Chapter 2
Interactions of Natural Enemies with Non-cultivated Plants

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2.1 Introduction

Conservation of natural enemies in agroecosystems is directly associated with farm management practices that provide more suitable resources and conditions to biological control agents. Using such strategy, it is expected that natural enemies provide the ecosystem the service of biological control, thereby reducing the need for external outputs (UN 2017). In this sense, strategies related with natural enemy diversity conservation are important tools to reduce negative trends in modern agriculture, including pesticide resistance among insect pests, environmental and human health impacts, biodiversity loss, and introduction of invasive exotic pests (Tscharntke et al. 2007; Bianchi et al. 2008). This perspective demands the improvement of ecosystem services via management strategies that increase and conserve the biodiversity of flora and fauna within and around crop fields (Gurr et al. 2003). Typically, management strategies to enhance vegetational diversity, which, subsequently, increase the biodiversity of associated beneficial arthropods, vary with crop type (perennial or annual) and region (temperate or tropical) at both local and landscape scales (Thies and Tscharntke 1999). Importantly, efforts to conserve the biodiversity may positively affect natural enemies that provide biological control of insect pests (Landis et al. 2000; Norris and Kogan 2000, 2005; Letourneau et al. 2011).

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A practice that has been widely adopted for a long time for habitat management in agroecosystems is the management of non-crop strips, which can increase beneficial arthropod populations (Altieri and Whitcomb 1978; Nentwig 1998; Liljesthröm et al. 2002; Gurr et al. 2003; Norris and Kogan 2000, 2005). Farmers can easily adopt the management of non-crop plants due to characteristics such as rapid plant growth and low investment (Amaral et al. 2013). However, non-crop plants are traditionally called and treated as weeds by some researchers, farmers, and citizens. Using this terminology implies that these plants have no obvious function in the agroecosystem and are indeed only deleterious to agriculture. Non-crop plants in agroecosystems provide resources and conditions to allow natural enemy survival, growth, and reproduction, even when their prey is scarce or absent. Thus, understanding the complex multitrophic interactions between natural enemies and non-crop plants provides a critical framework for the implementation of conservation biological control strategies.

In this chapter, we reviewed the direct and indirect effects of non-crop plant management on natural enemies. We addressed the main mechanism mediating the interactions among plants, herbivores, and natural enemies, focusing on examples from Latin America, mainly Brazil. We emphasized arthropod predators as model of action of non-crop vegetation on biological control. Thus, our specific objectives were firstly to examine how non-crop management improves the abundance and diversity of natural enemies, by the quantification of the specific mechanisms that mediated the interaction between non-crop plants and natural enemies. Secondly, we focused on possible applications on agroecosystems and effects upon evaluating plant characteristic or functional traits that may be chosen to improve key natural enemies.

2.2 Multitrophic Interactions Mediated by Non-crop Plants

The classical question “Why is the world green?” proposed by Hairston, Smith, and Slobodkin (HSS), in their influential 1960 study, was important to understand the role of natural enemies to regulate herbivore populations. In the HSS theory, or the *green world hypothesis*, Hairston and colleagues argued that plant biomass is not completely limited by herbivores, because natural enemies (third trophic level) regulate the populations of herbivores (second trophic level), reducing their impact on plants (first trophic level) (Hairston et al. 1960). This concept was previously defined as top-down regulation, where the third trophic level indirectly affects the populations from the first trophic level in a trophic cascade. Complimentary, Root (1973) demonstrated that brassica plots containing non-crop vegetation usually harbor a more diverse community of predatory and parasitoid arthropods than monoculture plots. The author also observed that the diversified plots presented less herbivore and associated damage, suggesting that plants can favor the diversity of natural enemies, which, in turn, reduces herbivore populations. After that, Price et al. (1980)

discussed that considering the role of natural enemies is imperative to understand the plant-herbivore interactions and the predator-prey dynamics due to direct and indirect effects of plants on natural enemies and vice versa. There are evidences that showed the importance of predators and other natural enemies' action against herbivores, reducing their negative effects on plants via trophic cascades (Dyer and Letourneau 1999; Costamagna and Landis 2011; Wilkinson and Sherratt 2016). Top-down forces, such as predation and parasitism, directly influence agricultural communities and can be managed to reduce pest outbreaks (Stireman et al. 2005; Macfadyen et al. 2009).

The top-down control is one of the most important theoretical bases to justify the implementation of conservation biological control in agroecosystems via non-crop plants. Beyond abundance of predator and other natural enemies, the effectiveness of biological control may increase with predator species abundance and diversity (Root 1973; Ives et al. 2005; Snyder et al. 2005). Specifically, modifications on leaf litter or crop residues, vegetation structure, and plant diversity (e.g., associated with polyculture, mulching techniques, or weedy cropping systems) all affect the diversity of beneficial arthropods (Uetz 1991; Denno et al. 2005) and, subsequently, the biological control service provided (Dornelas et al. 2009). However, simply adding plants and natural enemies to agroecosystems is not a guarantee of biological control (Letourneau et al. 2011) because the vegetational diversification by different techniques must be functional to attract and favor the performance of natural enemies in the farm (Venzon et al. 2015).

In this perspective, to attract and keep natural enemies in agroecosystems, practitioners often adopt habitat management strategies to conserve non-crop vegetation strips within or surrounding crop fields (Altieri and Whitcomb 1978; Nentwig 1998; Landis 2017). The manipulation of non-crop plants may be associated with a wide array of mechanisms that explain the attraction and maintenance of natural enemy populations as follows: (i) source of preferential prey species (Weyman and Jepson 1994); (ii) presence of patches used as refuge against competitors or as alternative for oviposition (Finke and Denno 2002; Langellotto and Denno 2006); (iii) provision of complementary and supplementary food resources (alternative prey and plat-provided food) (Jonsson et al. 2008; Lundgren 2009); (iv) access to favorable micro-climate conditions (Alderweireldt 1994; Chen et al. 2011); (v) reduction of the impact of negative interactions, such as cannibalism or intraguild predation, favoring synergistic or additive predation (Losey and Denno 1998; Finke and Denno 2006; Robinson et al. 2008); and (vi) the improvement of spatial structure that facilitates the web building, resulting in increase in prey capture (Robinson 1981; Mcnett and Rypstra 2000).

Agroecosystems are managed by human labor, which means that provisioning of biological control as an ecosystem service depends on cooperation between human and nature (Bengtsson 2015). The more the ecological theory is used as a management tool for pest control using ecosystem services besides artificial techniques (i.e., insecticide spraying), the less human counterpart is needed. In this perspective,

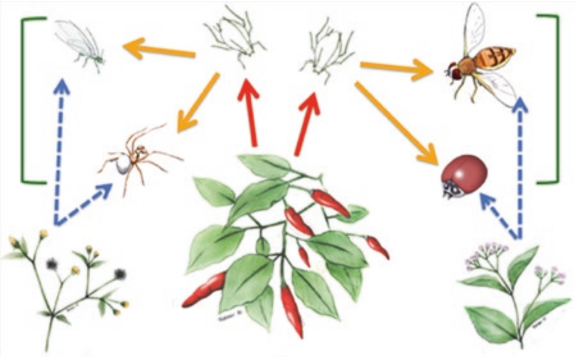

Fig. 2.1 *Next-to* effect (blue arrows) of non-crop plants contributing to top-down pest regulation (yellow arrows)

the strength of top-down control relies on the manipulation of the associated plant to the main crop, such as non-crop plants. Associated with top-down control, we predicted the *next-to hypothesis,* when the non-crop or another associated plant acts as a “scaffold” that helps to improve the coexistence of diverse natural enemy populations and promotes biological control (Fig. 2.1). *Why is the world green?* Because there is top-down control of herbivores, but complementary there are *next-to* traits on non-crop or other associated plants that build and reinforce the actions of natural enemies.

2.3 Non-crop Plants Affecting Natural Enemies

One of the main advantages of using non-crop plants to habitat manipulation is that plants are naturally present on agroecosystems; they grow rapidly and spontaneously, and farmers know them well. However, the effectiveness of this strategy depends on finding the functional role of each plant to specific biological control agents. To achieve this and successfully integrate non-crop plants into pest management decision-making, it is necessary to quantify and understand the ecological mechanisms that influence the response of natural enemies to such plants (Andow 1988; Snyder et al. 2005).

In temperate agroecosystems, there are several reported beneficial effects of non-crop plants on the distribution and abundance of beneficial arthropods (e.g., Wyss 1995; Nentwig 1998; Leather et al. 1999; Norris and Kogan 2000; Showler and Greenberg 2003; Silva et al. 2010). However, in tropical agroecosystems, there is a paucity of information pertaining to the resources provided by non-crop plants and their interactions with natural enemies. In the tropics, crops are grown all over the year with almost no interruption, and non-crop interactions with natural enemies are continuous in space and time. Herein, we sought to find and examine possible mechanisms associated with interactions between non-crop plants and natural enemies in tropical agroecosystems to clarify the role of such plants in cropped areas, mainly from South America.

2.4 Non-crop Plants as Resource to Natural Enemies

Results obtained from research carried out in chili pepper agroecosystems in Brazil revealed the role of non-crop plants as a resource and source of natural enemies. Amaral et al. (2013) observed that the presence of non-crop plants within or surrounding chili pepper fields differentially affected the abundance of different groups of aphidophagous predators by providing alternative prey, refuge, nectar, and pollen as a complementary resource. Coccinellidae were more abundant when aphids were present on non-crop plants, but the ladybirds were also observed foraging on flowers and extrafloral nectaries and using plants as refuge. Adults of Syrphidae were more frequently recorded feeding on nectar and pollen from flowers when compared to any other resource. Anthocoridae, Neuroptera, and Araneae were observed equally exploiting the resources from non-crop plants (Amaral et al. 2013).

Cycloneda sanguinea (Linnaeus) (Coccinellidae) was observed frequently preying on aphids commonly found on annual sow thistle (*Sonchus oleraceus*) and on American black nightshade (*Solanum americanum*) (Amaral et al. 2013). It was also observed on flowers of tropic ageratum (*Ageratum conyzoides)* and of beggarticks (*Bidens pilosa).* Feeding on flowers of *B. pilosa* increased predator survival in the absence of prey (Fonseca et al. 2017). In Central Mexico, *Coccinella nugatoria* Mulsant was more frequently observed interacting with aphids in maize crops with non-crop plants than in monocultures (Trujillo-Arriaga and Altieri 1990).

Complementary, non-crop plants may contribute to the diversification of plant communities, which may aggregate generalist arthropods with complementary foraging strategies, promoting functional diversity of natural enemies. Spiders exhibit a diversity of foraging characteristics and behavior (Uetz et al. 1999) that, acting together, may increase top-down control of pests. Studies on chili pepper agroecosystems in Brazil provided evidence for associations between spider families and non-crop plants (Amaral et al. 2016). The composition of non-crop plant communities altered the abundance and guild structure of spiders; the greatest number of spiders was found on Asteraceae plants (Amaral et al. 2016). These plants are attractive to spiders, particularly to the family Thomisidae, potentially due to complex inflorescences that act as sites to capture prey attracted to their flower resources (Nyffeler et al. 1994; Peterson et al. 2010). Additionally, spiders were also observed using non-crop plants as substrate to build webs, mainly on taller and ramified plants (e.g., *A. conyzoides*, *Leonurus sibiricus*) (Amaral et al. 2016).

Non-crop plants are important reservoirs of natural enemies for many crop systems due to the characteristics discussed above. For example, *B. pilosa*, *Amaranthus* sp., *Parthenium hysterophorus*, and *Alternanthera ficoidea* are important sources of many *Orius* species for crops such as maize, beans, and lettuce (Silveira et al. 2003). In soybean, stink bugs can oviposit on non-crop plants, such as *A. ficoidea*, adjacent to the crop field. These eggs can be used by Platygastridae parasitoids (e.g., *Telenomus podisi* Ashmead, 1881) and favor the biological control of stink bugs in soybean fields (Maruyama et al. 2002). Pollen of *Peltaea riedelii* (Malvaceae) can be used as supplementary food by the predatory mites *Euseius concordis* (Chant) and *Iphiseiodes zuluagai* Denmark & Muma (Acari: Phytoseiidae) on physic nut crops (Marques et al. 2014). Non-crop plants *S. americanum* and *Salpichroa origanifolia* harbor *Phytoseiulus longipes* Evans (Acari: Phytoseiidae), a potential effective candidate for augmentative biological control of *Tetranychus evansi* Baker & Pritchard in tomatoes (Furtado et al. 2006). Supporting these findings, traditional cornfields with a high non-crop plant diversity in the Colombian Andes presented a more diverse community of predators that could potentially act as biological control agents (Martínez et al. 2015). Moreover, the presence of non-crop plants can provide a great amount of non-pest species that can compete with pest species and serve as supplementary or alternative prey to natural enemies. In this sense, Sánchez-Monge et al. (2011) found 19 thrips species (mostly non-pests) associated with non-crop plants in Costa Rica.

2.5 Survival of Natural Enemies on Non-crop Plants

The survival parameters of arthropod predators may be directly affected by specific non-crop plants. The survival of *C. sanguinea* (native from America), in the absence of prey, differed between plant species, with significantly greater survival on *A. conyzoides* and *B. pilosa* than on *S. oleraceus* (Amaral et al. 2013). In the same study, any evidence was gathered to suggest that non-crop floral resources provided by these plants offered nutritional benefits to the exotic Coccinellidae *Harmonia axyridis* (Pallas). The non-crop plant species studied are native from the Americas, and *H. axyridis* is native from the Palearctic region, demonstrating that life history traits are important factors to be considered when selecting non-crop plants in conservation biological control strategies (Amaral et al. 2013).

Chrysopidae larvae can benefit by feeding on flower resources of non-crop plants during periods of prey scarcity. Salgado (2014) reported that these benefits vary with predator and non-crop plant species. Larvae of *Chrysoperla externa* (Hagen, 1861) had higher survival when *A. conyzoides* flowers were offered. *Ceraeochrysa cubana* (Hagen, 1861) larvae had higher survival with *A. conyzoides* and with *B. pilosa* flowers. Adults of both species did not benefit from the presence of these flower species. Larvae of *C. externa* completed their development and turned to adults when fed exclusively on pollen of elephant grass *Pennisetum purpureum* (Oliveira et al. 2010).

2.6 Spatial Distribution

The spatial distribution should be also considered when evaluating possible benefits of management of non-crop plants, by determining the natural enemy cover span from the source of the plant diversity (Holland et al. 2004; Thomson and Hoffmann 2013). More than intrinsic characteristic among species or life stages, the movement behavior may be influenced by environmental heterogeneity (Winder et al. 2001;

Park and Obrycki 2004). The strategy of manipulation of non-crop plant may be affected by the pattern of movement and spatial distribution of natural enemies, contributing to biological control. On a spatiotemporal experiment in chili pepper, the presence of non-crop plants affected positively the distribution of coccinellids and spiders, promoting more densities of arthropods in non-crop plant patches (Amaral 2014; Amaral et al. 2016). Non-crop plant strips influenced the aggregation tendencies of coccinellids and spiders on season crop, mainly from the middle to the end, when the non-crop plants were established. Other studies have also shown that the presence of vegetation surrounding crop fields increases predator colonization and abundance (Sunderland and Samu 2000). In Colombia, the presence of non-crop plants affected the predatory species turnover among habitat types, contributing to a higher diversity of potential biological control agents and to rare arthropod predatory species conservation in tropical landscapes (Martínez et al. 2015). Similarly, conventional soybean monoculture expansion across the Rolling Pampa, Argentina, threatened the occurrence of non-crop plants, and, consequently, non-crop plant removal imposed a risk to beneficial arthropod species and functional groups occurrence in the landscape (De La Fuente et al. 2010).

2.7 Behavior

Beyond the provision of food, non-crop plants may affect indirectly the survival of predators by reducing negative effect of cannibalism and intraguild predation. The diversification of vegetation mixing squash (*Cucurbita pepo*) and non-crop mugwort *Artemisia vulgaris* affected life-stage specific interactions between the American coccinellid, *Hippodamia convergens* (Guerin-Meneville, 1842), and the exotic *H. axyridis,* which overlap in spatial distribution in many crop systems (Amaral et al. 2015) (Fig. 2.2). In a small scale, the association of squash and non-crop plants promotes spatial heterogeneity and prey availability that reduce larval intraguild predation and cannibalism. The reproductive output of *H. convergens* was improved by reducing intra- and interspecific egg predation. The mugwort leaf morphology has complex architecture and provides better shelter for coccinellid eggs when compared to squash plants. Similarly, competition between several arthropods sharing similar resources and prey can be alleviated by the presence of non-crop plants that provides more resources besides the more complex spatial structure within the habitat (Tixier et al. 2013).

Aphidophagous coccinellids such as *Eriopis connexa* (Germar, 1824)*, C. sanguinea*, *H. axyridis*, and *H. convergens* share many prey types and, consequently, forage and oviposit in similar habitats. Sicsú et al. (2015) observed that, although adults from these species are found in many non-crop plants, each species oviposit on specific plants to avoid interspecific competition. Consequently, larval distribution is strongly related to the oviposition site on a preferred plant. Each plant also harbors different species of aphids. Therefore, there is an interaction between non-crop plant species and the availability of aphids, which can affect the ovipositional behavior of predatory coccinellids and the distribution of eggs and larvae.

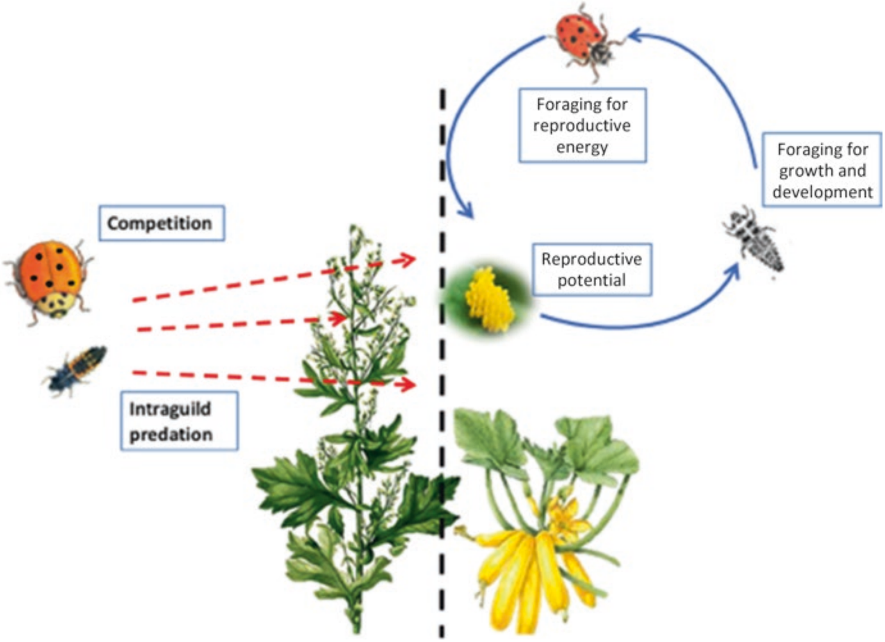

Fig. 2.2 Spatial guild division created by the management of non-crop plant (left), reducing negative effects of competition and intraguild predation between two species of coccinellids

In Mexico, Penagos et al. (2003) observed that the presence of non-crop plants favored the colonization of maize by natural enemies. The most common natural species associated with the reduction on *Spodoptera frugiperda* (J.E. Smith) (Noctuidae) and the presence of non-crop plants were the generalist predators *Doru taeniatum* (Dohrn) (Forficulidae) and *Chrysoperla* spp. (Chrysopidae) and predatory beetles such as carabid beetles. The authors also observed a significantly reduction on *S. frugiperda* eggs, on the number of aphid colonies, and on the number of sap beetles compared to maize plots without non-crop plants. However, the presence of non-crop plants reduced the parasitism rate of *S. frugiperda* eggs by *Chelonus insularis* (Cresson, 1865) (Braconidae) (Penagos et al. 2003). Similar results were found in the Peruvian Andes, where maize, bean, and non-crop plants treatments reduced the abundance of key herbivores similar to the conventional monoculture plots (Gianoli et al. 2006). These findings demonstrated that it is necessary to investigate specific traits of a given plant and its effects on target natural enemies.

2.8 Applications and Future Directions

Some growers can argue that non-crop vegetation can interfere on crop yield by the competition or the allelopathic effect. In fact, non-crop plants can be viewed as weedy, when they are not properly managed in agroecosystems. To avoid such problems, there is the need to encourage growers and researchers to search for the best design options when using non-crop plants as a diversification tool for pest management. For example, this could be achieved by maintaining strips of non-crop plants between crop rows or around the main crop. A selective removal of some species of non-crop plants can be also done in order to maintain only species that benefit natural enemies. Therefore, it is necessary to understand the ecological interactions among plants, herbivores, and natural enemies. Other complementary strategies, such as habitat manipulation at different spatial scales (e.g., using agroforestry systems, fallow areas, maintenance of natural areas), may broaden the positive effects of non-crop plants.

In a recent field study, Chiguachi et al. (2017) compared different pest management strategies for chili pepper pest control. Although pest population was lower in all sampled areas, the abundance and diversity of Coccinellidae were higher on cropped areas with non-crop plants without pesticides, compared with areas with and without pesticides but in absence of non-crop plants. Thus, the presence of non-crop plants contributes to the maintenance of biodiversity in cultivated areas.

In order to implement and recommend efficient strategies using non-crop plants and other habitat manipulation strategies, it is necessary to study deeply the biology and ecology of different natural enemies to identify factors disrupting biological control. This is an important challenge in tropical agroecosystems because there are much more species and possibilities of interactions with non-crop plants than in temperate regions. Non-crop plants are well known by growers, and it is also necessary that researchers focus their attention in their needs to produce applied research in accordance with real agricultural demands.

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