

Review

Effects of increased crop diversity using trap crops, flowering plants, and living mulches on vegetable insect pests

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ABSTRACT

In agroecosystems, increasing plant diversity is known to contribute to numerous ecological services, including regulation of insect pest densities directly or indirectly through the activity of their natural enemies. The objective of this review is to provide an overview and synthesis of the effects of crop diversification methods on insect pest management that can lead to more sustainable vegetable production systems. Focus is on trap cropping, flowering plants, living mulches and intercropping. This review highlights some of the most promising methods (e.g., trap crops supplemented with insecticide application or integrated with biological control, flowering plants that can support omnivorous predators, specific plantings that can act as a 'virus-sink') that can be readily implemented by farmers in support of ecologically-based pest management. Advantages and disadvantages associated with trap cropping are discussed in light of its effectiveness, simplicity, and cost considerations in various vegetable systems. Farmscape plants are reviewed in terms of their effects on fitness of parasitoids and omnivorous predators of insect pests, measures of success, and impact of natural enemies as biological control agents. The main mechanisms underlying the effects of living mulches and intercrops on pest suppression are discussed in terms of disruption of host-plant finding and chemically-based repellency, their effects on insect pests and their natural enemies, and potential competition between the cash crop and the neighboring non-crop. While each of these techniques can be a stand-alone approach to pest management, it is advisable to integrate approaches including chemical (if needed – e.g., in the case of trap cropping), cultural, and biological controls. Further development of such methods that promote biodiversity and provide favorable conditions for agriculture based on ecological principles are expected to reduce chemical inputs (e.g., insecticides), thus impacting positively the society and the environment to move towards sustainability in vegetable production systems.

KEYWORDS: crop diversity, trap crop, flowering plant, living mulch, intercrop, pest suppression, biological control, sustainable agriculture

1. Introduction

Increasing fruit and vegetable consumption is a global priority to prevent the world's most widespread and debilitating nutritional disorders. This, however, requires improved production and distribution systems, both of which represent major challenges [1]. To meet the current crop production challenge, modern agriculture systems have been intensified toward monocultures to produce more crops per unit area at the expense of greater inputs (e.g., high yielding varieties, fertilizers, and pesticides) and reduced biodiversity [2, 3, 4]. Thus, habitat management schemes are recommended to restore the functional aspects of plant diversity lost through crop intensification [2, 3].

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In agroecosystems, increasing plant diversity contributes to numerous ecological services, including regulation of insect pest densities directly or through the activity of their natural enemies [5, 6, 7, 8, 9]. An analysis of crop diversification studies showed that 53% of the pest species were less abundant compared to 18% that were more abundant in the diversified system [8]. A recent meta-analysis showed that overall herbivore suppression, natural enemy enhancement and crop damage suppression effects were significantly stronger on diversified crops than on crops with one or just a few plant species [7]. Non-crop habitats such as field margins, fallows (set-aside land), hedgerows and wood lots are relatively undisturbed and temporally permanent areas that hold a substantial proportion of the biodiversity in agricultural landscapes [2]. However, vegetables are annual cropping systems in which the nature and frequency of soil disturbance regimes can strongly influence above- and belowground diversity, especially in monocultures. Consequently, developing a general framework for increasing crop diversity that is economically and environmentally sustainable is an opportunity for vegetable cropping systems.

The philosophy of pest management in diverse crop habitats is largely based on two general hypotheses set forth by Root [10], which seek to explain why there are fewer herbivores in more diverse compared to simpler habitats: (1) the resource concentration hypothesis, and (2) the natural enemy hypothesis. The first hypothesis argues that the presence of diverse habitats has direct negative effects on the ability of the insect pest to find and exploit a particular resource. The second hypothesis argues that the presence of diverse flora supports greater abundance and activity of natural enemies (predators and parasitoids) as a result of the availability of diverse food resources (e.g., pollen, nectar, and prey). Various other hypotheses responsible for lower numbers of herbivores in diverse habitats have been discussed for specific habitat and pest combinations. A general theory has been developed, based on detailed observations of insect behavior and hostplant finding - the 'appropriate and inappropriate landing'. This theory suggests that host-plant selection involves three-linked chain of events in which the central link (landing on the host-plant) governed by visual stimuli is the key event [11].

In this review, we synthesize and interpret research papers published from the year 2000 onwards that report on methods of crop diversification with a focus on vegetable insect pest management. Methods concerning the effects of diverse habitats such as trap crops, flowering plants, living mulches and intercrops are discussed in light of the hypotheses being tested and its applicability at the field level (Table 1).

2. Trap cropping

Trap crops can be defined as "plant stands that are, *per se* or via manipulation, deployed to attract, divert, intercept, and/or retain targeted insects or the pathogens they vector in order to reduce damage to the main crop" [13]. In recent years, there has been renewed interest in trap cropping as an integrated pest management (IPM) tool due to concerns about the potential negative effects of pesticides on human health and the environment as well as pesticide resistance [17], and the interest/need to reduce production costs.

Main goal	Methods	Mechanisms
	Trap cropping	• Deployment of relatively attractive plant species to insect pests [12, 13]
	Use of flowering plants	• Enhanced biological control [10]
To increase crop diversity	Use of living mulches/ intercrops	 Disruption of host-plant finding behavior [11] Chemically-based repellency [14] Enhanced biological control [10] Specific plantings that can act as a "virus sink" [15, 16]

Table 1. Classification of crop diversification based on the methods that can reduce pest populations in the crops with associated mechanisms.

The trap cropping approach can be used in various ways based on its inherent characteristics and deployment methods, as discussed in Shelton and Badenes-Perez [13]. The inherent characteristics of a trap crop refer to their relative attractiveness and ability to retain pests on them as determined by their plant chemistry. The deployment methods refer to the timing and spatial arrangement and proportion of trap crop plants relative to the main crop. The success of trap cropping is directly influenced by the deployment strategy such as perimeter, sequential, multiple, and push-pull trap cropping. For the sake of space, this section focuses on perimeter trap cropping; for a detailed description of the other modalities see Shelton and Badenes-Perez [13].

One example of successful perimeter trap cropping is the use of collard greens (*Brassica oleracea* var. acephala L.) as a trap crop to protect cabbage (*Brassica oleracea* var. capitata L.) against the crucifer pest diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), in Florida [18]. In that study, the numbers of *P. xylostella* never exceeded the action threshold of 0.3 larvae per plant in any of the fields that were completely surrounded by collards, but did exceed the action threshold in three of the fields without collards on four sampling dates in one of the test years.

In general, guidelines for trap cropping recommend 10% of the total crop area to be planted with the trap crop [12]; however the actual needs of each particular system may vary [13]. It has been argued that for successful trap cropping systems, high trap crop retention is a more important criterion than attractiveness of a trap crop plant [19]. This may explain in part why trap cropping has failed to reduce insect density in the cash crop adequately, even when the pest shows a strong preference for the trap plants in the laboratory and semi-field experiments [20]. Insect pests congregating on trap crops need to be removed (i.e., killed) to prevent them from dispersing away from the trap crop or, in many situations, from killing the trap crops. Therefore, some systems use supplementary pest management strategies (e.g., insecticide application on trap crops) [13]. Specific examples on the development of dead-end trap crops, trap crops supplemented with insecticide applications and/or biological control and other efficient trap cropping systems are discussed below (Table 2).

2.1. Development of potential dead-end trap crops

Some of the disadvantages of trap crops may be the build-up of populations of the target insect pest on the trap crop plants and potential spilling over to the cash crop. To avoid this, the term 'dead-end' trap crops was proposed to describe plants that are highly attractive to insects but on which they or their offspring cannot survive [20]. An example of a dead-end trap crop is yellow rocket, Barbarea vulgaris (R. Br.) var. arcuata (Brassicaceae), a biennial invasive weed that occurs throughout the temperate region worldwide [21, 22]. This plant is more attractive to P. xylostella for oviposition with significantly lower larval survival compared to glossy collards and a cabbage cash crop [21, 23]. For example, the number of eggs laid on glossy collards, Indian mustard and yellow rocket were 3, 18 and 12 times greater than on cabbage with the percentage of larval survival from egg to pupation being 6.7% on glossy collards, 0% on yellow rocket, 24.4% on Indian mustard and 22.2% on cabbage [24]. Yellow rocket plants contain high levels of glucosinolates, which stimulate adult oviposition and larval feeding in P. xylostella, yet they also possess a high concentration of saponins, which are detrimental to the survival of P. xylostella larvae [25]. This triggered the development of potential dead-end trap crops in cruciferous vegetables [20, 21, 22, 24]. Results from research conducted in Taiwan showed the potential of using tropical soda apple, Solanum viarum Dunal. (Solanaceae), as a dead-end trap crop for tomato fruitworm, Helicoverpa zea (Boddie) (Lepidoptera: Noctuidae) [26]. Even though these plants showed characteristics of a dead-end trap crop, their invasiveness as a weed species limited its utility at a commercial scale.

More recently, an interesting area of research has been the development of transgenic dead-end trap crops. For instance, transgenic collards and Indian mustard plants expressing one or more proteins from the common soil bacterium *Bacillus thuringiensis* were developed and evaluated against *P. xylostella* by Cao *et al.* [27] and Shelton *et al.* [17]. Both plants resulted in significant suppression of a *P. xylostella* population over 3 generations in the greenhouse test and 2 generations in small cage experiments. Shelton *et al.* [17] concluded

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Table 2. Recent evaluations of the transmission of transmission of transmission of the transmission of transmi	ap cropping apl	proach for veg	getable insect pest management at the farm le	vel.	
Insect pest species	Country	Crop	Trap crop	Experimental set-up	References
Diamondback moth, Plutella xylostella (L.)	South Africa	Not specified	Cabbage, <i>Brassica oleracea</i> var. capitata L., cauliflower, <i>B. oleracea</i> var. botrytis L., broccoli, <i>B. oleracea</i> var. italica, Chinese cabbage, <i>B. perkinensis</i> (Lour.), Indian mustard, <i>B. juncea</i> (L.) Czern.	Laboratory and field oviposition and larval survival tests	[41]
Diamondback moth, <i>P. xylostella</i> (L.)	United States	Cabbage	Collards, B. oleracea var. acepahala	Perimeter trap cropping	[18]
Diamondback moth, <i>P. xylostella</i> (L.)	United States	Cabbage	Indian mustard, <i>B. juncea</i> , yellow rocket, <i>Barbarea vulgaris</i> var. acruta, collards, <i>B. oleracea</i> var. acepahala	Laboratory and field oviposition and larval survival tests	[23]
Diamondback moth, <i>P. xylostella</i> (L.)	United States	Cabbage	Yellow rocket, B. vulgaris var. arcuata	Green house, semi-field and field oviposition tests	[20, 21, 22, 24]
Tomato fruitworm, <i>Helicoverpa</i> armigera Hubner	Taiwan	Tomato	Tropical soda apple, Solanum viarum Dunal	Laboratory choice and no-choice tests	[26]
Diamondback moth, <i>P. xylostella</i> (L.)	United States	Cabbage	<i>Bt</i> collards. <i>B. oleracea</i> var. acepahala, <i>Bt</i> Indian mustard, <i>B. juncea</i>	Green house and caged tests	[17, 27]
Cabbage head caterpillar, <i>Crocidolomia pavonana</i> (Fab.)	Uganda	White cabbage	 Kale, B. oleracea var. acepahala, cauliflower, B. oleracea var. botrytis, broccoli, B. oleracea var. italica, Chinese cabbage, B. perkinensis (Lour.), Indian mustard, B. juncea 	Screen house and field tests (paired choice tests)	[28, 29]
Pepper maggot, Zanosemata electa (Say)	United States	Bell pepper	Cherry pepper, Capsicum annuum L.	Perimeter trap cropping	[30]
Squash bug, Anasa tristis (De Geer)	United States	Watermelon	Squash, C. pepo var. melopepo L.	Border trap cropping	[34]
Striped cucumber beetle, Acalymma vittatum (F.)	United States	Cantaloupe, squash, watermelon, butternut squash	Blue Hubbard squash, <i>Cucurbita maxima</i> Duchense	Perimeter trap cropping	[31, 32, 33]
Harlequin bug, Murgantia histrionica (Hahn.)	United States	Collards	Mustard greens, B. juncea, rapeseed, B. napus, Arugula, Eruca sativa, bean, Phaseolus vulgaris	Caged (choice tests) and field trials (border row trap cropping)	[35]

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Table 2 continued..

Tarnished plant bug, <i>Lygus rugulipennis</i> Popp.	Sweden	Lettuce	Alfalfa, Medicago sativa L., clover, Trifolium pratense L., Melilot, Melilotus officinalis (L.), mugwort, Artemisia vulgaris L., vetch, Vicia sativa L.	Field preference trial	[37]
Silverleaf whitefly, <i>Bemisia</i> argentifollii Bellows and Perring	United States	Tomato	Squash, <i>C. pepo</i> .	Intercropping	[38]
Tomato fruitworm, <i>Helicoverpa zea</i> (Boddie)	France	Tomato	Corn, Zea mays L.	Border trap cropping	[39]

that long-term suppression may be achieved with a small area planted to the dead-end trap crop.

2.2. Trap crops supplemented with insecticide application

An area of concern is when a trap crop plant is highly attractive and also accelerates insect pest reproduction, requiring insecticide application to trap crop plants. For example, in Uganda, Chinese cabbage and broccoli (*B. oleracea* var. italica) were the most suitable hosts for oviposition by cabbage head caterpillar, *Crocidolomia pavonana* (Fabricius) (Pyralidae). However, because of the shortest developmental time and highest pupal weight of offspring in these trap crops, *C. pavonana* larvae should be destroyed regularly to prevent pest reproduction [28, 29].

Perimeter trap cropping in combination with insecticide sprays to the trap crop has been shown to provide effective insect control while reducing insecticide use in the main crop. For example, a perimeter trap cropping system involving hot cherry peppers and border row application of insecticide provided the best protection of the main crop bell pepper from oviposition and infestation by the pepper maggot, *Zonosemata electa* (Say) (Diptera: Tephritidae) [30].

In cucurbits, Blue Hubbard (Cucurbita maxima Duchense) was the most effective perimeter trap crop for controlling striped cucumber beetle, Acalymma vittatum (Coleoptera: Chrysomelidae), in butternut squash (C. moschata Poir) in Massachusetts, USA [31, 32, 33]. In this system, by planting Blue Hubbard squash in the entire perimeter, insecticide use was reduced by 94% in the butternut squash compared to control fields involving applications to the cash crop [33]. Similarly, a border trap crop involving squash (C. pepo var. melopepo L.) with foliar applications of endosulfan significantly reduced populations of squash bugs, Anasa tristis DeGeer (Hemiptera: Coreidae), in the watermelon, Citrullus lanatus var. lanatus (Thunb.) Matsum. & Nakai, cash crop compared to the standard recommended practice involving soil application of carbofuran and foliar applications when pests exceeded a pre-set economic threshold [34]. More recently, Blue Hubbard and Red Kuri Hubbard squash planted at the row ends of cucumber (*Cucumis sativus* L.), zucchini (*Cucurbita pepo* L. var. cylindrica) and summer squash (*C. pepo*) in plasticulture systems were successfully used to control the three most significant pests of cucurbits in the Midwest USA: *A. vittatum*, spotted cucumber beetle (*Diabrotica undecimpunctata howardii* Barber) and *A. tristis* (J. C. Piñero, N. Miller, J. Legaspi, unpub. data).

In another example, mustard (*B. juncea*) cv. 'Southern Giant Curled' planted along perimeter rows was an effective trap crop for reducing feeding damage by harlequin bug *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae) on collards. However, spraying neonicotinoid insecticide on mustard rows provided no additional benefit for harlequin bug control [35].

2.3. Trap crops supplemented with biological control

An appealing trap cropping system is one in which unsprayed trap crop plants provide refuge for parasite/predator populations thereby enhancing the effectiveness of biological control by natural enemies. If a market exists for the trap crop, then applying a spot spray to the perimeter rows with a selective pesticide (i.e., microbial products like Bt or spinosad) may be beneficial. Only one example involving vegetables was found concerning the effective integration of biological control with trap cropping. In Florida, planting collards around the perimeters of cabbage fields helped reduce pesticide sprays for diamondback moth on cabbage by 75%-100% over cabbage fields treated with conventional insecticides, producing equivalent quantity and quality of cabbage. Interestingly, Diadegma insulare (Cresson) (Hymenoptera: Ichneumonidae), a naturally occurring parasitoid of P. xylostella, was found to build in high numbers in the collards, helping keep P. xylostella populations in check [36]. Thus, by not spraying the trap crops with conventional insecticides, farmers can also help conserve natural enemies in some vegetable systems (Figure 1). Further investigations in this area are needed.

2.4. Other efficient trap cropping systems

In general, plants from the same family or different varieties of same crop that are more attractive to the target insect are used in trap



Figure 1. Representative model of trap cropping that is assisted by biological control. Trap crop plants attract and retain herbivore pest insects in the perimeter rows, providing natural enemies (parasitoids and predators) with hosts and prey. This system reduces densities of herbivore pest on trap crop plants and the natural enemies can then disperse further to the cash crop to act on any spill over herbivore pest. Thickness of lines indicates the main expected colonization routes of both the pest herbivore and its natural enemies.

cropping systems. However, crop plants from different families have also been found to be effective trap crops. For example, clover, Trifolium pratense L., vetch, Vicia sativa L., melilot, Melilotus officinalis (L.) (all Fabaceae) and mugwort, Artemisia vulgaris L. (Asteraceae) were 6 to 40 times more attractive to tarnished plant bug, Lygus rugulipennis Popp. (Hemiptera: Miridae), than lettuce, Lactuca sativa L. (Asteraceae). These results stressed the potential of developing a trap cropping system for Lygus spp. in lettuce [37]. Schuster [38] found that the numbers of eggs and nymphs of silverleaf whitefly, Bemisia argentifollii Bellows and Perring (Hemiptera: Aleyrodidae), were generally lower on tomato plants when squash, C. pepo, was used as a trap crop compared to tomato alone. In turn, Rhino et al. [39] demonstrated that early planting of corn, Zea mays L., synchronized flowering with the main crop and reduced the infestation of tomato fruitworm, Helicoverpa zea (Lepidoptera: Noctuidae), on the main tomato crop. A trap cropping system has been developed to control stink bugs [*Euschistus servus* (Say), *Acrosternum hilare* (Say), *Nezara viridula* (L.)] and leaffooted bug [*Leptoglossus phyllopus* (L.)] in grain and fruit crops, as well as in vegetables, using triticale, sorghum, millet, buckwheat (*Fagopyrum esculentum* Moench [Polygonaceae]) and sunflower in the south-east United States [40].

Thus, trap cropping represents a simple, effective, and cost-saving alternative for reducing insecticides through the targeted application of insecticides to the trap crops as opposed to the entire crop area [18, 30, 33]. More studies that incorporate economic analyses are needed.

3. Use of flowering plants

Flowering plants that provide food (pollen and nectar), shelter from adverse environmental conditions, and alternate host/prey resources can enhance populations of natural enemies,

potentially resulting in pest suppression in agroecosystems [42, 43]. In general, flowering plants can enhance the longevity and fecundity of natural enemies (e.g., parasitoids and predators), and they represent one way to enhance conservation biological control [6, 44]. The method through which flowering plants are grown in the proximity of the targeted crop in some specific arrangement (such as intercropping and field borders) in order to promote conservation biological control is known as farmscaping [45]. However, field studies demonstrating that provisioning of floral resources reliably result in effective biological control of vegetable pests are scarce.

3.1. Criteria for selecting flowering plants

The suitability of flowering plants depends upon its olfactory attractiveness and accessibility of nectar to parasitoid species. Wackers [46] tested 11 flowering plants to three hymenopteran parasitoid species: Cotesia glomerata L., Heterospilus (both Braconidae) and Pimpla prosopidis turionellae (Ichneumonidae). Only two plant species, Aegopodium podagraria (Apiaceae) and Origanum vulgare (Lamiaceae) were optimal as a parasitoid food source, as they combine olfactory attractiveness with accessible nectar. Further, Vattala et al. [47] determined the accessibility of nectar based on the flower morphology (collar aperture and depth). Out of seven flower species coriander tested. buckwheat. [Coriandrum sativum L. (Apiaceae)] and white mustard [Sinapsis alba (Brassicaceae)] provided better access to Microctonus hyperodae (Braconidae), a parasitoid of the Argentine stem weevil Listronotus bonariensis (Coleoptera: Curculionidae).

Heimpel and Jervis [48] highlighted five criteria that need to be met in order to suppress herbivores, as a result of parasitoids utilizing floral resources: (i) parasitoids are sugar limited; (ii) parasitoids feed on floral nectar; (iii) nectarfed parasitoids have improved fitness, which leads to (iv) increased parasitism, and (v) decreased pest densities. Therefore, care should be taken in selecting appropriate non-crop flowering plants in agroecosystems to increase the effectiveness of natural enemies in light of evidence that sugarrich diets and floral resources may inadvertently increase the longevity of pests in the system [49]. Specific examples on the use of flowering plants to enhance natural enemies are discussed below (Table 3).

3.2. Effects on parasitoids of *Brassica* lepidopteran pests

Buckwheat has been mostly studied to examine the criteria set forth by Heimpel and Jervis [48] in the Brassica system to control lepidopteran pests, especially, P. xylostella. For example, the life expectancy of parasitoids D. insulare and C. glomerata were significantly increased when provided with buckwheat nectar compared to other sources of sucrose in the laboratory [50, 51]. and the longevity and fecundity of D. insulare collected from the cabbage fields planted with buckwheat borders were increased compared to the fields without borders [52]. Similarly, Winkler et al. [53] showed that the overall sugar content of D. semiclausum collected from Brussel sprouts B. oleracea var. gemmifera fields bordered by flowering margins was significantly higher than those of individuals collected from the grassbordered control plots. However, biochemical analyses of field collected D. insulare showed that buckwheat floral borders did not consistently increase the proportion of sugar-fed wasps nor correlated with parasitism [54]. Buckwheat borders did not significantly increase egg, larval or pupal densities of cabbage looper, Trichoplusia ni (Hubner) (Noctuidae), imported cabbageworm, Pieris rapae (L.) (Pieridae), or P. xylostella. In addition, parasitism rates of *P. xylostella* by D. insulare were shown to be unreliable in the cabbage field in a long-term field study [55]. These inconsistent results emphasize the need of examining whether factors such as dispersal or searching rates differ between sugar-fed and starved parasitoids in the floral habitats [54].

Furthermore, the distance of the main crop from flowering plants can also influence the outcome. For example, the number of *D. semiclausum* decreased significantly with distance away from buckwheat flowering strips [56]. In contrast, parasitism rates of *P. rapae* by *C. glomerata* on the collard cash crop did not differ with distance from the buckwheat strip [57]. Further, in an attempt to determine if the spatial arrangements of treatment plots can influence the results of

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Insect pest species	Country	Crop	Flowering plants	Effects	References
Diamondback moth, Plutella xylostella (L.)	United States	Cabbage	Buckwheat, Fagopyrum esculentum Moench	Buckwheat borders increased longevity and fecundity of <i>D. insulare</i> but did not consistently increase the proportion of sugar-fed wasps	[52, 54]
Diamondback moth, <i>P. xylostella</i> (L.)	Netherlands	Brussel sprouts	Buckwheat, F. esculentum Sweet alyssum, Lobularia maritima Dill, Anethum graveolens Brown knapweed, Centaurea jacea Perennial ryegrass, Lolium perenne (control)	Sugar content of <i>D. semiclausum</i> from the fields bordered by flowering margins was significantly higher than those from grassbordered control plots	[53]
Lepidopteran pest complex	United States	Cabbage	Buckwheat, F. esculentum	Although, buckwheat borders did not increase lepidopteran pest densities, the increase in parasitism of P . <i>xylostella</i> by D . <i>insulare</i> was inconsistent	[55]
Diamondback moth, P. xylostella (L.)	United States	Cabbage	Buckwheat, F. esculentum	D. semiclausum decreased significantly with distance away from the flowering strips	[56]
Imported cabbageworm, Pieris rapae (L.)	United states	Collards	Buckwheat, F. esculentum	Parasitism of <i>P. rapae</i> by <i>C. glomerata</i> did not differ with distance away from the buckwheat strip	[57]
Diamondback moth, P. xylostella (L.)	Indonesia	Cabbage	Coriander, Coriandrum sativum L.	Reduction in <i>P. xylostella</i> densities in the coriander mixed plots was not attributable to the increased parasitism by <i>D. semiclausum</i>	[58]
Aphids (species not indicated)	United States	Lettuce	Sweet alyssum, <i>L. maritima</i>	Sweet alyssum enhanced hoverfly, Eupeodes fumipennis (Thomson), populations and suppressed aphids in organic lettuce farms	[62, 63, 65]
Aphids (species not indicated)	Spain	Lettuce	19 flowering plants	Calendula arvensis L. and Coriandrum sativum were the most attractive to aphidophagous hoverflies [primarily, Sphaerophoria scripta L. and S. rueppellü (Wiedeman)]	[64]
European corn borer, Ostrinia nubilalis (Hubner)	United States	Bell pepper	Dill, A. graveolens L. Coriander, C. sativum Buckwheat, F. esculentum	Greater predation of <i>Ostrinia nubilalis</i> sentinel eggs by <i>Orius insidiosus</i> in the plots with border-planted flowering plants	[61]

Table 3. Recent evaluations of flowering plants for vegetable insect pest management at the farm level.

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se [68]	[72]	[73]	[74]	[66]	[67]
Increased abundance of hymenopteran wasp and predators in the border-planted floral habitats - results were not consistent	At one of the sites, the parasitism rate of P . rapae larvae was higher, whereas at the other site predation of M . brassicae eggs was higher in the intersown floral habitats compared to the control	Increased abundance of generalist predators (ground beetles and spiders) in the floral habitats compared to the control	Increased parasitism of <i>M. brassicae</i> larvae by <i>Microplitis mediator</i> and predation on herbivore eggs by generalist predators in the plots with flower strips compared to the control	Enhanced the parasitism rate of aphids and reduced the rate of increase of lepidopteran- caused foliar damage compared to the semi- natural habitats	Increased the abundance of bees and anthocorids but several other natural enemy group were not significantly enhanced compared to the control plots
Mixture of flowering annuals (California bluebell, buckwheat, dill, Plains coreopsis, <i>Coreopsis</i> <i>tinctoria</i> Nutt., garden cosmos and sweet alyssum)	Multiple species of wild flowers, including corn flower, C. cyanus	Multiple species of wild flowers in field margins with intersown corn flower, <i>C. cyanus</i>	Buckwheat along with corn flower, <i>C. cyanus</i>	Multiple species of wild flowers in field margins (buckwheat, common bean, hairy vetch, coriander, borage, fennel)	Multiple species of wild flowers including <i>C. jacea</i> L., <i>F. esculentum</i> , <i>Sinapsis alba</i> L.
Pumpkin	Cabbage	Cabbage	White cabbage	Tomato	Tomato
United States	Switzerland	Switzerland	Switzerland	Italy	Italy
Not specified	Cabbage moth, <i>Mamestra brassicae</i> L.; Cabbage butterfly, <i>P. rapae</i> (L.)	Not specified	Cabbage moth, <i>M. brassicae</i> L.	Multiple pest species	Not specified

Table 3 continued..

parasitoid activity, Lavandero et al. [56] found the parasitism rate of D. semiclausum to be lower in non-flower treated plots compared to flower treated plots, which were 60 m apart. In another study, more sugar-fed females of D. insulare were found in plots with flower strips when experimental plots were separated by 800 m compared to 67 m [54], whereas parasitism of P. xylostella larvae did not vary by spatial scale [55]. In Indonesia, the reduction in P. xylostella densities in the cabbagecoriander mixed cropping system was not attributable to the increased parasitism by D. semiclausum, suggesting that reduction may be due to the disruption in host searching behavior of female moths as influenced by the neighboring non-host plants [58]. These inconsistent results trigger the need of understanding the nature of landscape in providing services to natural enemies before altering the farmscape on a local scale [57].

3.3. Effects on omnivorous predators

Plant diversity through provision of floral resources allows omnivorous insects (e.g., *Orius* spp., hoverflies [Syrphidae]) to optimize fitness by exploiting various plant-based resources such as alternative prey that are attracted to the flowers as well as nectar and pollen [59, 60]. Various examples are discussed below.

Bickerton and Hamilton [61] found greater seasonal predation of Ostrinia nubilalis (Lepidoptera: Crambidae) sentinel eggs by Orius insidiosus (Hemiptera: Anthocoridae) in bell pepper when border-cropped with dill (Anethem graveolens L. [Apiaceae]), coriander, or buckwheat compared to a monoculture in New Jersey, USA. Syrphid fly larvae are highly efficient predators of aphids (Aphididae), while adults are highly attracted to floral resources for pollen. Among several tested flowering plants that are attractive to hoverflies, sweet alyssum, Lobularia maritima L. (Desv.) (Brassicaceae), was one of the most effective owing to its longer flowering period in California [62]. The presence of sweet alyssum in field cages enhanced Eupeodes fumipennis (Thomson) (Syrphidae) egg production, resulting in more hoverfly larvae and fewer aphids in lettuce [63]. In Spain, Calendula arvensis L. (Asteraceae) and coriander were the most attractive insectary plants to aphidophagous hoverflies [primarily

Sphaerophoria scripta L. and S. rueppellii (Wiedeman)] [64]. Gillespie et al. [65] found that a greater distance between two strips of sweet alyssum than that currently used in California, USA (48 m on organic farms) did not affect pollen consumption, syrphid dispersal, fecundity and aphid suppression, and could reduce costs involved in insectary plant management. Thus, incorporating floral resources in vegetable production systems has been shown to enhance the abundance of omnivorous predators, resulting in improved insect pest management. A better understanding of how flowering plants in the diverse habitats impact natural enemy abundance and subsequent increase in parasitism and/or predation at the farm level of pest is needed.

3.4. Effects of insectary mixtures and plants having extrafloral nectaries

Insectary plant mixtures comprising wild flowers have recently been used to examine their effects on natural enemies. The main purpose of using an insectary plant mixture is to increase the availability of functionally diverse floral resources across time, thus conserving beneficial arthropods [66, 67]. In Italy, the inclusion of strips of wild flower mixes adjacent to organically-managed tomato plots enhanced the parasitism rate of aphids and reduced the level of foliar damage caused by lepidopteran larvae on the tomato crop compared to a semi-natural habitat [66]. In a similar system, the inclusion of wild flower strips also increased the abundance of bees and anthocorids throughout the cropping system, but several other natural enemy groups (parasitoids, coccinelids, ground-dwelling predators, etc.) were not significantly enhanced compared to the plots with no wild flower strips [67]. In another study, border planting of flowering mixture comprising California bluebell [Phacelia campanularia A. Gray], plains coreopsis [Coreopsis tinctoria Nuttall], garden cosmos [Cosmos bipinnatus Cavanilles], buckwheat, dill and sweet alyssum suitable to New Mexico agro-climatic conditions did not consistently increase abundance of hymenopteran wasps and predators (anthocorids, chrysopids and coccinelids) in pumpkin plantings [68]. Furthermore, the use of flowering plants having extrafloral nectars has elicited interest among researchers because they may provide greater food resources to natural enemies than floral nectars [69]. In Switzerland, flowering plants having both floral and extrafloral nectaries [e.g., cornflower, *Centaurea cyanus* L. (Asteraceae)] had significantly increased the longevity of *Microplitis mediator* (Haliday) (Braconidae) and *Diadegma fenestrale* (Holmgren) (Ichneumonidae), and parasitism rates of cabbage moth, *Mamestra brassicae* (L.) (Noctuidae), larvae by *M. mediator* in laboratory tests [70, 71].

Mixtures of multiple species of wild flowers, along with plants having extrafloral nectaries, have been found to increase activity of both parasitoids and predators. For example, Pfiffner et al. [72] found that parasitism of P. rapae larvae and predation of *M. brassicae* eggs were higher at one of the two sites in cabbage plots with floral strips (multiple species of wild flowers, including C. cyanus) compared to the control. In another study, floral strips (multiple species of wild flowers) on field margins and intersown C. cyanus in cabbage positively affected abundance of generalist predators (ground beetles and spiders), with stronger richness along the field margin [73]. Similarly, planting cornflowers along with buckwheat as a non-crop flowering strip significantly increased parasitism of M. brassicae larvae by M. mediator and predation on herbivore eggs by generalist predators (carabids, staphylinids and spiders) in white cabbage [74]. Overall, these studies showed that the use of flowering mixtures along with plants having extrafloral nectars can enhance populations of both specialist parasitoids and generalist predators, resulting in increased pest suppression.

4. Use of living mulches and intercropping

Living mulches are cover crops planted either, before (undersown) or with a main crop (rowintercropped) and maintained as living ground cover throughout the growing season [75]. Living mulches can provide many benefits such as weed control, reduced erosion, enhanced soil fertility and improved soil quality [76]. When vegetables are undersown in living mulches or row intercropped with cover crops or other vegetable crops, they are found to reduce herbivorous insects and damage caused by them [77, 78, 79]. These systems (living mulches, intercropping) create diverse habitats that are generally less favorable for herbivores and/or more conducive for natural enemies [10]. However, herbivore response to diverse habitats could not be explained by a single ecological theory [5] and may depend on the behavior of herbivores (host finding, host acceptance, etc.) to the specific habitat type [11, 80]. Below, we discuss the main mechanisms underlying the effects of living mulches and intercrops on pest suppression (Table 4).

4.1. Disruption of host-plant finding

Unlike trap cropping, living mulches (undersown and intercropped) can be seen as a strategy in which the non-host plant disrupts the host-plant finding behavior of the insect pest, leading to reduced host plant colonization rates [11]. Disruption of host finding behavior of herbivores in diverse habitats is mainly attributed to the masking of visual or olfactory cues provided by the non-host plants. In UK, Finch et al. [81] showed that the ability of the cabbage root fly, Delia radicum, and the onion fly, D. antiqua (Meig.) (Anthomyiidae), to find host plants (Brassica and Allium) was affected by the color (green leaf) and size (leaf area, height, and weight), but not by the constitutive volatiles of the non-host plants. Further, behavioral studies with D. radicum showed that the time spent by the insect pest on the non-host plants was significantly longer than on the host plants [82]. Thus, much of the energy is allocated to assess the non-host plants [81, 82]. Some authors have suggested that among the three-linked chain of events in the 'appropriate and inappropriate landing' theory [11], the central link (visual stimuli) and the final link (cues from non-volatile plant chemicals) are crucial for landing on the host plant (colonization) and subsequent host acceptance (feeding and oviposition). In line with these findings, Bjorkman et al. [83] in Sweden found that intercropping cabbage with red clover (Trifolium pratense L.) resulted in reduced oviposition by turnip root fly, D. floralis (Fall.) (Anthomyiidae), by 42-55% on the cabbage crop compared to the monoculture. Further, lepidopteran egg and larvae densities were significantly lower

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Table 4. Recent evaluations c	of the use of	living mulch	les/intercrops for insect pest managem	ent in vegetables at the farm level.	
Insect pest species	Country	Crop	Living mulches / intercrops	Effects	References
Turnip root fly, Delia floralis (Fall.)	Sweden	Cabbage	Red clover, Trifolium pratense L.	Intercropping cabbage with red clover resulted in reduced <i>D. floralis</i> oviposition on the cabbage crop compared to the cabbage monoculture	[83, 94]
Lepidopteran pest complex	United States	Broccoli	Strawberry clover, T. fragiferum L. White clover, T. repens L. Yellow sweet clover, Melilotus officinalis L.	Lepidopteran egg and larvae densities were lower in the broccoli undersown in living mulches plots compared to the broccoli monoculture	[78]
Lepidopteran pest complex	United States	Broccoli	Yellow sweet clover, M. officinalis Tomato, Lycopersicon esculentum Miller Pepper, Capsicum annuum L.	Lepidopteran egg and larvae densities were lower in the broccoli undersown in yellow sweet clover plots compared to the tomato or pepper intercropped plots	[77, 79]
Colorado potato beetle, <i>Leptinotarsa decemlineata</i> (Say); Flea beetles, <i>Epitrix</i> spp.	United States	Eggplant	Crimson clover, T. incarnatum L.	Fewer numbers of Colorado potato beetle larvae, adults and eggs were found in the interplanted plots compared to the monoculture plots	[84, 85]
Striped cucumber beetle, Acalymma vittatum Fab.; spotted cucumber beetle, Diabrotica undecimpunctata howardi Barber	United States	Zucchini	Sunn hemp, <i>Crotalaria juncea</i> L.	Interplanting treatment reduced the numbers of striped cucumber beetle compared to monoculture	[86]
Whitefly, <i>Bemisia tabaci</i> (Gennadius)	Brazil	Tomato	Coriander, Coriandrum sativum	Intercropping treatment reduced the attractiveness of tomato plants resulting in lower numbers of whitefly adults and nymphs compared to monoculture	[87]
Whitefly, <i>B. tabaci</i>	China	Cucumber	Celery, <i>Apium graveolens</i> L. Malabar spinach, <i>Gynura cusimbua</i> (D. Don) Asparagus lettuce, <i>Lactuca sativa</i> L. Edible amaranth, <i>Amaranthus</i> mangostanus L.	Intercrops of celery and Malabar spinach reduced <i>B. tabaci</i> numbers on the cucumber crop compared to monoculture	[88]
Multiple pest species	United States	Tomato	Biological mulch of killed triticale, <i>Triticosecale</i> Wittm. Rye, <i>Secale cereal</i> L. and vetch, <i>Vicia sativa</i> L.	Increased spider densities in tomato field compared to a field that used reflective mulch	[89]

Effects of increased crop diversity on vegetable insect pests

[90]	[19]	[95]	[96]	[92, 99]	[100]	[15]	[79]	[86]
Increased weed seed and armyworm pupal predation by fire ants, compared to conventional practices (black plastic mulch and soil fumigation)	Increased actively hunting generalist predators but not 'sit and watch' predators	Reduced density of aphids in diverse habitats, but parasitism of aphids by <i>Diaeretiella rapae</i> did not explain the observed differences	Increased numbers of cabbageworm and its parasitoid, <i>Cotesia rubecula</i> , in killed rye mulch plots compared to killed vetch or bare-ground plots	Living mulches (white clover and sunn hemp) lowered the density of <i>B. argentifollii</i> resulting in reduced severity of silverleaf disorder in zucchini compared to bare ground	Living covers reduced the number of incoming whitefly adults and delayed the onset of <i>Tomato yellow mottle virus</i> compared to conventional methods (insecticide or reflective mulch)	Borders of maize and sorghum barrier plants reduced the transmission of the aphid-transmitted <i>Potato virus Y</i> and <i>Cucumber mosaic virus</i> to pepper plants	Greater reduction of pumpkin viruses when grain sorghum was used as an intercrop compared with border crop	Reduced incidence of <i>Papaya ringspot</i> virus-watermelon strain in zucchini when interplanted with buckwheat, white clover or sunn hemp compared to bare-ground
Killed cahaba white vetch, V. sativa L. Killed rye-vetch, S. cereale L V. sativa	Killed oat, Avena sativa L.	Potato, Solanum tuberosum (L.) Rye, S. cereal (L.)	Killed rye, <i>S. cereal</i> Killed vetch, <i>V. villosa</i>	Buckwheat, F. esculentum White clover, T. repens L. Sunn hemp, C. juncea Okra, Abelmoschus esculentus L.	Perennial peanuts, Arachis pintoi Cinquillo, Drymaria cordata Coriander, Coriandrum sativum	Maize, Zea mays Sorghum, Sorghum vulgare	Corn, Z. mays Soybean, Glycine max Peanut, A. hypogaea Grain sorghum, S. bicolor	Buckwheat, F. esculentum White clover, T. repens Sunn hemp, C. juncea Okra, A. esculentus
Bell pepper and collards	Cabbage	Broccoli	Cabbage	Zucchini	Tomato	Pepper	Pumpkin	Zucchini
United States	United States	Australia	United States	United States	Costa Rica	Spain	United States	United States
Armyworm, Spodoptera exigua	Multiple pest species	Cabbage aphid, Brevicoryne brassicae (L.)	Imported cabbageworm, Pieris rapae L.	Whitefly, <i>Bemisia</i> argentifollii Bellows and Perring	Whitefly, B. tabaci	Aphids, <i>Aphis gossypii</i> Glover and <i>Myzus persicae</i> (Sulzer)	Aphids (multiple species)	Aphids, A. gossypii Glover and M. persicae (Sulzer)

Table 4 continued..

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in the broccoli undersown in plots having living mulches compared to the broccoli monoculture [78]. Pest densities were also lower in plots with broccoli undersown in yellow sweet clover (Melilotus officinalis L.) compared to plots with broccoli intercropped with either tomato or pepper [77, 79]. Similarly, significantly fewer numbers of Colorado potato beetle, Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae), larvae, adults, and eggs were found in plots with eggplant interplanted with crimson clover (Trifolium incarnatum L.) compared to monoculture plots [84, 85]. In addition, interplanting sunn hemp (Crotalaria juncea L.) as a living mulch with zucchini significantly reduced the numbers of A. vittatum on zucchini plants compared to zucchini grown as monoculture [86].

4.2. Chemically-based repellency

Only a few studies have documented reduced pest numbers attributable to repellent effects of mulches or intercrops. A study in Brazil reported that intercropping tomato with coriander reduced the attractiveness of tomato plants resulting in lower numbers of Bemisia tabaci (Gennadius) adults and nymphs on the tomato crop compared to the monoculture plots [87]. Similarly, in China, volatile compounds emitted by the less-preferred intercrops of celery, Apium graveolens L. (Apiaceae), and Malabar spinach, Gynura cusimbua (D. Don) (Asteraceae), significantly reduced B. tabaci numbers on the cucumber crop compared to monocultures [88]. The authors found two major volatile constituent compounds, D-limonene from celery and Geranyl nitrile from Malabar spinach to be responsible for the observed repellent effects.

4.3. Effects on biological control

Living mulches can also influence in-field structural complexity affecting pests and their natural enemies. In Florida, USA, a mixture of cover crops killed using glyphosate herbicide significantly increased spider densities in tomato field compared to a field that used reflective mulch [89]. Similarly, in South Carolina, a cover crop mulch of either Cahaba white vetch, *Vicia sativa* cv. Cahaba (Fabaceae), or rye-vetch, *Secale cereale* L.- V. *sativa* (Poaceae), killed using glyphosate increased weed seed and armyworm, *Spodoptera exigua* (Hubner) (Noctuidae), pupal predation by fire ants, compared to conventional practices (black plastic mulch and soil fumigation) in bell pepper and collards [90]. In Michigan, USA, a complex habitat achieved through late killing of an oat, *Avena sativa* L. (Poaceae), cover crop with low herbicide intensity in a strip-tilled system increased actively hunting generalist predators but not 'sit-and-watch' predators (e. g., spiders) in a cabbage crop [91]. Thus, living mulch diversified habitats are more likely to support a population of generalist predators [77, 78, 79, 86, 92 but see Szendrei *et al.*, (93)], which may be one reason for having lower pest densities on crops grown in living mulch habitats.

On the other hand, Bjorkman et al. [94] found that neither predation nor parasitism rates of D. floralis eggs or larvae differed between a cabbage-red clover intercropping system and monoculture, suggesting that the lower densities of D. floralis observed were most likely due to disruption in oviposition behavior. Further, Broad et al. [95] found that cabbage aphid, Brevicoryne brassicae (L.), parasitism by Diaeretiella rapae (McIntosh) (Braconidae) did not explain the observed differences in the number of B. brassicae colonies in the treatments (broccoli intercropped with potato, broccoli planted in rye and monoculture) and indicated that the reduced density of aphids in diverse habitats is mainly due to differential rates of colonization. In contrast, Bryant et al. [96] found significantly higher numbers of P. rapae and its parasitoid C. rubecula in killed rye mulch plots compared to killed vetch mulch plots or bare-ground plots. However, increased parasitoid abundance in rye plots did not result in greater parasitism likely because of interference of the mulch with shortrange host finding odor cues. This provides further evidence that pest suppression in living mulch/ intercropping habitats is mainly due to the alteration in insect's behavior rather than to an increase in natural enemy activity as supported by the companion plants [11].

4.4. Specific plants that act as a 'virus sink'

The use of specific plantings called barrier or protector plants has been effective in managing aphid-transmitted non-persistent viruses in vegetables. One mechanism proposed for the lower incidence of non-persistent viruses on susceptible host plants grown with non-susceptible hosts is the 'virus sink hypothesis' [15, 16]. It suggests that the aphid vectors that land on the non-host plants (barrier plants) remove virus particles from their mouthparts while test probing. After probing/ feeding, the aphid becomes non-viruliferous and will not be able to transmit the virus to the susceptible host plant. For example, in Spain, Fereres [15] demonstrated that borders of maize and sorghum barrier plants reduced the aphidtransmitted Potato virus Y and Cucumber mosaic virus to pepper plants. In Oklahoma, USA, Damicone et al. [97] found a greater reduction of pumpkin viruses [Watermelon mosaic virus and Papaya ringspot virus – watermelon strain (PRSV-W)], when grain sorghum was used as an intercrop compared with border crop. This study also indicated that a higher proportion of barrier plants in the crop field might result in greater protection of the main crop. Similarly, in Hawaii, USA, Manandhar and Hooks [98] found reduced incidence of PRSV-W in zucchini when interplanted with cover crops (buckwheat, white clover or sunn hemp) compared to bare-ground cultivation. These studies consistently demonstrated that the reduced incidence of viruses in the main crop was only due to the barrier plant acting as a virus sink [15, 97, 98].

Unlike barrier crops acting as a virus sink, living mulches have also been found to reduce the incidence of phytoxemia or plant diseases. For example, in Florida and Hawaii, USA, living mulches (white clover and sunn hemp) lowered the density of *B. argentifollii* (egg, nymphs and adults) and reduced the severity of silverleaf disorder in zucchini compared to bare ground [92, 99]. Similarly, in Costa Rica living mulches represented by perennial peanuts, *Arachis pintoi*, cinquillo, *Drymaria cordata*, and coriander reduced the number of incoming *B. tabaci* adults and delayed the onset of *Tomato yellow mottle virus*, compared to conventional methods (use of insecticide or reflective mulch) [100].

5. Conclusion

This review synthesized recent information concerning the benefits and possible disadvantages associated with the use of trap crops, flowering plants, living mulches and intercrops. In many cases, the methods of increasing diversity implemented to manage insect pests were effective at reducing pest densities in vegetables crops. However, the associated mechanisms were largely found to be specific to each particular method and their effectiveness depended upon the particular crop-pest combination. Attractive trap crops supplemented with the application of insecticide effectively suppressed pest densities in some vegetables. The recent development of dead-end Bt trap crops (e.g., Bt collards and mustard) for the management of P. xylostella is promising given the expected reduction or even elimination of insecticide application to the trap crops. Omnivorous insects that use various plantbased resources (prey and pollen) were effective in reducing pest densities in floral habitats. The use of wild flower mixtures including plants having extrafloral nectars, have shown encouraging results in increasing parasitism and predation of multiple pests in vegetable crops. These results have applications for conservation biological control. Our synthesis also indicated that reductions in pest densities in living mulches or intercropped habitats seem to be largely due to the alteration of pest's behavior rather than to enhanced biological control, although in some cases living mulches have supported populations of generalist predators. While the techniques discussed can be a standalone approach to pest management, it is advisable to integrate approaches including the selective and judicious use of insecticides as well as cultural and biological controls through IPM implementation. Further development of such methods are expected to reduce chemical inputs (e.g., insecticides) leading to more sustainable and profitable pest management strategies.

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CONFLICT OF INTEREST STATEMENT

The authors claim no conflict of interest concerning this study.

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