

Review Article

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Plants and insects in interactions: multitrophic associations

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Abstract:

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Studying a biological species, we are very often obliged to examine many other species which are directly or indirectly related to the particular species in order to have broader perspective of its being. Interactions between organisms can be perceived on various levels concerning biological study areas, such as ecology, physiology, morphology etc. In this place, the authors have given some peculiar examples concerning parasitism. This specific interaction is very common in the animal kingdom, having in mind that about a half of all known organisms are parasitic. The importance of this phenomenon is reflected on many aspects of life, propelling evolution and speciation of each member in the relation.

Key words: parasitism, parasitoids, hosts, defending strategies

Apstrakt:

Žikić, V., Ilić Milošević, M., Lazarević, M., Stanković, S.S.: *Interakcije biljaka i insekata: multitrofičke asocijacije. Biologica Nyssana, 7 (2), Decembar 2016: 75-82.*

Proučavajući određene biološke vrste često smo primorani da izučavamo i mnoge druge koje su direktno ili indirektno povezane sa njom u cilju šireg sagledavanja njene celokupne biologije. Interakcije između organizama mogu biti proučavane na različitim biološkim nivoima, kao što su ekologija, fiziologija, morfologija itd. U ovom slučaju, autori su prezentovali neobične primere parazitizma. Ova specifična interakcija je veoma česta u životinjskom carstvu, imajući u vidu da skoro polovina poznatih organizama pripada parazitima. Značaj ovog fenomena se ogleda u mnogim aspektima života, podstičući evoluciju i specijaciju svakog člana posmatrane interakcije.

Ključne reči: parazitizam, parazitoidi, domaćini, odbrambene strategije

Introduction

The vast majority of plants have evolved along with insects. A lot of insect species directly depend on plants which represent a resource for the whole, or at least a part of insects' life cycle. In this trophic association plants can offer roots, bulbs, trunks,

branches, leaves, flowers, fruits and seed. Even dead plants or their parts can be of use for decomposing insects. Other connections between plants and insects imply symbiosis or mutualism.

A specific relationship between plants and most insects is pollination; this particular act can be performed by hymenopterans, butterflies and moths,

horned beetles, many flies etc., of which a great number represent very specialized forms as far as their morphology or behaviour is concerned (Bronstein et al., 2006). For example, moths from the family Sphingidae are associated with plants whose flowers have deep calyx forming tubes (Faegri & van der Pijl, 1979; Haber & Frankie, 1989). Hovering around the plants these moths suck nectar through a very elongated proboscis. This type of feeding is not unique in the animal world; convergent evolution has appeared four times in non-related nectar feeders. In mammals, bats are a very good example, while among birds there are hummingbirds, and also two groups of insects: hoverflies (Diptera: Syrphidae) and hawk moths (Kitching, 2002). The list of attended plants is huge, ranging from those with small flowers with short calyx such as *Verbena* L., *Lantana* L., *Lobelia* L. and *Buddleja* L., over *Petunia* Juss. or *Nicotiana* L., and furthermore to plants with very large flowers with deep calyx such as various species of *Datura* L. or Darwin orchid, *Angraecum sesquipedale* Thouars with a calyx which is 30 cm deep. Otherwise, the group of solitary bees (Megachilidae), e.g., *Eucera longicornis* (L.), some digger wasps (Crabronidae) and some mining bees (Andrenidae) specialize in the pollination of various orchids imitating the females; in the first place from the genus *Ophrys* L. (Willmer, 2011). For many snapdragon species the only solution of being pollinated was to establish an intimate relation with some bumblebees which are capable to open the “lips” of the flowers using their strong hind legs (e.g., Odell et al., 1999).

Myrmecochory is a special kind of ant-plant interaction where ants are engaged in seed dispersal. For this purpose myrmecochorous plants shaped their seeds to carry *elaiosomes*, various external appendages rich of nutrients such as lipids, amino acid, or other attractive substances to ants (Gibaldi, 2006). Some stick insects (Phasmida) have taken advantage of this ant activity by producing seed-like eggs which are carried by ants into their nests where the conditions are favourable for their development (Compton & Ware, 1991; Stanton et al., 2015). In Central America there is an example of true symbiosis between ants and plants. The acacia ant – *Pseudomyrmex ferruginea* F. Smith, lives in small colonies in the base of the horns of the bullhorn acacia – *Vachellia cornigera* (L.) finding a shelter there, but at the same time offering protection to its host (Janzen, 1967; Piper, 2007) as ants attack all approaching animals and plants by stinging them.

A specific way of insect parasitism takes place in galls. Galls or cecidia are transformations of plant parts (external tissues) such as leaves, branches,

roots, petals or flowers, caused by insect or mite activities. Plant tissues show abnormal outgrowths like tumours in animals. The most important gall-inducing insects are gall wasps, Cynipidae (Hymenoptera), gall midges Cecidomyiidae (Diptera), gall aphids Aphididae (Hemiptera) and some species from the group of leaf-miner flies, Agromyzidae (Diptera) (e.g., Spencer, 1973; Stone et al., 2002; Yukawa & Rohfritsch, 2005; Floate, 2010). Galls and cecidia arise after females inject cecidogenous fluid, along with egg, in the plant tissue, e.g. Tenthredinidae (Hymenoptera) (Kopelke, 1998). Afterwards, parasite larvae force the neighbouring plant cells into gall to start the division process of meristems. Parasites use the galls as their habitat and shelter; also exploiting the sugars accumulated in it, they also use the galls as a food source (Larson & Whitham, 1991).

A very bizarre relationship between plants and insects is found in carnivorous plants such as *Drosera* L., *Nepenthes* L., *Sarracenia* L. or *Dionaea muscipula* Ellis that “consume” insects. Leaves of those mainly bog inhabiting plants form traps, usually pitfalls, filled with water and enzymes (*phytotelmata*). All kind of traps in carnivorous plants are supplied with attractive colour, odour and specialized nectary glands. Those glands produce sweet smelling nectar to attract and catch insects later digesting them, using externally excreted enzymes. In this way, plants obtain minerals from insect’s body, since the boggy soil is poor. Once those plants have to be pollinated, they need insects again. Then, carnivorous plants suspend all the attractants in their traps, focusing on their flower equipment in order to attract pollinators. This convergent behaviour evolved independently in both dicotyle and monocotyle plant lineages, terrestrial and underwater plants (Albert et al., 1992).

Plants, hosts and parasitoids

Predators, parasites and parasitoids have an indirect connection with plants via their herbivorous prey or host which is essential for their life cycles (Price et al., 1980; Stotz et al., 1999). In the case of insect parasitoids, the host is usually required during the larval stage. The plant role in this play is to unintentionally help the host to become less attractive or even poisonous for its enemies. The six-spot burnet, *Zygaena filipendulae* L. is capable of sequestering alkaloids from the food plant *Lotus corniculatus* L. In this cases the cyanogenic glucoside linamarin, also lotaustralin are biosynthesized in poison thus decreasing predation of larvae and adults (Davis & Nahrstedt, 1979; Zagrobelny et al., 2007). This poison protects a

very high percentage of adult moths while larvae still remain exposed for various parasitoids such as various hymenopterans and tachinids (Tachinidae: Diptera) (Žikić et al., 2013).

The great majority of parasitoid insects belong to the Hymenoptera insect order. With some exceptions, they come from the division Parasitica. Parasitoid members of the other division Aculeata, are in minority and their kind of parasitism is a little different (e.g., Chrysididae, Sphecidae, etc.) (Wcislo et al., 1985; Winterhagen, 2015). The second important group of parasitoids are tachinid flies (Feener & Brown, 1997); also, there are some sporadic cases in Coleoptera, Lepidoptera, Trichoptera, Neuroptera and Strepsiptera (Pierce, 1995; Heraty, 2009). A simple association between a plant (primary food producer), an herbivorous host (primary food consumer) and a parasitoid (secondary food consumer) is being considered through trophic chains; this threesome is usually referred to as a tritrophic association. Higher trophic levels with more members include more than one parasitoid species and also hyperparasitoids primary food consumer forming a multitrophic association. Parasitoid larvae are carnivorous, feeding outside or inside the host body. Conversely, adults are free living organisms feeding on flowers (nectar) or honeydew produced by green aphids. The final effect of host-parasitoid interaction is death of the host, which makes these organisms very powerful biological weapon. Nowadays, several companies have developed technologies for commercial production of a few dozen parasitoid species on artificial nutrient medium. Those species are applicable both in open fields as well as in greenhouses (Olkowski et al., 2003; Hale & Hensley, 2010).

There are various classifications of parasitoids based on different criteria concerning their behaviour, life cycle or number of eggs laid per single host. On the basis of oviposition location parasitoids can be ecto- or endoparasitoids; whether or not parasitoid larvae alter hosts behaviour they could be idiobionts or koinobionts accordingly; according to the number of eggs laid per host there are two cases, solitary (a single egg per host) or gregarious (usually few to more than a hundred eggs laid per host) (Godfray, 1994). Ectoparasitoids lay their eggs on the host body surface. If the female causes a permanent paralysis of the host and parasitoid larvae feed outside the host body, those species represent idiobionts (many Ichneumonidae and some Braconidae). On the contrary, if the host continues its life after the larvae have been hatched on its body, those parasitoids are considered as koinobionts. Those are parasitoids which only temporarily

paralyse the host, and they are capable of regulating its behaviour and life cycle until they reach maturity (Desneux et al., 2009). Usually, parasitoid larva kills the host at the end of its larval stage. An example of ectoparasitic koinobionts is an ichneumonid wasp *Acrodactyla quadrisculpta* (Gravenhorst) which parasitizes a spider, *Tetragnatha montana* Simon (Miller et al., 2013). The majority of koinobionts represent endoparasitoids, which develop inside the host body. In some cases, such as the species *Macrocentrus* Curtis (Braconidae), the female lays only one egg in the host body which undertakes the process of polyembryony and ultimately gives dozens of individuals which are genetically the same (clones) and thus increasing its parasitic capacity (Howard, 1906; Cushman, 1913; Parker, 1931; Quicke, 2014). Another strategy of increasing parasitic capacity can be seen in gregarious parasitoids (e.g., Eulophidae, Encyrtidae, Braconidae) where females lay a couple of eggs per host, but their offspring is not genetically the same and both sexes are developed (Quicke, 2014).

Multitrophic associations usually include hyperparasitoids, the species that parasitize primary parasitoids. However, the hyperparasitism does not end here; on the highest level of trophic chains we are talking about hyperparasitoids of the second and the third level. Clearly, in the trophic chain with a maximum number of members in a row is consisted of: 1) primary food producer (plant), 2) primary food consumer (host), 3) secondary food consumer (primary parasitoid), 4) tertiary food consumer (secondary parasitoid = primary hyperparasitoid), 5) quaternary food consumer (tertiary parasitoid = secondary hyperparasitoid) and 6) quinary food consumer (quaternary parasitoid = tertiary hyperparasitoid). Harvey et al. (2009) explained this phenomenon working on the wasp *Cotesia glomerata* (L.) (Braconidae) as a primary parasitoid which is hyperparasitized by *Lysibia nana* Gravenhorst (Ichneumonidae) which is a secondary parasitoid. Furthermore, the species *L. nana* was hyperparasitized by another ichneumonid wasp *Gelis agilis* (Fabricius), appearing as a tertiary parasitoid. Finally, there are some other species from the same genus, *Gelis* attack *G. agilis*. Interspecific parasitism is considered in more details in Sullivan (1987).

A kind of parasitism which is known as kleptoparasitism is the interaction where one animal takes food from another. In parasitoids kleptoparasitism occurs in cuckoo wasps (Chrysididae). The cuckoo wasp *Omalus* Panzer is the parasitoid of the larvae of another hymenopteran family, Crabronidae (Winterhagen, 2015). This species does not oviposit directly in crabronid larva, but in aphids, even though an aphid is many times

smaller than the cuckoo wasp larva. Crabronid females collect the aphids and carry them in a previously made nest to serve as food for their larvae. Accidentally, a crabronid female picks up a parasitized aphid with the egg of a cuckoo wasp which has been laid inside its body. In this way a crabronid wasp brings the parasitoid in its own nest. Ultimately, when the cuckoo wasp larva emerges from its egg and then from the aphid body, it starts looking for food devouring the crabronid larva, and also the collected aphids.

Exceptions exist in almost every group of sibling organisms. Well known example of exception is panda – being herbivore among the mammal's order Carnivora. Similarly, among the large groups of Parasitica, there are some exceptions as well; many species of the family Agaonidae (fig wasps) have developed a unique mutualistic association with various *Ficus* L. trees, and more specifically with their flowers. The odour released from the fig flowers (*syconium*) attracts a fertilized female wasp to enter the syconium through a tiny opening in the centre. In this way, the wasp is carrying pollen from the flower from which it emerged. However, the main reason of its presence is to lay eggs in fig's female flowers turning a syconium to a fig fruit (Kjellberg et al., 2005).

Plant defending strategies and plant communications

There is a secret language in which plants communicate with each other in many ways (e.g., *allelopathy*) (Baluška & Ninković, 2010). Modern definition of allelopathy is “chemical interactions that involve toxic allelochemicals and should be distinguished from plant chemical communication” (Schenk et al., 1999; Schenk & Seabloom, 2010). A way of emanating evaporative chemical signals via air is the one that is best investigated (Vet & Dicke, 1992; Bruce et al., 2005). Fowler & Lawton (1985) found that the chemicals are a blend of organic molecules such as alcohols, aldehydes, ketones and esters which are known as volatile organic compounds (VOCs) also called kairomones (more recent, semiochemicals). Recent studies reveal that plants as the lowest trophic level, when attacked by herbivores such as aphids, scale insects or caterpillars, emit any substance produced by an individual of one species that benefits both the producer and the recipient which is of a different species - *synomones* which attract natural enemies i.e. parasitoids and predators in order to defend themselves (Vet & Dicke, 1992; Turlings et al., 1995). This group of authors also revealed that the signalling role probably evolved

secondarily as a result of plant responses that produce toxins and repellents against pests and also antibiotics against pathogens. Studying olfactory physiology and behaviour of a predaceous beetle *Thanasimus formicarius* (L.) (Coleoptera: Cleridae), the authors Zhang & Schlyter (2010) showed that the specific chemical substances from other non-target hosts and plants, which are not even a part of the particular trophic association, can inhibit the attraction of chemical signals of attacked host/prey. In other words, neighbouring target plants resort to mimicry, thus stopping to smell out, becoming less attractive for pests.

The other way of plant communication is through soil. They can do that directly by roots, or most often using an “internet” made of fungi. By linking to the fungal network, plants exchange information, nutrients and toxic chemicals with their neighbours (Song et al., 2010). Mutually-beneficial relationships between plants and fungi, known as mycorrhiza can be found in a great majority of plants.

Host-parasitoid coevolution

Under the pressure of parasitoids, hosts develop various defending strategies (Kraaijeveld et al., 1998). A simple type of protection that females use for their offspring is laying eggs in hidden places. For example, some Siricidae (Hymenoptera: Symphyta) have very long and strong ovipositors with which they drill wood and lay their eggs deep inside it, thus minimizing the chance of their larvae to be parasitized. Some other species, such as sawflies (Hymenoptera: Argidae and Tenthredinidae) saw plant stems where they will oviposit. In Symphyta there are also the species causing leaf mines or galls as it was previously explained (Hawkins, 1988; Hering, 2013).

The immune system can protect the host against parasitoids to varying degrees (Kraaijeveld & Godfray, 1999; Carton et al., 2008). In a process of encapsulation hosts can eliminate parasitoids, forming a multi-layered cyst made of hemocytes. The hemocytes found in insect's hemolymph are cells with the phagocyte function (Godfray, 1994).

Endosymbionts are present in many living beings, irrespective of whether they are algae, plants, fungi or animals. These are organisms that live within the body or cells of other organisms. The most famous examples of endosymbiosis are nitrogen-fixing bacteria associated with legume roots (Franche et al., 2009), single-cell algae living in reef-building corals (Rowan, 1998) and in some Turbellaria (Barneah et al., 2007), or some protists and prokaryotes which inhabit the intestine of termites

(Ohkuma, 2008) and other wood-consuming insects. There are also bacterial endosymbionts that protect host insects, e.g., aphids against parasitoids. Bacteria from the genus *Buchnera* overproduce tryptophan (plasmid borne enzyme) and other amino acids that minimize the exposure of aphids to parasitoids (Rouhbachsh et al., 1997). *Hamiltonella defensa* is a species of bacteria, that lives as an endosymbiont of aphids (most studied is the pea aphid – *Acyrtosiphon pisum* Harris) providing its host protection against parasitoids. Mechanism of protection implies that *H. defensa* is infected with temperate bacteriophages called *Acyrtosiphon pisum* secondary endosymbionts (APSEs) (van der Wilk et al., 1999; Vorburger, 2014). Those bacteriophages encode different toxin genes killing the parasitoid eggs or larvae thus protecting the aphid host (Degan & Moran, 2008). Endosymbiotic male-killing bacteria from the genera *Wolbachia* and *Rickettsia* eliminate only the male sex in parasitoid embryos defined by genetics. It is not yet clear why males are more sensitive to *Wolbachia*; it might be due to the fact that they have only one X chromosome or because they lack the whole garniture of chromosomes (haploids) (e.g., Hurst & Jiggins, 2000; Kondo et al., 2002; Belshaw & Quicke, 2003; Werren et al., 2008).

Parasitoids also have evolved a variety of strategies to overcome host immune responses, but on the other hand they developed strategies to defend themselves against hyperparasitoids. There are several strategies to accomplish host defending mechanisms: by avoiding oviposition in body parts accessible to host hemocytes or by disrupting the host immune system injecting specific chemicals into the host at the time of oviposition; for example: *Apanteles* (Hymenoptera: Braconidae) injects baculovirus-like nucleocapsids in the caterpillar body (Stoltz & Vinson, 1977). Also, remnants of polydnviruses found in larvae of some parasitoid taxa disrupt the capsule around the parasitoid which is made of host hemocytes (Bézier et al., 2009). Polydnviruses destroy those hemocytes or alter their ability to aggregate and form a strong layer around parasitoid larvae (Vinson, 1990). These endosymbionts played one of the main roles in evolution of host range and in defining parasitoid-host compatibility (Schlenke et al., 2007).

Conclusion

Although this overview represents only a glimpse of a fantastic array of interactions among insects themselves and plants, it gives an interesting insight and perspective of these phenomena. Beside the fact

that many details are concealed or maybe beyond our reach, the accumulated knowledge and permanent investigation of this topic has provided us with many benefits. The most useful is pest management and using biocontrol agents to combat pest insects. This has some serious repercussions in healthier food production and sustainable agriculture.

“Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life” (Darwin, 1872).

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