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Enhancing biological control: conservation of alternative hosts of natural enemies

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Abstract

Background There is a consensus that the conservation of natural enemies is the most important biological control strategy, but it has also been the least attended. The reason is simple: there is a strong contradiction between modern agriculture and biological control. Various strategies have been proposed for the conservation of natural enemies, among others, protection against pesticides and establishment of nectar plants as alternative food. Less attention has been paid to the conservation of alternative hosts for natural enemies.

Main body Natural enemies are not exclusive to pests, on the contrary, numerous species require alternative prey and hosts for their prevalence. Their conservation is a strategy widely referenced in scientific literature; however, this idea is not consistent with the studies developed. From 1973 to 2021, only 21 studies that emphasized the use of alternative hosts were recorded. Most focused on single phytophagous–natural enemy species, and little attention was given to the plant–phytophagous relationship. For example, *Asclepias curassavica* (Apocynaceae) hosts more than nine species of specialist phytophagous; and they, in turn, attracted 24 species of natural enemies. Although different studies demonstrate the potential of alternative hosts, some presume an adverse or doubtful effect on pest control; for example, additional vegetation in agroecosystems could act as a source, but also as a sink for natural enemies. This analysis tries to fit biological control to the modern agricultural paradigm, and not the other way around, as suggested by ecological theory. We support the idea that conservation biological control should be directed toward the conservation of multiple species, with the aim of controlling not only pest, but also the self-regulation of the agroecosystem. The path that should be followed by the study and application of alternative hosts as a strategy of biological control by conservation is discussed.

Conclusion The wide diversity of non-pest insect species suggests an enormous potential for their exploitation as alternative hosts. The evaluation of host plants of specialized phytophagous species could improve biological control and reduce the risk of pests for crops. This strategy would partly fill the huge gap that exists in modern agroecosystems in terms of biological diversity.

Keywords Alternative hosts, Classical biological control, Conservation, Natural enemies

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Background

The current paradigm of agricultural pest management is based on attacking their effects and not necessarily the causes that originate them (Gliesman 2007; Altieri and Toledo 2011; Sarandón and Flores 2014). The large extensions of monocultures established with genetically homogeneous varieties are recognized as one of the main causes that originate pests (Winkler 2005; Cerritos et al. 2012; Heinemann et al. 2014). The genetic manipulation of crops for purely productive purposes has made modern varieties highly susceptible to pests and diseases (Rosenthal and Dirzo 1997; Altieri and Toledo 2011; He et al. 2021). To attack the problem, for the last 80 years enormous amounts of organo-synthetic pesticides have been used to control crop pests and diseases; but contradictorily, these products are one more cause of the development of agricultural pests (Settle et al. 1996; Altieri and Nicholls 2019). Far from recognizing it, mainstream agricultural research disregards that the pest problem has an ecological origin and should be resolved as such (Flint and Van den Bosch 2012).

For example, since ancient times, keeping crops free of weeds is a widely recognized practice that should not be questioned. What should be up for debate are the pros and cons of maintaining crops free of spontaneous vegetation (*e.g.*, weeds) for long periods of time, ignoring the advances made to determine critical periods of weed-crop competition (Rojas 1990; Vaz Pereira and Leyva-Galán 2015). This tool could allow the predictive use of herbicides instead of the preventive practices commonly used in world agriculture. Thus, residual herbicides such as atrazine and, more recently, glyphosate-resistant transgenic plant varieties promise to keep crops weed-free for long periods of time (Cortez-Madriral 2004; Heinemann et al. 2014; Mall et al. 2019). Of course, a natural response is not long in coming and so, in these highly disturbed agricultural systems, a strong imbalance between populations occurs. Finally, modern agroecosystems could be classified as “green deserts,” where high populations of few species (*e.g.*, pests) and low populations of numerous species (*e.g.*, entomophagous and pollinators) occur. Under these conditions, beneficial insects could be classified as ecologically extinct organisms (Letorneau 1998).

A previously proposed solution is to take advantage of the endless war that occurs in the world of insects (Carson 2010), a biological interaction coined in economic entomology as “biological pest control.” Biological control (BC) is a part of the natural regulation or homeostasis of nature, where some organisms must necessarily feed on others (*e.g.*, pests). In BC, the biotic regulators called natural enemies (NE) of pests include predators, parasitoids and entomopathogens (Van Lenteren 2012). Due to various circumstances (*e.g.*, use of pesticides),

these organisms are absent or in low populations in ecosystems, the organisms they regulate can increase their populations to levels that cause significant damage to the trophic level they affect (*e.g.*, vegetation). Although sudden outbreaks of phytophagous usually occur in natural ecosystems, they still return to their original levels, mainly due to the action of biotic regulatory factors (DeBach 1964). There is a consensus that NE conservation is the most important BC strategy, but it has also been the least heeded (Ehler 1998). The reason is simple: there is a strong contradiction between the modern agricultural paradigm and BC. To alleviate all the above, biological control by increase or augmentation has been implemented, consisting in a massive increase in the laboratory and subsequent release of NE, with the intention of drastically reducing the population of a pest below the economic threshold (Parrella et al. 1992). Once again, this strategy moves away from ecological principles, since only the effects are cured, not the causes. From this perspective, the potential of BC is immense and, to take advantage of it, the *in situ* conservation of NE is seen as the main way forward.

Conservation biological control (CBC) has solid ecological bases and, once in action, the results can be wonderful and surprising, both in the regulation of pests and beyond: in the balance of the agroecosystem. CBC is defined as all those actions aimed toward adapting the environment to conserve and increase a plurality of NE populations in agroecosystems (Ehler 1998; Gurr and You 2016). Various strategies have been proposed for the conservation of natural enemies, among others, protections against pesticides (Van Emden 2002) and habitat manipulation (Fiedler et al. 2008). As for this last one, multiple studies document the importance of establishing plants as an alternative food source (nectar and pollen) for NE (Fiedler and Landis 2007; Villalaín et al. 2016); less attention has been paid to the conservation of alternative hosts of NE.

This review analyzes and discusses the potential role that conservation of alternative hosts could play in improving biological control, understood as the conservation of NE *in situ*. Biological control is consistent with a world that no longer supports huge amounts of chemical pesticides and has responded with such developments as pest resistance and global climate change.

Main body

The pest problem in modern agriculture

Agriculture is a process developing in time and space and is made up of three components: the biological-ecological, the technological and the socioeconomic (Hernández-Xolocotzi 1988). Modern agriculture emphasizes the technological and economic factors, and subordinates to

them the biological–ecological component (Gliessman 2007). Thus, this conventional agricultural paradigm is characterized by large extensions of monocultures with highly productive varieties, but also (due to their genetic homogeneity) highly susceptible to pests and diseases (Heinemann et al. 2014; He et al. 2021). This means adapting the environment to the variety, instead of the variety to the environment, as proposed by sustainability (Sarandón 2014). To this end, an arsenal of organo-synthetic compounds has been developed for the control of pests, diseases and weeds (Doménech 2004; Pimentel 2009a). Even after strong criticism of the use of chemical control (Pimentel and Edwards 1982; Pimentel 2009b; Altieri and Toledo 2011; Pizano 2014), this method currently remains the predominant strategy of phytosanitary management worldwide (Doménech 2004; Pimentel 2009b). Agroecosystems managed in this way maintain a strong imbalance between their organisms, with high populations of few species (pests) and low populations of numerous species, *e.g.*, NE (Letorneau 1998).

In tritrophic terms, an explanation to the pest problem in modern agriculture could be posed as follows: consider, as an example, a corn monoculture in an agricultural valley. After its establishment (maize only), the phytophagous insects of the crop arrive and, later, with the first populations of phytophagous, come the biotic regulators, not before. Remembering this information is crucial for good pest management, since, in practice, decision makers first detect the pest and its damage, and are unlikely to focus on biotic regulators because, furthermore, they disregard them. Additionally, if the variable “economic threshold” (ET) is included, defined as the pest population level to which control measures must be applied in order to avoid economic damages (Metcalf and Luckmann 1990), the situation becomes more complicated, since generally no NE are considered (Shakya et al. 2010).

For example, in crops of high economic value such as strawberries and avocado in Mexico, the tolerable population levels of phytophagous are so low that pesticide applications become preventive (*i.e.*, scheduled) (“better safe than sorry”) instead of predictive. Under this panorama of intense and frequent disturbances, NE populations are hardly favored. In other words, in modern monocultures, the breeding of specialized phytophagous insects is favored, like what happens in a pasture used for raising cattle.

This is how the constant disturbance to NE populations due to the use of pesticides is another of the main causes of the appearance of agricultural pests (Settle et al. 1996; Winkler 2005; Cerritos et al. 2012; Flint and Van den Bosch 2012; Altieri and Nicholls 2019). Agroecosystems managed this way remain in a vicious circle that is

difficult to escape from if the paradigm is not changed (Altieri and Toledo 2011). For this reason, modern agroecosystems are naturally incompatible with CBC, which has plant diversification as its fundamental basis (Ehler 1998; Landis et al. 2000).

Far from recognizing all this, the simplification of agriculture continues and even tends to become more simplified, *e.g.*, greenhouses, macrotunnels, plastic mulches, massive use of residual herbicides, enhanced using herbicide-tolerant transgenic plants. These pesticides have been barely analyzed in the field of integrated pest management (Nentwing et al. 1998; Ruberson and Nemoto 1998); however, they are the most widely used products in the world (Abrol and Shankar 2012). Herbicides are precisely one of the main causes of modern agricultural simplification, and their impact on pests and NE is indisputable, generally negative for the latter (Nentwig et al. 1998; Norris and Kogan 2000; Cortez-Madriral 2004). Thus, crops are protected from competing with weeds for long periods of time (>6 months), this magnified by the increase in areas cultivated with herbicide-resistant transgenic varieties (Kumar et al. 2019).

Although the idea of plastic mulches is justified by a reduction in the use of herbicides, they also contribute to the ecological simplification of agroecosystems. The ecological consequences are predictable: a reduction in populations of pollinators, NE (Letorneau 1998) and its alternative hosts (Nentwig et al. 1998). Consequently, larger populations of phytophagous that will eventually become pests occur.

A proposed alternative is BC, through the massive rearing of NE and their subsequent release, called “augmentative” or “inundative” biological control (Parrella et al. 1992; Collier and Van Steenwyk 2004) having as main characteristic to emulate chemical control, with large populations of NE being released to drastically reduce the pest population (Mora-Aguilera et al. 2017). However, these practices are palliative measures since the same agricultural design is maintained (monoculture and use of pesticides). Again, the causes are ignored and only the effects are addressed (*e.g.*, the presence of pests). To summarize, inundative biological control as the only expression of BC presents at least two disadvantages. The first is that the environmental conditions of modern agroecosystems are inadequate for the survival and beneficial activity of NE (Collier and Van Steenwyk 2004) and, therefore, its use is not sustainable. The multiple releases eventually required suggest so. The second problem is that only a limited number of NE species have managed to multiply in the laboratory (Van Lenteren 2000) while most of them only occur in marginally disturbed natural environments (Parrella et al. 1992; Hoffmann and Frodsham 1993; Van Lenteren 2012). Additionally, inundative

biological control is usually more expensive than the use of insecticides (Parrella et al. 1992; Collier and Van Steenwyk 2004), so its use is limited to certain agroecosystems, mainly under greenhouses (Van Lenteren 2000).

The problem of pest management raised up to this point is valid only for extensive monocultures with a high use of organo-synthetic pesticides, where NE have become ecologically extinct species (Letourneau 1998). However, that rule can be changed in agroecosystems with favorable environments for beneficial organisms (e.g., NE); this is achieved through rational plant diversification, within or near the agroecosystems (Doutt and Nakata 1973; Landis et al. 2000; Jacas and Urbaneja 2010). Scientific literature abounds in examples showing agricultural diversification favors the presence of NE and the reduction of pests (Landis et al. 2000; Letourneau et al. 2011).

In the new agricultural designs, there would be an abundance of phytophagous insects innocuous to the crop (Nentwig et al. 1998) that would function as alternative hosts for NE. Under the new paradigm, consortia of parasitoids and predators could permanently coexist in the agroecosystem, even before the establishment of the crop and its colonization by pests. This way, a diversified agroecosystem with high and varied populations of entomofauna can contribute to the self-regulation of pests and, even more, to the self-regulation of the agroecosystem (Sarandón and Flores 2014).

The nature of the natural enemies of pests

Biological control rests on solid ecological bases, where predators, parasitoids and entomopathogens are the main actors (De Bach 1964). Knowledge of their biology–ecology can be the difference between the success and failure of BC programs (Mora-Aguilera et al. 2017). The term “natural enemy” is accepted to name the biotic regulators deliberately used in biological pest control (Van Lenteren 2012). However, in ecological terms, it should be recognized that these organisms are not natural enemies of anyone, nor are they exclusive to pests. The organisms in question only participate with a certain function within the trophic web. Although it may seem trivial, this has not always been understood by technicians dedicated to the implementation of BC in the field. Some have the idea that the use of biological control should emulate the use of pesticides, which seeks the drastic reduction of pest populations below the ET (Parrella et al. 1992); this is not in accordance with the ecological principles of BC nor the nature of NE. From a worldwide analysis, more than 50% of cases of inundative biological control have been unsuccessful, while only 20% of them have succeeded (Collier and Van Steenwyk 2004).

As living beings, the NE require favorable environments for their survival and ecological function. It is widely documented that, at certain stages in their development, entomophagous require plant-based food, for example, nectar and pollen (Fiedler and Landis 2007; Gurr et al. 2017; Amala and Shivalingaswamy 2018). Flowering plants and those with extra floral nectaries can provide such resources. Nectar and pollen are necessary foods for adult parasitoids and some predators (e.g., Syrphids); their absence from the agroecosystem implies a delay in the appearance of entomophagous insects and, consequently, a delay and failures in the self-regulation of populations in those agroecosystems (Doutt and Nakata 1973).

On the other hand, when talking about NE of a particular pest, the idea of exclusivity of said NE becomes rooted. Conversely, a wide diversity of NE requires alternative host and prey for their prevalence (Williams 1984; Pell et al. 2010; Hoddle and Pandey 2014; Cortez-Madrigal et al. 2022). It has even been documented that their absence could be the cause of multiple failures in the establishment of exotic NE (Raffa 1977; Gurr and Wratten 1999). It is precisely this characteristic that provides stability to ecosystems (Van Emden 2002; Van Lenteren 2012) and it should not be different in agroecosystems. However, the fact that entomophagous also have NE (intraguild predation or parasitism) has been a cause for concern for various researchers, in the sense that CBC could interfere with biological pest control (Griffiths et al. 2008). We support the idea that CBC should be considered as the fundamental basis of Integrated Pest Management (IPM), similar in importance to plant resistance. Agroecosystems with various degrees of rationally planned diversification should show greater resilience against attacks by phytophagous pests than a conventional monoculture (Gliessman 2007; Sarandón 2014). However, it should not be surprising that, even with the conservation of NE, there could eventually be disruptions to some insect species (e.g., pests) due to various causes, such as intraguild entomophagy, or even due to the effect of climate. This has been documented in citrus agroecosystems, when the *Asclepias curassavica* L. plant was included for the conservation of alternative hosts (Cortez-Madrigal et al. 2016).

Due to the nature of NE, the CBC approach must be understood as part of a redesign of agroecosystems, without deviating from the principles of IPM; that is, to continue with insect sampling (pest and NE) in order to decide more rationally whether to include control strategies or not. We think that it is more beneficial to include CBC as a basis for the design of agroecosystems, than to maintain a conventional monoculture. Once there,

we can continue with all the strategies that IPM implies, even the use of pesticides, if necessary.

Although inundative biological control has been successful in some types of agroecosystems, *e.g.*, greenhouses (Van Lenteren 2000), in most agroecosystems this has not always been the case (Collier and Van Steenwyk 2004). The false idea of exclusivity attributed to NE is one of the main reasons for some failures or deficiencies in inundative biological control in the field. An example is the egg parasitoid *Trichogramma* spp. (Hymenoptera: Trichogrammatidae). These insects have been widely used worldwide against lepidopteran pests; however, the wide range of hosts (Lepidoptera) that occur in the field could distract the parasitoid from the intended target pest (Carrillo-Sánchez 1985); therefore, the BC of the target pest may not be as expected. It must be recognized that many NE have a wide range of host and prey, which supports the idea that the conservation of alternative hosts favors that of NE.

Preserving phytophagous conserves natural enemies

Although the idea of conserving NE through alternative hosts is frequently mentioned and recommended in the scientific literature (Ehler 1998; Landis et al. 2000; Kapadia 2001; Wyckhuys et al. 2013; Gurr and You 2016), the studies developed and their application in the field it have not been in accordance with this idea. For the most part, these studies have remained only as basic knowledge and some possibilities of application (Valladares and Salvo 1999).

A pioneer study on the importance of conserving alternative hosts is the one carried out by Doult and Nakata (1973) with the egg parasitoid *Anagrus epos* Girault, 1911 (Hymenoptera: Mymaridae) and leafhoppers *Erythroneura elegantula* Osborn, 1928 (Homoptera: Cicadellidae) and *Dikrella californica* (Lawson, 1930) (Hemiptera: Cicadellidae) as hosts. The first species is a key grapevine pest, where *A. epos* is one of its main biotic regulators; however, its highest levels of parasitism (67%) only occur in vineyards close to wild *Rubus* spp. (Rosaceae), host of *D. californica*. As it happens, while *E. elegantula* hibernates as an adult, *D. californica* does so as an egg; thus, this species functions as an alternative host for *A. epos* during winter. In spring, the parasitoid migrates again toward the vine, which coincides with the first ovipositions of *E. elegantula*. This system allows for an early and efficient BC of *E. elegantula*. Comparatively, in vine crops far from *Rubus* plants, economic damages caused by this pest are more frequent.

Alternative host is a practical-utilitarian term, which means that NE are not exclusive to one insect species. It turns out that *Anagrus* spp. (Hymenoptera: Mymaridae) has several hosts. Thus, in California, plants of the

European plum *Prunus domestica* L. (Rosaceae) occur next to vine plantations. These plants host leafhopper *Edwardsiana prunicola* (Edwards, 1914) (Hemiptera: Cicadellidae), also a host of *Anagrus* spp. *Prunus* shelters contribute up to 34% of *Anagrus* colonization in vineyards; the distance from the shelters and the direction of the wind were correlated to the extent of colonization in vineyards. Thus, specimens of *Anagrus* were captured 15 m away from the shelters while against a headwind and at 100 m with a tailwind (Corbett and Rosenheim 1996).

Something similar was recorded in vineyards in Italy; in the North, leafhopper *Empoasca vitis* (Gothe, 1875) (Hemiptera: Cicadellidae) is an important vine pest, while in vineyards in the center of the country the insect is considered a secondary pest. Traditionally, this region presents vineyards surrounded by hedgerows that support parasitoid *Anagrus atomus* (Linnaeus, 1767) (Hymenoptera: Mymaridae), the main NE of *E. vitis*. One of the main species in hedgerows is *Rubus ulmifolius* Schott (Rosaceae), host of leafhopper *Ribautiana tenerima* (Herrich-Schaffer, 1834) (Hemiptera: Cicadellidae), alternative host of the parasitoid (Ponti et al. 2003).

A group of insects that has gone from being secondary to a primary pest as a result of the massive use of pesticides are the leafminers of the Agromyzidae family, mainly due to the reduction of their NE (Salvo and Valladares 2007). Under natural conditions or in insecticide-free environments, leafminers have a wide diversity of NE, particularly parasitoids that efficiently keep them under BC. Thus, Chen et al. (2003) recorded a parasitism of 10–20% in crops treated with insecticides, while in plots without treatment or with reduced use of pesticides, parasitism was 48.5–68.8%. Although some evidence shows polyphagia in leafminers (Valladares and Salvo 1999), there are also monophagous species (Parkman et al. 1989b; Van der Linden 1992; Valladares and Salvo 1999). In other cases, they only damage wild plants, so they are not a risk to crops (Parkman et al. 1989a, b; Valladares and Salvo 1999). On the contrary, guilds of parasitoids can share several species of leafminers (Chen et al. 2003; Salvo and Valladares 2007), so leafminers could be a good example of the use of alternative hosts.

For instance, the species *Liriomyza sativae* Blanchard, 1938 (Diptera: Agromyzidae) and *Liriomyza trifolii* (Burgess, 1880) (Diptera: Agromyzidae) are considered pests of the celery crop *Apium graveolens* L. (Apiaceae) in Florida. However, *L. sativae* was more abundant in castor bean *Ricinus communis* L. (Euphorbiaceae) plants. Most parasitoid species obtained (11) were from weed miners, which could also impact crop miners. Since castor grows spontaneously near the crop, its conservation has been

recommended to enhance the BC of leafminers in celery (Parkman et al. 1989a, b).

There is no doubt that wild plants are of fundamental importance in the BC of pest leafminers. Chen et al. (2003) recorded 11 species of parasitoids in weed miners, with parasitism levels of 83.7%. Comparatively, parasitism in crops fluctuated from 10 to 68.8%, and was closely related to the use of pesticides. In this context, some researchers have proposed the idea of using non-pest (specialized) leafminer species as alternative hosts for NE, so that leafminer BC in crops can be enhanced (Salvo and Valladares 2007).

Plant–miner–parasitoid open breeding is a possibility, where specialized-miner host plants are used for breeding and increasing parasitoids, so that these systems can be introduced into crops where leafminers are pests and thus increase their BC, e.g., by breeding the specialized leafminer *Phytomyza caulinaris* Hering, 1949 (Diptera: Agromyzidae) on *Ranunculus asiaticus* L. (Ranunculaceae) plants, it was possible to efficiently produce the parasitoids *Dacnusa sibirica* Telenga, 1935 (Hymenoptera: Braconidae), *Opius pallipes* Wesm., 1835 (Hymenoptera: Braconidae) and *Diglyphus isaea* (Walker, 1838) (Hymenoptera: Eulophidae). Through this system, it was possible to control the leafminer *Liriomyza huidobrensis* (Blanchard, 1926) (Diptera: Agromyzidae) in tomato crops under greenhouse conditions. Unlike inundative BC, this system promises to be cheaper (Van der Linden 1992).

The Coccinellidae family includes important predatory species of insects, which provide an important service in the natural regulation of pests and in biological control programs (Hoffmann and Frodsham 1993; Giorgi et al. 2009). However, the Epilachninae subfamily is made up of phytophagous species; some of them, pests of great economic importance, e.g., Mexican bean beetle *Epilachna varivestis* Mulsant, 1850 (Coleoptera: Coccinellidae) (Gordon 1975; King and Saunders 1984; Giorgi et al. 2009). Within this group there are also secondary (non-pest) phytophagous that feed on wild plants; they should even be recognized as important natural regulators of weeds (Newman et al. 1998). In Mexico, the species *Epilachna difficilis* Mulsant, 1850 (Coleoptera: Coccinellidae) has been recorded for several decades, but without mention of its host plant (Gordon 1975); it was not until 2008 that the plant *Bonplandia geminiflora* Cav. (Polemoniaceae) was recognized as a host for *E. difficilis*. Associated with this phytophagou, six species of predatory Hemiptera were recorded, namely: *Podisus congrex* (Stål, 1862) (Hemiptera: Pentatomidae), *Podisus brevispinus* Phillips, 1982 (Hemiptera: Pentatomidae), *Oplomus dichrous* (Herrich-Schaeffer, 1838) (Hemiptera: Pentatomidae), *Oplomus pulcher* Dallas, 1851 (Hemiptera:

Pentatomidae), *Pselliopus nigropictus* Champion, 1899 (Hemiptera: Reduviidae), and *Rocconota* sp. (Hemiptera: Reduviidae) (García-Segura et al. 2017).

Various species of the subfamily Asopinae (Pentatomidae) are important NE of Coleoptera and Lepidoptera pests (Brailovsky and Mayorga 1994; Sant'Ana et al. 1997). Given the high specificity and ecological plasticity of *E. difficilis* and its host plant, it has been suggested that this insect be used as alternative prey for predators, which could enhance the BC of important agricultural pests, e.g., *E. varivestis* in beans (García-Segura et al. 2017). Apparently, *E. difficilis* is the main phytophagou of *B. geminiflora* and no potential pests or diseases were recorded for crops. Among others, this is one of the main requirements for a plant in order to be considered a candidate for the conservation of NE alternative hosts (Van der Linden 1992).

In Spain, at least two examples of conservation of alternative hosts in citrus crops are mentioned. The first one is based on the plant *Oxalis pes-caprae* L. (Oxalidaceae), host of the mite *Petrobia harti* (Ewing, 1909) (Acari: Tetranychidae), alternative prey for predators of the Phytoseiidae family. They also feed on the mites *Panonychus citri* (McGregor, 1916) (Trombidiformes: Tetranychidae) and *Tetranychus urticae* Koch, 1836 (Trombidiformes: Tetranychidae), important citrus pests. The second example is the “laurel rose” plant, *Nerium oleander* L. (Apocynaceae), which establishes itself at the edges of citrus groves. This shrub hosts the aphid *Aphis nerii* Boyer de Fonscolombe, 1841 (Hemiptera: Aphididae), a species harmless to orange trees, but a host for parasitoids that eventually impact populations of pest aphids in citrus (Jacas and Urbaneja 2010).

The use of alternative hosts can also be useful in classical biological control. The gypsy moth *Lymantria dispar* (Linnaeus, 1758) (Lepidoptera: Erebyidae) is a major, exotic forest pest in the USA. Two of its parent NE are parasitoids *Apanteles liparidis* (Bouche, 1834) (Hymenoptera: Braconidae) and *Apanteles porthetriae* Muesebeck 1928 (Hymenoptera: Braconidae). Multiple attempts to achieve their establishment have failed, presumably due to the absence of alternative hosts to sustain the parasitoids in the absence of *L. dispar*. After evaluating more than 40 species of native Lepidoptera as alternative hosts, only three were parasitized by *A. porthetriae*, but *Orgyia leucostigma* (Smith, 1797) (Lepidoptera: Lymantriidae) was the most acceptable host. These alternative hosts would allow the exotic parasitoid to be reared in a laboratory for subsequent mass releases to control the afore mentioned pest (Raffa 1977).

Although the original definition of the CBC implies the conservation of a plurality of “natural enemies,” most studies have been directed toward single species of

phytophagous–NE. We support the idea that CBC should be directed toward the conservation of multiple NE species, with the aim of controlling not only pest species, but also the self-regulation of agroecosystem populations (Settle et al. 1996). The focus on the conservation of alternative hosts should also center on this; however, few studies have been conducted with multiple species of alternative hosts.

For example, a group of insects that has received little attention in agroecosystems is the Order Collembola. Springtails can play an important beneficial role, in this case, as alternative hosts for predators. For instance, in agroecosystems in England, various species of springtails functioned as the major alternative prey source for spiders of the family Linyphiidae. Thus, these insects helped retain and increase important populations of spiders for the regulation of aphids in cultivated fields (Agusti et al. 2003).

A special agroecosystem is the cultivation of inundated rice in some regions of tropical Asia. Important populations of insects occur in these systems, among others, chironomids, culicids and springtails that feed on detritus and plankton. During the first period of cultivation, they function as alternative prey for NE and, when their populations are reduced, the NE impact phytophagous rice insects, which keeps them below the economic threshold. The increase in organic matter favored the increase in populations of detritivorous insects, and eventually the populations of NE (Settle et al. 1996).

Of the plant banks used for the conservation of alternative hosts, monocots have been the most used (41%) (Huang et al. 2011). For example, potato crops intercropped with barley maintained lower populations of pest aphids than those established in monoculture. The populations of wingless and winged aphids were up to three times higher in the monoculture than in those intercropped with barley. This is arguably due to the presence of parasitoids and predators in barley aphids (alternative hosts) that later migrated to the potato crop (Nakahira et al. 2012).

Although the previous studies demonstrate the potential in the use of alternative hosts, some presume an adverse or doubtful effect in their application in pest BC. For example, in California, the plant *Polygonum aviculare* L. (Polygonaceae) hosts the specialized aphid *Aphis avicularis* Hille Ris Lambers, 1931 (Hemiptera: Aphididae) which may eventually function as alternative prey for various species of Coccinellids. Although the plant is an important floral resource for NE (29 taxa), it is argued that the presence of alternative prey on the plant could discourage BC in crops. However, it is also proposed that its conservation could be a source of predators that could colonize agricultural fields (Bugg et al. 1987).

In other cases, additional vegetation in the agroecosystems could act as a source, but also as a sink of NE, which will depend on the spatial and temporal availability of resources. For example, the broad bean, *Vicia faba* L. (Fabaceae), hosts aphids *Aphis fabae* Scopoli, 1763 (Hemiptera: Aphididae) and *Acyrtosiphon pisum* (Harris, 1776) (Hemiptera: Aphididae), which can function as alternative hosts for NE. When intercropped with the hop crop *Humulus lupulus* L. (Cannabaceae), it favored the attraction and increase in various species of aphid predators; however, the presence of the broad bean did not reduce the populations of the hop pest aphid *Phorodon humuli* Schrank, 1801 (Hemiptera: Aphididae). The explanation was that these NE prefer to oviposit on the broad bean, which reduced their predatory capacity on the hops. It was not until after bean harvest that predators dispersed and increased on the primary crop (Goller et al. 1997).

Toward the complexity of agroecosystems: conservation of multiple alternative hosts

Until now, most studies on alternative hosts have focused on single species of phytophagous–NE, and little attention has been paid to the plant–phytophagous relationship. It is important to remember that plant–herbivore coevolution has led plants to develop morphological and biochemical defense mechanisms that limit herbivory; but also, it encourages some phytophagous to overcome this resistance and adapt to some plant species (specialist herbivores; Coley et al. 1985). Such is the case of *Asclepias curassavica* L. (Apocynaceae), a plant of American origin with a high content of poisonous cardenolides (Dobler et al. 1998). Like the related species *N. oleander*, *A. curassavica* hosts the aphid *A. nerii* (Hemiptera: Aphididae) and other specialist phytophagous, such as the monarch butterfly, *Danaus plexippus* (Linnaeus, 1758) (Lepidoptera: Nymphalidae), a complex of stink bug species (Hemiptera: Lygaeidae), the hairy worm, *Euchaetes antica* (Walker, 1856) (Lepidoptera: Erebiidae), the leafminer *Liriomyza asclepiadis* Spencer, 1969 (Diptera: Agromyzidae), the beetle *Tetraopes discoideus* LeConte, 1858 (Coleoptera: Cerambycidae) and the mite *Eotetranychus typhae* Tuttle, Baker and Abbatiello, 1976 (Trombidiformes: Tetranychidae; Cortez-Madriral et al. 2016). Recently, the scale *Planchonia stentae* (Brain, 1920) (Hemiptera: Asterolecaniidae) (Cortez-Madriral et al. 2020), of exotic origin, and a mite from the family Eriophyidae, still unidentified, have been added to the list.

More than 21 NE species associated with phytophagous were documented; among them, the parasitoids *Trichogramma pretiosum* Riley, 1879 (Hymenoptera: Trichogrammatidae) in *D. plexippus* eggs, and *Lysiphlebus*

testaceipes (Cresson, 1880) (Hymenoptera: Braconidae) in *A. nerii* stand out. Associated with the aphid, various predators of the Coccinellidae and Syrphidae families, among others, are included (Cortez-Madrigo et al. 2016). In addition, species of Cecidomyiidae (Diptera) and mites of the family Phytoseiidae are included as mite predators (unpublished data). The non-exclusivity of the aforementioned NE species suggests their importance in the regulation of a wide diversity of pests, e.g., *T. pretiosum* is one of the main species used in inundative BC against lepidopteran pests (Collier and Van Steenwyk 2004; Devi et al. 2020).

In order to know the potential of *A. curassavica* and its specialized phytophages as alternative hosts in the conservation of NE and in the BC of pests, a study was established in a Persian lemon plantation, *Citrus × latifolia* (Yu. Tanaka) (Rutaceae), with and without the inclusion of *A. curassavica*. In the absence of insecticides, low populations of *Toxoptera aurantii* Boyer de Fonscolombe, 1841 (Hemiptera: Aphididae), *Aphis spiraeicola* Patch, 1914 (Hemiptera: Aphididae), the Asian psyllid *Diaphorina citri* Kuwayama, 1907 (Hemiptera: Liviidae) and leafminer *Phyllocnistis citrella* (Stainton, 1856) (Lepidoptera: Gracillariidae) were recorded. During the first half of the year, the low pest populations did not allow us to distinguish a clear effect of *A. curassavica* on the pest and NE populations. On the other hand, during the second semester, significant differences were registered in the populations of aphids and psyllids between the two systems. In crops with *Asclepias*, there was a 46.3% reduction in aphid populations, while psyllid populations increased by 77% (Godoy-Ceja and Cortez-Madrigo 2018).

The suggested explanation is that both, psyllids and aphids, compete for the same niche (vegetative shoots). The presence of *A. nerii* in *Asclepias* as an alternative host for the parasitoid *L. testaceipes* favored the BC of aphids in citrus, as has been reported for *N. oleander* in citrus from Spain (Jacas and Urbaneja 2010). Thus, the availability of empty niches was greater in the presence of *Asclepias*; these niches allowed a greater colonization by the insect subject to less biocontrol; in this case, the psyllid. Unlike the first half, the diversity of NE of *D. citri* was lower in the second semester (hibernal stage) and, although its parasitoid *Tamarixia radiata* (Waterson, 1922) (Hymenoptera: Eulophidae) was present, its low populations were insufficient to reduce the pest. Even so, the inclusion of *A. curassavica* in the citrus plantation favored the significant reduction of insecticides during the study period, which was reflected in a greater development and production (Godoy-Ceja and Cortez-Madrigo 2018).

The result of the previous study suggests that the conservation of alternative hosts involves complex trophic relationships, e.g., phytophagous–plant, NE–phytophagous, phytophagous–phytophagous, NE–NE, as well as climatic factors (Mora-Aguilera et al. 2017). Future studies should aim to have a better understanding of these relationships as well as the pros and cons in pest BC. In the end, the conservation of alternative hosts should be seen as one more IPM tool, and not as a definitive solution to the pest problem, so basic tools such as sampling should be maintained; host plants for specialized phytophagous could also be used as auxiliary “sentinel” plants in NE sampling.

Various species of Lepidoptera constitute some of the most important agricultural pests (King and Saunders 1984); as an alternative to the use of chemical compounds, the inundative release of NE for their control stands out. One of the main groups used are the egg parasitoids of the Family Trichogrammatidae (Cano-Vásquez 2001); the species *T. pretiosum* recorded in *D. plexippus* eggs in *A. curassavica* could be an interesting innovation in CBC. This species recorded parasitism levels of up to 100%, with multiple individuals per egg (Cortez-Madrigo et al. 2014). The frequency of *T. pretiosum* in monarch butterfly eggs is proposed as the fundamental cause of the low populations of lepidopteran pests in citrus (Godoy-Ceja and Cortez-Madrigo 2018), strawberry (Romero 2021) and tomato (unpublished data), where it has been evaluated.

A criticism of CBC is the poor understanding of its economic feasibility in highly technical crops (Cullen et al. 2008; Griffiths et al. 2008). In this regard, the inclusion of *A. curassavica* and *Lobularia maritima* L. (Brassicaceae) in the incidence of pests in organic strawberry from “Valle de Zamora,” Michoacán, México was evaluated. In all cases that included accompanying plants, pest populations were lower than a conventional system with pesticide application. For example, the adult and egg populations of the *T. urticae* mite were up to 14 times lower in the milkweed system than in conventional strawberry cultivation. This coincided with the highest number of mite predators, although the Phytoseiidae family explained the highest correlation ($r = -0.96$) with the phytophagous. This low population of pests was reflected in production and in the benefit/cost ratio (B/C). It was higher in the systems with accompanying plants, although *A. curassavica* stood out with a B/C ratio of 38/1 while, in the conventional system, it was 5.6/1 (Romero 2021). It has been known for some time that the use of organo-synthetic pesticides reduces populations of predatory mites (Phytoseiidae) and consequently favors the increase of pest mites (Nyrop et al. 1998).

Perspectives

Various strategies have been proposed for the conservation of NE (De Bach 1964; Kehrlí et al. 2004; Huang et al. 2011), but perhaps one of the least heeded is the conservation of alternative hosts, even though it is widely reported in the scientific literature (Ehler 1998; Van Emden 2002; Gurr et al. 2017; Altieri and Nicholls 2019). From 1973 to 2021, only 21 studies emphasizing the importance of phytophagous species as alternative hosts of NE were recorded. A higher percentage (76%) followed an atomistic approach; that is, studies with single NE–host species focused on the control of a specific pest or, at most, with groups of parasitoids and hosts of similar groups, *e.g.*, aphid parasitoids. This even though insects are the most numerous and diverse group of organisms on the planet (Stork 2018). However, only 5000–10,000 species are considered economically important pests (Hoffmann and Frodsham 1993; Pimentel 2009a; Van Lenteren 2012), which barely represents 1% of the total estimated insect species [($> 1,000,000$) (Stork 2018)]. The obligatory question should be: What role do most non-pest insect species play? In addition to the widely documented value of NE and pollinators (Altieri et al. 2015), there is increasing evidence of the benefits that numerous insect species provide to human development (Klein 2022).

Within this miniature universe, there are phytophagous insects not valued as beneficial since they play a double role; on the one hand, in the regulation of native weeds (Newman et al. 1998), and on the other, as alternative hosts of NE (Nentwig et al. 1998). Most of the orders Lepidoptera and Homoptera (= Hemiptera) are phytophagous (Triplehorn et al. 2005), although not necessarily pests. *E.g.*, out of 86 species of aphids recorded on weed edges, 58% were non-pest monophagous species, 42% polyphagous, and only five species were crop pests. Similarly, most of the Coleoptera registered corresponded to species innocuous to crops (Nentwig et al. 1998). This suggests an enormous potential in the use of alternative hosts in enhancing biological control, so this important CBC strategy should be reassessed in the future.

Some researchers argue that the lack of studies demonstrating the economic validity of CBC has been one of the main reasons farmers disregard conservation strategies (Cullen et al. 2008; Jonsson et al. 2008). Others see intraguild entomophagy as a limitation for biological pest control (Shakya et al. 2010). This analysis tries to adjust CBC to the modern agricultural paradigm, and not the other way around, as suggested by ecological theory. Some also forget that agriculture did not arise with the green revolution; on the contrary, there are multiple agricultural paradigms around the world where these

arguments are not valid; for example, traditional Mexican agriculture (Hernández-Xolocotzi 1988).

One path would be to demonstrate, through scientific evidence, that using CBC as the basis of IPM can provide important economic benefits for any type of agriculture; for example, with a more lax ET (Shakya et al. 2010). In addition to this, it could also be demonstrated that the occurrence of intraguild entomophagy is offset by the benefits that CBC can provide in the regulation, not of single pests, but entomofauna in general and beyond, in the regulation of spontaneous vegetation, where secondary phytophagous play an important role (Settle et al. 1996; Newman et al. 1998).

A second path for CBC is to demonstrate that traditional agriculture has what modern agriculture lacks: a greater diversity of NE. As we begin to understand how traditional agricultural practices influence NE conservation, not only will traditional agricultural systems be reevaluated, but also some of these practices could be exported to more disturbed agricultural systems.

Countries like Mexico have agricultural systems based on smallholdings (*i.e.*, small property), where a variety of agricultural systems can be identified throughout the country, in accordance with the prevailing edaphic-climatic and cultural conditions (Hernández-Xolocotzi 1988). They are based on the use of native varieties, adapted to local conditions and, presumably tolerant to pests and diseases (Winkler 2005; Nord et al. 2020). In these environments, an ancient agriculture known as “milpa” is practiced, where corn is diversified with beans, broad beans, squash, tomatoes, among others. These diversified systems are presumably more resilient to the incidence of pests and disease than monocultures with high use of agrochemicals, which is suggested to be largely due to the conservation of ecologically functional NE (Letourneau 1987; Trujillo-Arriaga and Altieri 1990); that is, these agricultural systems have an empirical CBC (Trujillo-Arriaga 1992).

Small Mexican agricultural areas frequently maintain native plant species close to their crops, *e.g.*, mesquite, *Prosopis* spp. y guamúchil, *Pithecellobium dulce* (Roxb.) (Fabaceae); *Senecio salignus* Kunth (Asteraceae); as well as live fences composed of species of *Bursera* spp., (Burseraceae); *Gliricidia* spp. (Fabaceae); but also, stone fences among other elements that could contribute to the conservation of NE. However, farmers and technicians are not always aware of the benefits derived from these agricultural practices. In any case, in this type of agriculture, it could be less challenging to implement CBC programs, as has been suggested in other countries with similar agricultural areas (Van Emden 2002; Ponti et al. 2003; Wyckhuys et al. 2013). If these traditional practices are lost, it will be more difficult to implement

conservation strategies. To keep a scientific record of these traditional practices and convey the knowledge that they can aid the conservation of NE, and, consequently, the biological control of pests has a fundamental importance for the future of CBC.

A third path CBC can advance through is precisely the weaknesses of modern agricultural systems; among others, the resistance of pests, pathogens and weeds to pesticides, and the use of varieties not adapted to the environment, resulting in environmental and health problems. As a result, in recent decades there has been a greater social awareness of the risks of the massive use of pesticides in agriculture and—the icing on the cake—global climate change. A first outcome is the prohibition on various pesticides, *e.g.*, methyl bromide (Meadows 2013), and glyphosate (Fogliatto et al. 2020). Consequently, greater efforts have been made in the search for sustainable strategies for phytosanitary management, *e.g.*, CBC, as more and more attention has been shown in countries that were the cradle of the green revolution, such as the USA (Fiedler et al. 2008).

Achieving greater acceptance of the conservation of alternative hosts as a fundamental strategy of CBC necessarily has to do with the modification of other widely used phytosanitary technologies, *e.g.*, pesticide application techniques. For instance, the spraying technique is the main strategy for the application of pesticides, even though it has been pointed out that it is the least efficient (Bateman and Chapple 2001); it has been estimated that only 1% of insecticide sprays reach the target insect (Pimentel and Edwards 1982) while the rest can negatively impact nontarget organisms (alternative hosts). Also, the “management” of weeds bets on preventive application, where the crop is practically kept free of weeds throughout the cycle (Heinemann et al. 2014; Mall et al. 2019). In this way, the two main causes of the appearance of pests are maintained: monoculture and pesticides.

Until now, the strategy followed in studies of alternative hosts has focused on the selection of unique host–NE–pest species, without including the phytophagous–plant relationship. Using this strategy, it would be impossible to advance the search for individual alternative hosts. On the contrary, it would be more logical and practical to evaluate groups of plants that support specialist phytophagous insects without constituting a problem for crops. There are countless plants that harbor this type of insect and that could be used in CBC programs. The Apocynaceae family, for example, has more than 300 plant species, many endemics to the American continent (Juárez-Jaimes et al. 2007). In addition to *A. curassavica*, *A. angustifolia* Schweigg, *A. linaria* Cav. (Apocynaceae) and *Mandevilla foliosa* (Muell.Arg)

Hemsl. (Apocynaceae) have been recorded in Mexico. But there are also species with food potential, such as “chicuipos” *Gonolobus pectinatus* Brandegees and “chiche de burra” *Funastrum pannosum* Schltr. (Apocynaceae). All of them host specialized phytophagous, among others, the aphid *A. nerii*.

If we choose to work with and not against nature, CBC using alternative hosts has an important role to play in the fight we maintain against pest insects. Insects and humans have probably competed for food since the invention of agriculture and in this sense, we must recognize that they have a vast advantage over us: insects have evolved for more than 300 million years, which has allowed them to adapt and survive in the most adverse conditions, including chemically synthesized pesticides. Compared to this, man is barely a newcomer to the planet (DeLong 1960), but what distinguishes us from other animals is our ability to reason. If we follow the same path hitherto chosen for food production, it is almost certain that insects will be the winners.

Conclusions

Even though there are relatively few documented studies on the conservation of alternative hosts of natural enemies, the wide diversity of non-pest insect species suggests an enormous potential for their use in pest management. The evaluation and use of host plants for specialized phytophagous could improve biological control (insects and weeds) and reduce the risk of pests for crops. This strategy would partly fill the enormous gap that exists in agroecosystems in terms of biodiversity.

Abbreviations

BC	Biological control
CBC	Conservation biological control
ET	Economic threshold
IPM	Integrated pest management
NE	Natural enemies

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