

Evolution of biological control agents following introduction to new environments

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Abstract The introduction of biological control agents (BCAs) creates the potential for adaptive evolution in translocated organisms. BCAs are confronted with new environments that can promote adaptation to exploit novel resources, even within short ecological time frames. In particular, insect BCAs are amenable to rapid evolution due to their short generation times and relatively large population sizes. These factors hypothetically increase the likelihood that, when exposed to novel habitats, environmental selection could cause BCAs to extend their range to non-target host species. Alternatively, insects may simply extend their range as their generalist or polyphagous habits are fully realized. In this review, we consider recent literature that addresses these topics. Adaptations to environmental conditions have been demonstrated in a number of BCAs. Mechanisms of adaptation include founder effects, hybridization, and endosymbiosis. Yet, there is little evidence of adaptive host range expansions among insect and weed biological control agents to non-target species, albeit existing examples are from limited numbers of studies. Important future directions and current

developments in the field incorporate next generation sequencing technology that can promote better resolution of population divergence, possible mechanisms involved in adaptation to novel resources, and insect hybridization. Future studies should also include a careful consideration of the influence of microbes on BCA efficacy and environmental adaptation.

Keywords Biological control agent evolution

Introduction

The inadvertent global movement of organisms through trade and travel results in environments continually being colonized by newly adventive organisms, many of which become invasive. Adventive species typically escape their natural enemies that regulate their populations, leading to large unconstrained invasive populations. All too often this is to the detriment of indigenous species, local and global economies, and human health in the invaded environment (Hill et al. 2016). Classical biological control—the introduction of natural enemies of invasive pests, usually from the place of origin of the pests—is a frequent management option that is employed to address these issues (Messing and Wright 2006). Classical biological control has resulted in many highly successful pest management efforts and it is generally considered to be an economical and

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environmentally compatible option (Messing and Wright 2006).

Adaptation of organisms to changing, or new environmental conditions is inevitable, and adaptation can occur over very brief time spans (i.e., ecological time-scales). The ability of a wide range of organisms to evolve rapidly via adaptation to changing environment has been clearly demonstrated in a number of systems. Some of the most distinct and compelling case studies arise from relatively long-lived organisms that include birds and their food plants on the Galapagos Islands (Grant and Grant 2002; Hendry et al. 2006). In these cases, rapid adaptation results from intense environmental selection on traits associated with the availability of food and resources (Grant and Grant 2006). In contrast, animal populations can also experience relaxed selection from reduced competition and abundant food resources. They may then be able to expand their range through ecological release or non-adaptive range expansion (Bolnick et al. 2010; Warren et al. 2015). In this scenario range shift may involve little to no measurable genetic divergence, at least initially, but could lead to selection to use newly available resources, reproductive isolation, and eventual speciation (Warren et al. 2015). The interplay between adaptive and non-adaptive processes in driving long-term local adaptation may be challenging to tease apart. Nevertheless, they are both likely to be important mechanisms in shaping adaptation of populations to new environments.

The practice of classical biological control of pests creates situations wherein purposefully introduced organisms have new opportunities to undergo significant evolutionary change. It would not be surprising to discover that insects, which have rapid generation times and large population sizes, can evolve readily to fill novel environments and ecological opportunities (e.g., host plants or insects)—even within several generations (e.g., Turcotte et al. 2011). In the context of classic biological control, various sub-populations of insect species are routinely subjected to novel habitats. Insects are expected to evolve more rapidly than many other animals, and may indeed undergo rapid adaptive changes in response to changes in their selective environments.

In biological control programs, natural enemies of pests are trans-located, reared in captivity, and introduced as biological control agents (BCAs). Following release in their new ranges, insect populations are

subjected to new environmental conditions, novel potential hosts, and other interacting organisms that could promote rapid evolution. Whether adaptations following purposeful introductions are advantageous or deleterious depends on the nature of the change. Introduced BCAs may face a number of selective pressures to adapt their host range as outlined above. Alternatively, they may face reduced selection and can expand their range through non-adaptive processes. Switches to novel hosts may impose little to no selection pressure if host defenses are weak, or if competition and predation by other organisms are reduced, allowing BCAs to expand their realized niche (Tingley et al. 2014). The introduction of biological control agents often occurs with a small number of individuals relative to naturally occurring insect populations. This reality could impose a population bottleneck (also known as founder effect) that can reduce genetic diversity and even lead to the loss of beneficial alleles (Franks et al. 2011). Populations may then simply undergo non-selective genetic drift and begin to diverge from conspecifics in the native range. This process could lead to eventual speciation and local adaptation. Thus, it is hypothetically possible that BCA populations might adapt to utilize non-target species in the place of introduction and to other local environmental conditions.

It has been suggested that classical biological control constitutes “intelligent pollution”, as introduced species are able to adapt to their environment, and if they include native non-target species in their host range, be considered environmental pollutants (Howarth 1991). Howarth (1991) was primarily concerned with possible negative impacts that BCAs might have. However, there may well be beneficial outcomes of post-introduction adaptations. Adopting an evolutionary perspective in natural enemy introductions can contribute to increased biological control success while reducing potential non-target exploitation (Vorsino et al. 2012). This information provides a predictive element that can better guide the principles and applications of BCA approaches. The importance of evolutionary change in BCAs has indeed received attention, including an entire issue of *Evolutionary Applications* (2012, volume 5) dedicated to a series of studies of environmental adaptation in biological control systems. Since this time, there have been additional studies of post-introduction adaptation in BCAs, not only with regard to non-target impacts, but also

adaptation to variable climates, pesticides, different habitats, and also impacts of hybridization and outcrossing. These works provide new insights into the biology BCAs and also new critical areas of research in the field.

The main goal of this review is to provide a contextual overview of recent studies and summarizes their main findings, seeking to identify significant adaptations in BCAs. We draw in literature that has explicitly investigated BCA evolution post-introduction. Tables 1 and 2 summarize the key findings of

papers that document demonstrable adaptations in insect and weed BCAs, respectively. Owing to space constraints, selected studies are discussed in more detail for natural enemies of insects, and weed biological control agents. The possibility that insect BCAs have evolved to exploit non-target species is addressed, as well as other cases of demonstrated adaptation in new environments. Finally, we aim to identify and highlight emerging areas of future research and technologies that will be important in the development of the field.

Table 1 Post-introduction adaptations in arthropod predators and parasitoids respectively, listed alphabetically

Natural enemy taxon	Quantified adaptation	References
Predators:		
<i>Metaseiulus occidentalis</i> , Phytoseiidae	Adaptation of predacious mites to pesticides; development of pesticide resistance	Caprio and Hoy (1994), Roush and Hoy (1981)
<i>Cryptolaemus montrouzieri</i> , Coccinellidae	Positive selection/recent selective sweep; potential for local adaptation	Li et al. (2016)
<i>Harmonia axyridis</i> , Coccinellidae	Hybridization between flightless and invasive individuals; hybrids with reduced development time; larger size; greater genetic variance, survive starvation	Facon et al. (2011)
<i>Harmonia axyridis</i> , Coccinellidae	Genetic admixture with invasive US strain, “Bridgehead effect”—USA population adapted, reinvaded Europe	Lombaert et al. (2010)
<i>Laricobius nigrinus</i> , Derodontidae	Hybridization with native species	Havill et al. (2012)
Parasitoids:		
<i>Aphidius ervi</i> , Braconidae	No adaptation to host resistance; No local adaptation to hosts	Hufbauer (2001)
<i>Aphidius ervi</i> , Braconidae	Non-adaptive evolution—reduced ability to parasitize hosts on certain plants	Hufbauer (2002)
<i>Aphidius ervi</i> , Braconidae	Reduced rare alleles; mild genetic bottleneck; genetic change associated with founder events, even with large founder numbers	Hufbauer et al. (2004)
<i>Aphidius ervi</i> , Braconidae	Lack of host adaptation; role of phenotypic plasticity in fitness on alternative hosts. Host phylogeny effect?	Zepeda-Paulo et al. (2013)
<i>Aphidius transcaspicus</i> , Braconidae	Geographic structure among populations; no host-associated diversification	Lozier et al. (2009)
<i>Cotesia rubecula</i> , Braconidae	Complementary sex determination resulting from inbreeding depression	Boer et al. (2012)
<i>Cotesia sesamiae</i> , Braconidae	Cryptic species	Kaiser et al. (2015)
<i>Diachasmimorpha tryoni</i> , Braconidae	Geographic structure between place of origin and introduction; no host-associated adaptation	Vorsino et al. (2014)
<i>Diaeretiella rapae</i> , Braconidae	Low allelic length and frequency variation; founder effect; genetic bottleneck	Baker et al. (2003)
<i>Lysiphlebus testaceipes</i> , Braconidae	Geographic structure; no host-associated adaptation	Mitrovic et al. (2013)
<i>Microctonus hyperodea</i> , Braconidae	Adaptation to local environmental conditions; increased target pest mortality	Phillips et al. (2008)
<i>Trichogramma chilonis</i> , Trichogrammatidae	Hybridization among populations; heterosis; inbreeding depression	Benvenuto et al. (2012)

Table 2 Post-introduction adaptations in insects used as weed biological control agents, listed alphabetically

Natural enemy taxon	Quantified adaptation	References
<i>Agasicles hygrophila</i> , Chrysomelidae (L) ^a	Decreasing genetic diversity with sequential introductions	Ma et al. (2013)
<i>Aphthona nigricutis</i> , Chrysomelidae (L)	Possible effects of <i>Wolbachia</i> producing genetically distinct groups	Roehrdanz et al. (2006)
<i>Boreioglycaspis melaleucae</i> , Psyllidae (S)	Loss of mtDNA diversity and rare microsatellite alleles; no genetic bottleneck effect despite demographic bottleneck	Franks et al. (2011)
<i>Chrysolina quadrigemina</i> , Chrysomelidae (L)	Increased larval survival on non-target host (within fundamental host-range)	Andres (1985)
<i>Diorhabda carinulata</i> , Chrysomelidae (L)	Critical day length for diapause induction	Bean et al. (2012), Dalin et al. (2010)
<i>Diorhabda elongata</i> , Chrysomelidae (L)	Reduced host acceptance threshold	Thomas et al. (2010)
<i>Eccritotarsus catarinensis</i> , Miridae (S)	Recovered, or retained genetic variation following bottleneck	Taylor et al. (2011)
<i>Larinus cynarae</i> , Curculionidae (P)	Host shifts in place of origin (potential for post-introduction host range changes)	Olivieri et al. (2008)
<i>Longitarsus jacobaeae</i> , Chrysomelidae (L)	Increased fitness in hybrids	Szűcs et al. (2012)
<i>Phenrica guerini</i> , Chrysomelidae (L)	No variation in fitness on different host genotypes	Paterson et al. (2012)
<i>Prosopidopsylla flava</i> , Psyllidae (S)	Genetic limitations on aspects of life history limit ability to colonize new plant hosts	van Klinken (2000)
<i>Tyria jacobaeae</i> , Arctiidae (L)	Reduced egg to pupa development time at increased elevation	McEvoy et al. (2012)

^a Feeding guilds: L: leaf-chewer, S: sap-sucker, P: seed-predator

Overview

BCA adaptation to non-target species: parasitoid
 BCA adaptation to novel host insects

The possibility that BCAs may evolve the ability to exploit non-target species is a significant issue in the selection of particular species for introduction (Messing and Wright 2006). Although non-target host or prey exploitation may occur because a BCA is fundamentally polyphagous, it may also result from true adaptive host-range expansion as a BCA evolves to exploit novel resources. In the former case, phenotypic plasticity rather than evolutionary change may create the impression of adaptation, and care should be taken to distinguish these outcomes (Thomas et al. 2010).

There have been relatively few cases of putative BCA host-range shifts that have been examined in an evolutionary framework. In such cases, a reasonable hypothesis is that if host-mediated adaption has occurred, genetic differentiation should be observed between BCA populations associated with distinct

hosts. One recent study that explicitly tested this hypothesis examined *Diachasmimorpha tryoni* (Braconidae) introduction to Hawaii from Australia in the early 1900s (from ~15 founder females) to control fruit flies (Tephritidae: *Ceratitus capitata*). Within about 60 years of its introduction, *D. tryoni* began to utilize a unique host, *Eutreta xanthochaeta* (Tephritidae) that is a gall-forming natural enemy of *Lantana camara* (Verbenaceae) introduced as a BCA to Hawaii from Mexico. Early work (Duan et al. 1998) indicated that there might be populations of *D. tryoni* that adapted to use *E. xanthochaeta* preferentially, based solely on behavioral observations. Vorsino et al. (2014) later examined this system using mitochondrial DNA sequencing and microsatellite DNA to assess whether there were indeed genetically distinct populations of *D. tryoni* associated with the different host species. Their results indicated that there are genetic differences between the populations in Australia (their place of origin) and those found in Hawaii. Despite potential behavioral differences, no genetic differentiation was observed between populations associated with *C. capitata* and the non-target *E. xanthochaeta*

(Vorsino et al. 2014). The possibility remains that the original *D. tryoni* population is able to parasitize a range of fruit fly species, including gall-forming ones in Australia. However, even if that is the case, Vorsino et al. (2014) investigated multiple sources of fast evolving genetic markers that were unable to detect genetic differentiation associated with the exploitation of a novel host in a new environment. These results suggest that *D. tryoni* may not have undergone an adaptive shift to use *E. xanthochaeta* as a host.

Several other recent works have also found limited evidence for the role of BCA adaptation in host range expansion. For example, *Lysiphlebus testaceipes* (Braconidae), introduced to control citrus aphids in Europe, exploited a number of native aphid species in the introduced range, leading to some distinct population level impacts (Mitrović et al. 2013). The authors used mitochondrial and microsatellite markers to investigate the possibility of host-associated lineages, but found only geographic population structure and not host-mediated genetic structure (Mitrović et al. 2013). Lozier et al. (2009) also demonstrated geographic structure among populations of *Aphidius transcaspis* (Braconidae), with no evidence for host-associated diversification. Other work on aphid parasitoids (Braconidae: *Aphidius ervi*) comparing preferences and virulence on various hosts also showed no host-adaptation in the parasitoids, but rather underscored the potential importance of phenotypic plasticity in maximizing fitness (Zepeda-Paulo et al. 2013).

BCA adaptation to non-target species: adaptation of phytophagous BCAs to novel host plants

Phytophagous insects may have considerable potential to adapt to new host plants, and cautionary suggestions have been made based on the apparent instability of host use in some (e.g., Olivieri et al. 2008). However, it should be noted that most examples of putative host-shifts in phytophagous BCAs are not the result of genetic change, but rather the result of inadequate assessment of fundamental host ranges in their native habitats (Marohasy 1996; van Klinken and Edwards 2002). Regardless, there are still likely to be genetically defined limits that preclude phytophagous insect species from freely adapting to new host plant lineages (van Klinken 2000).

For BCA introductions to control weeds, there have been isolated cases where introduced species appear to

have switched to new hosts, although none appear to be examples of adaptive host switches (Table 2). In illustration of this point, Andres (1985) showed that *Chrysolina quadrigemina* (Chrysomelidae) had increased larval survival on a non-target host in the area of introduction—but that species was within the predicted fundamental host range of the insect. In a more recent chrysomelid example, Thomas et al. (2010) demonstrated a reduced host acceptance threshold in *Diorhabda elongata* (Chrysomelidae), which appeared to result in improved performance on the target weed. In this case, the BCA was initially slow to establish in an area dominated by a non-target weed, and a shift in its host-acceptance threshold onto that non-target resulted in eventual successful establishment in the region. Despite the occurrence of some non-target utilization by several other weed BCAs, none are considered to be true “host shifts” (van Klinken and Edwards 2002). Furthermore, no cases of changes in fundamental host range have been recorded for weed BCAs (van Klinken and Edwards 2002). Thomas et al. (2010) emphasize the important caveat that the differences in host acceptance that they documented may have been the result of phenotypic plasticity rather than evolutionary change in the new environment. Marohasy (1996) blames reports of “host switches” on poor use of terminology and inadequate research in some cases.

Conclusion: limited evidence for BCA adaptation to non-target hosts

To date, there is little conclusive evidence for an introduced insect and weed BCAs undergoing evolutionary adaptation that resulted in a true host shift or adaptive host range expansion. Expansion of non-target ranges that classical biological control agents may realize in certain cases are often emphasized by those concerned about the impact of BCAs. It is reassuring that observed range shifts and expansion are attributable to the generalist nature of those early BCAs, rather than documented evolutionary change. Negative impacts from generalist BCAs can easily be avoided through careful selection of agents and quarantine screening.

It may seem surprising that parasitoid insects have not been found to rapidly adapt to new hosts in new environments, as many parasitoid groups have high diversification rates (e.g. Mardulyn and Whitfield

1999). It has been proposed that highly specialized life styles such as parasitism are “evolutionary dead-ends”, and this may be a tenable hypothesis, although no unequivocal evidence that parasitism limits potential for diversification exists (e.g. Wiegmann et al. 1992; Rainford and Mayhew 2015). Rainford and Mayhew (2015) present data that demonstrate that parasitic insects have undergone fewer origination events in geological time than other feeding guilds of insects. This provides some support for the notion that the parasitic guild is less likely to undergo dramatic evolutionary dietary (host) shifts. The abilities to hone in on new hosts, overcome host defenses, out compete local species, and to find mates present significant adaptive challenges that are apparently difficult for BCAs to overcome. One must also bear in mind that a little more than a century has passed since the first classical biological control programs were put in place, a brief period in evolutionary terms. Demonstrable adaptation of BCAs to their new environments may still be sorting out. Nevertheless, the evidence currently available suggests that host-switching evolution in parasitoids does not occur within that timeframe.

Other environmental influences on local adaptation: Non-adaptive evolution of BCAs

As mentioned above under non-target aspects, there are examples of BCAs that have adapted to local conditions other than new hosts in their novel environments. Hufbauer (2001) observed that *Aphidius ervi* (Braconidae) underwent non-adaptive evolution in introduced ranges, with reduced ability to parasitize target aphids on certain plant hosts. The researchers showed that *A. ervi* had not undergone any correlated adaptation to local hosts in places of introduction, and that the parasitoids had not demonstrated any signs of adapting to host resistance (Hufbauer 2002). Despite the lack of evidence for adaptive transitions, genetic information revealed that rare allele frequency was reduced in *A. ervi*. These results indicate that genetic changes resulting from genetic bottlenecks during founder events are detectable, even with relatively large founder population numbers (Hufbauer et al. 2004) (Table 1). This is an important consideration because a stochastic change in genetic frequency can confound inference of population structure and even host adaptation. Non-adaptive evolution of BCAs has

received relatively little attention, but is an area that deserves more, as the results can have important implications for effective biocontrol.

Adaptation to the environment

Evolutionary changes related to adaptations to environmental conditions have been demonstrated repeatedly in BCAs introduced to control weeds. One such example includes *Microctonus hyperodea* (Braconidae) introduced to control *Listronotus bonariensis* (Curculionidae) that was indeed found to have undergone adaptation to local conditions, and target pest mortality increased as a result (Phillips et al. 2008). Reduced developmental time has also been demonstrated for *Tyria jacobaeae* (Arctiidae), introduced to control *Senecio jacobaea* in Oregon, USA, at higher elevations (McEvoy et al. 2012). This was shown to be a clear case of adaptation at the genetic level, using common garden experiments with reciprocal transplants of the insects. Dalin et al. (2010) and Bean et al. (2012) also demonstrated adaptation of a weed BCA, *Diorhabda carinulata* (Chrysomelidae), to environmental conditions following introduction to the USA. Using carefully designed experiments, they showed that the beetles had evolved reduced critical day length required for diapause induction, permitting colonization of a larger geographic range than originally anticipated. This adaptation had positive impacts for biological control of the target weed, as efficacy of the BCA was increased and they were able to colonize a wider geographical range than originally expected (Bean et al. 2012).

Influence of microbial symbionts on BCA evolution

The role of microbial endosymbionts in biological control is an area currently receiving much attention with significant potential for future work. The microbial associations of insects, particularly their gut microbiota, have wide-ranging ecological and evolutionary implications for insect populations that certainly include BCAs (see review by Engel and Moran 2013). For example, the gut microbiota of the Western corn rootworm (Coleoptera: Chrysomelidae: *Diabrotica virgifera*) facilitated rapid adaptation to novel food plants, particularly those used in crop rotation (Chu et al. 2013). Although this latter example is from a pest

species, such outcomes can be envisioned for BCAs when introduced outside of their native ranges. Another consideration is that pest insect species targeted by parasitoid BCAs can themselves harbor microbial symbionts that could provide protection against them. An example of microbe-mediated parasitoid protection occurs in pea aphids where a facultative bacterial symbiont (defined as not required for reproduction), *Hamiltonella defensa*, encodes bacteriophage genes that inhibit parasitoid egg development of *Aphidius ervi* (reviewed by Oliver et al. 2010). Many different strains of *H. defensa* occur in the natural environment and are known to infect a handful of other aphid species, providing protection against other parasitoid species (reviewed by Oliver et al. 2014). Furthermore, other widespread facultative symbiont species (e.g., *Regiella insecticola*) are known to provide various protections against microbial pathogens such as environmental fungi and also to increase insect tolerance to heat (Oliver et al. 2010). The potential for symbionts to protect their hosts against fungi is an important consideration for the effective use of microbial BCAs. Clearly there is potential for microbes to enhance BCA effectiveness in introduced ranges, or to protect target hosts from BCAs. However, the role of facultative microbes in driving BCA evolution remains largely unexplored.

Finally, parasitic bacteria can also interact with insect population demography and genetic structure in significant ways (Werren et al. 2008). For example, Roehrdanz et al. (2006) showed that *Wolbachia* infection of leafy spurge natural enemies (*Aphthona nigricutis*, Chrysomelidae) may contribute to limiting genetic diversity in some beetle populations. They suggest that the *Wolbachia* infection may in fact result in the development of genetically distinct beetles, with limited genetic diversity. Uninfected beetle haplotypes had high genetic diversity in their study (Roehrdanz et al. 2006). *Wolbachia* is considered to be one of the most commonly occurring microbial symbionts of insects, infecting upwards of 65% of all insect species, with extreme potential to influence host adaptation and population structure (Werren et al. 2008). Its role in shaping the evolution and effectiveness of BCAs should be a critical consideration in future research. It may also be considered a form of microbial biocontrol for application against a range of insect hosts, including mosquitoes (World Health Organization 2016).

Host and microbial mediated pesticide resistance

There are clear benefits in terms of integrating pesticide resistant BCAs into cropping systems that rely on pesticides for management of other pests. Although examples of BCA adaptation to overcome pesticides are limited, several examples do exist. An interesting adaptive response in BCAs that may be exploited in some circumstances is the ability of the organisms to evolve resistance to pesticides. Caprio and Hoy (1994), and Roush and Hoy (1981) have demonstrated that predacious mites can be selected for resistance to pesticides.

A growing body of research has also clearly demonstrated that insect microbiota can confer resistance to certain pesticides in a range of insect hosts (Broderick et al. 2009; Kikuchi et al. 2012). The range of interactions may be complex and dependent on the host insect. For example, the effectiveness of *Bacillus thuringiensis* toxin (commonly sold over the counter as BT toxin and applied as an organic bio-pesticide for control of lepidopteran pests) is partly dependent on the species present in the bacterial gut microbiota of larvae (Broderick et al. 2009). Although the mechanisms are unclear, the authors suggest that BT may disrupt interactions with the normal gut microbiota, rendering it pathogenic to the host. In contrast, another emergent pattern is that beneficial microbial symbionts can metabolize and breakdown chemical insecticides. For example, the legume pest *Riptortus pedestris* (Hemiptera: Coreoidea) obligately acquires environmental *Burkholderia* bacterium from the soil (Kikuchi and Yumoto 2013). Some *Burkholderia* strains retain the ability to breakdown the commonly used insecticide, fenitrothion, conveying a direct adaptive advantage to the host insect (Kikuchi et al. 2012). Similarly, the oriental fruit fly, *Bactrocera dorsalis*, can also obtain insecticide resistance by acquiring specific gut bacteria capable of degrading other phosphate-based insecticides (Cheng et al. 2017).

The extent to which microbes underlie BCA pesticide resistance is a growing area of research. Insect BCAs may be able to rapidly obtain insecticide resistance by developing symbiotic relationships with certain microbes. Bacterial communities are immensely diverse as is their range of metabolic capabilities (e.g., reviewed by Fierer and Lennon 2011; Wang et al. 2016). They are also rapidly evolving and

mutable, providing opportunities to quickly adapt to novel environmental conditions such as pesticide degradation. In theory, these adaptations could be conferred rapidly to select BCAs either in the environment or through inoculation experiments. This potential should be considered as an important element of effective application of novel BCAs.

BCA hybridization with local species and populations

The possibility for BCAs to hybridize with local insect populations or closely related species is another potentially important evolutionary outcome of introductions. However, there have been few documented cases of introduced biological control agents hybridizing with indigenous or other introduced species. Havill et al. (2012) report hybridization of an introduced Derodontidae beetle with an indigenous species in the same genus. Hybridization may have diverse impacts, including reduced fitness and impacts on target pest populations. On the other hand, hybrids may have improved characteristics for certain traits, such as reducing Allee effects and reducing loss of genetic variation (Havill et al. 2012). Hybridization among populations of *Trichogramma chilonis* (Trichogrammatidae) with varying genetic and phenotypic distances has been shown to have somewhat predictable fitness effects (Benvenuto et al. 2012). While Benvenuto et al. (2012) demonstrated a slight but significant negative relationship between both genetic distance and phenotypic distance, and female wasp fitness, they found surprising heterosis in hybrids from geographically distantly related populations. Szűcs et al. (2012) similarly showed heterosis effects in a weed BCA (*Longitarsus jacobaeae*, Chrysomelidae) when populations from geographically distant regions in Europe were crossed. They suggest that hybrids with higher fecundity may be beneficial, as they may increase establishment success and rapid population growth (Szűcs et al. 2012). This suggests that adaptive alleles may introgress between populations that provide advantages to some populations. Hybridization and genetic admixture of populations of *Harmonia axyridis* (Coccinellidae) has indeed produced some remarkable adaptations. Genetic admixture between beetles from Europe crossed with invasive populations from the USA, produced a re-invasion of Europe by fitter individuals resulting from

hybridization (Lombaert et al. 2010). Hybridization between flightless and invasive *H. axyridis* produced progeny with shorter developmental times, larger size and increased ability to survive starvation (Facon et al. 2011).

Microbial pathogen BCAs

Microbial biological control agents, including viruses, bacteria and fungi, are a group of organisms that have considerable potential for adaptation to new hosts and environments. Evolution of pathogens in insect host populations has received some attention, underscoring the fact that the impact that insect pathogens have on their hosts is dependent on a wide range of environmental conditions, and that the factors influencing pathogen diversity are largely unknown (Myers and Cory 2016). Among the various insect pathogens used in biological control of insect pests, fungi (e.g. *Beauveria bassiana*) and bacteria such as *Bacillus thuringiensis* have received considerable research attention. Resistance to *B. thuringiensis* in the target pests has been documented, perhaps most famously in diamond back moth (*Plutella xylostella*) (Tabashnik et al. 1990), but there appears to have been no work on possible adaptation of the pathogen to overcome resistance in the insects. In their review of evolution of insect pathogens used in insect biocontrol, Cory and Franklin (2012) state that there have been no records of host-range evolution of impacts on non-target species resulting from the use of microbial BCAs. They further suggest that long-term studies of pathogen population structure and virulence should be conducted.

With the genetic diversity that microbial BCAs may harbor, there has been some effort to identify isolates with variable virulence to certain pests. For example, Valero-Jimenez et al. (2016) has shown that virulence of selected isolates of *B. bassiana* toward mosquitoes varies by an order of magnitude, and that multiple genes and molecular processes govern the virulence. Hudson et al. (2016) examined genotype-by-genotype (G×G) interactions between numerous isolates of baculovirus and gypsy moth (*Lymantria dispar*), and showed that virulence varied among the isolates, and also found evidence for differential susceptibility in the host, supporting the presence of G×G effects in the study system. As these few examples show, pathogen-host evolution is clearly a research area with huge

potential to investigate important questions in biological control of pests. The recent examples cited underscore the potential value of using advanced genomic tools in understanding pathogen-host interactions and the evolution of the systems.

Future research directions

While historically the study of adaptation has been constrained by availability of technology or costs of procedures such as DNA sequencing, current technology permits rapid and relatively cheap acquisition of large amounts of DNA sequence data. Next generation sequencing technologies (e.g., Illumina short-read sequencing) that permit analysis of whole genomes, large numbers of select genes, and many individuals, are now becoming routine. These methods offer significant possibilities for analyzing genetic change and population structure on a broad-scale in BCAs. But more importantly, they offer the opportunity to identify particular loci under selection that may be involved in local adaptation to novel hosts in BCAs—even when host-specific population structure is not detectable or fixed. NGS approaches have been used successfully to detect insect adaptation to novel host plants and other environmental conditions in a wide range of systems (e.g., Soria-Carrasco et al. 2014; Feng et al. 2015). In BCA studies, such approaches can provide deep insights into the biological underpinnings of successful introductions and the possible long-term outcomes of these applications.

Selective breeding of BCAs using genetic marker technology is also worth consideration. It is possible to predict microevolutionary change in organisms, if traits in offspring from selected groups can be reliably quantified (e.g., Grant and Grant 1995), which is becoming increasingly viable with captive insect populations and new sequencing technology. Massively parallelized, deep sequencing can then identify particular genes that underlie these changes within and between populations with relative ease, even if they have occurred over the short time frames of a few years or generations (Soria-Carrasco et al. 2014; Lamichhane et al. 2015).

Another important consideration is epigenetic effects that can alter gene expression in the absence of heritable change. With recent technological developments and biological understanding, epigenetic approaches are an expanding area of research that

should also be considered in BCA research. These mechanisms are currently sometimes invoked as underlying otherwise unexplained adaptations, such as modified host preference, and corresponding genetic change. Epigenetic effects can occur within as short a period as the life cycle of an individual, inducing behavioral and developmental changes that are influenced by diet, environmental conditions, and stress (reviewed by Mukherjee et al. 2015). For example, in eusocial insects, epigenetic responses to food and environment are known to govern queen and worker development, as well as insect memory and responses to environment (reviewed by Yan et al. 2015). It is easy to imagine that in BCAs, when faced with entirely new environments, epigenetic modifications could permit rapid environmental tolerance and novel host interactions. Although several epigenetic mechanisms are currently recognized, methylation appears to be the dominant method in insects (Mukherjee et al. 2015). Current shot-gun sequencing methods are easily adapted to survey genome-wide changes in DNA methylation sites between target BCA populations, potentially identifying certain functional elements and loci involved underlying behavioral changes (see Lister et al. 2008; Xiang et al. 2010). Previously researched parasitoid-host expansion systems, such as *D. tryoni* which showed no detectable genetic change with a host expansion (Vorsino et al. 2014), may be good candidates for investigating epigenetic effects, and may provide clarity on the mechanisms involved in changes in host preference. Subsequent experiments, such as RNA-seq and reverse-transcription quantitative PCR (RT-qPCR), could then be used to validate changes in the expression of identified genes between target populations.

Finally, new sequencing technologies also permit rapid, culture-independent approaches to understand the role of microbial partners in BCA success and evolution (Sloan et al. 2013). An understudied component of BCA biology and evolution is the role that microbial endosymbionts play in mediating the BCAs interactions with their target species and the local environment. Endosymbionts can mediate BCA success by enhancing environmental tolerance and by providing novel abilities to overcome host defenses (insect or weeds). BCAs may be able acquire new endosymbionts when introduced to novel environments that can provide a diverse array of

environmental advantages (Oliver et al. 2014). It is possible to select for specific interactions between natural enemies and target species by selecting species that have certain endosymbionts that promote target specificity. Furthermore, target pests may also carry defenses against potential parasitoids that could render introductions ineffective and should be considered as part of the BCA selection process. Thus, increased understanding of the interactions between insects and their endosymbionts offers enormous potential for future research in biological control.

Incorporating evolutionary studies into biological control research has much to offer in terms of further improving classical biological control. With greater understanding of genetic systems in BCAs, and also insects more broadly, it is conceivable that we could identify genetic characteristics associated with monophagous or polyphagous life styles in prospective introductions prior to introduction. Nevertheless, the biological control research community should see the elucidation of evolutionary adaptations that BCAs have undergone, and the evidence indicating that evolutionary changes have not generally been environmentally deleterious, as a significant achievement. The work that has been conducted to detect and characterize evolutionary change in BCAs demonstrates a willingness by the community to responsibly deal with issues that relate to the long-term environmental impacts of biological control. Advance technologies offer the opportunity to greatly expand this work at an accelerated rate. Traditional approaches (e.g., transplant and phenotypic studies) have continued value in the field and can be used in tandem with advanced technologies to better understand BCA systems. The use of advanced sequencing technologies provides more mechanistic explanations for field observations, which can provide deep biological insights as opposed to more pattern-based observations in transplant and phenotypic studies. Understanding the underpinnings of adaptive (or not) evolution in BCAs can only provide better predictive science. In our experience, the expense of next generation sequencing is no longer that great and should not be seen as a hurdle, but a method that offers new opportunities and understanding for the field.

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