

Insects in agroecosystems – an introduction

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Accepted: 9 January 2020

Key words: agriculture, plant defense, plant domestication, weed control, biological control, volatile organic compound, sustainability, ecological complexity, habitat modification, intercropping, preference–performance, damage quantification

Abstract

Agroecology is the study of linkages in agricultural systems and it derives from the need to understand and restore natural connections and ecological complexity to control insect and other pest populations. The present special issue addresses a rich variety of agroecosystems spanning the globe, involving the roles of a range of insects on a great many crops. The overview will further improve our understanding of the complex ecology of the players and the ecological complexity of the crop systems.

Of all the habitable land on earth about 37.5% is used for agriculture (The World Bank, 2019), with crops accounting for 23% of agricultural lands used whereas the remaining 77% are for livestock. The Food and Agriculture Organization (FAO) estimates that 1.6 billion ha is currently under cultivation (FAO, 2011). It is estimated that at any one time there are over 10 quintillion (10×10^{18}) insects on earth (EO Wilson, quoted on Howstuffworks, 2019). The human world population is 7.7 billion. This means insects outnumber humans by roughly 1.5 billion to one. Considering that many of these insects are phytophagous, it is inevitable that people and insects will compete for the same food plants. Insect pest densities in a crop can be enormous. In the USA Midwest, for instance, soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a major soybean pest that can reach high population densities (in the peak of summer a single plant may support more than 6 000 aphids; Yoo & O'Neil, 2009), producing a density of approximately 100 million aphids ha⁻¹. Densities of the invasive little fire ant, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae), in a tropical fruit orchard in Hawaii, USA, were estimated at 244 million ha⁻¹ (Souza et al., 2008).

Herbivorous insects are extremely diverse, with species number estimates ranging from 500 000 to 2 million (Schoonhoven et al., 2005; Bernays, 2009; Stork et al.,

2015). Most plant species in the wild support complex faunas of herbivores (Strong et al., 1984). The amount of damage sustained is quite small as plants appear to have broad-spectrum physical and chemical defenses against insect herbivores and pathogens (Giron et al., 2018). However, plant domestication and breeding involving selection for improved yield and quality have diminished the defensive capability of the crops making them more susceptible to pest damages (Chen et al., 2015). The pre-adapted traits providing protection from insect pests may still exist in the plant genome and finding and exploiting these traits forms the basis of host plant resistance (Mitchell et al., 2016). Whereas plant defenses may determine the diversity and abundance of insects attacking a plant species, natural enemies and interactions within the ecological community are of key importance in regulating insect populations (Rosenheim, 1998). Crop production systems result in a significant alteration in food webs and the number and diversity of insect species, as well as various modifications of the soil, water, and topography. Crops are maintained by high-energy inputs that involve practices such as tillage, fertilization, cultivation, irrigation, and pesticide use, which greatly simplify and/or alter food webs (Tilman et al., 2002; Desneux et al., 2007; Tsiafouli et al., 2015; Zytynska & Meyer, 2019), and the linkages that normally keep insect populations in check are often lost. Agroecology is the study of the linkages in agricultural systems and derives from the need to understand and – at least partially – restore natural connections and ecological complexity to control insect and other pest populations.

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The present special journal issue addresses a rich variety of agroecosystems involving the roles of insects from a range of orders (Diptera, Hemiptera, Heteroptera, Lepidoptera, Coleoptera, Hymenoptera), a great many crops (potato, onion, African peach, wheat, strawberry, alfalfa, chickpea, rice, tomato), truly spanning the globe (Brazil, Mexico, USA, Canada, Benin, Iran, India). In many cases, insects are pests, but in some the insects are the good guys, helping in the control of weeds or pest insects. The overview of systems and detailed investigations of mechanisms will further improve our understanding of the ways in which the complex ecology of the various players as well as the ecological complexity of the crop systems as a whole can be used to the benefit of farmers, consumers, and the environment alike.

The importance of healthy soils for natural pest control is reviewed by Alyokhin et al. (2020). Agricultural practice and soil deterioration have long gone hand-in-hand and have led in many cases to decrease of complexity and stability of agricultural ecosystems, making them more vulnerable to pest outbreaks. Focusing on potato and onion crop systems, the authors illustrate how soil conservation techniques may help improve crop production. Examples of such techniques are organic soil amendments (making soils rich in organic matter, enhancing the complexity of soil food webs and the diversity of soil-dwelling organisms, making crops less susceptible to insect herbivory) and mulching (also reducing soil erosion and water evaporation, suppressing weed growth, hampering pest infestation and disease transmission in the crops, and stimulating the abundance of natural enemies of the pests). Although the authors convincingly demonstrate the benefits of soil improvement, they also explicitly indicate where more research is needed – not all effects are equally strong at all times and in all crop systems (calling for a better understanding of the underlying mechanisms), and aside from the relatively well studied effects of mulching and organic soil amendments, much remains to be expected of, for instance, conservation tillage (reducing soil disturbance and erosion, leading to more complex habitats, providing additional resources – alternative prey, shelter – to biological control agents), cover crops (often leading to reduced insect herbivory, more sustainable production, and higher crop yields), and mycorrhizal fungi [crop plant symbionts, often stimulating plant (re)growth and defense].

The effect of habitat modification on insects and crops is further explored in three research studies. Mama Sambo et al. (2020) investigate which biotic and abiotic factors affect *Fopius caudatus* Szépligeti (Hymenoptera: Braconidae), a parasitoid wasp of the pest fruit fly *Ceratitis cosyra* Walker (Diptera: Tephritidae) in orchards of *Sarcoccephalus latifolius* (Smith) Bruce (Rubiaceae) shrubs in

West Africa. Both parasitoid and pest population levels appear to be associated with various biotic and abiotic factors, some of which can be manipulated to influence parasitism rate, such as cultivation intensity, topography, and vegetation composition and coverage. The relevance of habitat structure for the abundance and interactions of herbivorous and predaceous insects also stresses the importance of natural habitats close to cultivated areas: they may function as sources of natural enemies.

Habitat structure may also be modified within arable fields, by intercropping (e.g., Lai et al., 2019). In a carefully controlled laboratory study, Mansion-Vaquié et al. (2020) set out to test the disruptive crop hypothesis, stating that the ability of herbivores to find and settle on host plants is reduced by the presence of non-host plants. In two intercropping systems – soft winter wheat (*Triticum aestivum* L., Poaceae) combined with winter pea (*Pisum sativum* L., Fabaceae), and soft winter wheat combined with white clover (*Trifolium repens* L., Fabaceae) – the behavior of wingless *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) was compared to the behavior in soft winter wheat-only stands. When intercropped with clover, the aphids were found to take longer to locate their wheat host plants, and aphid densities stayed lower than in the wheat-only control. This was not the case when the wheat was intercropped with winter pea. Hence, the disruptive crop hypothesis was accepted in one of the two systems; the species of non-host used as intercrop has a decisive effect. The next step will be to take the study to the field, where for instance natural enemies of the aphid come into play.

Generalist predators in a strawberry field (*Fragaria ananassa* Duchesne, Rosaceae) intercropped with alfalfa (*Medicago sativa* L., Fabaceae) were the focus of a study by Hagler et al. (2020). Alfalfa is a highly preferred host plant of various *Lygus* species (Hemiptera: Miridae), and the use of alfalfa as a trap-crop in strawberry fields may lure the pest away from the focal crop, and form a sink for *Lygus* predators at the same time. The abundance of generalist predators of six taxa was assessed on alfalfa and strawberry, as well as their dispersal through the field, on two strawberry farms in California, USA. Recapture of protein-marked predators indicated that most predators were collected less than 2 m from a central alfalfa trap-crop row. This demonstrates that the trap-crop indeed forms a predator sink, which may be taken in account when plotting conservation biocontrol strategies.

Generalist predators also feature in a wheat field study in western Canada, where the cereal leaf beetle, *Oulema melanopus* L. (Coleoptera: Chrysomelidae), has recently been reported. This leaf beetle causes great concern, as it is a major pest of cereal crops. To explore the relevance and importance of naturally present generalists as predators of

the cereal leaf beetle, Keirodin et al. (2020) developed primers to detect the DNA of cereal leaf beetle in the predator gut. Of six common predator taxa in wheat fields, the species *Nabis americanoferus* Carayon (Hemiptera: Nabidae) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) were the most abundant, and a positive association was found between the abundance of the cereal leaf beetle and the proportion of *N. americanoferus* and *C. septempunctata* specimens with cereal leaf beetle DNA in their guts. The molecular method proves a useful tool in monitoring field predation, and may help to incorporate the natural predators into programs of pest management of the cereal leaf beetle.

Many legume crops are victim to the pod borer *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae). In an Iranian field study with chickpea, *Cicer arietinum* L. (Fabaceae), Allahyani et al. (2020) tested the control efficacy of members of two guilds of pod borer natural enemies. Two pathogens, *Helicoverpa armigera* nucleopolyhedrosis virus and *Bacillus thuringiensis* Berliner ssp. *kurstaki*, and the parasitoid *Habrobracon hebetor* Say (Hymenoptera: Braconidae) were released in chickpea fields, both separated and combined. The best pest control was achieved when the parasitoid was released with either of the pathogens, indicating synergistic effects. As the study also included various economical parameters, it was demonstrated that also the costs of these combined treatments were highest. The authors conclude that an increase of the net benefit of the combined application of the pathogens and the parasitoid depends on more efficient mass production of especially the pathogens.

Three studies explore the role of plant-produced volatile compounds, two in a rice crop and one in tomato. The first studies the role of airborne plant signals on direct and indirect plant defense strategies of rice plants in Brazil (Ulhoa et al., 2020). Chemical analyses demonstrate the overlap and differences in headspace volatiles of rice infested with each of two species of stink bug, *Tibraca limbativentris* Stål and *Glyphepomis spinosa* Campos & Grazia (both Heteroptera: Pentatomidae), and olfactometer analyses investigate the effect of volatiles on the behavior of the same stink bug species (direct defense), as well as on the egg parasitoid *Telenomus podisi* Ashmead (Hymenoptera: Platygasteridae) (indirect defense). The rice plants were found to produce different headspaces in response to infestation by the two stink bug species, and that based on the volatiles conspecific stink bugs are less attracted to infested rice plants, whereas the egg parasitoid wasps are attracted to rice plants infested with each of the two stink bugs. These results indicate that these herbivores possibly use the plant signals to avoid competition with conspecifics and parasitization by natural enemies.

The second study of the role of plant volatiles in a rice production system uses different components. Weeds in rice fields in India may reduce grain yield seriously, therefore these weeds need to be controlled, for instance by the use of a biocontrol agent. Mitra et al. (2020) studied the host preference of the leaf beetle *Altica cyanea* (Weber) (Coleoptera: Chrysomelidae) based on their behavioral response to volatiles from each of three *Ludwigia* weed species (Onagraceae), a pantropical genus that is considered invasive throughout the world. The goal of this laboratory study is to develop traps with synthetic blends that may lure the leaf beetles to target the weeds during their early emergence in rice fields. Chemical headspace analyses of the three weed species identified ca. 25–35 compounds, some common, some plant species specific. The behavioral response of the beetles toward these volatiles was tested in olfactometer assays. Subsequently, the olfactory responses to artificial blends of subsets of synthetic compounds mimicking each of the three weeds were assessed. This has resulted in several simplified blends that will be good candidates for lures to monitor the presence of the beetle in the field.

The third study including plant volatiles focuses on a test of the preference–performance (‘mother knows best’) hypothesis with the generalist cabbage looper moth, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), and three varieties of tomato, *Solanum lycopersicum* L. (Solanaceae), in Mexico. The hypothesis states that females select host plants on which the performance of their offspring – incapable of moving large distances – is best. Meneses-Arias et al. (2020) were interested in the role of plant volatiles in host selection of the moths, and that of glandular trichomes on the plant leaf surface. The results did not support the hypothesis: neonate larvae did best on the tomato cultivar with the lowest density of leaf trichomes, yet egg-laying female moths did not prefer any of the three (uninfested) cultivars of tomato in a cage experiment, despite (quantitative) differences among the volatiles in the three headspaces. The authors discuss possible explanations for the lack of support for the preference–performance hypothesis in this study (and some others), in light of various previous studies that did find support.

The issue closes with a technical note introducing a new and simple method for the quantification of insect damage to plant storage organs, which may be instrumental in the study of belowground herbivory. Quantifying aboveground herbivory (leaf damage) is often straightforward, as (two-dimensional) image analysis software can be used. May plant storage organs – such as potato tubers or cassava roots – are decidedly three-dimensional, which makes a volumetric method more appropriate. Dray & Goldstein (2020) demonstrate the accuracy of their method by

quantifying the feeding damage by *Lilioceris egena* (Weise) (Coleoptera: Chrysomelidae) to air potato, *Dioscorea bulbifera* L. (Dioscoreaceae). This invasive Asian vine has spread throughout the southeast USA and *L. egena* seems a good candidate biocontrol agent. The method is based on the injection of water in sliced tubers (bulbils) and compared to water-injected intact tubers and resin-injected slices. This method allows direct quantitative measures of insect damage, thus providing a valuable tool for biological control practitioners.

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