

# Problems Inherent to Augmentation of Natural Enemies in Open Agriculture

JP MICHAUD

Dept of Entomology, Kansas State Univ, Hays, KS, USA

## Keywords

Conservation biological control, ecological pest management, habitat manipulation, parasitoids, predators, sustainable agriculture

## Correspondence

JP Michaud, Dept of Entomology, Kansas State Univ, 1232 240th Ave, Hays, KS67601, USA; [jpmi@ksu.edu](mailto:jpmi@ksu.edu)

Edited by Eliana MG Fontes – Embrapa/CENARGEN

Received 31 October 2017 and accepted 10 January 2018

Published online: 25 January 2018

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## Abstract

Augmentation biological control has successfully replaced a lot of insecticide use in ‘closed system’ agriculture (e.g., greenhouses). The profitable commercialization of biocontrol agents in greenhouses has created an incentive to expand markets for mass-reared beneficial insects into open agricultural systems, often without sufficient scientific justification. However, the semi-contained nature of greenhouse culture is often critical to the success of augmentation and can serve to mask potential pitfalls and intrinsic limitations of this approach in open systems. Factors contributing to greenhouse successes include the reduced biological diversity of contained agroecosystems, the prevention of agent dispersal, the ability to maintain environmental conditions within a range favorable for the agent, the exclusion of competitors and natural enemies of the agent that might otherwise diminish its efficacy, and the absence of alternative prey/hosts that could divert predation/parasitism from the target pest. There are also problems arising from collection of source material from locally adapted populations, and the inadvertent imposition of artificial selection in the course of laboratory rearing. Besides highlighting these pitfalls, this paper aims to encourage more consideration of conservation approaches prior to investment in augmentation programs which entice farmers into perpetual cycles of ‘rear and release.’ I argue that although augmentation can benefit agriculture whenever it replaces pesticide applications, it does not constitute an ecologically sustainable solution because it requires continued inputs, and it can distract research attention away from more sustainable objectives. Sustainable biological control is best achieved through modifications to cultural practices that increasingly ‘naturalize’ agroecosystems, thus facilitating the natural recruitment and persistence of beneficial arthropod fauna, combined with habitat management geared to increasing overall plant and arthropod diversity in the agroecosystem.

## Introduction

The integrated control concept developed by Stern *et al* (1959) led to the development and successful implementation of integrated pest management (IPM) as a scientifically based, and economically justified, approach to controlling pests in agriculture. IPM was a twentieth century landmark of applied ecology that yielded many benefits for agriculture and society at large, primarily by recognizing and utilizing

the actions of beneficial species in pest control strategies and diminishing reliance on toxic pesticides with broad-spectrum activity. Although IPM strategies are preferable to chemically dependent alternatives, they are not truly sustainable when they require continued inputs in order to function. The terms “environmental pest management” (Coll & Wajnberg 2017), or “ecological pest management” (Shennan *et al* 2005), have been proposed to refer to truly sustainable solutions that, once integrated into an

agricultural system, will continue to function without further human intervention. Thus, ecological pest management embodies a naturalistic philosophy of agroecosystem management that can be extended beyond pest control to include weed control and soil health management (e.g., Meng *et al* 2016).

In its best iterations, the classical form of biological control (BC), the introduction of an exotic, but highly coadapted, natural enemy of the pest, can meet the criteria of an ecological solution. However, history suggests only a small fraction of invasive pests, typically those with one or two highly specific and effective natural enemies, can be successfully targeted with this approach (Michaud 2002a, Cock *et al* 2016). I believe a broader range of agricultural and environmental benefits have been achieved through conservation BC, where cultural modifications bring about permanent reductions in pest abundance with the assistance of naturally occurring beneficial species. Augmentation BC is not an ecological solution, because it does not move agriculture closer to becoming a self-sustaining ecosystem that naturally retains pests below economic thresholds without continued human intervention. Some of the intrinsic impediments to augmentation have been previously itemized (Collier & Van Steenwyk 2004), although by no means exhaustively. The augmentation approach also entails certain fundamental and inherent pitfalls likely to be more problematic in field crops than in closed systems, including genetic and epigenetic effects arising from mass-rearing procedures, and ecological mismatches between source populations and release sites. Whereas continuous releases of beneficial species may be an attractive proposition for those commercially producing them, more sustainable solutions would provide greater benefits to producers. Although often incentivized by government agencies, facilities for mass-rearing beneficial insects are increasingly operated by private companies, raising the specter of profit-driven, rather than science-driven, applications as these companies seek to expand their markets. Whereas the promotion of augmentation BC programs to agricultural producers as a desirable alternative to pesticides is a laudable enterprise, we should not set the bar too low and settle for partial solutions. The ephemeral nature of annual crops can present impediments to conservation BC, especially in ecologically depauperate landscapes, which may justify inoculative releases of key natural enemies, but the greater permanence of perennial cultures should facilitate more permanent BC solutions. Augmentation BC in open systems is perhaps best considered an interim measure—when it can serve as an economically viable alternative to insecticide applications—but it is not a final solution because it locks farmers into a perpetual cycle of purchasing and releasing insects. And if the crop requires continued releases of beneficial insects, then the agroecosystem has intrinsic ecological deficiencies that should be identified.

Unfortunately, these deficiencies will not be addressed if we claim success and walk away every time we replace a cycle of insecticide dependency with a cycle of rear and release.

#### *Species identity versus population differentiation*

Species identity is often the sole justification for developing a rear-and-release program. Once a predator or parasitoid is determined to be an effective natural enemy of a particular pest, it is axiomatically assumed that augmentation of that species will improve control of the pest. However, taxonomic identity alone provides no information on the extent to which populations may be regionally specialized in biology and behavior. Critical attributes such as foraging behavior, prey range, and plant or habitat preferences may all exhibit geographic variation among local populations of a given species. Commercial mass-rearing operations often collect source material from the most convenient locations, and then distribute their product to customers over a much wider geographic area, often without consideration of significant ecological disparities among locally adapted populations. Such disparities can result in augmentation of arthropods that are ecologically mismatched to particular regions or target pests, even though the same species occurs naturally at the release site.

Many species of Coccinellidae are quite easy to rear on a diet of lepidopteran eggs, usually *Ephestia kuehniella* Zeller or *Sitotroga cerealella* (Oliver), making them popular candidates for augmentation programs. However, their patterns of prey use, and their ability to reproduce and develop on particular prey species, can vary greatly among different populations of the same coccinellid species (Michaud 2012). A prime example of the misguided use of augmentation that has persisted for more than a century is the widespread redistribution of *Hippodamia convergens* Guerin-Meneville across North America (e.g., Fink 1915, Hatch & Tanasse 1948, Randolph *et al* 2002). The beetles are easily harvested in large numbers from overwintering sites in the Sierra Nevada mountains of California, but post-hibernation they have low reproductive potential, combined with a strong tendency for immediate dispersal (Obrycki & Kring 1998, O'Neil *et al* 1998). Pre-release conditioning treatments have been tested to improve their retention at release sites (Starks *et al* 1975, Driestadt & Flint 1996), usually to little effect. However, regional populations of *H. convergens* differ considerably in their dietary habits, nutritional requirements, foraging behavior, and diapause and hibernation habits that render them unsuited to function as biocontrol agents, or even survive, in many other parts of their range. Do we really expect that *H. convergens* adapted to central California will prey more effectively on citrus pests in Florida than their Florida-adapted counterparts, even if they are willing to consume them (Qureshi & Stansly 2011)? There are also the

potentially adverse consequences of genetic admixture with local populations (Sethuraman *et al* 2015), to say nothing about the potential impact of mass-harvesting on local populations. Indeed, the potential risk of augmented insects negatively impacting naturally occurring populations of the same or other beneficial species is rarely explored, despite the glaring example set by years of *Harmonia axyridis* Pallas augmentation in Europe (Camacho-Cervantes *et al* 2017). For example, when *H. convergens* from the Sierra Nevada are redistributed geographically, so are their parasitoids and diseases (O'Neil *et al* 1998, Bjornsen 2008), and beetles at release sites may well be more vulnerable to these than are beetles endemic to collection locality. If there is potential for *H. convergens* to control a particular pest in a particular agroecosystem within its geographic range, the goal should be to understand the factors that are limiting the natural response of the local population within that agroecosystem, rather than releasing beetles collected from remote, non-adapted populations. There is also a negative impact on public perceptions of biological control more broadly whenever such poorly conceived augmentation programs fail to deliver results.

#### *Domestication phenomena*

The rearing of successive generations of arthropods in captivity inevitably exerts inadvertent and artificial selection on a broad suite of traits, both biological and behavioral, leading to various domestication phenomena, many of which can be quite cryptic (e.g., Sepulveda *et al* 2017). These problems are inevitably exacerbated when large numbers of insects are commercially produced in confined spaces where many elements of the natural environment are lacking. Mass-produced arthropods are commonly reared on factitious diets, which can lead to changes in behavioral responses to the target pest, potentially diminishing their efficacy. These problems are often implicitly recognized by various efforts to 'condition' natural enemies prior to release with learning experiences that involve exposure to cues originating from either the target pest or its host plant complex (e.g., Kruidhof *et al* 2014, Giunti *et al* 2015, 2016). Plant-specific responses can be a key first step in host-finding by both predators and parasitoids (Segura *et al* 2016), yet many species are reared in the absence of any plant material for the sake of expediency, which can lead to loss of appropriate plant responses. Plant responses can also be key to accessing supplementary or alternative foods that can be critical for sustaining arthropods in the release environment, foods that are typically provided via artificial delivery systems in mass cultures.

An illustrative example is provided by lacewings (Chrysopidae), many species of which are commercially produced. On the High Plains of the USA, adult *Chrysoperla carnea* Stephens commonly utilize extrafloral nectar from

wild sunflowers, *Helianthus annuus* L., to stave off dehydration during hot, dry periods. This behavior creates a potential route of exposure to systemic insecticides when these are used as seed treatments on commercial sunflowers (Gontijo *et al* 2014). Our attempts to use commercially supplied *C. carnea* in seed treatment bioassays failed because the adults did not respond to sunflower plants and desiccated without provision of water on a cotton wick. On closer examination, even the larvae displayed abnormal behavior in comparison to feral individuals; they were less active in exploring their arenas, less photo-negative, and less likely to seek shelter in concealed locations, a behavior presumably important for avoiding intraguild predation. Mass-rearing of lacewings requires the isolation of the larvae in cells to prevent cannibalism, and the regular provisioning of food that requires no active searching to discover. These conditions eliminate the selective forces likely needed to maintain normal larval foraging and defensive behaviors, leading to their eventual diminution, and potentially negative effects on both the biocontrol efficacy of these insects, and their odds of survival under more natural conditions. No matter how carefully protocols are crafted, it is biologically impossible to rear continuous generations of insects in captivity without relaxing natural selective forces and imposing artificial ones; eventually, organisms become domesticated. Despite well-developed methodology for "quality control" of *Trichogramma* spp. (Bigler 1994), problems remain widespread in commercially supplied wasps (Schmidt *et al* 2003). It would be difficult to determine how often, or how many, feral individuals would need to be introduced to a culture to prevent or ameliorate domestication phenomena in any particular species.

#### *Lessons from Trichogramma*

Egg parasitoids of the Trichogrammatidae are perhaps the insect group most intrinsically suited for large-scale augmentation programs. Cheaply and easily produced in large numbers, their efficacy is aided by the fact that they kill the host in its earliest life stage, before any plant feeding occurs. The augmentation of various *Trichogramma* spp. against stalk-boring lepidopteran pests has successfully replaced insecticide applications over large acreages of field and cereal crops around the world for many years (Li 1994, van Lenteren & Bueno 2003). Although these releases continue in many developing countries, their use has decreased substantially in North America since the advent of transgenic *Bt* crops that are essentially immune to such pests. However, inundation with *Trichogramma ostrinae* (Pang and Chen) against the European corn borer, *Ostrinia nubilalis* Hubner (Lepidoptera: Pyralidae) remains an option in processed sweet corn where use of *Bt* traits is considered unacceptable to consumers (Gagnon *et al* 2017). The basic biology of this

group, combined with many decades of refinement in rearing procedures (Flanders 1929), has enabled large numbers to be produced very cheaply, and has facilitated inundative releases, where the agroecosystem can be flooded with densities of wasps orders of magnitude higher than might naturally occur (Smith 1994). However, other programs were developed to carefully time ‘inoculative’ releases of smaller numbers of wasps that would then multiply on either the pest or alternative hosts, and continue to provide seasonal-long control in the agroecosystem, or even in adjacent ones (Li 1994). To the extent that inoculative releases can be effective, they are inherently more sustainable than other forms of augmentation BC, and a worthwhile improvement over inundation. However, the ecological requirement for survival and reproduction of multiple generations following a single release means that success will ultimately depend on much the same conditions that are required for ‘natural’ (unassisted) BC: the local availability of resources that support adult feeding as well as immature development, and a crop production cycle free of broad-spectrum insecticides. This was usually not possible in the case of programs against *O. nubilalis* in field and sweet corn (Hawlitzky & Voegele 1991), but see Wright *et al* (2002). Despite some early claims of success, largely from France and Switzerland (Vonderheyde 1991, Hawlitzky *et al* 1994), efforts to scale up releases of *T. ostriniae* in field corn production in North America were largely unsuccessful. Problems likely included insecticide applications targeting other pests, the large spatial scales involved, and an emigration rate of up to 40% of female wasps per day from release fields (Andow & Prokrym 1991). The level of corn borer control achieved with *T. ostriniae* releases in field corn was never sufficient to completely supplant insecticide usage (e.g., Gardner *et al* 2007), although the development of *Bt* field corn eventually did. Most likely, this was due to the fact that corn in North America is grown as a vast, synchronous monoculture without sufficient plant and insect diversity nearby to provide adequate adult food sources and alternative hosts for naturally occurring egg parasitoids that have limited dispersal capacity. In China, inundative releases of *Trichogramma* spp. have been successfully and widely utilized for many years (Wang *et al* 2014). It has also been argued that augmentation of *Trichogramma* spp. in Chinese apple orchards “supplements the natural control provided by the existing natural enemy community” (Zhou *et al* 2014), although other recent work has examined landscape-level factors that correlate with improved levels of natural egg parasitism in small-scale Chinese farming systems (Liu *et al* 2016).

#### Augmentation in Latin America

In Latin America, augmentation has been widely adopted and vigorously promoted (e.g., van Lenteren & Bueno 2003),

primarily to reduce the hazardous use of insecticides. Until recently, Mexico had more than 50 biological control laboratories operated by the national agricultural agency “INIFAP” and tasked with the mass-production of a wide range of exotic and native biocontrol agents and entomopathogens. A number of classical introduction programs were notable early successes in Mexico and engendered considerable respect and veneration for biological control among agricultural producers (Arredondo-Bernal & Rodriguez del Bosque 2008). Primary among these was the establishment of three exotic parasitoids to control the citrus blackfly, *Aleurocanthus woglumi* Ashby (Hemiptera: Aleyrodidae), an invasive pest of citrus. Conducted in coordination with the USDA, this was probably the first successful and widely publicized example of classical biocontrol in Mexico. A form of augmentation was continued long after the establishment of these parasitoids which involved periodic collections of mummified blackflies from regions with high levels of parasitism and their redistribution to areas with low levels of parasitism, the latter often caused by injudicious pesticide use (Arredondo-Bernal *et al* 2008). Other efforts to respond to emerging pest problems with augmentation of natural enemies, both native and introduced, soon followed, although typically without any follow-up efforts to quantify impact.

The Mexican response to the invasion of the Yucatan peninsula by the brown citrus aphid, *Toxoptera citricida* Kirkaldy, in the late 1990s was a program to mass-rear and release in citrus groves hundreds of thousands of larval stages of *H. axyridis*, itself an invasive species that had recently established in Mexico (Lopez-Arroyo *et al* 2008). The potential for negative impacts of *H. axyridis* on indigenous coccinellid species were not yet widely recognized (e.g., Michaud 2002b, Koch *et al* 2006), but widespread augmentation of *H. axyridis* in European countries eventually resulted in a severe case of ‘buyers remorse’ (e.g., Soares *et al* 2008, Camacho-Cervantes *et al* 2017, Kenis *et al* 2017). In Mexico, the objective of these releases was to reduce the rate of spread of *T. citricida* northward and westward to more important citrus-producing regions, although they likely had little effect in this regard. However, program leaders had arrived at a new realization: widespread respect for biological control had provided them with a powerful means of controlling the relatively indiscriminate and frequently unsafe use of dangerous insecticides, which has long been a persistent problem throughout Latin American agriculture (Nicholls & Altieri 1997). Farmers selected to receive beneficial insects enjoyed local prestige and, although provided free by government agencies, these insects were always available in limited numbers. Questions about efficacy and actual impact of the releases became moot, simply because they were effective in diminishing pesticide use. Deliveries of beneficial insects were contingent on an

agreement to refrain from insecticide applications, which at the time typically employed inexpensive, broad-spectrum pyrethroids and organophosphates that were probably exacerbating many pest problems in the first place. In this manner, augmentation became more of a political tool than a scientific one, sufficiently effective in combating bad management practices that agronomic benefits emerged which, in many cases, had no direct connection to any impact provided by the released insects.

Programs augmenting egg and larval parasitoids of stalk-boring *Diatraea* spp. (Lepidoptera: Crambidae) over large areas of sugar cane production have been relatively successful in Central America (Badilla 2002, Rodríguez *et al* 2004) and South America (Botelho & Macedo 2002, Vargas *et al* 2015). Although these releases have reduced insecticide usage, there is also evidence that repeated introductions of the exotic *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae) against *Diatraea saccharalis* F. have led to some competitive displacement of native tachinid species that share host species (Rossi & Fowler 2004). But if releases are continually required, we should again dig deeper and ask what features of the sugarcane agroecosystem are preventing populations of these parasitoids from sustaining themselves in the crop. Again, the most likely answer is a lack of plant diversity and floral resources required to provide adult food and alternative hosts within, or adjacent to, sugarcane monocultures. It is also conceivable that improved floral diversity in the landscape would simultaneously increase the efficacy of the parasitoid release programs. The greater evenness of natural enemy populations across organic agroecosystems compared to industrial-scale monocultures (Crowder *et al* 2010) is most likely a function of their greater plant diversity. Ironically, the success of some classical BC programs with exotic parasitoids has been linked to the simplified nature of the food webs present in commercial agroecosystems beleaguered by combinations of exotic pests (Hawkins *et al* 1999).

A recent historical review of BC efforts in Brazil illustrates how focusing too narrowly on augmentation can distract from more sustainable approaches. Parra (2014) essentially synonymized “applied biological control” with the augmentation approach, and posited that augmentation of mass-produced natural enemies could provide faster control of pests than the classical importation approach, noting that it was generally more acceptable to Brazilian farmers. It is true that, in general, native natural enemies should be better ecologically suited than exotics for controlling native pests, but unlike augmentation, the classical approach can provide truly sustainable solutions, even if it is appropriate for only a subset of exotic pests that happen to have “silver bullet” natural enemies (Michaud 2002a). Despite an all-encompassing title, the review by Parra (2014) focuses

almost exclusively on augmentation at the expense of more ecologically based BC approaches; conservation BC is not mentioned even once, nor is there any mention of habitat management or cultural modification as viable strategies for supporting beneficial insect populations. Why not give some thought to how different Brazilian agroecosystems might be re-designed in order to facilitate the activities of the incredibly diverse community of beneficial arthropods that is locally indigenous? Resources exist that can help pest managers think about local ecological factors that might limit biological control services and develop experimental approaches for testing improvements (e.g., Bengtsson 2015, Tschamntke *et al* 2016, Gurr *et al* 2017).

As long as we judge the success of BC in terms of merely displacing pesticides, we sell short its true potential—the natural suppression of pest species without need for human intervention. The very phenomenon of “secondary pest resurgence” (e.g., Hill *et al* 2017) is evidence enough that a lot of natural biological pest control probably goes completely unnoticed under our nose—until, of course, it is disrupted by pesticide use or some other environmental insult. Granted there may be agronomic constraints that render certain pests impossible to manage via conservation BC in some agroecosystems, but in many cases, small changes in agronomic practices might tip the balance in favor of a more permanent solution, a solution that may never be discovered if we claim victory every time we implement a rear-and-release treadmill. For example, natural enemies will often be more abundant in edge habitats that provide alternative foods and shelter (e.g., Griffiths *et al* 2008, Ingrao *et al* 2017), which implies that field subdivision into smaller units could facilitate their penetration into planted areas by virtue of increasing edge habitat. Although efforts to foster greater local plant diversity often require some reduction of the area planted to crops, marginal areas around fields are often underutilized and could be planted to species that provide floral resources for both pollinators and natural enemies. A misguided philosophy of BC can obscure alternative approaches that might be more sustainable. For example, although Garcia & Ricalde (2013) document a large number of native parasitoid species as “important biological control agents” of tephritid fruit flies in Brazil, they do little more than list them, along with a few details on their host range and life histories. Because the focus is again on augmentation, they overtly discount their utility because “mass rearing of these native species is difficult” and choose to focus on an introduced species, primarily because of its “ease of laboratory rearing”. However, an improved understanding of the biology, behavior and ecological requirements of these native species could suggest cultural measures to improve their natural effectiveness in fruit orchards and potentially preclude the need to rear them at all.

### *Natural enemies can adapt to agricultural systems*

Natural enemies are capable of evolution just the same as pests, and sometimes we can assist this process when we understand their needs. A good example of an ecological solution obtained through holistic agroecosystem analysis is provided by organic lettuce production in the central valley of California. It has long been known that various syrphid flies could reduce populations of the lettuce aphid, *Nasonia ribisnigri* Mosley, (Nelson *et al* 2012), but it was the interplanting of lettuce with sweet alyssum, *Lobula maritima* (L.), timed to flower in synchrony with aphid colonization, that has provided a permanent solution with minimal displacement of the crop (Brennan 2013). Once provided with floral resources that support their foraging behavior (nectar) and egg maturation (pollen), adult hoverflies arrive in sufficient numbers to provide sustained aphid control, and the same technique has now been adapted for control of cabbage aphids, *Brevicoryne brassicae* (L.), in broccoli production (Brennan 2016). One can safely assume that hoverflies are not the only beneficial species utilizing sweet alyssum flowers, and that their presence benefits other pollinator species and contributes to overall arthropod diversity. Now consider a hypothetical program in which mass-reared syrphids are provided to farmers for releases timed to coincide with periods of aphid colonization. It is unlikely to be successful without providing the flies with their requisite floral resources in the field, a tactic already demonstrated to completely negate the need for fly releases in the first place. This is the type of truly sustainable BC solution that merits emulation.

Various populations of Coccinellidae now express multiple types of insecticide resistance in both North America (Rodrigues *et al* 2013a, Barbosa *et al* 2016) and South America (Rodrigues *et al* 2013b, Spindola *et al* 2013), ostensibly as a consequence of repeated exposure in crops such as cotton where pesticide use is heavy. Although such insects have the potential to function in agroecosystems where pesticide use deters other natural enemies, they do not present a desirable opportunity for augmentation, as implied by some authors (e.g., Lira *et al* 2013). Rather, the existence of these insects should serve as a wake-up call that pesticide loads in these cropping systems are unacceptably high. Do we really want insecticide-resistant natural enemies that will encourage the continued use of compounds that remain toxic to so many other organisms? This seems diametrically opposed to the original reason for promoting biological control—less insecticide use, not more—but it serves as another example of how an augmentation mindset can lead us away from more fundamental objectives. However, the evolution of insecticide-resistant ladybeetles does provide a nice illustration of something that is often overlooked: the ability of natural enemies to evolve novel adaptations that enable them to forage more effectively

within our agroecosystems, however disturbed and unnatural they may be. If coccinellids can evolve resistance to insecticides, they can also potentially evolve to tolerate many other environmental insults associated with agricultural activities, which likely explains their ability to make such large contributions to control of cereal aphids on the central High Plains of North America (e.g., Rice & Wilde 1991; Michels Jr *et al* 2001), despite these crops being grown as sterile monocultures. Various evolutionary adaptations to agriculture by natural enemies have likely gone unnoticed in many agroecosystems, simply because natural BC is far more apparent in its absence than in its presence.

The adaptation of aphid natural enemies to cereal cropping systems on the Great Plains of the USA provides a good example of natural enemy evolution and eventual adaptation (Brewer & Elliott 2004). Here, cereal crops dominate the landscape in synchronous monocultures of immense spatial scales, conditions which are seemingly ideal for exploitation by many cereal aphid species capable of rapid colonization and explosive population growth. Historically, the evolution of natural enemies to provide sustained BC of some aphid species (e.g., greenbug) took decades, and for many years aphids remained serious, perennial pests that elicited heavy pesticide usage (e.g., Morrison & Peairs 1998; Michels Jr & Burd 2007). The broad-spectrum insecticides in use at that time likely impeded the evolution of natural enemies to better control the aphids. The Russian wheat aphid, *Diuraphis noxia* Mordvilko, became a widespread scourge of wheat in the 1980s (see Quisenberry & Peairs 1998), but is now little more than a curiosity across much of its former range, largely due to the responses on indigenous predators aided by plant resistance. Over time, gradual changes in agronomic practices over large geographic scales (e.g., adoption of no-till cultivation, reduced flood irrigation, and reduced insecticide use in *Bt*-protected crops), combined with advances in breeding aphid resistant plants, and the emergence of more selective aphicides for managing outbreaks, have collectively enabled a broad guild of natural enemies to provide quite consistent control of more than a dozen aphid species (Michaud 2017). Except for periodic disruptions when new species invade, insecticide applications for aphid control in grain crops are now rare, even though aphids are invariably present in low numbers. In fact, outreach efforts now encourage farmers to view as beneficial sub-economic densities of aphids in spring-maturing crops (e.g., winter wheat and alfalfa), as these facilitate the multiplication of natural enemies that then move in larger numbers to summer crops where aphid control is potentially more problematic.

The invasion of a sorghum-feeding strain of sugarcane aphid, *Melanaphis sacchari* Zehntner (Hemiptera: Aphididae), in 2013 represented a major disruption to the insect community in the crop. The problem began near the

Mexican border and there were predictably some misguided efforts to augment lacewing populations (as larvae released onto soil!), with no justification beyond the fact that mass-reared chrysopids were locally available. Populations of *M. sacchari* peaked on the High Plains in 2015 and 2016, but began to come under natural control region-wide in 2017, with much less acreage affected and fewer fields requiring treatment. Among the various coccinellid species responding strongly to the invasion was *H. axyridis*, a species not previously observed in this crop. Significant numbers of *H. axyridis* appeared in Kansas sorghum again in 2017, despite the absence of *M. sacchari* from most fields, and turned their attention to feeding on secondary aphid species. We can infer that *H. axyridis* has rapidly evolved novel responses to sorghum, a crop that it previously ignored, and now associates this plant with the presence of other suitable prey. Similarly, *H. axyridis* only became a familiar resident in soybean fields of the American midwest after the invasion of the soybean aphid, *Aphis glycines* Matsumura, attracted it into the crop (Koch and Costamagna 2017), along with a wide range of indigenous aphid natural enemies (Kaiser *et al* 2007).

#### *Toward a philosophy of natural biological control*

There is currently a pervasive tendency for many BC workers to view augmentation as an end point for laboratory studies of beneficial insect life histories. This view seems to reflect a commercially derived philosophy of beneficial insects as potential ‘biopesticides,’ organisms that can be reared on demand and applied as needed, in the same manner as insecticides. Countless papers cite the potential for mass-rearing and augmentation of a predator or parasitoid as rationale and justification for *fundamental studies of prey range, nutritional ecology, functional responses, development and reproduction*, etc. Why is any such justification necessary, when this knowledge is valuable in its own right for better understanding the ecological requirements of beneficial species? This phenomenon reflects a completely misguided philosophical premise that amounts to little more than hand-waving: “Look, this work is important for BC because we might be able to artificially augment the numbers of this species...”. It betrays a mindset predicated on achieving narrow, short-sighted goals rather than seeking deeper ecological understanding of cultural impacts on insect communities that will potentially yield broader, and more permanent, BC solutions. Others compile lists of commercially produced beneficial species available for “use” against agronomic pests and then bemoan their lack of “uptake” by the agricultural community (van Lenteren 2012). I prefer to analyze specific cropping systems for various features that may encourage, or inhibit, natural recruitment of beneficial species.

A focus on the potential for augmentation becomes like a shiny object of superficial value that distracts attention away from the higher goal of sustainable ecological solutions (Tshernyshev 1995). As soon as the rearing procedures are refined for a beneficial species, new applications are sought for it. When you carry a hammer, everything starts to look like a nail. Those who focus exclusively on augmentation risk selling short the true potential of BC. If continued releases are required, then fundamental problems in the agroecosystem remain unaddressed. All agriculture constitutes a manipulation of natural ecosystems for human ends, and will invariably create ecological problems that require human interventions. Accepting this, a conceptual analysis of the fundamental issues giving rise to pests is warranted—the nature of the agroecosystem and the cultural practices imposed upon it. Ask not what a single beneficial insect can do for you; ask what you can do for the entire beneficial insect community. It can be argued that conservation biological control, at present, is ineffective against a large number of serious agricultural pests. To some degree, this is due to varietal selection for agronomically desirable traits that often leads inadvertently to a high degree of plant vulnerability to pests, but it is also due in large part to the structuring of our agroecosystems as phenologically synchronous monocultures with a paucity of floral resources for beneficial species. Monocultures concentrate plant resources for pests in both time and space, and across many spatial scales (e.g., at the levels of fruit, plant, and field), thus favoring pests with good colonizing abilities and high rates of reproduction, and rendering natural BC more challenging.

A quotation from Stern *et al* (1959) is worth revisiting: “By changing or manipulating the environment, man has created conditions that allow certain species to increase their population densities.” More than 50 years later, I would make a stronger assertion: Modern, industrial-scale agricultural practices are the primary selective forces driving the evolution of our pest problems. We strive to mass-produce highly vulnerable plants in the cheapest and most convenient ways that are typically dependent on many undesirable inputs, including fossil fuels and inorganic fertilizers. In so doing, we continually diminish the area occupied by natural ecosystems, the last, shrinking vestiges of biotic diversity in the landscape, and the primary reservoirs of beneficial species, whether natural enemies or pollinators. However, it may still be possible to achieve sustainable ecological pest control in many such systems, and indeed, many pests of great importance historically are now held below economic levels without human intervention. This is because beneficial insects, as well as pests, can adapt in response to selection, and can sometimes evolve improved functionality within our agroecosystems. The natural evolution of beneficial species is perhaps one of the most overlooked and underappreciated

facts in the entire discipline of pest management. Rather than singling out particular species for rear-and-release programs, we should devote more attention to understanding and characterizing ecological impediments to the timely, natural colonization of our crops by beneficial species. Many of these impediments may be amenable to mitigation via minor cultural modifications, but first they must be identified. This approach can then be complemented by efforts to identify and eliminate plant traits that increase crop vulnerability to pests, traits often inadvertently selected in the course of domestication, and introduce new traits that improve plant resistance. Although augmentation programs have provided benefits by substituting released insects for pesticides in various field crops, their net benefits for agriculture will be diminished if they distract us from seeking more permanent ecological solutions.

**Acknowledgments** This is contribution No. 18-279-J from the Kansas Agricultural Experiment Station.

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