PLANT-INSECT MUTUALISTIC ASSOCIATIONS AND THEIR EXPLOITATION BY ROBBERS AND CHEATERS

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Abstract

This study reviews existing research findings on the diversity of plant insect mutualistic associations and the use of deceit in the exploitation of such associations. A multitude of plant-insect mutualistic associations, including plant-insect pollinators, ant- myrmecochore mutualisms, digestive mutualism of carnivorous plants with insects and protective mutualism between ants and myrmecophytes are disrupted by the exploiting plant / insect species. While insect robbers / cheaters deprive the plants of resources without providing any beneficial services, many plants use deceit to obtain services from insects without providing them the desired resource, in return. The review reveals that a variety of partner choice mechanisms at the levels of morphology, physiology and behaviour are used by the exploited species to impose host sanctions and to filter out the robbers / cheaters so as to avoid costly association with exploiters and to interact and invest predominantly with the cooperators. It is, therefore, abundantly clear that elucidation of 'cooperation and conflict' between plants and their insect associates is possible only by considering mutualistic associations as part of the complex network involving multispecies guilds and multitrophic interactions.

Keywords

Cooperation, deceit, ant plants, plant-insect pollinators, extrafloral nectar, myrmecophytes, myrmecochory.

Introduction

Plant-insect mutualistic associations (involving cooperative interactions) are widespread in nature. These include i) plant-insect pollinator mutualism (Kremen *et al.*, 2002), ii) mutualism between seed-dispersing ants and myrmecochores (ant-dispersed plants), the seeds of which are dispersal by ants (myrmecochory) (Beattie, 1985), iii) digestive mutualism between carnivorous plants and insects (Anderson and Midgley, 2002), iv) and, protective mutualism between ants and myrmecophytes (plants which offer shelter in the form of domatia and food in the form of Beltian bodies and/or extrafloral nectar (EFN), to the ants) (Janzen, 1966; Heil and McKey, 2003). While bees (also wasps, butterflies, flies and beetles) are significantly implicated in pollination, ants play the dominant role in seed dispersal and myrmecophyte protection. However, the mutualistic associations are frequently riddled by instances of conflicts between the two partners which resultantly shift the nature of the association from mutualistic to exploitative (Doebeli and Knowlton, 1998; Bronstein, 2001; Sachs and Simms, 2006; Douglas, 2008). Thus, many insects exploit plants by utilising food (pollen/nectar/Beltian bodies) and /or domatia (as shelter) and not providing pollination / seed dispersal / herbivore protection service(s) to the host plant, in return. At the same time a variety of plants are documented to use deceit in order to avail the

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services of insects. There are also instances of exploitation of plants by one of the interacting insect partners which changes the trophic behaviour of the insect mutualist.

The present review aims at providing a brief synthesis of recent information on mutualistic plant-insect associations and the prevalence of deceit in such associations. At the same time, the mechanisms used by the exploited partner to reduce exploitation and to increase cooperation are highlighted to give an insight in the 'cooperation and conflict' involved in such associations. A cheater is an individual of a partner species that receives the benefit of mutualism but does not reciprocate (Mainero and del Rio, 1988). Hereafter, the term cheater would be used for an exploiter irrespective of whether it has/does not have mutualistic ancestors since phylogenetic information is not available for a large majority of exploiting species.

Plant-insect pollinator mutualism

More than 75% of crop species depend on pollination by animals (Kremen *et al.*, 2002; Klein *et al.*, 2007). Animal pollinators include birds, bats and insects. Insect pollination is known as entomophily (Gullan and Cranston, 2004). Pollinating insects obtain nectar and/or pollen, or may utilise the flowers for laying eggs. They thus obtain nutritive or reproductive benefits while aiding sexual reproduction of the flowering plants. Most pollinators visit the flowers for obtaining nectar and pollen. However, in some cases the objective of the floral visit is mating and oviposition, the most well known being *Ficus* (Moraceae) (Janzen, 1979) and *Yucca* (Agavaceae) (Baker, 1986).

Anthophilous (flower-visiting) taxa include bees, wasps and ants (Hymenoptera), butterflies and moths (Lepidoptera), flies (Diptera) beetles (Coleoptera) and thrips (Thysanoptera) (Gullan and Cranston, 2004).

Hymenopteran insects

Melittophily (bee pollination) is well known. Honey bees especially *Apis mellifera* is an important pollinator of crop worldwide though stingless bees (*Melipona* spp.), bumble bees (*Bombus* spp.) and many solitary bees also play significant role in crop pollination (Klein *et al.,* 2009). Pollination by wasps (sphecophily) is reported in some plants such as those belonging to the genus *Eucomis* (Hyacinthaceae) and African milkweed *Xysmalobium orbiculare* which are specialized for pollinated by pompilid wasps (Shuttleworth and Johnson, 2008). Mutualism between figs (*Ficus* spp.) and fig wasps (Chlocloids: Agaonideae) is a classical example of species-specific plant-pollinator association. Each species of fig is associated with a unique species of fig wasp. Figs and their wasps depend upon each other to reproduce. Fig inflorescence is in the form of an urn-shaped receptacle, the syconium (which has tiny flowers inside). It has a small hole through which fig wasps enter. Inside the syconium the wasps lay their eggs in the fig's ovules. Thus, each maturing larva galls and feeds on the developing seeds. The larvae destroy the developing fig seeds but when the adult wasps finally emerge from the fig, they pick up pollen and take it to another tree.

Ants are reported as pollinators only in some cases (Peakall and Beattie, 1989; Peakall *et al.,* 1991; Bosch *et al.,* 1997; Gómez, 2000; Schürch *et al.,* 2000). It is suggested that to minimize the interference caused by ants to insect pollinators (Ghazoul, 2001) and/or to avoid the negative impact of the extrafloral nectary visiting ants on pollen function (Beattie *et al.*, 1985) insect-pollinated plants have evolved various strategies to avoid ant visits to the flowers. Ants are,

however, found to be effective pollinators of some orchids (Peakall, 1989; Sugiura *et al.,* 2006). A guild of ant species are also recorded as dominant pollinators of *Cytinus hypocistis* (Cytinaceae), a Mediterranean root holoparasite (de Vega *et al.,* 2009).

Non-hymenopteran insect pollinators

Lepidopteran pollinators

Butterflies are diurnal and use vision to locate brightly coloured but odourless flowers while moth being nocturnal use odour (usually sweet) to find the flowers which are usually white or pale-coloured. While butterfly pollination (psychophily) occurs in flowers exhibiting diurnal anthesis, moth pollination (phalaenophily) occurs in nocturnal anthesis flowers. Butterflies pollinated flowers are usually arranged in clusters and provide a landing platform (such as those belonging to compositae). Moths are hover-feeders so moth pollinated flowers are characterized by deep tubular structures. Some plants such as the *Lantana camara* ((Schemske, 1976) and wild carnation, *Dianthus carthusianorum* (Bloch *et al.,* 2006) are predominantly pollinated by diurnal Lepidoptera. The cabbage white butterfly (*Pieris rapae*), notorious as a pest of cabbage also happens to be a pollinator of many wild and cultivated plants (Conner *et al.,* 1995). The Karner blue butterfly, *Lycaeides melissa samuelis*, the larvae of which feed only on wild lupine leaves is endangered pollinator. The monarch butterfly, *Danaus plexippus* is a pollinator of common milkweed, *Asclepias syriaca*. Obligate pollination mutualism between yuccas and yucca moths is extensively documented (Pellmyr and Leebens-Mack, 1999; Pellmyr and Leebens-Mack, 2000). Yuccas are pollinated exclusively by yucca moths, whose larvae in turn consume some of the developing yucca seeds. Female yucca moths possess unique tentacular mouthparts that are used to actively pollinate host flowers where they oviposit (Pellmyr and Krenn, 2002). The sticky pollen is scrapped off the anthers and then compacted with the help of tentacles and occasionally the forelegs legs. It is then placed on the concave posterioventral surface of the head. Next, the moth searches flowering yucca plants where she oviposits into or near the pistel. After oviposition she uses the apical portion of the tentacles to transfer a small portion of pollen load on to the floral stigma.

Dipteran and coleopteran pollinators

Myophily (fly pollination) is exhibited by large flies belonging to the families Bombyliidae, Syrphidae, Anthomyiidae, Tachinidae, Calliphoridae, and Muscidae as well as small nematoceran fly pollinators (Kevan and Baker, 1983). Flies are documented as regular visitors and pollinators of a variety of flowering plants including mango, tea, cashew, cacao and onions (Kearns, 2001 and references therein). *Aristolochia*, the most diverse genus of the family Aristolochiaceae is found to be pollinated exclusively by flies belonging to at least five different families.

Beetle pollination or cantharophily is reported in the *Magnoliaceae, Annonaceae, Eupomatiaceae* and *Calycanthaceae* (Gottsberger, 1989). Bimodal pollination by wasps and beetles has been reported in African milkweed *Xysmalobium undulatum* (Shuttleworth and Johnson, 2008). Thrips which feed on nectar and pollen were earlier regarded as minor pollinators but are now documented to be important pollinators of a number of flowering plants (Moog *et al.,* 2002; Williams *et al.,* 2001).

Nectar and/pollen robbing insects and adaptive strategies by plants to prevent robbing

Nectar robbers deprive the plants of nectar without playing a role in pollination. Nectar robbery has been defined as the consumption of nectar from flowers without contacting the sexual parts of the flower by physically damaging the flower in a way that is not done by legitimate pollinators (Inouye, 1983). Floral robbers are commonly viewed as acting as plant antagonists. They have been placed into three categories on the basis of the resource robbed and occurrence /absence of floral damage caused by the robbing insect (Barrows *et al.,* 1976). These include: i) nectar-foraging which restricts the robbing insects' visits to individual flowers thereby reducing outcrossing (Heinrich and Raven, 1972), ii) nectar-foraging-perforating (which bites holes in corollas through which nectar is imbibed, though it does not necessarily restrict the visits to individual flowers, and iii) pollen-foraging, where the insect robber collects pollen and, restricts its visits to individual flowers (Barrows *et al.,* 1976). Nectar-foraging-perforating robbers not only deplete nectar from flowers but also facilitate theft by secondary robbers which use the holes made by the former to access nectar (Hawkins, 1961). Some short-tongued bumblebees utilise the holes left by the hole-biting *Bombus terrestris* for nectar collection (Stout *et al.,* 2000).

Nectar robbers include the stingless bee, *Trigona* (*Trigona*) *fulviventris* (Barrows, 1976) bumble bees, *Bombus* spp. (Inouye, 1983; Zhang *et al.,* 2009) carpenter bees, *Xylocopa* spp. (Dedej and Delaplane, 2004) and ants (Norment, 1988.). Nectar robbing reduces the nectar standing crop and also diminishes the visits by legitimate pollinators. Primary robbers can cause even legitimate pollinators such as honey bees to access nectar by making visits through holes such as those made by *Xylocopa* spp. and thus act as secondary nectar thieves (Delaplane and Mayer, 2000). Nectar robbing may cause floral changes. The sugar concentration of nectar available to other pollinators also changes in some cases (Pleasants, 1983). Other pollinators including humming birds are known to avoid nectar robbed plants (Irwin, 2000).

Plants have evolved a wide variety of strategies to avoid being robbed. These include physical mechanisms in the form of longer corolla tubes (Lara and Ornelas, 2001), thicker corolla tissue (Inouye, 1983) and floral nectar barriers (Coombs and Peter, 2009). Chemical mechanisms include production of floral repellents (Agarwal and Rastogi, 2008a) including volatile scents (Junker and Blüthgen, 2008) and nectar unpalatable to potential robbers (Shuttleworth and Johnson, 2009a). One hypothesis put forward is that plants may be selected to provide their nectar reward in many small flowers to keep away large nectar robbers (Pettersson, 1999). In this way the plants may discourage visits by large hovering foragers since it may be too costly for them to collect the scattered nectar. Moreover, the plant can direct this energy in the production of more number of flowers.

Plant resource exploiting insects and adaptive strategies of the host plants

There is a possibility of cheating by the fig wasps by using too many ovules. To prevent seed production from ceasing and thereby causing extinction of mutualism, fig trees must prevent

the wasps from ovipositing in all flowers. Fig trees use a number of strategies to prevent wasps from ovipositing in all flowers and reduce galling. In the hot summer, wasps have shorter life spans and therefore, fail to oviposit in many flowers. During winter although the longer lifespans permit the wasps to exploit more number of flowers interference competition among the competing wasp foundresses reduces the proportion of flowers that are galled. It is found that the fig trees encourage the entry of multiple foundresses by delaying ostiole closure of the syconia during the low temperature conditions of winter (Wang *et al.,* 2009).

Cheating by wasps is also prevented since there is another player in this game in the form of parasitic wasps which lay eggs in the outer ovules. To escape being parasitized fig wasps only use the seeds closest to the center of the fruit. Thus the parasitic wasps help to prevent cheating by the fig wasps and ensure cooperation between the pollinating wasps and the fig plants.

Deceitful plants

Many orchids exploit existing plant-pollinator relationships and use deception to accomplish pollination. Most common mechanisms include: i) 'generalized food deception' (Steiner, 1998; Brodmann *et al.,* 2008), ii) Batesian floral mimicry, where the flowers resemble rewarding plant species (Johnson *et al.,* 2003), or even mimics pollinating insects (Schiestl, 2005) iii) sexual deceit, where the flowers mimic female insect mating signals, especially their pheromones (Ayasse *et al.,* 2000; Schiestl *et al.,* 2003) and or shape and colour patterns (Paxton and Tengö 2001) and are pollinated by the lured male insects, which often try to copulate with the flower. The flowers of orchid *Ophrys sphegodes* 'double dupes' the males of the bee, *Andrena nigroaenea.* After attracting them by production of odour similar to that produced by the female sex pheromones the pollinated flowers repel the pseudocopulating males by production of chemical compounds similar to those produced by impregnated females (Paxton and Tengö 2001). The orchid *Leporella fimbriata* Lindle, exploits the winged male *Myrmecia urens* Lowne ants, which are observed to pseudocopulate with the flowers (Peakall, 1989). In a rare strategy, the deceptive orchid, *Disa nivea* successfully exploits a reciprocally specialized mutualism between a nectar-producing plant (*Zaluzianskya microsiphon*) and its long-proboscid fly pollinator (*Prosoeca ganglbaueri*). *Disa nivea* is a rare southern African orchid known only from habitats that support large populations of *Z. microsiphon*, which the exploiting species closely resembles in both general morphology and floral spectral reflectance. The orchids *Epipactis helleborine* and *E. purpurata* show chemical mimicry to attract wasp pollinators (Brodmann *et al.,* 2008). They emit green-leaf volatiles which are attractive to prey-hunting foragers of the social wasps *Vespula germanica* and *V. vulgaris.*

The perianth of the zygomorphic flowers of *Aristolochia* has three sepals which together form a tubular calyx. The basal part of this forms a chamber (utricle) around the fused styles, stigmas, and anthers. The utricle is connected to a tube which ends as an expanded limb, which is often colorful and presumably attracts the pollinators (Brantjes, 1980). The flies being saprophagus the plants apparently use deceit to lure the flies for pollination (Endress, 1994; Vogel, 1990)

though in a few species the flies oviposit and develop on the decomposing flowers (Sakai, 2002). Immediately after opening the flowers use odour to attract the flies and trap them inside the utricle. On the second day, the anthers dehisce and the flies are released with the pollen load.

Ant-plant mutualistic interactions

Seed dispersal mutualisms

About 70 plant families are known to have ant-dispersed (myrmecochorous) seeds (Beattie, 1985). The seeds of myrmecophores bear a lipid-rich appendage known as the elaiosome. Since the fatty acid composition of elaiosomes is similar to that of insect hemolymph (Hughes *et al.,* 1994), it is attractive to ants. Thus the elaiosome is suggested to function as a dead-insect analogue. Ants and the myrmecochorous seeds have a reciprocal association. The ants benefit by getting a lipid-rich reward resource while the plant propagule gets dispersed in refuse heaps or in nest chambers (Handel, 1976). Additionally the seeds get a nutrient-rich microsite for germination.

Although it is often generalized mutualism recent studies indicate the occurrence of keystone ant mutualists (Ness *et al.,* 2009). It was demonstrated that *Aphaenogaster* ants (predominantly *A. rudis*) collect about 74 % of the myrmecochorous seeds in eastern North American forests.

Seed predators/ robbers

Ants which remove seeds but destroy them act as seed predators since they kill the potential plants. Recent studies demonstrate that the red imported fire ant, *Solenopsis invicta*, is attracted to and destroys many ant-dispersed seeds (Zettler *et al.,* 2001). The ants consume elaiosomes and either scarify or destroy the seeds thereby preventing seed dispersal by native ant species. Thus they act as seed robbers.

Digestive mutualistic insect-carnivorous plant associations

Carnivorous plant, *Roridula gorgonias* uses sticky traps to capture insect but lacks digestive enzymes for the digestion. It has digestive mutualism with hemipterans, *Pameridea* sp. (Hemiptera: Miridae). The hemipteran feeds on the captured prey and then defecates on the leaves of the carnivorous plant which absorbs the nitrogen directly from the leaves. Hemipterans are also the major pollinators of *Roridula* and are responsible for up to 65% of seed set in *R. dentata* (unpublished data as given in Anderson and Midgley, 2002). The combination of nutritional and pollination benefits of this mutualism indicates that hemipterans may be crucial for plant survival. Pitcher plant, *Nepenthes* suffers from putrifaction on capturing excess prey, but the specialist ants living on theses plants reduce the incidence of putrification by upto 12 fold by removing excess prey and thus are regarded as carnivorous plant mutualists (Clarke and Kitching, 1995).

Cheaters involved in digestive mutualistic associations

Many insects act as cheaters by taking the reward offered by the plants but not providing digestive services to the carnivorous plants. Thus the cheaters exploit the mutualistic association. *Roridula dentata* is associated with a unique species of hemipteran (*Pameridea marlothi*) (Anderson

and Midgley, 2002). Here, a specialist spider (*Synaema marlothi* Dahl., Thomsidae) which is also associated exclusively with *R. dentate* acts as a cheater. It reportedly decreases the numbers of hemipteran individuals inhabiting *Roridula* plants and also decreases efficiency of indirect prey digestion by up to 30%.

Ant-plant protective mutualism

Many plants are involved in 'biological warfare' since they attract and reward ants (by providing food and/or shelter) to deter or kill insect herbivores (reviewed by Bronstein *et al.*, 2006). A large number of studies have documented the obligate associations of ants with myrmecophytes (Janzen, 1966; Beattie, 1989; Bronstein, 1998; Heil and McKey, 2003). Ants provide protection against herbivores and in some cases from competition with other plants (Hölldobler and Wilson, 1995 and references therein). Ants are also involved in facultative protective associations with annual (Agarwal and Rastogi, 2008b, 2009) and perennial, extrafloral nectary-bearing plants (Gaume *et al.,* 1997).

Ants as exploiters and adaptive strategies of the ant-plants to avoid exploitation

While the mutualistic ant, *Pseudomyrmex ferrugineus* protects the Acacia, the myrmecophytes is exploited by the ant, *Pseudomyrmex gracilis* which colonises the plant thus preventing the colonization of the mutualist (Clement *et al.,* 2008). The exploiting ant species not only has adverse effect on the growth of the myrmecophyte but also does not defend it. Ants belonging to genus *Allomerus* though providing protection from insect herbivores to the host plants are also castration parasites since they destroy flowers on the branches they inhabit (Yu, 2001; Izzo and Vasconcelos, 2002). However, its host plant, *Hirtella myrmecophila* (Chrysobalanaceae) drops domatia from older leaves, to minimize the effects of cheating by *A. octoarticulatus* (Izzo and Vasconcelos, 2002).

Acacia ant-plants defended by the symbiotic *Pseudomyrmex* ant mutualists secrete sucrose-free extrafloral nectar which excludes exploiters (Kautz, 2009). Experiments reveal that the mutualist workers avoid sucrose due to the absence of the sucrose-cleaving enzyme invertase while the exploiters and generalists with no particular affinity toward *Acacia* myrmecophytes prefer sucrose. Thus *Acacia* plants are specialized with respect to their ant partners and the digestive specializations prevent mutualists from becoming cheaters. The extrafloral nectary-bearing sponge gourd plants, *Luffa cylindrica,* involved in facultative association with a guild of liquid sugar loving aggressive ants species prevents the exploitation of floral nectar (and also deterrence of pollinators) by means of floral repellents (Agarwal and Rastogi, 2008a).

In the Ant-acacia mutualism, *Acacia mayana* while guarded by the ant *Pseudomyrmex ferrugineus* also harbours the generalist ant, *Camponotus planatus*. *C. planatus* appears to be a parasite of the *Acacia–Pseudomyrmex* mutualism since it occupies the swollen thorns on the host tree, and harvests nectar from extrafloral leaf nectaries but does not protect it from insect herbivores. However *C. planatus* is unable to harvest the second trophic reward in the form of protein-rich food (Beltian) bodies produced by the tree for its *Pseudomyrmex* ant-guards (Raine *et al.,* 2004). The specialised

larval adaptations needed to use Beltian bodies as brood food, is absent in the parasitic ant species. Thus this resource is apparently more resistant to exploitation by generalists than extrafloral nectar.

Conclusion

Plant-insect mutualistic associations generally regarded as pair-wise associations are actually rather complex involving other species which influence the associations. Thus these associations should be regarded as part of the complex network involving multispecies guilds and multitrophic interactions (Stanton, 2003). Attempts are being made to elucidate the ecological and evolutionary dynamics of mutualisms in the context of exploitation (Jones *et al.,* 2009). Recent studies focus on how mutualists use various mechanisms to target rewards preferentially at mutualists (Pellmyr and Huth, 1994; West *et al.,* 2002; Edwards *et al.,* 2006; Bever *et al.,* 2009). Extra-floral and floral nectar composition serves to attract and fulfill the physiological requirements of mutualists while deterring and protecting the resource from robbers and exploiters (González-Teuber and Heil, 2009). In *Acacia–Pseudomyrmex* system a study of 23 *A. cornigera* and 24 *A. hindsii* plants (all of which were inhabited by *P. ferrugineus*) showed that high reward hosts produce significantly more extrafloral nectar, food bodies, and nesting space than low-reward hosts (Heil *et al.,* 2009). Moreover, exploiter ants were recorded to be less dependent on the host-derived rewards and were able to colonize many of the low-reward hosts.

Finally it must be pointed that the evolution of cooperation in fact is itself a puzzle which poses a challenge to evolutionary biologists since natural selection should favour cheaters who can receive benefits without reciprocating the services (Foster and Wenseleers, 2006). Partner choice mechanisms are fundamental to the evolution of cooperation since these permit individuals to invest in cooperating partners and avoid cheaters (Edwards, 2009). A variety of partner choice mechanisms have been implicated in the evolution of mutualism. These include i) host sanctions - selection imposed by hosts rewarding cooperation or punishing less cooperative behaviour (Kiers *et al.,* 2003), ii) sensory traps which are signal mimics that exploit the adaptive, neural responses of signal receivers to elicit out-of-context behaviours (Edwards and Yu, 2007) and, iii) filters - mechanisms which allow individuals to prevent or to avoid costly association with parasites, allowing mutualists to solely interact with and invest in cooperators (Yu, 2001). Paradoxically, occurrence of cheaters may facilitate the maintenance of partner choice (Foster and Kokko, 2006). Thus cheaters may be instrumental in stabilising cooperation in mutualistic associations. It appears that cheating persists when the cheaters are able to avoid host sanctions (Denison and Kiers, 2004). Punishment has been documented to enforce cooperation and prevent cheating in both social insects and human societies (Henrichet *et al.,* 2006; Wenseleers and Ratnieks, 2006). Recent evidences thus suggest that failure to punish leads to cheating in plant- insect mutualism also (Edwards *et al.,* 2009). Since the exploited partner suffers a loss on account of nectar/pollen robbing and deceitful exploitation of its resources (without getting benefit in return) further investigations need to focus on the fitness consequences on the exploited species taking into account the network of interacting species.

Acknowledgement

I thank the University Grants Commission, New Delhi for funding the field studies on

elucidation of insect behaviour and ecology, the research findings of which has stimulated and led to the present review.

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