**NEOTROPICAL ENTOMOLOGY**

**FORUM ARTICLE**

**TITLE: COMPANION AND SMART PLANTS: SCIENTIFIC BACKGROUND TO PROMOTE CONSERVATION BIOLOGICAL CONTROL**

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**Abstract**

To attain sustainable agricultural crop protection tools such as host plant resistance, enhanced ecosystem services (i.e. conserving natural enemies), and the deployment of companion plants should be promoted in pest management programs. These Agro system manipulations could be based on chemical ecology studies considering the interactions with natural enemies and pests, regarding specifically plant defense signaling. Further, new crop protection strategies might rise from widening the knowledge regarding how herbivore-induced plant volatiles can govern a multifaceted defense response including natural enemy recruitment, pest repellence or induced defense in neighboring plants. It is crucial to use a multitrophic approach to understand better the interactions involving companion plants, herbivores and natural enemies in the field, increasing the knowledge to build more efficient and sustainable pest management strategies. In this Forum, we explore the perspectives of companion plants and their semiochemicals to promote conservation biological control according to the ‘smart plants’ concept. Further, we discuss the advantages and disadvantages of using companion plants and explore the application of companion plants in different agroecosystems using several case studies.

Keywords: Sustainable agriculture systems, natural enemies, herbivores, plant diversity

**Plant diversity and Biological Control**

 Increasing the diversity of plants in agroecosystems has been studied extensively in recent decades as a strategy for promoting conservation biological control of invertebrate (insect, mite) pests (*e.g.,* Sheehan 1986; Andow 1991; Poveda et al.2008; Letourneau et al.2009;2011; Isbell et al.2017). Here, more suitable resources and conditions for pest natural enemies are provided (Venzon et al. 2019b), and the need for external inputs e.g. pesticides is reduced (Shields et al., 2019). However, the effectiveness of this strategy has met with variable levels of success (Letourneau et al.2009; 2011). Although general positive effects on pest management have been observed in different systems, there are examples where increasing plant diversity in agroecosystems can lead to difficulties for natural enemies (mostly specialists) to locate their prey (Letourneau et al. 2011). For example, plant diversity can in some instances promote antagonistic interactions, such as intraguild predation or apparent competition, which can reduce the impact of natural enemies on pest populations (Venzon et al. 2001; Koss and Snyder 2005; Janssen et al.2007). Plant diversity can also increase unfavourable conditions for natural enemies (Corbett and Plant 1993). Additionally, some plants may provide additional resources to phytophagous insects, increasing their attraction and damage to the main crop (Norris and Kogan 2000). Therefore, increasing plant diversity *per se* is sometimes insufficient to reduce pest populations, and there is a need to better understand the ecological interactions underlying this management strategy (Venzon et al. 2019a; 2019b) (Figure 1).

 Although ecological interactions that operate in natural ecosystems are also present in agroecosystems, interactions in the latter are often characterized by continuous disturbance due to agriculture intensification. Agroecosystems can have high species turnover, frequent introduction of germplasm with low genetic variability, disturbance of natural communities caused by synthetic pesticides, and continuous exportation of biomass from the system through harvesting (Nicholls and Altieri 2004). To understand better the ecological interactions operating in agroecosystems, it is necessary to elucidate main factors that affect interactions within guilds and between trophic levels (Venzon et al. 2001). Most interactions related to pest management may involve cropped plants (e.g. main and secondary crops), natural vegetation, weeds, herbivorous pests, non-pest herbivores and natural enemies (Venzon et al. 2019b). In such food webs, bottom-up (a lower trophic level influences a higher trophic level) and top-down (a higher trophic level influences a lower trophic level) effects can directly and indirectly operate simultaneously upon populations of insect pests (Figure 1).

Achieving a better understanding of specific interactions in food-webs is an important first step for manipulating plant diversity and enhancing pest management (Begg et al.2017). Moreover, it is known that semiochemicals (naturally-occurring behaviour-modifying compounds eg herbivore-induced plant volatiles (HIPVs)) play a central role in mediating the interactions between plants, pests and their natural enemies. Understanding the chemical ecology of plant-pest-natural enemy interactions, specifically the role of inducible or primed host semiochemicals in plant resistance, has advanced rapidly in recent years, thereby increasing the use of semiochemicals in pest management (Birkett and Pickett 2014) (Figure 1). Therefore, improving our understanding of the synergies between the use of companion plants and the interactions mediated by semiochemicals could stimulate a new generation of conservation biological control strategies.

In this review, we seek to explore the use of companion plants and their associated semiochemicals to promote conservation biological control within the framework of ‘smart plants’, i.e. selected plant varieties that present traits allowing them to respond earlier to pest colonisation (Birkett and Pickett 2014). We believe that smart plant deployment is an important innovation for sustainable pest management, as it is based on the manipulation of ecological processes rather than relying predominantly on deployment of pesticides. We present (i) a theoretical discussion on the background related to companion plants, semiochemicals and smart plants, in order to find possible complementary effects between their use in agriculture (ii) successful case studies, with a primary focus on experiments carried out in Brazil. Finally, we provide a future perspective on opportunities for research in conservation biological control and possible routes for innovation in agricultural food production.

From a bottom-up effect perspective, phytophagous insects use a wide array of signals and stimuli from different distances and sources to locate and colonise a host plant (Bernays and Chapman 2007). At long distances, insects mostly use olfactory and visual signals to orient towards an appropriate habitat containing their host plants (Borges and Blassioli-Moraes; 2017, Prokopy et al 1983), and then at a short distance, plant traits start to play an important role (Borges and Blassioli-Moraes 2017, Prokopy et al. 1983).

In a more complex environment with a variety of plants (i.e., other than the target crop), visual cues may be difficult for phytophagous insects to exploit in differentiating between host and non-host plants, and therefore may waste time and energy in finding a host (Dethier et al. 1960). Therefore, it is expected that tritrophic interactions that rely on chemical volatile information could be more advantageous in complex environments. However, a mixed blend of plant odours promoted by plant diversity in agroecosystems could also act as a repellent stimulus (Robinson et al. 2008; Ratnadass et al. 2012), thereby causing individuals to move to other habitats or patches. Additionally, plant volatiles from non-preferred or non-host plants can produce a masking effect of the cues from the host plant, thus producing an associational resistance effect (Thiery and Visser 1987). This phenomenon is more restricted to polyphagous insects, where decision-making ability is less accurate than that of specialist insects, possibly because they need to deal with more complex and diverse information in the environment to benefit from the exploitation of different hosts (Bernays and Minkenberg 1997). There is a certain neural limitation to integrate information and make choice in complex environments over a simpler environment (Bernays 2001). According to Rosado et al.(1973) and their Resource Concentration Hypothesis, monoculture crops are easier to be found than polycultures. Phytophagous insects tend to colonize and be retained in such areas because they find resources that are more suitable and conditions ideal for survival and reproduction.

 At shorter distances, for phytophagous insects to be retained in the habitat, chemical (including volatile and non-volatile chemicals), physical and visual stimuli can be used. Finch and Collier (2000) summarized the theoretical ecology involved in host plant selection at short distance. The choice of a host consists in accumulating several positive stimuli (*e.g.,* olfactory, tactile and visual) when landing on different plant parts after arriving in a patch within the habitat. When an insect consistently gains more positive stimuli, when probing a host plant several times, it can decide to use the plant as a host i.e., start egg laying. However, when non-preferred or non-host plants are present during the acceptance phase, an insect can deal with multiple negative stimuli, including barriers to movement and as well as mechanical plant defence against feeding. After balancing the negative and positive stimuli, when plant diversity is present, phytophagous insects tend to move to another area. Therefore, plant diversity in agroecosystems can affect host plant selection and insect retention.

Natural enemy top-down effects, in a given crop location, are engendered by species that can effectively colonize hosts and be retained within the crop field (Tscharntke et al.2005 a; 2005b). Some habitats in the landscape such as natural vegetation areas (Rand et al.2006), fallow areas (Sarthou et al.2014; Togni et al.2019a; 2019b), agroforestry systems (Harterreiten-Souza et al.2014; 2021; Rezende et al. 2014) and field margins nearby the crop (Amaral et al.2016) can act as sources of natural enemy species where they can spill over to the cropped area (Tylianakis et al.2005; Tscharntke et al.2012; 2016). Consequently, the effects of plant diversity on natural enemies can depend on spatial variables, often at the landscape level. As most of the strategies related to the increase of plant diversity are connected to farm scale level, we will therefore focus our discussion on the attraction and retention of natural enemies inside the crop area.

 According to the natural enemies’ hypothesis, increasing plant diversity in agroecosystems raises the abundance of natural enemies, as there are more resources and conditions to harbour larger populations of different species in the area (Root 1973; Andow 1991). As a consequence, there is a higher mortality of phytophagous insects (Root 1973). However, some predictions created by this hypothesis are not always confirmed (e.g., Andow 1991; Letourneau et al.2011). Thus, a multitrophic approach should be adopted to increase the positive effects of plant diversification in agroecosystems. Focusing on how different natural enemy species can co-exist in the same area, and increase the population regulation of phytophagous insects, is a key factor for conservation biological control research.

 The attraction of natural enemies to crops depends on cues related to the provision of suitable resources and conditions (Begg et al. 2017). The attractiveness of a crop can be increased by provision of edible resources (pollen and nectar), favourable conditions (shelter for eggs) and plant diversity (Togni et al.2016; Venzon et al. 2019a). HIPVs can be used as a reliable signal to attract natural enemies (Dicke et al.1990; Karban and Baldwin 1997). However, retention of natural enemies is not guaranteed. For example, some parasitoids can be attracted to a given crop by its volatiles, but they need first to gain energy from food sources, such as pollen and nectar, to go after their hosts. Nectar, for example, can be present in floral and extrafloral nectaries that can selectively attract natural enemy species (Rezende et al.2014), due to differences in the nutritional quality and accessibility to different species (Patt et al.1997). Thus, introducing plants with edible pollen and suitable nectar, including spontaneous vegetation, can increase the attraction, retention and efficiency of natural enemies in controlling pest populations (Simpson et al.2011; Venzon et al. 2019b). As more species of natural enemies are attracted to a given habitat, multiple negative interactions, such as intraguild predation and apparent competition, are also prone to occur with negative effects on biological control (Janssen et al.2007). Therefore, specific plant traits should be considered when introducing or managing plant diversity to avoid such interactions. Moreover, alternative prey, such as non-pest insects can increase the retention, and survival, of natural enemies (Biondi et al.2016). Besides the provision of food, plant diversity can improve the provision of shelter, and microclimatic conditions, to natural enemies (Gontijo 2019).

When resources are not limited to natural enemy species, there is no competition within, and between, species allowing their coexistence in the same habitat. Plant architecture, and shelters provided by increasing plant diversity, can also reduce the rate of encounter between individuals from the same guild and reduce intraguild predation due to changes in the habitat structure (Janssen et al.2007; Gontijo 2019).

 Moreover, plant diversity can increase the movement of phytophagous insects within and among plants in agroecosystems because the habitat has a more complex architecture and the presence of non-host species make the individuals move. Consequently, phytophagous insects tend to be more exposed and vulnerable to predation by different species (Straub et al.2014). All the positive effects of plant diversity on natural enemies should depend on the knowledge about the phenology synchrony between populations of pests and natural enemies dispersing in different crops at a regional/landscape scale (Begg et al.2017).

**Development of the smart plant concept for agroecosystems**

Besides physical and visual effects, plant semiochemicals are probably the most important factors mediating the interactions and processes described above, in particular HIPVs. The use of HIPVs and other semiochemicals can be an alternative, or complement, to increase diversity in agroecosystems. HIPVs have the potential to be exploited in biological control of agricultural insect pests, either as direct attractants for natural enemies, inducers of crop defense to increase their attractiveness to natural enemies, targets for breeding or genetic engineering of crop plants, or as targets for companion cropping (Turlings and Erb 2018). Attempts to use HIPVs for natural enemy recruitment have been increasingly explored in recent years with some success e. g. companion cropping for management of pests on cereals (Pickett and Khan 2016).

The concept of using smart plants that can respond to insect damage by rapid HIPV emission and recruitment of natural enemies from natural habitats has been described previously (Birkett and Pickett 2014) (Figure 1). A number of underpinning studies have given a platform for developing the smart plant concept, by providing an understanding of the role of plant defence signalling in plant/insect/natural enemy interactions, the smart defence response trait in crop genotypes, the deployment of companion plants alongside smart main crops for semiochemical-based crop protection, and genetic engineering of a crop plant to produce a natural enemy recruitment cue (Pickett and Khan 2016; Khan et al.2014; Birkett and Pickett 2014; Bruce et al. 2015; Tamiru et al. 2011). In a further development of the smart plant concept, HIPV emission can be exploited in the design of sensitive companion (‘sentinel’) plants for rapid, early and reliable detection of insects that are hard to detect before recognisable symptoms appear. Here, HIPV emission from sentinel plants is a target for airborne plant/plant communication, where the sentinel plant induces defence in smart crops that have been tailored or selected to respond rapidly to the emitted HIPVs, for the recruitment of natural enemies (Birkett and Pickett 2014).

For successful development of the smart plant concept in pest management, hypothesis-driven science, together with field experiments, is needed to meet the challenge of upscaling companion plant concepts into intensive agricultural systems and inform the next steps in development of smart plants for inclusion in the deployment of sentinel-based cropping systems. Furthermore, experimental farm platforms are needed to test the viability of smart crop/sentinel plant cropping systems in managing pest populations. Trap crops, nurse crops or cover crops, as well as flowering field margins, are required to investigate for sentinel plant effects. Research is needed to address key questions relating to (i) planting arrangements, density and proportion of sentinel plant vs main crops (ii) the ability of the main crop to respond to sentinel plant signals under field conditions.

Semiochemicals and HIPVs have the potential to be exploited in biological control of agricultural pests and can also be considered as direct indicators of early plant stress events (eg. insect colonisation). The strategic value of developing an accurate early warning system to aid with crop pest management is of vital importance to the global economy. With current crop management practices, around 30-40% of crop yield worldwide is lost to pests (Savary 2019). Having accurate and reliable information on when to apply pesticides will reduce environmental impact (Barzman et al. 2015) and allow target precision application of crop protection tools. The idea of exploiting plant response to stress volatile organic compounds (VOCs) fits well with the smart plant concept where known VOCs can be biomarkers for real-time sensor technologies (plant as biosensors) (Volkov and Ranatunga 2006).

Biotic and abiotic stress factors significantly impact crop production worldwide. Mitigation strategies work effectively when there is a known problem. However, the problem is not always visible. Cryptic pests, disease infected plants and abiotic factors cannot be seen in crops until there are visual symptoms at which point it may be too late for effective mitigation. The exploitation of plant VOCs as indictors of stress will allow detection at earlier time points, as plants react to stresses which results in changes to VOC profiles (potential biomarkers) (Kollist 2019).

Over the last three decades, volatile analysis technology has rapidly moved away from traditional laboratory-based GC and GCMS instrumentation to non-invasive real-time analysis systems e.g. proton-transfer-reaction mass spectrometry and selective ion flow tube mass spectrometry (Niederbacher et al. 2015; Materić et al. 2015). These techniques have allowed real-time analysis of plant volatile emission, thus providing an understanding of diurnal cycles in VOC emission, and changes in VOC emissions as a result of biotic or abiotic stress conditions. However, a major limitation to these technologies is that they are laboratory-based systems. VOC gas analysers (based on electronic nose sensor devices), which have developed rapidly over the last 3 decades, offer a solution to this limitation, by enabling rapid monitoring of VOCs at the source of emission (Cui 2019). Such analysers cannot discriminate between compounds within a headspace sample. Sensor designs can be optimised for particular groups of compounds but still cannot truly distinguish between compounds, as can be achieved with mass spectrometry-based systems. However, with advanced statistical models the analysis of whole head space samples can be categorised and give indications of plants stress (cryptic herbivore infestation and disease status). This sensor technology offers the ability to quantify VOC changes rapidly on location, and, if needed, traditional MS methods can be used to identify the compounds of significance.

As with all sensor technologies, problems with sensitivity and efficient sample collection provide barriers to widespread acceptance in agricultural settings (Cellini 2017). For successful deployment in pest management, hypothesis-driven science and proof-of-concept field testing are required to fully characterise crops and smart sentinel plants under different biotic and abiotic stressors. Next generation advanced statistical models, AI identification and discrimination between stressors, can be used to create digital libraries to help with farm management decisions on when and where to use crop protection tools.

**Case studies**

*Companion and smart plants to manage pest in maize crops*

Maize, *Zea mays* L. (Poaceae), is one of the most important cultivated plant worldwide (Ranum et al.2014). One of the biggest constraints to improving the yield of maize crops in smallholder and family-run farms is the high number of pests attacking maize, mainly herbivores and weeds. In Brazil, maize plants are attacked by several insect pests both aboveground and belowground (Moreira and Aragáo 2009), with the fall armyworm, *Spodoptera frugiperda* Smith, 1797 (Lepidoptera: Noctuidae), being considered as the primary pest in Brazil (Cruz et al.2010). Farmers have few alternatives to manage these pests other than intensive insecticide applications, which are usually not fully effective because of the development of insecticide resistance (Lira et al. 2020). Use of Bt maize in Brazil has significantly reduced lepidopteran populations and insecticide application (Farias et al.2014). However, this technology is still not accessible to smallholder and family-run farms due to its high cost. In addition, failure of Bt maize to control fall armyworm populations has been reported (Farias et al.2014; Bernardi et al.2015).

The International Centre of Insect Physiology and Ecology (ICIPE) successfully developed the use of companion plants to protect maize crops in Sub-Saharan countries against lepidopteran pests, based on plant semiochemicals in a push-pull system. The target species to be controlled were the exotic stemborer *Chilo partellus* Swinhoe, 1885 (Lepidopetra: Crambidae), the indigineous *Busseola fusca* Fuller, 1901 (Lepidoptera: Noctuidae) and the weed *Striga hermonthica* Benth. (Orobanchaceae). Napier grass *Pennisetum purpureum* Schumach. (Poaceae), was selected as a trap plant from a group of natural hosts of the borers (Schulthess et al. 1997). *Desmodium uncinatum* Jacq.DC (Fabaceae) was used as the push plant, as it repels the herbivores and reduces emergence of *S. hermonthica* in maize fields. Chemical ecology studies showed that Napier grass and maize plants release a blend of green leaf volatiles (hexanal, (*E*)-2-hexenal, (Z)-3-hexen-1-ol, (Z)-3-hexen-1-yl acetate) that attracts the herbivores. However, Napier grass produces higher levels of these compounds in the first hour of nightfall, when lepidopterans actively forage for host plants. On the other hand, *D. uncinatum* produces a blend of repellent volatiles including (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (*E*)-ocimene, (*E*)-caryophyllene, α-humulene and α-terpinolene. In addition, studies reported that *D. uncinatum* flowers are attractive to the natural enemy, *Cotesia sesamiae* Cameron 1906 (Hymenoptera: Braconidae). Finally, the striga weed is controlled by a complex mechanism involving different isoflavonones released by the roots of *D. uncinatum* (Khan et al. 2008, 2007).

 Another alternative to manage lepidopteran pests on maize could be to explore the genetic variability of different cultivars that can influence the secondary metabolites that are involved in insect-plant interactions. Michereff et al.(2019) showed that from six different neotropical maize genotypes, only one genotype, i.e. Sintetico Spodoptera (SS), produced a specific blend of herbivore induced plant volatiles (HIPVs) after *S. frugiperda* feeding damage, that attracts its natural enemy, the egg parasitoid *Telenomus remus* (Nixon, 1937) (Hymenoptera: Platygastridae). The study suggests that two factors could be involved in this natural enemy attraction, i.e., the higher concentration of the compounds in the SS genotype and the ratio between the compounds in the HIPV blend. The SS maize genotype appear to have a great potential as a sentinel and smart plant, since it produces higher level of HIPVs, and this genotype is primed by HIPVs released by neighbour plants, triggering earlier and stronger defence against herbivory of *S. frugiperda* (Michereff et al. 2021).

 Recently, several field studies have reported that the stink bugs *D. melacanthus* and *D. furcatus* move from harvested soybean to seedling maize. A potential trap crop for these pests is pigeon pea, *Cajanus cajan* (Millsp.) (Fabaceae). Nymphs of *D. melacanthus* are not able to develop when fed with pigeon pea pods (Borges and Blassioli-Moraes unpublished data). To test the potential effect of this trap crop and other companion plants (CP) as border plots on maize insect pests and natural enemy diversity, a field experiment with four different treatments was set up in small (25 m2) plots. The treatments were: 1) maize as a monocrop, 2) maize with *C. cajan*, 3) maize with *P. purpureum* and 4) maize with *Crotalaria spectabilis* Roth. (Fabaceae). Plots with maize and *C. spectabilis* as the border crop showed a smaller number of plants with severe injury from *S. frugiperda* compared to monocrop maize, *C. cajan* maize plot and to *P. purpureum*/maize.

Other studies have shown a negative effect on *S. frugiperda* population in maize when cultivated with *Crotalaria* sp. The mechanisms underlying the effects of these CP with maize are still to be determined. Therefore, more laboratory studies are required to understand these interactions, and more field studies are necessary to establish the use of CPs in maize crops on smallholder and family-run farms in Brazil.

*Companion and smart plants to manage stink bugs in soybean crops*

Stink bugs are oligophagous or polyphagous insects that use a wide variety of plants belonging to more than 10 families (Panizzi and Lucini 2017; Esquivel et al.2018). Host plants i.e., plants where the insects feed and can complete their development are decisive for stink bug biology. It has been demonstrated that alternative hosts, i.e., plant species where the insects feed but do not complete full development, could have a complementary and fundamental role in stink bug biology. These alternative plants offer a substitute and complementary source of food that may positively influence biological parameters of their population dynamics (Panizzi and Slansky 1991; Panizzi and Saraiva 1993; Panizzi and Lucini 2017; Velasco and Walter 1993; Silva et al.2018). As most of the plants used by stink bugs are either annual or semi-perennial herbs and bushes, these resources are not continuous in both space and time, so stink bug ecology is characterized by a continuous displacement between areas with cultivated plants and areas with native or spontaneous vegetation (Panizzi 1997). This switching between more and less preferred plants has been exploited to develop trap crops as a stink bug management strategy. Trap cropping consists of the use of an attractive plant species to arrest the insects and reduce the colonization of crop fields (Hokkanen 1991).

In the Nearctic region, trap crop systems have been successfully implemented for stink bug management in both organic and conventional cultures. Many plants in the Brassicaceae e.g., white mustard, *Sinapis alba* (L.) and black mustard, *Brassica nigra* (L.), the Fabaceae e.g., pea, *Psium sativum* (L.), *Vicia villosa* Roth, crimson clover, *Trifoliumin carnatum* L. and soybean *Glycine max* (L.), the Poaceae eg sorghum, *Sorghum bicolor* (L.) and pearl millet, *Pennisetum glaucum* (L.) R.Br., sunflower, *Helianthus annuus* L. (Asteraceae) and buckwheat, *Fagopyrum esculentum* Moench (Polygonaceae) have been used successfully to manage *Nezara viridula* (Linnaeus, 1758), *Euschistus servus* (Say, 1832) and *Chinavia hilaris* (Say, 1832) stink bugs (Bundy and McPherson 2000; Rea et al.2002; Tillman 2006; Mizell et al.2008; Tillman and Cottrell 2012). However, despite these successful examples of stink bug management and the wide knowledge of host and alternative plants in the Neotropical region (Panizzi and Silva 2012, Panizzi and Lucini 2017), trap cropping has been not used with soybean until now in cultivated areas.

 Egg parasitoids (Hymenoptera: Scelionidae) are the main natural enemies of stink bugs. In the Neotropical region, there is a high diversity of these native parasitoids (Cingolani 2012) which provides an opportunity to develop augmentative biological control programs. However, because of the difficulty in rearing these insects and their high mobility and susceptibility to insecticides (Corrêa-Ferreira et al.2010), conservation biological control using natural populations of parasitoids is likely a better option. A common approach to promote conservation biological control is to use attract-and-reward strategies, which allows the spill over of parasitoids attracted by semiochemicals to be managed. Here, additional resources such as shelter and food (nectar) via flowering plants are offered (Simpson et al.2011). Some semiochemicals have shown their potential to attract stink bug parasitoids in the laboratory and field, e.g., plant volatiles (Blassioli-Moraes et al.2005; 2008; Michereff et al.2015; 2016), host sex pheromones (Borges et al.1998) and host defensive compounds (Laumann et al.2009). Plant volatiles are of particular interest because of their potential to underpin the development of smart plants with enhanced volatile production through breeding and genetic engineering. However, although the application of semiochemicals under field conditions increases the recruitment of egg parasitoids, it does not increase parasitism rate (Vieira et al.2013; 2014); probably because attraction alone is insufficient to increase the performance of parasitoids. The use of flowering plants in combination with semiochemicals could be an efficient way to solve this problem. Foti et al.(2017) have shown the beneficial effect of some flowering plants, especially buckwheat and sweet basil, *Ocimum basilicum* (L.) (Lamiaceae), to increase the offspring of the egg parasitoid *Trissolcus basalis* (Wollaston, 1858) (Hymenoptera: Scelionidae). The authors also showed that flower volatiles of buckwheat are attractive to the parasitoid. In a two-year experiment, it was demonstrated that strips of buckwheat cultivated in combination with tomato plants increase the parasitism by *T. basalis* in *N. viridula* eggs. In contrast, this plant appears to repel another egg parasitoid, *Ooencyrtus telenomicida* (Vassiliev, 1904) (Hymenoptera: Encyrtidae). This shows that flowering plants, specifically flower volatiles, could mediate intra guild competition favouring some species of egg parasitoids (Foti et al.2019), an aspect that needs to be considered for the design of attract-and-reward strategies. Similar beneficial effects of buckwheat flowers have been observed for the Neotropical parasitoid *Telenomus podisi*. In laboratory experiments it was demonstrated that feeding on buckwheat increases the survival and fecundity of the parasitoid and that buckwheat volatiles are attractive to *T. podisi* females. In preliminary field test plots of soybean with buckwheat as a border plant, higher parasitism indices were observed compared to control plots (without buckwheat), and no negative effect on the parasitoid community structure was observed (Aquino, Blassioli-Moraes, Borges and Laumann, unpublished data).

*Companion plants as reservoirs for natural enemies in organic crops*

The use of companion plants can enhance the efficiency and reliability of conservation biological control in organic farms. In Brazil, crops such as garlic, onion, lettuce, tomatoes, cabbage/collards, cucumber and sweet pepper have been grown in association with african marigold, *Tagetes erecta* (L.), pot marigold, *Calendula* sp. (Asteraceae), coriander, *Coriandrum* sp., dill, *Anethum* sp. and anise, *Pimpinella* sp. (Apiaceae), basil (*Ocimum* sp.), forage turnip, *Raphanus* sp. (Brassicaceae) and spontaneous plants (weeds) as companion plants.

 In a crop system including onions and african marigold (Silveira et al.2009), the proximal (until 5m) and distant (30 m) effects of the companion plants were assessed. The results showed that phytophagous populations, mainly *Thrips tabaci* Lindeman, 1889 (Thysanoptera: Thripidae), were two-fold greater in onion plants distant from the companion plant, and that entomophagous species were more abundant in onion plants close to the companion plants. In another experiment with lettuce as the main crop instead of onions, it was demonstrated that african marigold plants could contribute to natural enemy abundance in lettuce beds until distances ranged between five to six meters (Zaché 2009).

In another experiment where african marigold(a single line 1.7 m long) were installed across a lettuce field it was demonstrated that this arrangement was more suitable for spreading natural enemies across a whole field (Haro 2015; Haro et al. 2018). The proximity of the companion plants mediated shifts in the food webs, since they became stronger and more intricate when close to african marigold (Haro et al.2018).

The effect of companion plants on arthropod food web composition and attractiveness of natural enemies appears to be influenced by volatiles from essential oils of plants. Haro (2015) found that oils of african marigold, extracted from leaves and flowers resulted in positive olfactory responses of various natural enemies as the parasitoids *Aphidius colemani* Viereck, 1912 (Hymenoptera: Braconidae), *Aphelinus abdominalis* (Dalman, 1820) (Hymenoptera: Aphelinidae) and *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae). Also, the predators *Adalia bipunctata* (Linnaeus, 1758) (Coleoptera: Coccinellidae) and *Orius laevigatus* (Fieber, 1860) (Hemiptera: Anthocoridae) responded positively to the presence of these oils.

The association of african marigoldwith tomato also led to reduced herbivorous injury on tomato plants (Haro 2011). In a greenhouse experiment, enhanced tomato production (ca 30%), was observed when tomatoes were accompanied by african marigold. The production increase was likely mediated by various factors, but mainly by the reduction of important pests. Thrips, aphids and leaf miners did not reach pest threshold levels in the african marigoldtreatment, whereas for tomato monocultures, herbivore threshold levels were reached during experiments (Haro 2011).

These data clearly suggest that african marigold can be used as a companion plant in horticulture with benefits to natural enemies and conservative biological control. Other species also have potential to fulfil the same role, and when comparing the effects of *african marigold* with *C. officinalis* (also an Asteraceae species), and the Apiaceae species dill (*A. graveolens*) and coriander (*C. sativum*), incidence of the aphid *Lipaphis erysimi*, was significantly lower in the kale - african marigold system when compared with all other treatments (Silva et al. 2016). One of the possible reasons for this was aphid predation and parasitism; the kale - african marigold system resulted in a higher incidence of predators in comparison with the other treatments, while the number of parasitized aphids was highest in the kale-african marigold and kale - calendula systems.

Members of the Apiaceae i.e., coriander, dill and fennel (*Foeniculum vulgare* Mill.) were studied to determine the assemblage of predators associated with them (Resende et al.2012). Fennel showed the higher diversity of species (Shannon H’), while coriander was more abundant in important species such as *Orius insidiosus* (Say, 1832) (Hemiptera: Anthocoridae), an important thrips predator.

Other species of vegetable pest predators were found in all Apiaceous species, especially adults and larvae of coccinellids, which are important aphid predators. Also, the flowers of Apiaceae species can serve as sources of pollen for predators as adults of *Chrysoperla externa* Hagen, 1861 (Neuroptera: Chrysopidae) and larvae and adults of *Eriopis connexa* (Germar, 1824) (Coleoptera:Coccinellidae) as shown in Resende et al.(2015, 2017). Larvae and adults of ladybeetles were shown to survive in the presence of only coriander flowers, while adult chrysopids may survive and reproduce up to the third generation by feeding only on resources provided by flowers of dill, coriander and fennel.

Haro et al.(2015) studied the parasitoids of important horticultural pests associated to these Apiaceae. The authors found higher richness and abundance in coriander and dill and also important parasitoids of pest species in fennel. Therefore, parasitoids and predators could contribute to the biological control of pests when Apiaceous species are used as companion plants.

 Basil, a plant used for cooking and medicinal purposes, has also good potential to preserve natural enemies, especially parasitoids (Souza et al.2019). Parasitoid diversity was studied in organic sweet pepper associated with basil and african marigold , and it was reported that sweet pepper monoculture, sweet pepper-basil intercropping, and sweet pepper-marigold intercropping hosted 40, 98, and 130 individuals respectively, with similar richness of species between them. Furthermore, the insects of greater abundance in basil and marigold were different to those collected in the monoculture, resulting in distinct groups of similarities amongst the treatments, as shown in the non-metric multidimensional scaling (NMDS) analysis and with significant similarity analysis (Anosim). Therefore, the number of parasitoids increased in the associations of sweet pepper with basil and marigold, providing advantages in the use of vegetable diversification for organic pepper production.

*Companion plants for intercropping with tomatoes in organic cropping systems*

In Costa Rica, Hilje and Stansly (2008) reported the reduction of the incidence and damage caused by the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) on tomato crops when intercropped with coriander plants. The intercropping effects on pest incidence and damage were comparable to the use of synthetic insecticides, but with the advantage of returning an extra income to farmers for the sale of the coriander and ease of handling (Hilje and Stansly 2008).

In Brazil, this intercrop was adapted for managing whiteflies and tomato pinworm *Tuta absluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae), mostly in organic tomato crops through bottom-up and top-down effects on these pest insects (Medeiros et al.2009a; Togni et al.2009). Coriander should be planted, intercropped with tomatoes, 15 days before the tomato seedlings are transplanted in the field. After 50-55 days, the coriander plants can be harvested, leaving about 6-10 plants to bloom between every pair of tomato plants. Coriander seeds are sown again so that, when the previous plants become senescent, new flowers will be available and the growers can harvest the coriander seeds (see details in Medeiros et al.2009b; Togni et al.2009).

*Tuta absoluta* oviposited approximately twice as many numbers of eggs on tomato plants in the conventional system than in the organic system, with no detectable effect from coriander plants in the conventional system (Medeiros et al.2009a). In the organic system the intercrop with coriander reduced the number of eggs of *T. absoluta* by 34% (Medeiros et al.2009a) and the number of *B. tabaci* nymphs by 48% (Togni et al.2009). Additionally, the abundance of natural enemies of both pest species was almost three-fold higher in the organic system (Togni et al.2009), and more species were found in the intercropped plots (Togni et al.2010a).

These results suggest that bottom-up and top-down effects acted together in reducing the populations of *B. tabaci* and *T. absoluta* when coriander plants were added to the cropping system. However, each species responds differently to plant diversification and the cultural practices used. In a free-choice experiment in a greenhouse, *T. absoluta* exhibited a clear preference for laying eggs on tomato plants cultivated in soils from the conventional system (Medeiros et al.2009c). For *B. tabaci*, coriander volatiles produces an odour masking effect on adults when presented together with tomato volatiles, making host choice more difficult and causing individuals to colonize areas with coriander plants (Togni et al.2010b). Another cultural practice that can be integrated with the tomato and coriander intercrop system is the use of sprinkler irrigation, which causes mortality of *T. absoluta* eggs (Medeiros et al.2011)as well as reduces *B. tabaci* colonization and nymph settlement on plants in organic systems (Togni et al.2018).

As the flowers of coriander are abundant with natural enemies able to access resources (pollen and nectar) easily (Patt et al. 1997), several natural enemy species can be attracted. Predators such as *C. externa*, *Hippodamia convergens* Guérin-Menéllive, 1842 (Coleoptera: Coccinellidae) and *Cycloneda sanguinea* (Linnaeus, 1763) (Coleoptera: Coccinellidae) can use the pollen of coriander plants as food sources, increasing their survival (Medeiros et al.2010; Togni et al.2016). Some predators such as *C. sanguinea* exhibit an innate attraction to coriander volatiles because these plants can be used as oviposition sites and shelter for the larvae (Togni et al.2016). When coriander is intercropped with tomato plants, there is an increase in *T. absoluta* egg predation but no increase in the parasitism by *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) was observed (Medeiros et al.2011). Similarly, predation is a key mortality factor of *B. tabaci* populations and it is positively related with the abundance and richness of *B. tabaci* natural enemies (Togni et al.2019c).

The tomato and coriander intercrop did not affect the yields of tomato plants in comparison with monocultured plots, even when it is irrigated by sprinklers (Togni et al.2009; Marouelli et al.2011). However, coriander plants can provide an extra income to the farmers and increase land use occupancy and efficiency (Hilje and Stansly 2008; Medeiros et al.2009b). In conclusion, the increase in the vegetation diversity in organic tomato crops provided by coriander plants can favour positive interactions between natural enemies and the population regulation of pest insects and disrupt the host-plant interactions with direct benefits to farmers.

*Companion plants and conservation biological control in Brassica crops*

*Brassica* spp. plants comprise the most economically important cruciferous group among the 51 genera in the tribe Brassicaceae (Gomez-Campo 1980). In general, brassicas are attacked by a variety of arthropod pests, especially aphids and lepidopterans.

Due to increasing demand for organic vegetables in Brazil (Oelofse et al.2010) and the fewer options of insecticides registered for brassicas, more biological control studies have been warranted. In this sense, conservation biological control of brassica pests has been a continuous research effort in many parts of Brazil. Some related studies presented herein have been carried out in open fields, mostly at the Federal University of Viçosa, Campus Florestal.

In general, these studies have investigated how intercropping either flowering or non-flowering plants with brassicas can affect the conservation biological control of herbivorous pests such as aphids, thereby prompting applied and fundamental implications. The flowering species used in these studies has been alyssum *Lobularia maritima* (L. Desv.) (Brassicaceae), which forms a low-growing mat with high flower density, attracts several natural enemies and very few pests; and is unlikely to become a weed (Chaney 1998; Gontijo et al.2013). In fact, this flower species has often been used as an insectary plant in the United States to enhance conservation biological control (Hogg et al.2011; Gontijo et al.2013; Brennan 2016).

Ribeiro and Gontijo (2017) investigated in Goias State, how strip intercropping alyssum flowers with collards would influence the conservation biological control of multiple brassica pests, including aphids, diamondback moth larvae, and whiteflies. This study showed that the attractiveness of alyssum flowers to generalist predators mediated a significant reduction of those pests, especially aphids. The abundance of generalist predators in this study was significantly higher in treatments associated with strips of alyssum, which likely served as a source of alternative non-prey food (i.e., pollen and nectar) and shelter. In a similar study, Silva et al.(2021) investigated whether the intraspecific variation of general morphology in a mixture of brassicas (i.e., collards + broccolis + cabbages) could influence lepidopteran and aphid infestation/suppression. Additionally, in some treatments alyssum plants were added to the brassica mixture to assess if the interspecific variation of multiple plant traits (i.e. plant morphology and flower availability) could further enhance natural enemy activity and pest suppression. The results suggest that adding alyssum flowers to fields planted with either monoculture or mixture of brassicas was important to enhance aphid suppression. Moreover, while the results indicate that brassica mixture (i.e., variation of single plant trait) was enough to promote predator abundance it was not able to drive pest suppression alone. In this specific study, collards associated with alyssum also had higher leaf fresh weight as well as higher number of marketable leaves per plant. Taken together, these results indicate promoting the interspecific variation of distinct plant traits can engender stronger pest suppression than the intraspecific variation of single plant traits in regard to promoting biological control.

Gontijo et al.(2018) studied how non-flowering parsley intercropped with collards would affect different guilds of natural enemies (diurnal and nocturnal) and consequently the conservation biological control of aphids. The results showed that the absence of flowers on the companion plants was not detrimental in attracting and sheltering generalist predators, which contributed significantly to a reduction in the aphid population. Furthermore, this suggests that non-flowering plants may still contribute to conservation biological control by providing natural enemies with adequate microclimate and alternative prey/host. Nonetheless, this study showed that companion plants forming the low stratum can hamper the movement of non-flying natural enemies in the short term (e.g., nocturnal predators), and thus impair their ability to encounter pests on the focal host plants at the high stratum. Using a similar experimental design where non-flowering parsley was intercropped with collards, Saldanha et al.(2019) investigated how companion planting could affect natural infestation by aphids, natural enemy activity and parasitoid emergence. The results indicate that non-flowering parsley is important to shelter generalist predators that will form the first line of defence against aphids early in the season. Additionally, the effect of companion planting covaried with the on-plant aphid density to influence the numerical response from specialist natural enemies, which was weaker in the intercropping treatment. Although not detrimental to conservation biological control in the short term, companion planting appeared to mediate an increase in intraguild predation of immature aphid parasitoids. These results were likely due to companion plants promoting the breakdown of the prey dilution effect and making the mummified aphids more prone to predation.

 Taken together, all these studies indicate that companion planting can be an important strategy to promote conservation biological control of pests. Despite some negative interactions mediated by companion planting (e.g., intraguild predation, hampering non-flying predators), the overall benefits of its implementation to enhance conservation biological control still outweigh those potential short-term adverse effects. The results also suggest that companion planting and natural shelter could be more important for generalist natural enemies, which are more likely to arrive sooner in the agroecosystem after crop emergence. Therefore, implementing efficient companion planting or natural shelter may entail methods that will ensure their field establishment prior to pest arrival. In respect to improving brassica production, advancing the conservation biological control of cruciferous pests is paramount to enhancing quality and safety for this group of vegetables, which is widely consumed and vulnerable to excessive insecticide applications.

*Companion plants and conservation biological control in coffee agroecosystems*

Coffee, which is cultivated mainly in tropical developing countries, is an important cash crop. Brazil is the leading global producer of coffee, and this crop has predominantly been cultivated in monocultures under full sun in the country. However, environmental and social harms caused by conventional agricultural practices have encouraged the development of other cultivated systems that aim to recover the soil, reduce erosion, improve nutrient recycling, enhance pest control and increase food security and sovereignty (Souza et al.2012; Rezende et al.2014; Gomes et al.2020).

 Increasing plant diversity in coffee agroecosystems can reduce damage caused by the main coffee pests (Rezende et al.2014; Venzon et al.2019a). Amaral et al.(2010) investigated in two organic coffee production systems the effects of plant diversification on the population coffee leaf-miner *Leucoptera coffeella* (Guérin-Mèneville, 1842) (Lepidoptera: Lyonettidae), one of the key coffee pests in Brazil. One system consisted of coffee intercropped with banana trees, *Musa* spp. (Musaceae) (shaded system) and the other consisted of coffee intercropped with pigeon pea, *Cajanus cajan* (Fabaceae) (unshaded system). The increase in plant diversity on both systems was achieved via introduction of cover crops, i.e., perennial peanut, *Arachis pintoi* Krapov. and W.C. Gregory, sun hemp, *Crotalaria juncea* L., and Brazilian lucerne, [*Stylosanthes guianensis*](https://keyserver.lucidcentral.org/weeds/data/media/Html/stylosanthes_guianensis.htm). A positive and significant relationship between plant diversity and coffee leaf miner predation by wasps on the unshaded coffee system (without banana trees) was observed, whereas a negative relationship on the shaded coffee system found the opposite effect.

 Further studies were carried out in order to select the most suitable cover crops to introduce into coffee agroecosystems, with the aim of selectively increasing natural enemy performance via provision of plant provided food. Venzon et al.(2006) evaluated the suitability of leguminous cover crop pollen to the green lacewing *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae), a common predator species in coffee agroecosystems (Ecole et al.2002; Ribeiro et al.2014). Both adults and larvae of *C. externa* can feed on plant-material, whilst larvae can feed on a variety of soft-bodied arthropod prey including the coffee leaf miner and coffee berry borer (Ecole et al.2002; Carvalho et al.2020; Botti et al. 2021). The presence of alternative plant food sources for lacewings is especially important in times of prey scarcity. Pollen of pigeon pea and sun hemp were equally suitable for *C. externa,* especially when they were complemented with a carbohydrate source (indicate here the type of carbohydrate used). The results suggest that to successfully enhance predator effectiveness, coffee crops should be diversified in a manner of combining plants that provide pollen with plants that provide nectar. In fact, laboratory (Rosado, 2007) and field experiments (Rosado et al. 2021) confirm that when sun hemp, a pollen source, was associated with buckwheat, *Fagopyrum esculentum* Moench (Poligonaceae), a nectar and pollen source, an increase in coffee leaf miner parasitism and predation rate was observed.

Besides increasing diversity by adding cover crops, the introduction of trees in coffee agroecosystems can also provide pest control services. Trees play an important role within coffee agroforestry systems, providing resources to natural enemies that enhance natural regulation of coffee pests (Railsback and Johnson 2014; Rezende et al.2014). Many trees selected for intercropping with coffee, as those of the genus *Inga* Miller (Leguminosae), possess extrafloral nectaries (Soto-Pinto et al.2001; Souza et al.2010), that are accessible and available during all stages of plant growth, thereby extending food availability (Wäckers 2005). Plants bearing extrafloral nectaries are known to suffer less from herbivory than plants lacking these structures (Mathews et al.2007).

Rezende et al.(2014) showed that extrafloral nectaries of associated trees can boost natural pest control in agroforestry systems. While species richness had no significant effect, leaf miner parasitism increased significantly with the abundance of nectary visitors, and the proportion of mined leaves decreased significantly with this abundance. The proportion of bored fruits decreased with increasing abundance of visitors, but this trend was not significant. Inga trees host an important natural enemy of coffee berry borer, *Hypothenemus hampei* (Ferrari, 1867) (Coleoptera: Scolytidae), i.e., predatory thrips of the genus *Trybomia* (Thysanoptera: Phlaeothripidae) (Rezende et al.2014; Pantoja 2018).

Research has been carried out to select more plant species to be used in coffee agroecosystems (Venzon et al.2018; 2019a), with the aim of reducing coffee pest populations using diverse strategies such as the use of ecological corridors and agroforestry (according to the production system). Understanding about the ecosystem services provided by individual plant species will help in unravelling the mechanisms which enhance pest control in diversified systems, and can also help in the design of pest-suppressive coffee systems (Rezende et al. 2021).

*Plant diversification as a tool for smallholder farmers: a successful case for perennial and annual crops*

The development of a productive, resilient and affordable agricultural system is essential to assure smallholder farmers sustainability as well as maximize the economical, environmental and social long-term benefits. As plant diversification can also help mitigating the impact of climate change, the Santa Catarina State Agricultural Research and Rural Extension Agency (Epagri) has been encouraging the provision of multifunctionality in agricultural landscapes, ecosystem services and biodiversity for the cultivation of perennial and annual crops in the Itajaí River Valley (Lichtenberg et al. 2017; Rusch et al. 2016). Smallholder farmers in Itajaí River Valley grow mainly vegetables such as lettuce, arugula, tomatoes, cabbages, spices and aromatic plants, which are supplied to all coastal cities in that region. Usually, an excessive number of pesticides are used to control pests and diseases, potentially damaging these crops (Ngowi et al. 2007). However, there is a growing concern about food safety and environmental contamination, due to the proximity of these cropping fields to water sources and urban areas (Huang et al. 2006).

As part of a response to those concerns, some researchers have suggested the intercropping of vegetables with african marigold, *Tagetes* *erecta* L (Asteraceae), which has been shown in previous studies to enhance pest suppression without pesticides (Silveira et al. 2009; Haro et al. 2018). The conservation biological control provided by this specific intercropping, successfully extinguished insecticide spraying for pests such as: thrips as *Frankliniella occidentalis* (Pergande) and *Frankliniella schultzei* (Trybom) (Thysanoptera: Thripidae) on spring onion and lettuce; vegetable leafminer (*Lyriomiza* spp. (Diptera: Agromyzidae) on lettuce, spring onion and arugula; *Tetranychus urticae* Koch (Acari: Tetranychidae).

In banana production systems, intercropping with companion plants could improve soil physical quality and structure, control nematode population and reduce *Fusarium oxysporum* incidence, the causal agent of *Fusarium* wilt (Pattison et al. 2014; Quaresma et al. 2015; Almeida et al. 2018). All these benefits can effectively reduce the need for external inputs as a result of using natural resources for long-term management of farmland, and thereby promote a sustainable farming system (Quaresma et al. 2015; Orr and Nelson, 2018). The main species used in the intercropping are *Calopogonium mucunoides* Desv. (Fabaceae), *Raphanus sativus* L. var. oleifera Metzg (Brassicaceae), *Avena strigosa* Schreb (Poaceae), *Vicia sativa* L. (Fabaceae) and *Lolium multiflorum* Lam (Poaceae). Additionally, producers are associating lower damages caused by banana rust and eruption thrips with intercropped farms. Previous studies indicate a higher diversity and abundance of insects in intercropped banana systems (Casaril et al. 2019), and such beneficial effect on thrips population control is currently being studied.

Therefore, there is an immediate need to implement companion plant technologies that have already been tested (eg, *african marigold* as companion plants) mainly through the effort of extension agencies. Additionally, it is necessary to investigate techniques currently used by producers for other primary purposes (e.g.: intercropping to improve soil quality and control plant diseases in banana crop system), which could have some potential to be used as a pest management tool. These integrated procedures can contribute for the optimization and long-term sustainability of the agricultural environment, especially for smallholder farmers.

**4. General conclusions and synthesis**

Increasing plant diversity in agroecosystems has been linked to increased pest management, however, in some cases increasing plant diversity is not directly related to reduction of pest populations. To better understand the underlying natural process and mechanisms regulating this effect it is necessary increase our scientific knowledge. The effects of plant diversity in pests populations is associated with ecological processes of the diversity components within guilds and between trophic levels, including host specificity and selection, species competition or displacements, intraguild predation and apparent competition. For insects and mites, most of these ecological processes are mediated by semiochemicals that drive and modulate insect/mite behaviour. Based on this framework, the concept of deploying smart plants that can respond rapidly to pest damage by releasing or responding to HIPVs has been developed. Within this strategy, smart plants could be used to repel herbivorous pests, attract natural enemies or even to promote plant-plant communication i.e., plants emitting HIPVs blends signaling imminent danger to neighboring plants. In addition, with technological development, some of this knowledge could be applied to insect monitoring and early pest detection, especially for cryptic pests that are otherwise difficult to detect and / or manage.

The case studies presented herein show the potential of applying companion plants agriculture as tools for pest management. Moreover, these studies provide several examples of repellent or attractive plants, and the provision of resources by these plants, in various cropping systems, to different insects. From this position, the basic information for landscape management is now available for crops such as maize, fruits, vegetables and coffee. In addition, for some crops, as in the case of maize, fundamental knowledge of HIPVs and their effect on pests and their natural enemies can be applied to the development of pest management strategies based on the concept of smart plants. Companion plants, real time detection of pests and injured plants using advanced technology such as electronic noses and image detectors bring a cleaner and efficient tool to a more sustainable agriculture. It is expected that identification and characterization of semiochemicals in real time could help to better understand the role of companion plants and the behavioural mechanism of insects/mites mediated by these compounds. This can contribute to establish more efficient and profitable mixtures of crops (i.e., polycultures), and for new tactics for pest management based on insect interactions, plant defences, insect behavioural manipulation and biological control.

It is crucial to mention that some of the studies reported here are already implemented in the field and are part of the farmers’ management strategies in several regions in Brazil. Basic research was fundamental in developing effective and reliable strategies that can be used in conventional and organic systems. The challenge is to upscale these technologies to large cropped areas. Another important issue is that scientific cooperation and the interplay among research fields and researchers play a central role in developing such technologies.

With recent advances in fields such as ecology, conservation biology, agronomy and biotechnology, we can now look forward to new opportunities that we did not previously view. We are aware that the initial cost of implementing the smart plant technologies in complex environments with companion plants may be challenging in a first moment. However, this is one of the multiple ways to move from the perspective of pest control based on the use of pesticides to a truly sustainable pest management grounded in the use and manipulation of ecological interactions with a solid scientific background. In this sense, multidisciplinary studies and actions among several research areas, extension agencies, governmental and non-governmental entities, and the private sector allied with the farmers needs may play a pivotal role.

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**Author contribution**

This work was conceived during the workshop "Stakeholders engagement workshop: ‘Companion plants and their semiochemicals for pest control in agriculture’. All authors participate in the elaboration of the first draft and revised versions of the ms. All authors approved the version considered for publication.

**Declarations**

Conflict of interest: The authors declare no competing interests

Ethics approval: Not applicable.

**Figure Legends**

Figure 1. General overview of ecological interactions in crops systems with increased plant diversity by introduction of companion plants (left) and botton-up and top-down effects on herbivorous populations. The relevance of identification of semiochemicals mediating these interactions to develop smart plants to strengthen bottom-up and top-down effects.

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