured structures [49]. Flowers pollinated by bee are usually bright in colour which reflect light in the blue to purple part of the spectrum and have nectar guides that formed during the daytime. Due to their sturdy physical adaptation, flowers coloured in blue, lilac, and purple flowers are often visited by bees. Bees are driven to flowers by nectar cues that resemble a bull's-eye or stripes in the core of the flower, and they commonly involve UV coloration that humans cannot perceive [53]. The flower seems yellow to human in visible light, however, there is a gleaming yellow edge and a duller, darker centre under UV light, which only bees can sense [54]. For example, a yellow aster (*Asteraceae* sp.) were seen as yellow coloured flower by human, but appear different under UV light [53]. As mentioned by Miller [54], Yellow sorrel (*Oxalis fontana Bunge*) also visibily yellow in human eye (Fig. 1a) but has a darker center under UV light (Fig. 1b). Besides, yellow-flowered crops such as melons, oilseed rape are also often considered to interest a variety of insects due to the high reflectance of yellow [50,55]. Bright or light-coloured flowers are pollinated by moths and bats, with appropriate odour, and have nectar guides with nectar produced during the night time. Meanwhile, birds (particularly hummingbirds) are more attractive to red-coloured flowers that open during the day compared to blue-coloured flowers. The association of butterflies with pink and red flowers is well known [47]. In addition, successful pollination could result as specialized colour attractants will intensify the likelihood of pollinator constancy by guaranteeing pollinators visit one conspecific after another [56].

Shape and size

Equally, the flower shape and size are closely linked to pollinator attraction. Flowers are derived in many diverse forms, with different structures, and in various arrangements. This variety of flower forms has developed to perform pollination tasks. Flowers are formed mainly by natural selection from their pollinators, and the flower form varies based on the flowering plant and from the outcome of convergent evolution [37]. Flower shape can increase attraction to pollinators and facilitate pollen deposition, flower handling, and the degree of pollinator specialization, as well as influence the electrostatic properties of pollen deposition [56]. Moreover, flower shapes could offer a hint as to what animals have the potency to perform as pollinators for a plant. Flowers that are animal-pollinated usually have larger showy petals of different sizes and shapes to attract pollinators. For example, study on two yellow melon hybrids showed that tropical hybrid has larger flowers that could be more attractive to bee species such as *A. mellifera*, [57] large solitary bees of genus *Xylocopa* by providing larger landing platform [58,59] compared to the other melon hybrids from Brazil. There is a positive connection between the size of flowers, inflorescences, or flower fields and attractiveness to insects. The smaller flowers or inflorescences are thought to suffer lower visitation rates due the insect's incompetence to detect them [50]. Meanwhile, larger flowers are easier to be detected and offer more rewards [60,61] and as an outcome some findings have acknowledged pollinator-mediated phenotypic selection for larger flowers [62,63]. Large flower such as *Cistus ladanifer* obtains great benefits in visitation rates and diversity that resulted in increasing fruit and seed production but it also increased florivory costs since they are more prone to be attacked by hostile insects like pollen-eating ants (Fig. 1c) and petal- eating beetles (Fig. 1d) that may cause damage to the flowers [61]. Nevertheless, there are some factors selecting for smaller flowers [45] as such theory predicts that when the pollinators are plentiful and competent, smaller flowers could be gainful in relations to water balance particularly. Moreover, these small, inconspicuous flowers are regularly assembled into large inflorescences to more effectively attract pollinators [7]. If not, larger flower are commonly preferred by pollinators by increasing the pollen dispersion level [64].

The aspects of floral morphology such as the arrangement of the reproductive parts and petals can be important in limiting access to floral reward [48]. Floral traits such as floral designs or corolla entrance diameter likely evolved to enable and increase the effectiveness of pollination [45]. Moreover, lipped, or labiate, flowers can provide a platform on which bumblebees can land before entering the flower, while hummingbirds visit long tubular flowers, that hover while probing the deep flowers with their long beaks [9]. For example, Alberto and others [65] determined that different types of bees such as *Apis mellifera* and native bees have different preferences of landing zone on strawberry flowers whether on top of flowers, stamen zone and on the petal zone. Besides, pollen detachment from pollinators would be facilitates by increased style length, along with its deposition on the stigma that could accelerate pollen transmission between the contrarily-charged flower and pollinator [56]. Flowers symmetry is another main visual trait where selection performs based on pollinator perception, information processing and activity patterns. Insect pollinators detect and perceive symmetrical patterns, radial or bilateral in comparison to flowers that differ from symmetry and such floral patterns were found to receive higher visitation rates and better pollen transfer resulting in efficient pollination [7,40]. Commonly, floral colour, size and shape are closely linked to attract potential pollinator. For example, the flower form that appealing to hummingbirds tend to have a red-orange colour, a long flower tube form, a sweet scent with a nectar reward at the base of the flower tube. In addition, bee-pollinated flowers often have coloured guides on a landing podium shaped by the lower petal where the nectar is at the base of the tubular flower where bees usually enter. Certain flowers fit pollination by butterflies, moths, or hummingbirds take advantage of the insects' long mouthparts and have nectar spurs at the base of the flower [37].

Fig 1 The diversity of plant attractant. (**a**) A yellow aster (*Asteraceae* sp.) under human vision and (**b**) under UV light [54]. (**c**) An ant species picking stamens by consuming pollen and (**d**) betteles eating petals degrade the flower attractiveness and caused damage to the flowers of *Cistus ladanifer* [64].

Olfactory attractants

Apart from colour and shape, floral scent or fragrance also responsible for the attraction of specific pollinators. Olfactory signals advertise reward goods to pollinators often synergistically and in concert with visual cues. Compared to colours and colour patterns, olfactory signals are adapted faster more precisely chosen [38], making them more resilient. Scent is a complex element of the floral phenotype that is primarily involved in communication amongst flowering plants and their pollinators. It encourages specialization in plant-pollinator relationships (via secretive channels with uncommon connections) and outcrossing and reproductive isolation (via flower perseverance) [66]. Floral scents are likely to be a necessary determining factor of communication network structure because they are among the most significant cues used by pollinators to trace nectar and pollen rewards from a distance [7,67]. These odorous substances are nearly always a mixture of numerous volatile organic compounds (VOCs), consist of over 100 different mixtures [66]. The VOC emission can alter quantitatively (total emission rate) and qualitatively (ratio between odorants) over the diurnal cycle in both flowers and fruits [68]. The repeated association of odour with food and the integration of gustatory and olfactory pathways may have developed neuronal structures that facilitate olfactory reactions in insects which permitting animals with food-related learning abilities[10]. Moreover, in both flowers and fruits, odour production possibly will be particularly important in plants species that lack perfect visual attraction and in species that depend on nocturnal pollinators [40]. Usually the flowers that open at night are pleasantly fragrant, attracting pollinators to pollinate and providing them with a fragrant reward and sometimes an essential oil [37]. Besides, for nectar-less crops that relatively unattractive to insect pollinators like kiwifruit, they tend to produce staminate or pistillate pollen that have odour in order to attract them [69,70]. Flowers pollinated by insects often emit fragrance, while flowers pollinated by birds are usually scentless. For moth pollination, night-blooming plants with characteristically strong and penetrating floral scents are necessary for long-distance advertising. In day-blooming plants, the floral scents are not as strong and these scents could act as attractants for landing that connected with nectar ladders [47].

At both long and short distances, the scent of flowers and fruits can attract animals. For flowers that depend on nocturnal pollinators, long-distance attraction is mutual in the surroundings where visual signals are unnoticed [56]. In addition, floral scent can also provide nuanced information about the quality of reward in nearby proximity. Studies of primate pollinator behaviour, for example, have also found that certain species consciously smell fruit at close range [71]. Moreover, flower scent is an essential chemical trait for modifying the flower visitors' behaviour and signifies an evolutionary trade-off between attracting mutualists and deterring competitors. Both pollinators and herbivores might be attracted toward the identical odorants [72]. Flowers that normally have a pleasant-smelling fragrance use it to attract moths, butterflies, and bats. Certain flowers produce such strong scents that can be detected by insects more than half a mile away. Plants that use scent to attract pollinators may perhaps not have colourful flowers as the scent is the primary method of attracting pollinators [9]. Plants may also emit unpleasant odours that mimic the smell of rotting meat or manure that attract flies and beetles [47]. As the insect inspects the flower to trace the source of these odours, it indirectly comes in contact with pollen. This relationship is rather communalistic, with the plant benefiting from the interaction as pollen is transferred but the pollinator receives no profit at all. There are variety of crops that produce fragrant flowers to attract pollinators, for example, flies (Diptera) which are the main pollinator crops for mango are attracted to the plant due to the scent produce compared to honey bee (Apidae) that more attracted towards nectar rewards [73]. Moreover, although less is identified about the stone fruit crops pollinators, El-Sayed and others [74] showed that stone fruits plants (plum, *Prunus domestica* L.; apricot, *Prunus armeniaca* L.; peach, *Prunus persica* L.; cherry, *Prunus avium* L.) produce floral scents that perform as a common chemical attraction to a wide range of possible pollinators. Previous study investigates the effects on inbreeding in *Solanum carolinense* and resulted in altered floral traits and this caused the reduction in floral rewards (pollen) and negatively affect pollinator visitation [75]. The flower itself offers their own rewards that targets certain insects, thus, any changes to the plant may affect the rewards offered and reduce pollinators visitors.

Floral attraction by deceit

Not all plant species attract their animal pollinators on reward bases; instead, several mutualisms are exposed to "deception" by one partner or another, and interactions between plants and pollinators are no exception. Deceptive pollination has developed in 4-6% of angiosperms and is based on the incapability of pollinators to differentiate between a real resource such as breeding sites, mating partners, food and the flower that imitates the reward [76–78]. These plants have therefore evolved signals to deceit insects to carry out pollination process. Mimicry is the common pollination strategy in which the flower does not provide a pollination reward (pollen or nectar) in this type of adaptation, but deceptively lures the pollinator to visit the flower [79]. Flower mimicry is a very diverse phenomenon, including Batesian mimicry, in which an unrewarding flower mimics a rewarding one, and Mullerian mimicry or signal normalization, in which two distinct rewarding flowers display similar signals [79,80]. The deception system has developed in different flowering plants families where about one-third of the species in the Orchidaceae family are well known to deceive their pollinators [80–82]. These deceiving flowers have therefore developed the capability to discharge cues that elicit essential reactions toward targeted insects [83]. One of the examples of mimicry acts in angiosperms includes the imitation of floral features. For instance, in begonia, only male flowers provide pollen rewards. To initiate visitation by animal visitors to the female flower, both twisted pistils and stigmas emit the presence of male stamens, also identified as flower automimicry [37]. In addition, the different morphologies of stamens within the same flowers in crape myrtle (Lagestroemia) serves as a signal to attract pollinators where the inner spiral of the male reproductive organ is on short filaments which assembled in the middle of the flower and the external whorl of stamens is on lengthy pigmented filaments [37]. Certain melittophilous flowers display pollen and stamens imitations include colorations on the petals that bear a resemblance to the stamens, typically as a bright yellow spot on the petals, patterns of flowers, stamen-like pistils and staminodes [79].

Meanwhile, sexually deceptive plants secure pollination by sexually attracting male insects through chemical and/or physical mimicry of the pollinator's female [84,85]. Sexual mimicry is the most widespread among the orchid genera. For example, sexually deceptive orchids like *Cryptostylis* spp, which are pollinated by haplodiploid wasps (*Lissopimpla excelsa*), enticing male to mate with flowers that provide no reward which frequently lead to sperm loss [86]. Other than that, orchid species *Ophrys heldreichii* flowers tend to resemble bees in form and coloration. The tactic is to draw male bees to undergo pseudocopulation with female bees [87]. Brood-flower mimicry is a particular sort of reproductive illusion in which the flower imitates a spot that insects mistakenly think is a place to breed. A common characteristic of brood flowers is the creation of a foul odour to appeal to carrion flies (sapromyophilia), dung beetles (coprocantharophilia) and fungus gnat flowers (mycethophily) [78]. In addition, visual cues play an important role in attracting pollinators because a larger flower exemplify extra odour-producing features and the quantity of odour formed is positively correlated with insect attraction. For example, *Rafflesia arnoldii* which is the largest single flower in the world (up to one meter in diameter) emits a rotten, decaying flesh odour to attract potential pollinators [88]. Besides, the diurnal species of *Nymphaea*, attract beetles, flies or bees by floral trap mechanism where there is a stigmatic liquid that fills the flower cup. Visiting insects particularly bees and flies would fall into the cup and finally drown. The liquid may wash away all the pollen that the insects or pollinators visit to pollinate the plants [89,90]. Basically, flowers mimic the signals that pollinators use to find other flowers or substrates that they routinely visit for feeding or oviposition, initiating the distinctive or learned foraging behaviour to hunt for a non-existent reward.

Rewards for Pollinator

Plant and pollinators interactions affect the morphological as well as physiological adaptations to a great extent [4]. The interactions involved a mutualistic relationship where both parties gained benefits. As previously described, pollinators rely on plant ads such as visual, chemical, or structural cues to attract them and give information to possible pollinators regarding the location of and access to flower rewards [7]. Flowering plants provides reward for pollinator to encourage them to make return visits and with the increased number of regular visits, greater awards will be provided [91]. Pollinators visits and forage on flowers mainly for food rewards such as nectar that contains variety of compounds including sugars, and pollen that provides an important protein resources, however some visits are made for non-nutritive reasons, including as breeding grounds, shelter, and gathering places [7]. Pollinators visit flowers for a variety of reasons, including caloric reward, energy, protection, and oviposition sites [10,92].

Food rewards

Pollinators usually feed on plants to gain nutritional resources mainly pollen and nectar [93]. Pollinators generally relies on plant attractant to guide them to the food resources as the rewards are often concealed within a flower, which cannot be seen directly by pollinators [94]. Animal-pollinated flower usually provide nectar to pollinators as a reward [95]. Furthermore, the most recorded resources offered to insects to encourage plant pollination are nectar [93]. Nectar are also an important nutritional and energy sources for pollinators [92]. Pollinators that visit flower usually rewarded with carbohydrate-rich nectar even when other rewards such pollen or wax were offered [96]. Dipterans feed on nectar to gain carbohydrates with high sugar concentrations for short terms energy needs such as mating, migration and oviposition, as well as to obtain lipids that able to provide energy, also they feed on nectar containing protein-building amino acids for longevity especially for mosquitos as amino acids may reduce the needs for blood meal and apart from that, vitamins, minerals and salts in nectar are equally important for their nutritional sources [7]. As mentioned by Prasifka [48], many pollinator-dependent fruit and vegetable crops shows a positive correlations between bee visits and volume of nectar such as blueberry, watermelon, raspberries and blackberries. According to bee behavioural research utilising nectar sugar concentrations reported in *Vicia faba*, showed a weak but significantly positive relationship where bumblebee (*Bombus terrestris*) favours 55 % w/w sugar solution over 40 % w/w sugar solution, but has no preference between 55 % w/w and 68 % w/w sugar solution [97]. In addition, the increased frequency of bee that visits zucchini flowers (*Cucurbita pepo* L.) was associated with higher nectar volumes and sucrose/hexose ratios, which seemed to be excellent markers of pollinator choices [98].

Apart from nectar, pollen also regards as the important floral reward that showing intraspecific variation [48]. Pollen contains nutritional sources like proteins, carbohydrates and lipids that benefit animal forage on them. Animal pollinator especially bees rely on pollen as the sole protein source for larvae development [3]. Besides, sterols which is a lipid in pollen are important for insects to have the ability to produce hormone or pheromone [92]. In addition, pollen proteins contains enzymes that helps pollen tube growth and undergo fertilization [99]. The enzyme responsible to support the growth of pollen tube are called proline which also helps insects pollinators to gain energy for flight [7]. Other pollinators puncture on the pollen grains to draw out the protoplasm while on the contrary, Diptera consume the entire grains and they may eat a lot of pollen until their belly becomes bloated and yellow, and the pollen digested can be seen in their excrement [7]. Pollen-foraging bees have been shown to favour certain flowers over others and are able to discern variations between pollen(-like) samples with various chemical, colour, and/or mechanosensory properties [100]. The ability of *Eristalis tenax* L. to distinguish between pollen and nectar is studied, as well as the triggering of pollen ingestion on sunflower (*Helianthus annuus*), in behavioural preference tests extracted pollen is ingested in lesser amounts compared to than untreated pollen, demonstrating that water-soluble compounds are necessary for acceptability. Pollen that is dry is favoured over pollen that is moist where the grains clump together, implying that the pollen's mechanical features play a part in its sensory evaluation [101].

There is a significant association between pollen quality and reproductive system where pollen from insect-pollinated plants had increased protein content, while pollen from plants frequented by pollen-collecting bumblebees provided the best pollen [102]. However, a study of how floral abundance and resource quality influence pollinator choice found that bees preferred good nectar over pollen as the main driver of floral choice. Furthermore, the abundance of floral in a given area is important as a resource selection, even though the quality of rewards often influences forager choices [93].

Warmth, heat and energy rewards

Energy balance for pollination involves energy intake as in rewards pollinators gained from flowering plants and pollinator’s own energy used while foraging. Body temperature is a measure of the amount of energy expended as heat [92]. Energy is supplied as food or as heat and most pollinators' energy requirements are determined by factors such as cost of living, locomotion, thermoregulation, and behaviour, which is primarily influenced by body size. Pollinators often forage on warmer flowers to gain net rate of energy and reduce the amount of energy needed to get their bodies to flight temperature before leaving the flower [96]. Thermogenic flowers offers energy rewards to pollinators which able to retain insect pollinators longer compared to protogynous plant and thus endothermic pollinators benefited from increased independence from environmental conditions, allowing them to forage in cooler and wetter conditions as well as enable them to have a high energy level to distribute pollen in wider weather tolerance and longer distances [2]. Researched done by Abrol [103], stated that pollinators' foraging profitability appears to be linked to the relationship between energy cost and reward in which *Apis dorsata*, which is larger in size and tongue length, forages high-energy-rewarding flowers while *Apis florea* forages low-energy-rewarding flowers [103]. *Apis dorsata* clearly spends more energy while foraging than *Apis florea*, hence its energy requirements and foraging rate are higher.

Apart from energy, some plants also provide warmth to ectothermic pollinators. While the flower release heat to provide warmth for the pollinators, it is similar as providing extra metabolic, however, floral warming may also be a process to increases the production of flower nectar as nectar secretion often reduced at low temperatures [96]. Actively thermogenic flowers, such as the sacred lotus *Nelumbo nucifera*, may provide a consistent supply of predicted warmth [104]. Besides, when visiting the solar-heated flowers of *Narcissus longispathus*, an early-flowering montane species, the mining bee *Andrena bicolor* showed a positive correlation between visit length and floral temperature [105]. During the colder hours of the day, warm flowers are favoured by insect pollinators. Flower species that bloom at cooler times of the year or develop in colder habitats would be benefitted, where providing heat not only boosts the rewards offered to attract pollinators, but it may also be required to retain any pollinators present in the environment [96].

Not to mention, a study stated the *Oncocyclus* iris flowers that are partially or completely dark in colour do not produce nectar and have hidden pollen, so no pollinators will visit during the day and will pollinate only at night, but they can gather heat by absorbing solar radiation, and this heat acts as a reward for pollinators [5]. For example, scarab beetles, *Cyclocephala colasi* requires additional energy for activity that are 2.0-4.8 times greater outside flower *Philodendron solimoesense* (Araceae) than inside [106]. Scarab beetle spend the majority of their time inside floral chambers of heat-producing flowers, where they feed and mate at night and rest during the day, so flower heat are important energy rewards for the beetle to reduce energy expenditure for its activity [106].

Protection, brood sites, oviposition and mating location

Besides, plant blossoms are responsible in providing protection to most insects including thrips, beetles and flies. According to Liker [92], insects pollinators that requires protection from plant includes, *Taeniothrips ericae* that spends the majority of its life in *Colluna vulgaris* blooms, as well as mutualism between the *Tegiticula* moth and *Yucca*, and aganoid wasps and fiscus. Protective mutualisms with ants are common in the *Macaranga* genus. *Macaranga* have a type of inflorescence called ‘enclosing’ in which bracteoles cover flowers including all the thrips- and hemipteran-pollinated species, bracteole "chambers" also protect thrips or hemipteran pollinators that use these structures as feeding and breeding sites. Furthermore, pollinators may be physically protected from natural enemies such as ants by the bracteoles of the 'enclosing' form [104,107].

During flower visitation, pollen movement may occur and resulted in flower breeding. Flower also offers rewards for pollinators in terms of breeding sites as individual flies visit multiple flowers during mating, oviposition, or it may occur concurrently with the plant reproductive systems and, for example, pollen transfer occurs while flies move from female-phase inflorescences where they mate and oviposit to male-phase inflorescences where they consume nutritional pollen, as demonstrated in the pollination of protogynous *Peltandra virginica* Kunth (Araceae) by *Elachiptera formosa Loew* (Chloropidae) [7].

Flowers also often provide benefits to pollinators in terms of oviposition and mating sites. Previous studies were done to examine the hoverfly preferences in ovipositional sites using three model flowers that exhibits attributes by real flowers in terms of colour, pollen and nectar resources and from the observations, hoverfly laid eggs on flowers that has a bright visual which means colour are important in eliciting oviposition response compared to olfactory stimuli of pollen and nectar [108]. Besides, female diptera are required to visit flowers in order to obtain nectar and pollen; therefore, flowers may be an excellent location for males to find mates [7]. Some males diptera usually lingers around and repeatedly flying near the flower and acts like a pollinator but instead searching for mate.

Other rewards

Some flowers also offer fatty oils as rewards for pollinators and mainly for bees where they use the oil mixed with pollen for larval provisioning and for water-resistant call lining and these bees generally has specialization to gather oils with their forelegs that equipped with special combs, brushes, and hair tufts [95]. Apart from that, weeds can also act as a source of floral reward in order to maintain the survivability of pollinators to maintain diversity and enhance crop yields by providing food sources for pollinators that requires pollen and nectar to survive and to prepare their food, this can be done letting the weeds to grow on roadside or fallow land and also through a proper planned establishment on bunds in agriculture land to support pollinators diversity [109].

Conclusion

In conclusion, the plant-pollinator interactions may result in successful crop pollination where the attractant and rewards are heavily dependent on each other. Most pollinators attracted to plants that invest more on advertisement and/or rewards such as larger display, bright colour, good scent compared to those that does not and while visiting the flower both parties will gain benefits in pollination and plant reproduction as well as pollinators fitness. Pollinators may also revisit and return to plant that provide greater rewards based on the experienced and this indirectly ensure the pollination process to occurs effectively. Even after decades of studies, there is still a vast knowledge and great opportunity to uncover about the pollination and pollinators. Many more questions are likely to arises especially involving the pollination and pollinator relationships in environment affected by human activities. The investigation of the issues requires new approaches and methods that resulted in better understanding of the significance of insects in pollination, especially plant strategies to attract pollinators as well as how pollinator react and responds to it. It is important to study the behavioural of insects, their neurological processes and routes with regards to the attractant and rewards. Moreover, more detailed investigations must be done in determining the content of carbohydrates, lipids, proteins and other compound in pollen and nectar and how it can greatly influence pollinator's visitations. Thus, further studies into the chemical interactions between pollinators, visitors, and flowering plants with the recent advancement in technology is required in order to develop best pollinator management techniques for the cultivation of human food crops. Identifying nutrient rewards in fruits and connecting them to plant attractants may provide more information into the relationship between fruit nutrients and attractants. Although flower provide their own rewards for insects, studies such as addition of fragrance or attractant in fruits may also increase visitation by insects and improve fruit quality that may contributes to the successful of crop production and increase economic value of pollination services. Therefore, additional fragrance or attractant such as sugar solution or even palm wine may be also useful in attraction of insect's visitation.

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Availability of data and material
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