

A REVIEW OF NONTARGET EFFECTS OF INSECT BIOLOGICAL CONTROL AGENTS: CONCEPTS AND EXAMPLES



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Top row: The polyphagous parasitic tachinid fly *Compsilura concinnata* (Tom Murray); gypsy moth (*Lymantria dispar*) larva (USDA APHIS PPQ - Oxford, North Carolina, USDA APHIS PPQ, Bugwood.org); two of the nontarget moths attacked by the tachinid *Compsilura concinnata*: the silkmoth *Hyalophora cecropia* (Pennsylvania Department of Conservation and Natural Resources, Forestry Archive, Bugwood.org) and the buck moth *Hemileuca maia* (Gerald J. Lenhard, Louisiana State University, Bugwood.org).

Middle row: *Trichopoda pennipes (pilipes)* (Russ Ottens, University of Georgia, Bugwood.org); *Nezara viridula* (Clemson University - USDA Cooperative Extension Slide Series, Bugwood.org); Koa bug, *Coleotichus blackburniae* (nymphs and one adult) (Forest and Kim Starr, Starr Environmental, Bugwood.org).

Bottom row: Two introduced coccinellids, *Harmonia axyridis* (Scott Bauer, USDA Agricultural Research Service, Bugwood.org) and *Coccinella septempunctata* (David Cappaert, Michigan State University, Bugwood.org); yellow pecan aphid, *Monelliopsis pecanis* (Louis Tedders, USDA Agricultural Research Service, Bugwood.org); two of the native species the coccinellids displaced: *Adalia bipunctata* and *Coccinella novemnotata* (Whitney Cranshaw, Colorado State University, Bugwood.org).

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INTRODUCTION

Whether, when, and how frequently introductions of biological control agents have important population-level effects on nontarget species is a question of continuing importance to both biological control scientists and conservation biologists. This issue was first raised by Howarth (1991), who outlined evidence for significant nontarget impacts from biological control agents. While breaking new ground in raising the issue, this article was, in our opinion, flawed. First, rather than assessing whether nontarget impacts had occurred regularly or to what degree on average, Howarth (1991) advocated strongly for the proposition that they had occurred, supporting the article's assertion by selectively assembling instances of possible impact. While it alerted society to this unintended risk, Howarth (1991) did little to objectively assess the magnitude of the problem posed by natural enemy introductions. Second, the author grouped vertebrate introductions, some made as far back as the 1700s by farmers, with introductions of biological control agents made by government scientists after biological control began to develop as a science (post 1920s). This greatly enhanced the perceived negative impact of biological control as most vertebrate introductions for pest control did cause ecological damage. Third, the article did not adequately differentiate between simple use (feeding or parasitism to any degree) and evidence-based, population-level impacts on nontarget species. Fourth, Howarth (1991) greatly overstated the risk of extinctions from introductions, by emphasizing the effects of vertebrate and mollusk introductions, as opposed to arthropods (e.g., herbivores, parasitoids, and predators) that are used most commonly for biocontrol of pest plants and arthropods. While

this article opened a conversation on the potential environmental effects of classical biological control, it did not provide a definitive answer. Further discussion of this issue ensued in the following decades (Follett and Duan, 2000; Follett et al., 2000; van Lenteren and Loomans, 2000; Louda et al., 2003; Hoddle 2004a,b,c; Stewart and New, 2007; Parry, 2009; Barratt et al., 2010; Suckling and Sforza, 2014).

Here we focus on potential nontarget impacts of parasitoids and predacious arthropods introduced as classical biological control agents. The impacts of these agents are less understood than those of herbivorous insects and pathogens released against invasive plants. Releases of plant biocontrol agents are well documented (Winston et al., 2014), and population-level impacts of herbivorous biocontrol agents on native plants have been rare (Suckling and Sforza, 2014). Analysis of all 512 species known to have been released for weed biocontrol worldwide found no evidence of impact for 99% of the agents. Of the few known cases of impacts, most (>90%) were only of minor importance, without long-term harm to nontarget plant populations. Important population-level effects are known only in the cases of some thistle and cacti-attacking insects, principally *Cactoblastis cactorum* (Bergroth) (Figure 1A,B) on some native cacti (Figure 2) (Stiling et al., 2004; Pemberton and Liu, 2007) and *Rhinocyllus conicus* Fröelich (Figure 3) on some native thistles (Figure 4) (Louda, 1998; Louda et al. 2005). In contrast, for parasitoids and predators, whose actions are generally invisible to any but specialists, we have less information on population-level impacts. This has led to speculation that nontarget impacts are high, based largely on extrapolation from several

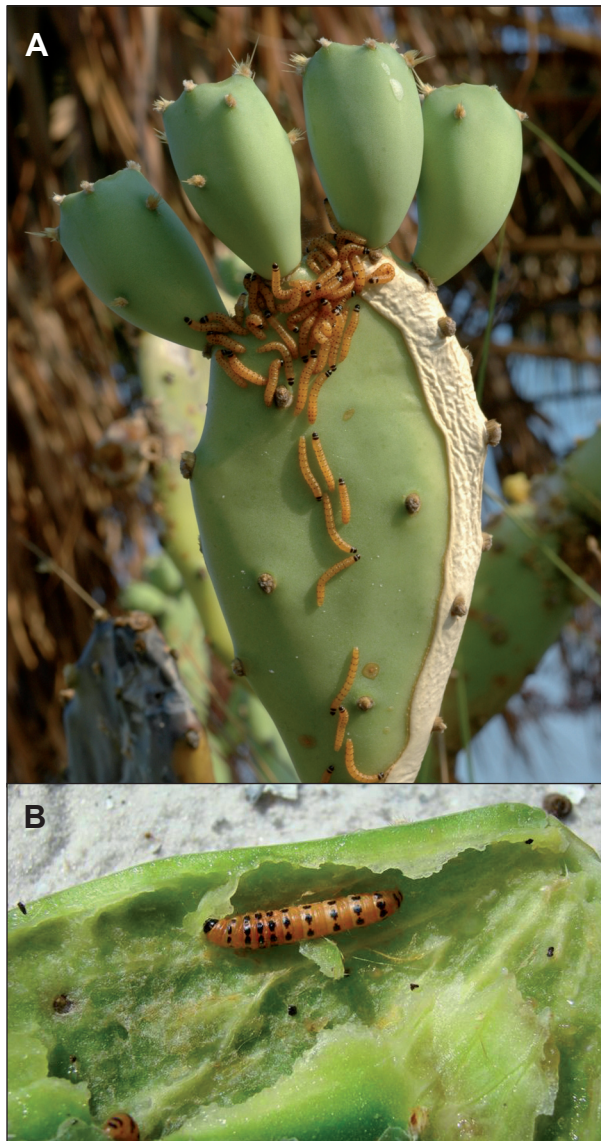


Figure 1. *Cactoblastis cactorum* larvae (A) (photo of Ignacio Baez, USDA Agricultural Research Service, Bugwood.org); feeding damage (B) (photo of Rebekah D. Wallace, University of Georgia, Bugwood.org).



Figure 2. *Opuntia hemifusa*, attacked by *Cactoblastis cactorum* in Florida (photo of Kristen E. Sauby).



Figure 3. An oligophagous thistle feeding weevil, *Rhinocyllus conicus* (photo of Eric Coombs, Oregon Department of Agriculture, Bugwood.org).



Figure 4. A rare native thistle, *Cirsium canescens*, fed on by *Rhinocyllus conicus* (photo of Irene Shonle).

cases of likely or presumed high-level impact, especially the coccinellid beetles *Harmonia axyridis* (Pallas) and *Coccinella septempunctata* (L.) (Harmon et al., 2007; Losey et al., 2007) and the tachinid flies *Compsilura concinnata* (Meigen) (Boettner et al., 2000) and *Bessa remota* (Aldrich) (Kuris, 2003; Hoddle, 2006), as discussed below.

Past summaries of impacts of parasitoids and predators on nontarget insects and mites include a mini-review for the island of Guam (Nafus 1993a); global literature reviews (Lynch and Thomas, 2000; van Lenteren et al., 2006), and a detailed analysis of releases of both weed and insect biocontrol agents in Florida (Frank and McCoy, 2007). Lynch and Thomas (2000) state that nontarget effects are recorded for 1.7% of the ca 5000 recorded cases of parasitoid or predator introductions (species x country releases of about 2000 natural enemy species), as detailed in the database “BIOCAT” (van Lenteren et al., 2006a). Of these 87 records ($87/5000 = 1.7\%$), most were recorded as causing only minor effects (that is, “host use” but not “population-level impact”).

Seventeen cases ($17/5,000 = 0.34\%$), however, were classified as causing population reductions or other severe impacts. (However, below, we show that some of these cases were in fact of no ecological concern). No credible cases of extinction were found; one such case is claimed by Howarth (1991), but see Hoddle (2006). For introduced parasitoids and predators successfully established in Florida (Frank and McCoy, 2007), grouping cases by 20-yr intervals (data from Table 4 in Frank and McCoy, 2007), found no detectable trend in either the average severity of impacts (categories 1 through 6) or the frequency of instances in high-impact categories suggestive of population-level effects; there were 2 to 5 such events per 20-yr period. No further reviews of nontarget effects of insect biocontrol have been published since 2007. Here we discuss known or alleged cases of nontarget impacts of parasitoid or predator introductions and review trends in host specificity of such agents since 1985 (Appendixes 1 and 2). We conclude with some caveats and recommendations.

TYPES OF IMPACTS

Several types of impacts of parasitoids and predators on nontarget arthropods have been discussed: (1) direct attacks on native insects, (2) negative foodweb effects, such as competition for prey, apparent competition, or displacement of native species, (3) positive foodweb effects that benefited nontarget species, (4) hybridization of native species with introduced natural enemies, and (5) attacks on introduced weed biocontrol agents. After discussing these categories as concepts, we describe instances of each in the section “How Common Have Population-Level Nontarget Effects Been.”

Type 1. Direct Attacks on Native Insects

The concept

Direct attack by a parasitoid introduced for biological control is shown by measuring rates of parasitism in a nontarget native species by the introduced natural enemy. Estimating the population-level consequence of various levels of parasitism is not easy (Van Driesche, 1983), but rates below 10% are probably of little importance, while high rates (>50%) may reduce populations. Actual impacts on long-term population densities, however, may vary depending on other factors present in the life system of a particular host and may vary among hosts, years, or geographic regions. For introduced predators, rates of predation are more difficult to determine because there is usually little evidence remaining of attacks (in contrast, parasitism can be measured more easily because hosts can be collected and parasitoids reared out). Once measured, predation rates, as with parasitism, require further analyses to estimate the likely population-level consequences (Van Driesche et al., 2008; Van Driesche, 2016).

Examples

Three examples of direct nontarget impact have been widely discussed in the literature, and the scientific documentation is best for these three parasitoids: *Compsilura concinnata* (Meigen) (Diptera: Tachinidae), *Microctonus aethioides* Loan (Hymenoptera: Braconidae), and *Trichopoda pennipes (pilipes)* (F.) (Diptera: Tachinidae). Details of these cases are discussed below individually because impacts vary spatially, temporally, or among nontarget species.

(a) *Compsilura concinnata*. *Compsilura concinnata* (Figure 5), released in North America in 1905, was one species among a large group of parasitoids and predators introduced against the gypsy moth (*Lymantria dispar* [L.]) (Lepidoptera: Erebididae), a defoliating forest pest (Fuester et al., 2014). *Compsilura concinnata* is a highly polyphagous tachinid fly, and at the time of its release was recognized as parasitizing >50 insect species (MacClaine, 1916; Culver, 1919),

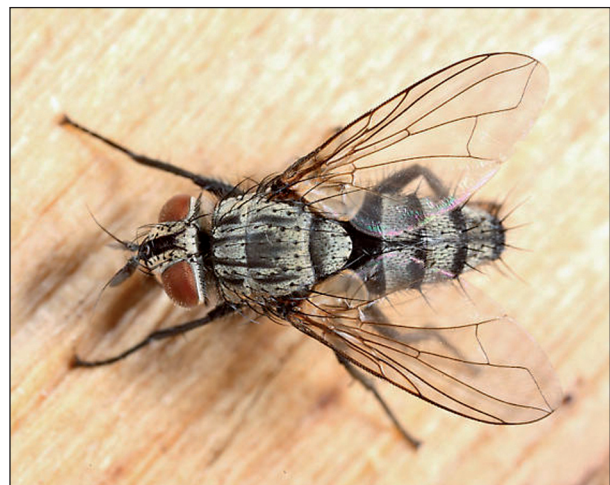


Figure 5. The polyphagous parasitic tachinid fly *Compsilura concinnata* (photo of Tom Murray).

a number now significantly increased to several hundred (Boettner et al., 2000). The highest rates of parasitism by this fly have been recorded on larvae of native saturniid moths—including silk moths (Figure 6A), (Boettner et al., 2000), buck moths (Figure 6B) (Stamp and Bowers, 1990), and the luna moth, *Actias luna* (L.) (Figure 6C) (Kellogg et al., 2003). Rates of parasitism vary within group and by region, and this fly has likely affected some nontarget species' populations in some areas, but not others (Parry, 2009).

For the buck moth *Hemileuca lucina* H. Edwards, Stamp and Bowers (1990) found attack rates in Massachusetts (USA) of 26 to 53%, which likely would reduce populations if sustained for several consecutive years. For *Hemileuca maia* (Drury), also in pitch pine habitats in Massachusetts, Selfridge et al. (2007) found low and inconsequential levels of parasitism by *C. concinnata*. In contrast, Boettner et al. (2000) found 36% parasitism by *C. concinnata* of this species in the same habitat, also in Massachusetts.

For luna moth (*A. luna*), experimental deployment of larvae at sites in Virginia by Kellogg et al. (2003) resulted in high levels of attack on some groups, particularly of older instars. Larvae were deployed on separate leaves, at four per small tree, and left in the field for one instar period only. Of all detected parasitism, 78% was caused by *C. concinnata*, and the level of parasitism suffered by deployed caterpillars varied from 0 to 62%, depending on instar and deployment date. The higher of these rates of attack, if sustained, might be sufficient to depress populations, and more information is needed to determine how attack rates vary over time, habitat, and location, and if densities of experimental cohorts affect outcomes.

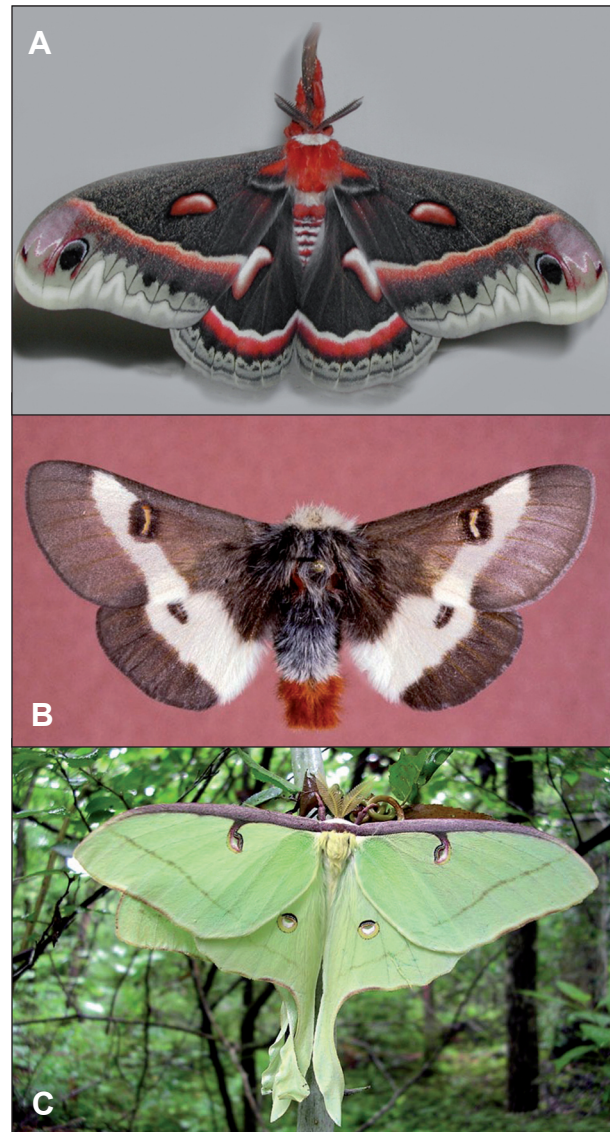


Figure 6. Some of the nontarget moths attacked by the tachinid *Compsilura concinnata*: the silkmoth *Hyalophora cecropia* (A) (photo of the Pennsylvania Department of Conservation and Natural Resources, Forestry Archive, Bugwood.org); the buck moth *Hemileuca maia* (B) (photo of Gerald J. Lenhard, Louisiana State University, Bugwood.org); and the luna moth, *Actias luna* (C) (photo of Tom Coleman, USDA Forest Service, Bugwood.org).

For giant silkmoths, some of North America's largest and most attractive moths, Boettner et al. (2000) found high levels of attack on cohorts of larvae of both promethia (*Callosamia promethea* Drury) and cecropia (*Hyalophora cecropia* [L.]) moths. For cecropia larvae placed five per tree in the field and left for their lifetimes, none (of 500) survived beyond the fifth instar. When individual instars were deployed for one instar period, *C. concinnata* parasitized 81% of the larvae in each of the first three instars. When larvae of *C. promethea* were deployed in groups of different sizes for 6 or 8 days, 70% and 66% of larvae, respectively, were parasitized by *C. concinnata*. These rates, if representative of nature, suggest a high level of impact on populations of these silk moths. Lower levels of attack (25-30%) on these same species are reported from New York by Parry (2009). Goldstein et al. (2015) report that the island of Martha's Vineyard (Massachusetts) retains an intact macrolepidoptera fauna that includes the imperial moth (*Eacles imperialis* Drury), a species that has declined or disappeared throughout much of New England, and Goldstein et al. (2015) related the persistence of this population to the absence of *C. concinnata* on Martha's Vineyard, as evidenced by tachinid captures in traps.

These studies collectively support the view that *C. concinnata* has had population-level impacts on several species of macrolepidoptera in the northeastern United States. Further documentation of the variation of this impact in time and space would be useful, especially contrasting areas with and without outbreaks of gypsy moth. Population modeling may provide useful insights here.

(b) *Microctonus aethioides*. Biotypes of this parasitoid (Figure 7A) were introduced into several countries for control of invasive pest weevils in forage crops, including the alfalfa

weevil, *Hypera postica* (Gyllenhal) (Figure 7B) in the United States in 1958 (Clausen et al., 1978; Kingsley et al., 1993); *Sitona discoideus* Gyllenhal (Figure 7A) in Australia in 1977 (Cullen and Hopkins, 1982; Waterhouse and Sands, 2001) and New Zealand in 1982 (Stufkens and Farrell, 1989; Barlow and Goldson, 1993); and *Sitona lepidus* Gyllenhal (Figure 7C) in New Zealand in 2005 (Gerard et al., 2007). These introductions successfully suppressed their target pests in all locations. Barratt and her co-workers have extensively investigated the effects of this parasitoid on native weevils in New Zealand and, to a lesser degree, Australia. No nontarget studies have been carried out with this species in the United States. In general, nontarget attacks were found in New Zealand (Barratt et al., 1997, 2007) on several native weevils, while no significant effects were found in Australia (Barratt et al., 2005, 2012). In New Zealand, laboratory tests found that a variety of native weevils (9 species) were attacked and yielded offspring (suggesting they were in the "physiological host range"), while field collections found 14 species of nontarget weevils that were parasitized, showing use under natural conditions (Barratt et al. 1997; Ferguson et al., 2016) (Figure 8). Extensive surveys covering altitudinal gradients in three locations collected 12,000 weevils comprising some 36 species, and, of these, eight weevil species were parasitized by *M. aethioides* (Barratt et al., 2007). Overall, parasitism of nontarget species was very low (~2%), but varied by region, collecting site, and season. Of nine sites surveyed, for six years, a moderately high level (24%) of parasitism was found for only one species of native weevil (*Nicaeana fraudator* Broun), at just one site. *Irenimus egens* (Broun), another species known to be susceptible to attack, was present at that site, at similar densities, but was attacked at a much lower rate.

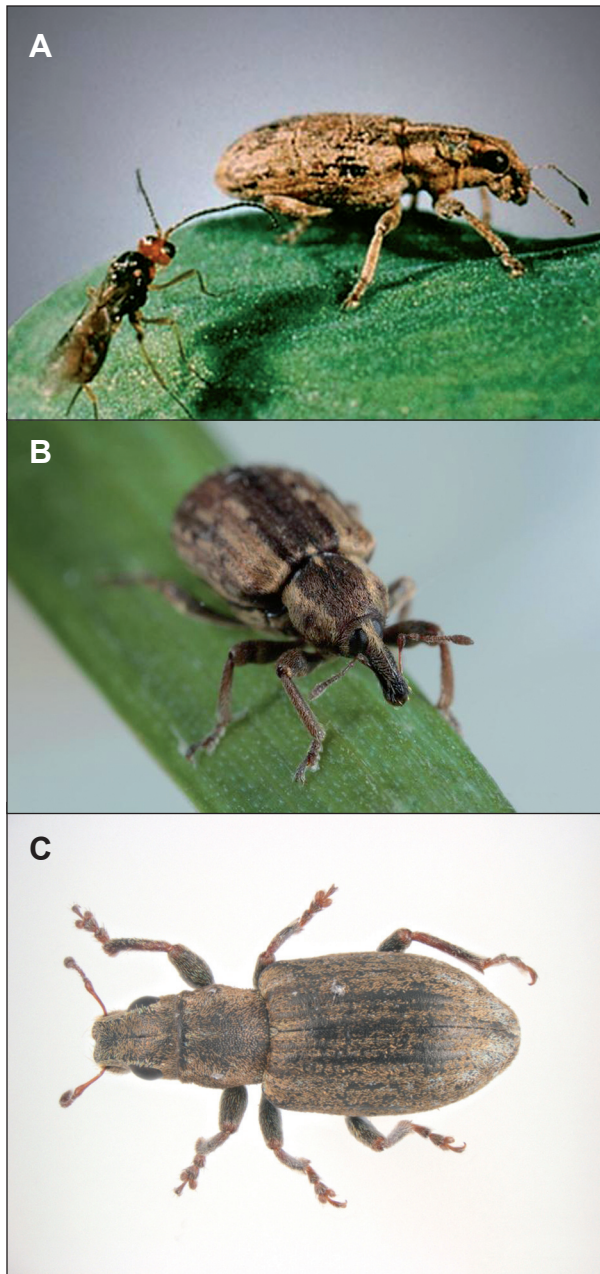


Figure 7. The braconid parasitoid *Microtonus aethiopoides* (A), an effective control agent for several pest weevils, including *Sitona discoideus* (A) (photo of Mark McNeill, AgResearch Invermay, Bugwood.org); *Hypera postica* (B) (photo of Joseph Berger, Bugwood.org); and *Sitona lepidus* (C) (photo of Pest and Diseases Image Library, Bugwood.org).



Figure 8. *Irenimus aequalis*, a native New Zealand weevil within the host range of *Microtonus aethiopoides* (photo of Caroline Harding, Ministry for Primary Industries, New Zealand).

Population models were developed for *N. fraudator* and used to estimate levels of population impact associated with particular levels of parasitism. The model indicated that field parasitism rates of 30% implied various levels of population impact depending on the weevil population's reproductive rate, being a 30% population reduction when reproduction rates were low but only an 8% reduction when reproduction rates were high (Barlow et al., 2004). Therefore, the level of parasitism sometimes seen in New Zealand on some species of weevils would likely have a greater impact on populations at higher altitudes, where rates of weevil reproduction (measured as intrinsic rate of increase) are lower.

In contrast to New Zealand, in southeastern Australia a survey by Barratt failed to find any evidence of significant impact on native weevils. Some 197 nontarget weevils, comprised of 29 species from 15 collection sites, produced just a single nontarget weevil (*Prosayleus* sp., Curculionidae: Entiminae: Leptopiini) parasitized by *M. aethiopoides* (Barratt et al., 2005). A second, later survey in Australia (Barratt et al., 2012) detected no further cases of nontarget parasitism.

(c) *Trichopoda pennipes (pilipes)*. Howarth (1991) correctly noted that the native Hawaiian “koa bug,” *Coleotichus blackburniae* White (Hemiptera: Scutelleridae) (Figure 9AB), was a suitable host for the egg parasitoid *Trissolcus basalis* Wollaston (Hymenoptera: Scelionidae) (Figure 10) (Davis, 1964; Shahjahan and Beardsley, 1973) and for the nymphal/adult parasitoid *Trichopoda pennipes (pilipes)* (Diptera: Tachinidae) (Figure 11), two species that were introduced into Hawaii in 1962 against the invasive pest stink bug *Nezara viridula* (L.) (Hemiptera: Pentatomidae) (Figure 9C). From these relationships and circumstantial evidence of decline of koa bug on Oahu following the introduction of these parasitoids (Figures 12, 13), Howarth (1991) assigned blame for this decline to the biological control project, particularly to the tachinid *T. pennipes (pilipes)*. However, a field investigation by Johnson et al. (2005) found only partial evidence in support of Howarth’s (1991) assertion (Figure 14). Johnson et al. (2005) measured parasitism of lifestages of koa bug in several habitats and found that egg parasitism due to *T. basalis* never exceeded 26% and was only detected at sites below 500 m and only on one host plant; in contrast, egg predation by a spider and several species of ants (accidental introductions) was as high as 87%. Parasitism of adult bugs by the tachinid *T. pennipes (pilipes)* was near zero at 21 of 24 sites, but did reach high levels (up to 70% of females and 100% of males) at three sites, where bug density was high, suggesting that dense populations of koa bug may no longer be ecologically possible because of density-dependent attacks by *T. pennipes (pilipes)* on koa bug aggregations.

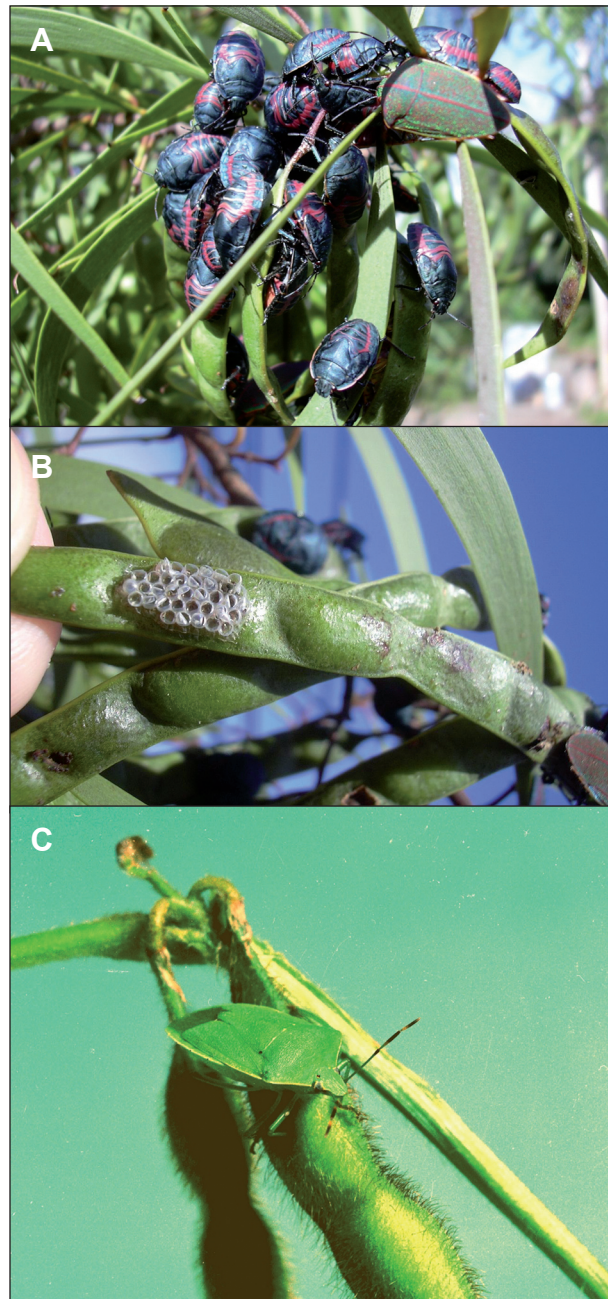


Figure 9. Koa bug, *Coleotichus blackburniae* (nymphs and one adult) (A) and its egg mass (B) (both photos of Forest and Kim Starr, Starr Environmental, Bugwood.org); *Nezara viridula* (C) (photo of Clemson University - USDA Cooperative Extension Slide Series, Bugwood.org).



Figure 10. *Trissolcus basalisis* (photo of David Reed, www.dreedphotography.com).

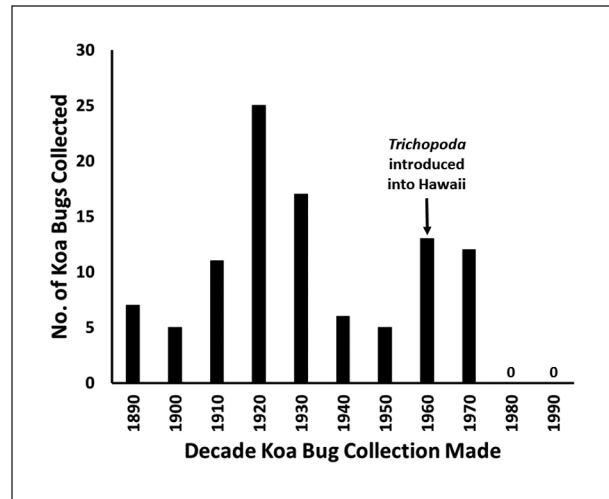


Figure 12. Numbers of koa bugs, *Coleotichus blackburniae*, added per decade to the insect collection at University of Hawaii, Honolulu (unpublished data of Adam Asqui).

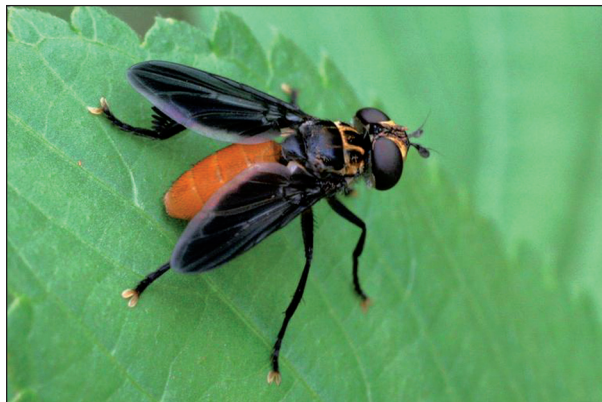


Figure 11. *Trichopoda pennipes (pilipes)* (photo of Russ Ottens, University of Georgia, Bugwood.org).

Taxon	N No. Parasitized %		
Alien Pentatomidae			
<i>Nezara viridula</i>	302	52	17.2
<i>Plautia stali</i>	160	7	4.4
<i>Thyanta custator accerra</i>	58	3	5.2
<i>Brochymena quadripustulatus</i>	62	1	1.6
<i>Eysarcoris ventralis</i>	3	0	0.0
Native Pentatomidae			
<i>Oechalia pacifica</i>	46	0	0.0
<i>O. virigula</i>	12	0	0.0
<i>O. virescens</i>	9	0	0.0
<i>O. grisea</i>	4	0	0.0
<i>O. patreulis</i>	4	0	0.0
<i>O. hirtipes</i>	3	0	0.0
Native Scutelleridae			
<i>Coleotichus blackburniae</i>	107	9	8.4

Figure 13. Numbers of *Trichopoda pennipes* eggs on Hawaiian museum specimens of various species of pentatomids and scutellerids collected between 1965 and 1995 (unpublished data compiled by Adam Asquith).

Insect species	Host plant	Elevation of sites (m)	No. sites w/bugs	No. sites w/parasitism	Percent parasitism ^a , mean per site ± SEM (no. sites)			
					Male adults	Female adults	Fifth instars	Fourth instars
<i>C. blackburniae</i>								
	<i>Dodonaea viscosa</i>	60-360	2	1	3.6 (1)	0 (1)	0 (1)	0 (1)
		600-1,100	5	4	31.2 ± 13.1 (3)	12.0 ± 7.4 (4)	18.5 ± 8.0 (3)	5.4 ± 3.2 (3)
		1,050-2,050	6	2	1.2 ± 0.8 (6)	0 (6)	0 (2)	0 (2)
	<i>Acacia confusa</i>	10-300	5	3	7.2 ± 6.0 (4)	5.3 ± 3.9 (4)	0.8 ± 0.5 (4)	0 (4)
	<i>Acacia koa</i>	760-1,200	5	2	0 (1)	0 (1)	0 (1)	0 (1)
		1,960	1	0	0 (1)	0 (1)	0 (1)	0 (1)
<i>N. viridula</i>								
	<i>Crotalaria</i> spp.	60-100	2	2	70.0 ± 13.3 (2)	47.1 ± 14.8 (2)	4.0 (1)	–
	<i>Ricinis communis</i>	800-1,000	2	2	40.2 ± 30.3 (2)	11.9 ± 9.5 (2)	–	–

^a Percent of bugs with *Trychopoda* eggs out of total number examined per site, excluding sites with fewer than six total bugs.

Figure 14. Rates of parasitism of *Trichopoda pennipes* on *Coleotichus blackburniae* on different host plants and at different elevations on the island of Hawaii, 1998-1999 (from Johnson et al., 2005; *Oecologia* 142: 529-540, redrawn with permission).

Putting direct attack by parasitoids in context

Whether the type of impact seen in the case of *C. concinnata* is rare or common is critical to determine if impacts of insect biocontrol agents are likely to harm populations of nontarget insects. While the above cases make it clear that nontarget attacks are possible (by species first used as biocontrol agents in 1905, 1958, and 1962, respectively) and that at certain times and locations these attacks may be of sufficient magnitude to locally reduce population densities, they don't clarify if such impacts are likely for agents released since nontarget effects of introduced arthropod agents for pest insect control became of concern (ca 1995) and better regulated. Below, in "How Common Have Population-Level Nontarget Effects Been?" we discuss a longer series of cases to put potential risk from introduced natural enemies to nontarget species into perspective.

Mitigation of direct attacks

Since ca 1995, requirements for determining the likely host ranges of insect biocontrol agents have increased in countries most commonly practicing insect biological control (Sheppard and Warner, 2016). Our summary of host range information on parasitoids introduced from 1985 to 2015 (Appendix 1) suggests a reduction in the proportion of agents with family-level specificity and an increase in agents with genus or better level of specificity. Few insect biological control agents, however, are monophagous, and most are likely to have host ranges that include some other species that are taxonomically related or ecologically similar to the target pest, which may be attacked, but likely at lesser degrees than the target pest. The key to mitigating direct impacts of introduced parasitoids and predators is to correctly estimate likely host ranges relative to the nontarget fauna (i.e., native species or valuable introduced species such as weed biocontrol agents) in the area of release. The goal is not to avoid all host use, but to avoid damaging population-level effects on nontarget species.

Type 2. Negative Food Web Effects

The concept

Introduced species can affect native species through food webs (Holt and Hochberg, 2001). In some cases, they may directly attack native species, but the level of such attack may be significantly increased by the introduced species' ability to maintain larger populations by attacking, but not suppressing, the target pest or other species, a situation termed *apparent competition*. In other cases, the introduced species never (or rarely) attacks nontarget species, but their populations are still reduced through competition with the introduced natural enemy for food or hosts, a situation often termed *displacement*.

Apparent competition grades into simple direct attack and may be difficult to recognize except by an enhanced level of impact when the natural enemy is in association with the other host. For example, *C. concinnata* directly parasitizes larvae of various native moths and butterflies, as discussed above, but *C. concinnata* numbers, and hence the numbers of such attacks, are likely to rise and fall with the local density of gypsy moth, the target host. Here we have arbitrarily considered this case as one of simple direct attack because the link to gypsy moth densities, while quite likely, is supported by only very limited data (Redman and Scriber, 2000). A better example of apparent competition by an introduced biological control agent is that of *Cotesia glomerata* (L.) (Hymenoptera: Braconidae), *Pieris rapae* (L.), and *Pieris oleraceae* Harris (both Lepidoptera: Pieriidae) in southern New England, as discussed below (Benson et al., 2003a; Van Driesche et al., 2003; Herlihy et al., 2014).

Displacement of one species of parasitoid by another introduced later has been observed during biological control projects (DeBach and Sundby, 1963; Bennett, 1993; Herlihy et al., 2012). This has generally been viewed as a favorable process, as each more efficient parasitoid drives the invasive host insect to lower levels and excludes less efficient biocontrol agents. However, if

the displaced species are native parasitoids exploiting exotic pests, this could be viewed as an undesirable impact on a native species whose "commonness" declines due to the introduced agent. However, such observations typically are made in the context of studies of mortality of the introduced pest insect, often in a crop. Decline of a native parasitoid (or predator) from former abundance on a non-native host on an introduced crop plant is not by itself evidence of significant ecological impact because both the host and its crop habitat are an artificial human construct. The important question is whether or not the superior introduced parasitoid displaces the native parasitoid from its native hosts in natural habitats. Unfortunately, because the focus of most studies is on pests on crops, observations of displaced native parasitoids in non-pest hosts in native habitats are rare and should receive more emphasis. Therefore, further study is needed to determine the status of affected native parasitoids in non-crop habitats.

(a) Apparent competition. This interaction is named apparent competition because superficially after a new herbivore arrives, a related local native herbivore begins to decline, making it appear as if the invasive species is competing with the native one for some resource, while in reality the negative population impacts on the native species are mediated through unequal effects of a shared natural enemy. Evidence for apparent competition has been sought in a variety of systems in which one member of a pair of herbivores is invasive and one native, and the parasitoid attacking them both is a local native species. Apparent competition has been found in some cases (Péré et al., 2010) but not others (e.g., Péré et al., 2011).

The link to biological control is the subset of apparent competition cases in which the parasitoid (or predator) mediating the interaction is a species introduced for classical biological control of the non-native member of the herbivore pair. Few such cases have been documented, possibly because of a lack of work in this area. Redman and Scriber (2000) noted that if they

artificially deployed larvae of the butterfly *Papilio canadensis* (Rothschild and Jordan) (Lepidoptera: Papilionidae), those larvae placed near gypsy moth populations suffered higher rates of parasitism (45%) (mostly from *C. concinnata*) than larvae deployed in areas without gypsy moths (16%). This difference was statistically significant, although there was no significant effect on the percentage of larvae reaching the adult stage (3.8% vs. 4.3%), suggesting the action of some compensatory mechanism later in the life cycle.

A well documented instance of apparent competition due to a biological control agent is that of the parasitoid *C. glomerata* (Hymenoptera: Braconidae) (Figure 15A), introduced to control

the invasive brassica pest *P. rapae* (Figure 15B). This parasitoid appears to have caused the decline of a related native white butterfly, *P. oleracea* (formerly *Pieris napi oleracea*) (Figure 15C) in Massachusetts, but not in northern Vermont (USA) due to differences in voltinism (Benson et al., 2003a; Van Driesche et al., 2003; Herlihy et al., 2014). Interestingly, this effect was later reversed by *P. oleracea*'s use of a non-native host plant (Herlihy et al., 2014) and the displacement of *C. glomerata* from its position as the dominant parasitoid of *P. rapae* in crops by the introduction of *Cotesia rubecula* (Marshall) (Figure 15D), another biological control agent that is a specialized parasitoid of *P. rapae* (Herlihy et al., 2012).

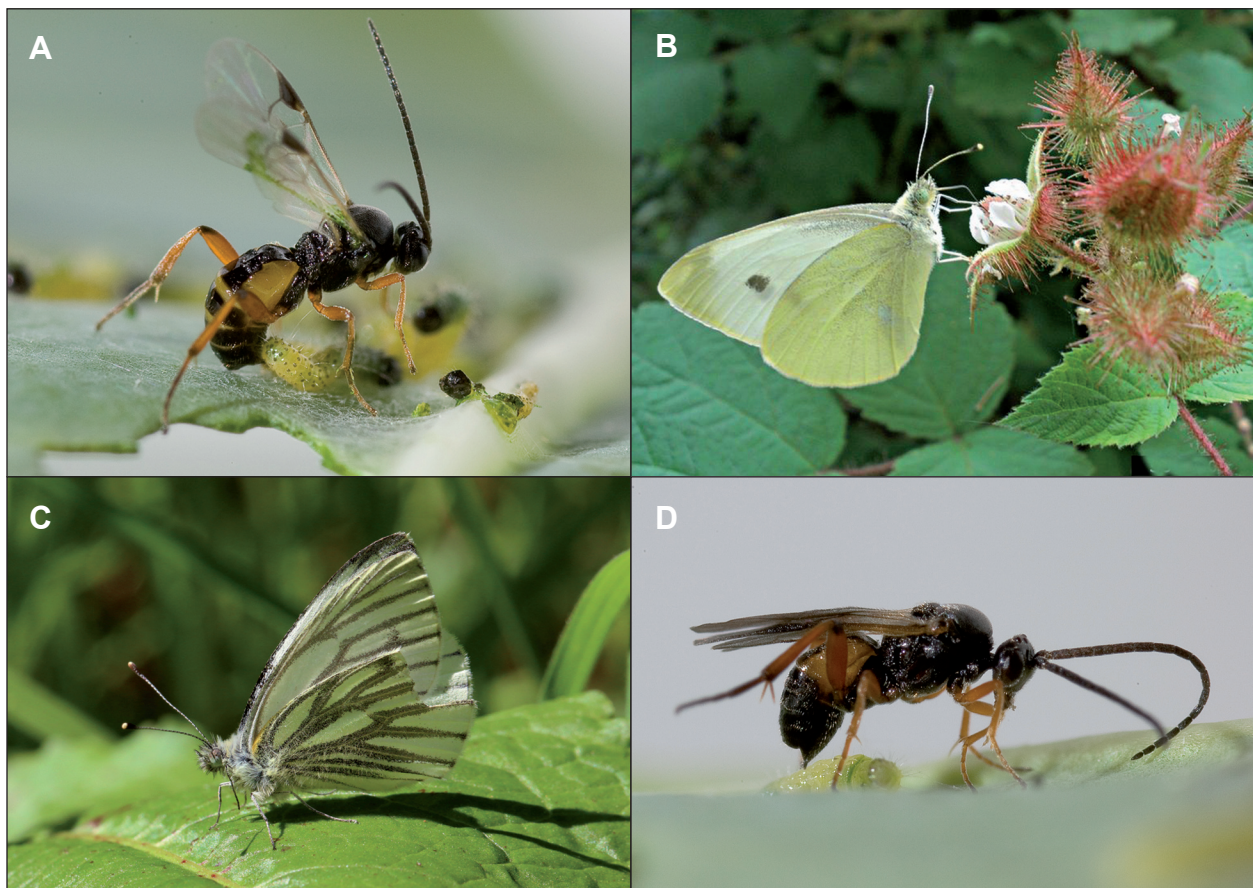


Figure 15. A case of apparent competition: *Cotesia glomerata* (A) (photo by Hans Smid /Bugsinthepicture.com) is an introduced parasitoid in North America of both the invasive butterfly *Pieris rapae* (B) (photo: Ansel Oommen, Bugwood.org) and of the native *Pieris oleracea* (C) (from [https://commons.wikimedia.org/wiki/File:Green-veined_white_butterfly_\(Pieris_napi\)_underside_worm_first.jpg](https://commons.wikimedia.org/wiki/File:Green-veined_white_butterfly_(Pieris_napi)_underside_worm_first.jpg)); *Cotesia rubecula* is another introduced, but more specific, parasitoid of *P. rapae* (D) (photo by Hans Smid/Bugsinthepicture.com).

(b) Displacement via competition for prey.

Perhaps the best-studied example of displacement of native species by introduced predators is the case of two introduced ladybird beetles, *H. axyridis* (Figure 16A) and *C. septempunctata* (Figure 16B), in North America and Europe (*H. axyridis* only). In North America, these species replaced native ladybirds as the common species in a wide variety of crops, causing formerly common native ladybirds to become rare at the study locations (Wheeler and Hoebeke, 1995; Elliott et al., 1996; Turnock et al., 2003; Harmon et al., 2007; Fothergill and Tindall, 2010). Among

the most widely affected species were *Adalia bipunctata* (L.) (Figure 16C) and *Coccinella novemnotata* Herbst. (Figure 16D). More recently, the invasion in Europe of *H. axyridis* has also begun to affect native ladybirds there (Brown et al., 2011). To explain why displacement of native ladybird species happened, several mechanisms have been proposed and to some extent tested, including direct predation effects on native ladybirds (“intraguild predation” or IGP), apparent competition mediated by pathogens, and displacement due to reduction of available prey in sampled habitats.

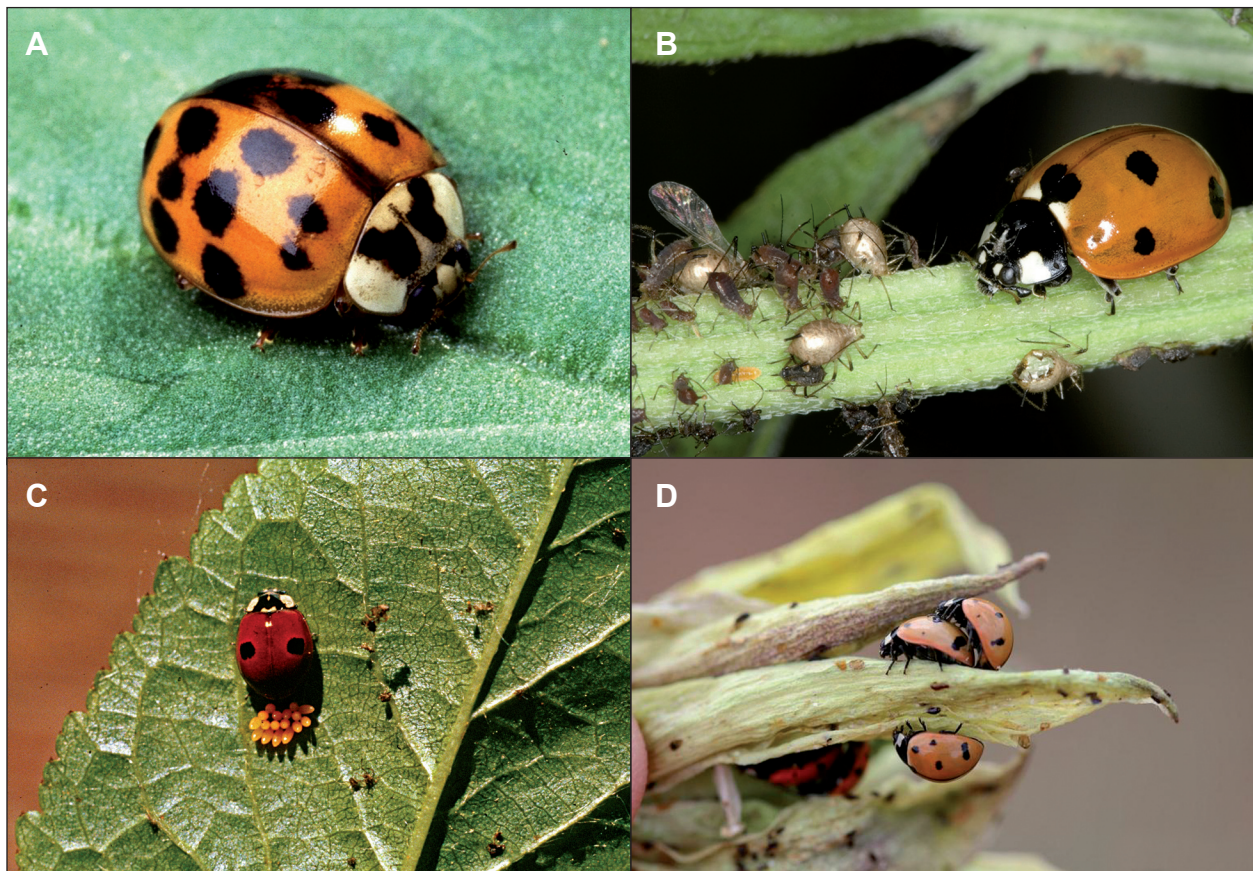


Figure 16. Two introduced coccinellids (A and B) and two of the native species they displaced (C and D): *Harmonia axyridis* (A) (photo of Scott Bauer, USDA Agricultural Research Service, Bugwood.org); *Coccinella septempunctata* (B) (photo of David Cappaert, Michigan State University, Bugwood.org); *Adalia bipunctata* (C) (photo of Whitney Cranshaw, Colorado State University, Bugwood.org); *Coccinella novemnotata* (D) (photo of Whitney Cranshaw, Colorado State University, Bugwood.org).

Asymmetrical IGP effects (ones that are more severe on the native species) have been demonstrated, showing that larger non-native species often have the advantage over smaller native ones (Snyder et al., 2004; Katsanis et al., 2013). However, while asymmetrical IGP is well demonstrated (Gagnon et al., 2011), whether it has caused population declines of native species is not. Limited attempts to test IGP as the factor responsible for the decline in native ladybirds in crops have not supported the idea (Smith and Gardiner, 2013).

Another possible mechanism, apparent competition mediated by a pathogen, is a novel idea supported by one study (Vilcinskas et al., 2013). In Europe, the microsporidian *Nosema thompsoni*, found in but harmless to *H. axyridis*, is lethal to *C. septempunctata*, a local native species. When *C. septempunctata* adults or larvae eat eggs or larvae of *H. axyridis*, they die. There is no evidence that pathogens associated with non-native ladybirds affect additional native species of North American or European ladybirds, but this possibility merits investigation.

The third possible mechanism postulated for disappearance of native species following the appearance of non-native ladybirds is that these competing species drive densities of shared prey to levels too low to support the native species. For example, Mizell (2007) states that *H. axyridis*' presence on crape myrtle (*Lagerstroemia indica* L.) in northern Florida 8-9 years after its arrival was associated with much lower abundances of both the main aphid on the plant, *Sarucallis kahawaluokalani* (Kirkaldy), and of various native ladybirds, especially *Hippodamia convergens* (Guérin-Méneville), *Olla v-nigrum* (Mulsant), *Coleomegilla maculata* (DeGeer), *Cycloneda sanguinea* L., and *Cycloneda munda* (Say), suggesting that low prey density on crape myrtle plants exposed to *H. axyridis* may have been insufficient to attract or support the native species. Similarly, Alyokhin and Sewell (2004) recorded both a substantial reduction in aphid density and of

two native ladybirds (*Coccinella transversoguttata* Brown and *Hippodamia tredecimpunctata* [Say]) in potatoes in Maine following the arrival of *H. axyridis* in the region, circumstantially implicating loss of prey as an important factor in the observed decline of the native species. In alfalfa, the decline of various native ladybirds may also be due to a decline in the density of pea aphid (*Acyrtosiphon pisum* Harris) (Evans, 2004; Day and Tatman, 2006), an invasive insect that was brought under biological control through introductions of parasitoids, especially *Aphidius ervi* Haliday (Hymenoptera: Braconidae), released first in the eastern United States in 1959 (Angelet and Fuester, 1977).

The hypothesis of displacement due to competition for prey has as a corollary that either native habitats or some particular subset of agricultural habitats may remain suitable for the declining native species. Consequently, surveys for native ladybird beetles have concentrated on surveying for native species in such locations. For example, in western South Dakota and Nebraska, Bartlett et al. (2015) found reproducing populations of one highly suppressed native species, *C. novemnotata*, in sparsely vegetated small-grain fields.

A second corollary of prey-depletion as the cause of decline of native ladybird beetles in crops is that if aphid densities in such crops rebound for any reason, the native ladybird beetles should recolonize such cropping areas. This was confirmed by Evans (2004) in Utah using perturbation experiments in alfalfa fields, conducted after the invasion of the region by *C. septempunctata* in 1992-2001, which had been associated with declines of native ladybirds in alfalfa. This decline in native ladybirds paralleled declines in pea aphids, the ladybirds' principal prey in alfalfa. Artificially induced outbreaks of pea aphids caused native ladybirds to rapidly re-accumulate in alfalfa, until *C. septempunctata* again suppressed pea aphid numbers. In Maine, Finlayson et al. (2008) surveyed ladybirds and found native species to be present in both native

vegetation and crops, but at low densities in both. The ability of native ladybirds to reach high densities in native habitats would require both the presence there of a high-density prey species and the absence of the highly competitive non-native ladybirds. Hesler and Kieckhefer (2008) surveyed putative native ladybird habitats (fields and areas of woody vegetation) in South Dakota but found that the targeted native ladybirds were rare in the habitats surveyed and that both *H. axyridis* and *C. septempunctata* were present in many of the putative refuge habitats. In contrast, Bahlai et al. (2015), analyzing a 24-yr data set from Michigan (with larger acreage of semi-natural forest habitats than South Dakota), found that only two species of ladybirds showed statistically significant declines (*A. bipunctata* and *C. maculata*) after the establishment of these two exotic ladybird species. They also found that in semi-natural forested habitats ladybird assemblages were unique in both composition and variability from those in crop fields and concluded that such forested areas acted as refuges for native coccinellids.

The sum of evidence suggests that these two non-native coccinellids, *H. axyridis* and *C. septempunctata*, have greatly lowered the abundance of several native ladybirds in agricultural fields. While the same native coccinellids also seem rare in natural habitats, earlier estimates of their abundance there are lacking, and we cannot, therefore, know if significant changes have occurred in those habitats. Finally, a question not yet raised by researchers on this topic is whether the density of these native coccinellids in crops, where they previously exploited high density prey species that were often themselves invasive, is the right benchmark against which to measure impacts, or if a more appropriate standard might not be densities of native coccinellids in non-crop habitats (e.g., native forests or grasslands) where these native ladybirds presumably exploited native prey.

(c) Displacement via competition among parasitoids for hosts. Introduced parasitoids may displace local species (either native or previously introduced species) if they are more efficient at exploiting hosts (see examples below, “Group 3. Displacement or Other Indirect Impacts”). There is, however, no clear well-documented example in which an introduced parasitoid has had dramatic population-level impacts on a native parasitoid where it is acting on its native hosts in their native habitat. Rather, displacement has only been documented in crops, where an introduced parasitoid displaces native parasitoids that are usually exploiting invasive hosts. However, one case exists where such displacement of native parasitoids from native hosts is likely to have occurred but has not yet been adequately documented: the release of the American braconid *Lysiphlebus testaceipes* (Cresson) (Figure 17) in Europe. This aphid parasitoid (attacking mostly species in the Tribe Aphidini [pers. comm., Starý]) was introduced (1973-74) from Cuba to France for control of pest aphids in citrus (Starý et al., 1988a). In addition to providing control of the target pests, *L. testaceipes* spread into non-crop habitats and became the



Figure 17. The New World aphid parasitoid *Lysiphlebus testaceipes* after its introduction to Europe parasitized many species of native aphids, mostly in the Tribe Aphidini in a wide range of natural habitats (photo of Peter Bryant).

dominant parasitoid on a number of native aphids inhabiting various types of vegetation, including forests (Starý et al., 1988a). The list of aphid species parasitized by *L. testaceipes* increased as it spread, reaching at least 32 by 1986 (Starý et al., 1988b), and continued to increase as the parasitoid's range expanded into the Iberian Peninsula (Starý et al., 2004). In southeastern Europe, a total of ten host species were recorded (among 115 aphid species sampled from 422 plant species), and this parasitoid was found principally on species of *Aphis* (*A. craccivora* Koch, *A. fabae* Scopoli, *A. nerii* Boyer de Fonscolombe, *A. ruborum* [Börner], *A. urticata* Gmelin, *A. gossypii* Glover, *Aphis* sp.), but also occurred on species in *Rhopaloshihum* and *Toxoptera* (Kavallieratos et al., 2004). It is possible that *L. testaceipes*, which attacks many native European aphids in various habitats, may suppress some species of native parasitoids exploiting native hosts in native habitats. However, this has not yet been documented, in part because the collection of information on the native aphid parasitoids—their presence, abundance, phenology and host ranges—requires an extremely high level of taxonomic training and ecological knowledge and several years of work to understand temporal and spatial effects.

(d) Parasitoid host shifts caused by competitive displacement. *Diachasmimorpha tryoni* (Cameron) (Hymenoptera: Braconidae) (Figure 18A), a parasitoid of frugivorous tephritids, attacked larvae (Figure 18B) of the lantana gall fly (*Eutreta xanthochaeta* Aldrich [Diptera: Tephritidae]) (Figure 18C), in the laboratory but did not do so in the field in Hawaii after its release until a superior competitor, *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae), was introduced. After that release, competition apparently caused *D. tryoni* to shift onto lantana gall fly, which was a more available host in the presence of *F. arisanus* (Messing and Wang, 2009).

Putting risk in context

Polyphagous and oligophagous parasitoids likely pose risk to native parasitoids. Documenting such events, however, is difficult because of the high level of taxonomic skill needed to separate parasitoid species and make sense of the survey results. Projects assessing these types of nontarget effects, especially population-level consequences, require work spanning several consecutive years with study sites that are representative of the various habitats within which the agents of interest are operating.

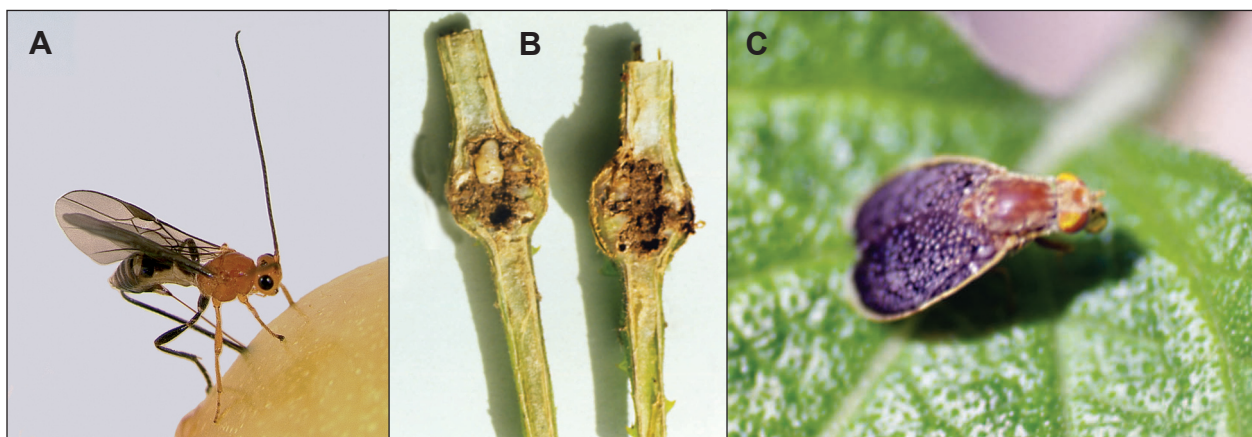


Figure 18. A field host-switch by *Diachasmimorpha tryoni* (A) (photo of Russell Messing) towards use of larvae inside galls (B) (photo of Jian Duan) of the lantana gall fly, *Eutreta xanthochaeta* (C) (photo of Jian Duan), was driven by the introduction of *Fopius arisanus*, a superior parasitoid attacking frugivorous tephritids.

Mitigation

Looking forward, regardless of what past introductions may have done, the solution to minimize unwanted nontarget effects is to introduce parasitoids with narrow host ranges, as estimated by adequate pre-release testing in quarantine and, if reliable data are available, host use in the natural enemy's area of origin.

Type 3. Beneficial Food Web Effects

Beneficial indirect effects on native species can also follow biological control of invasive pest insects. Schreiner and Nafus (1993) observed population increases of native moths following biological control of *Penicillaria jocosatrix* Guenée (Lepidoptera: Noctuidae) on mango in Guam by the tachinid *Blepharella lateralis* Macquart. Pest suppression led to a large increase in flowering by mango which caused several native moths to increase in abundance because this resource had improved.

In Queensland, Australia, biological control of invasive crop-pest scales (*Ceroplastes destructor* Newstead and *Ceroplastes rubens* Maskell [both Hemiptera: Coccidae]) provided benefits in forest

ecosystems by reducing densities on native forest plants of invasive ants that were attracted to honey dew produced by invasive scales (Figures 19a and 19b). Uncontrolled scale populations tended by invasive ants reduced vigor of forest plants and decreased use of plants by larvae of native lycaenid butterflies, such as *Hypochrysops miskini* (Waterhouse) and *Pseudodipsas cephenes* Hewitson. These native butterflies must be tended by native ants, and invasive ants disrupt this important mutualism (as described by Sands in Van Driesche et al. [2010], with further details in Waterhouse and Sands [2001]).

In Tahiti, invasion (due to movement of infested plants) of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) (Figure 20A), posed a significant risk for native spiders (Figures 20B,C), for whom this hyper-abundant sharpshooter proved to be a poisonous prey (Suttle and Hoddle, 2006). Biological control of the invader by release of the mymarid egg parasitoid *Gonatocerus ashmeadi* Girault (Figure 20D) greatly reduced the pest's densities (Grandgirard et al., 2009), which subsequently lowered this threat to native spiders.

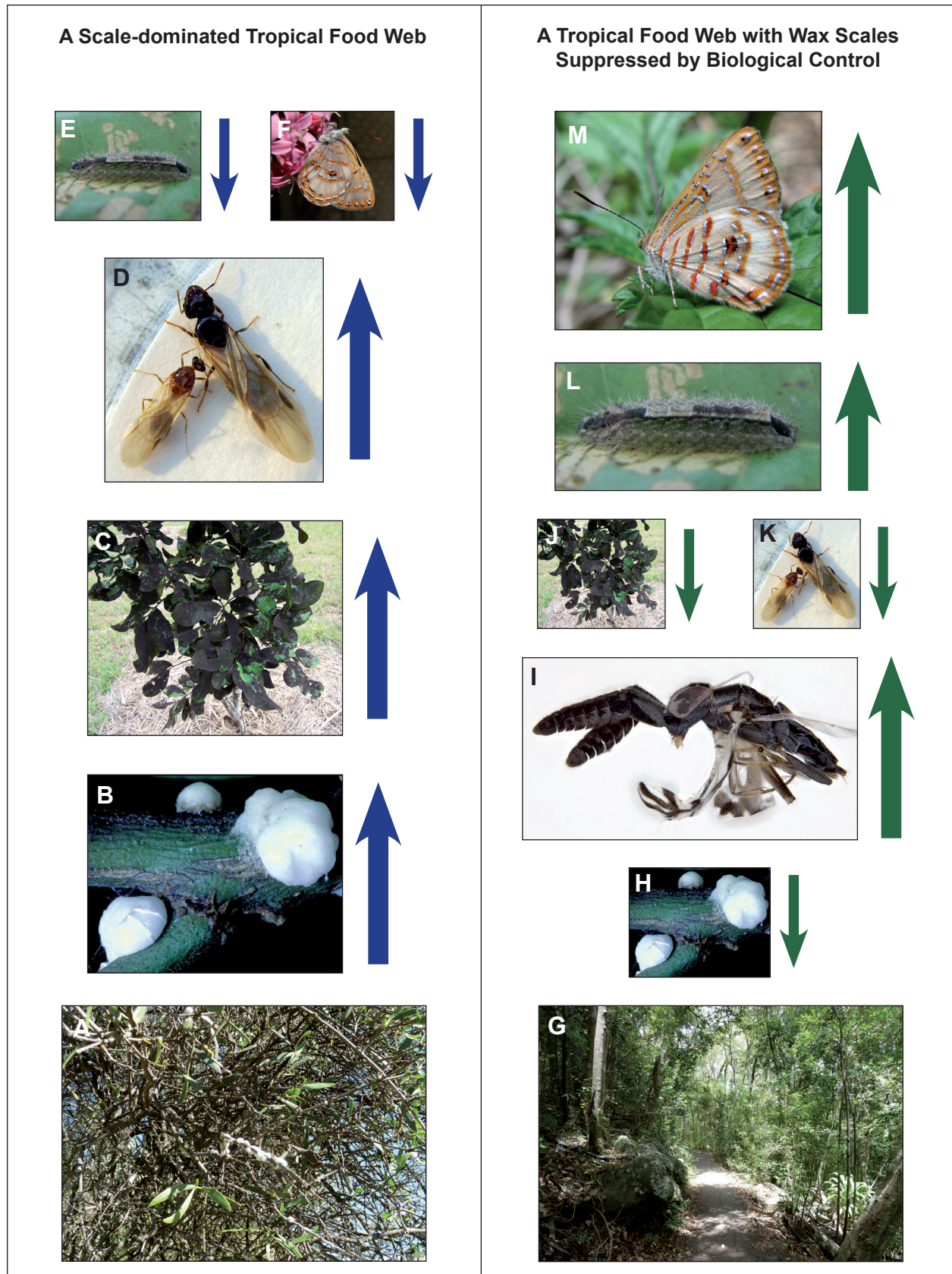


Figure 19a. See caption on next page.

Figure 19a. Food web before scale biocontrol (left): Native Australian rainforest plants defoliated by an invasive scale (A) (photo by Don Sands)—close up of scale (B) (photo by Rosa Henderson, Landcare Research, Bugwood.org)—were the consequence of the invasion of the white wax scale, *Ceroplastes destructor*, in preserved natural areas in Queensland. Dense scale populations produced copious sugary waste, leading to coverage of foliage by sooty mold (C) (photo of Don Sands), which was attractive to the invasive big-headed ant, *Pheidole megacephala* (D) (photo of R.H. Scheffrahn, University of Florida). Big-headed ant foraging made plants unsuitable for feeding by the larvae of several native lycaenids (E) (photo of Bob Miller, Bobsbutterflies.com.au), including the coral jewel, *Hypochrysops miskini* (F) (photo of Bob Miller, Bobsbutterflies.com.au). Direction of arrow denotes increase (up) or decrease (down) of population, and size of arrow suggests the magnitude of the change.

Food web after scale biocontrol (right): Foliage quality of native plants in rainforests formerly affected by wax scale improved (G) (photo of Don Sands) following reduction in density of the invasive scale (H) (photo by Rosa Henderson, Landcare Research, Bugwood.org) caused by the introduction of a biocontrol parasitoid, *Anicetus nyasicus* (I) (photo of Museums Victoria, Australia). Lower scale density reduced honeydew and sooty mold contamination of foliage (J) (photo of Don Sands), which reduced density of big-headed ant, *Pheidole megacephala*, foragers (K) (photo of R.H. Scheffrahn, University of Florida). These changes improved the health and foliage quality of native plants and the absence of big-headed ant foraging made native plants' foliage suitable for feeding of larvae of native lycaenids (L) (photo of Bob Miller, Bobsbutterflies.com.au), leading to recolonization and population expansion of the coral jewel, *Hypochrysops miskini* (M) (photo of Bob Miller, Bobsbutterflies.com.au) at Burleigh Head National Park in Queensland.

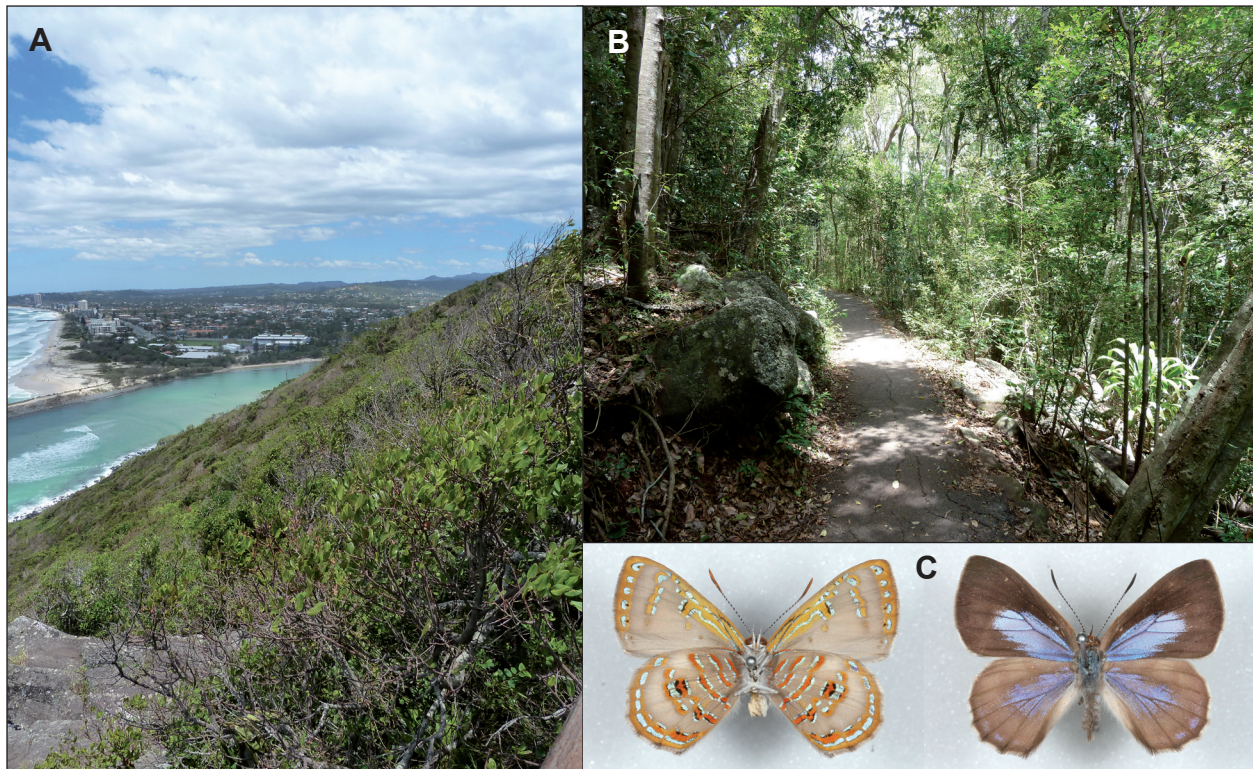


Figure 19b. Burleigh Head, a national park in Queensland in a built-up coastal area, lost several species of native blue butterflies due to ant-tending of wax scales on butterfly host plants (A,B). Lost species included the coral jewel (C) (all photos of Don Sands).

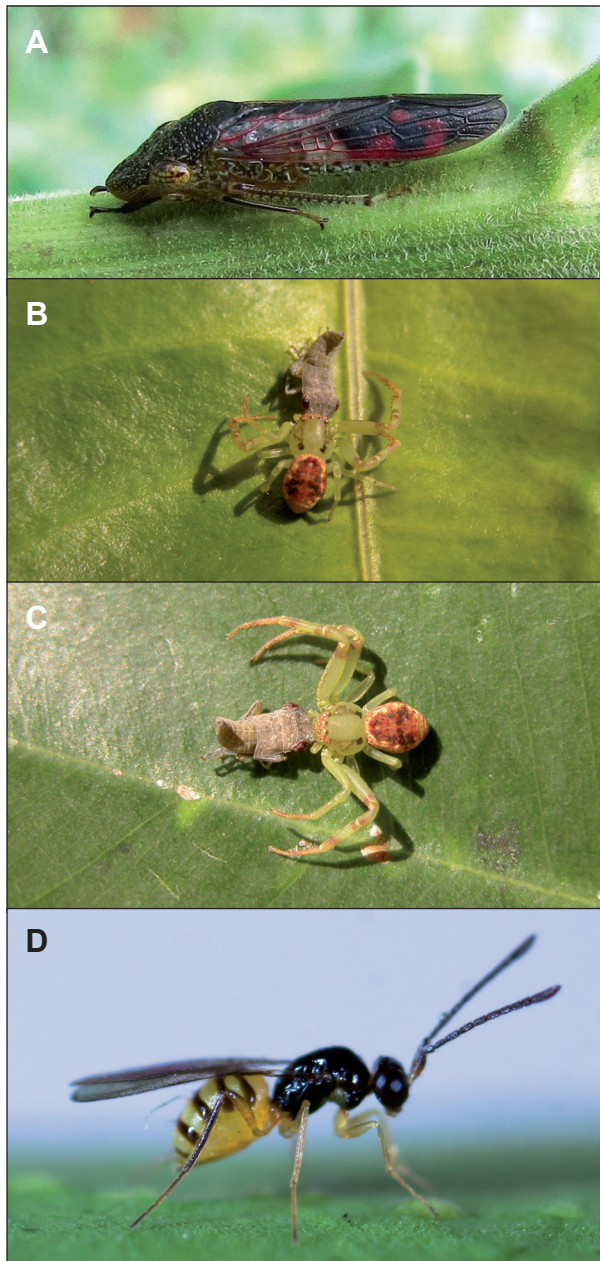


Figure 20. The toxic effect of an invasive leafhopper, *Homalodisca vitripennis* (A) (photo of Charles Ray, Auburn University, Bugwood.org), leading to extensive mortality of native spiders of Tahiti (B shows a crab spider, *Misumenops mellolaito*, attacking a glassy wing sharpshooter and C shows a colonial orb weaver, *Cyrtophora moluccensis* lies, lying dead, having fallen from its web after eating a sharpshooter) (photos of Kenwyn Suttle). The harm to spiders was eliminated when a biological control agent, *Gonatocerus ashmeadi*, was released that greatly suppressed sharpshooter densities (D) (photo of Mike Lewis, Center for Invasive Species Research, University of California Riverside).

Type 4. Hybridization with Native Congeners

The concept

Natural enemies may sometimes be introduced into areas that contain closely related species that may have different host or prey ranges. If these species have been geographically separated, they may lack the pre-mating barriers needed to sustain their separate species identities, and inter-species mating may occur, leading to hybridization and genetic introgression. Hybridization is common in some groups in nature. For example, the eastern and Canadian tiger swallowtails (*Papilio glaucus* L. and *Papilio canadensis* Rothschild & Jordan), whose distributions are generally distinct, have a hybrid zone along their common border (Mercader et al., 2009).

When individuals of distinct species mate, several outcomes are possible: (1) Mating may occur but be infrequent due to differences in habitat or host plant affiliations, allowing separation of the species even in partial sympatry. In this case a stable, low rate of hybridization may occur due to overlap, accidents, or chance where the species' distributions overlap. This outcome is probably of little or no ecological consequence; (2) In other cases, there may be substantial contact between the species due to similarity in habitat, and mating may be relatively frequent. If offspring are infertile, there may be selection on mating behaviors to reduce the rate of hybridization over time; and (3) If overlap is substantial, selection for pre-mating segregation is ineffective due to lack of variation in mating behaviors, and offspring are fertile, species may fully introgress with each other and one or both species may cease to exist in their previous taxonomic status, leading to a reduction in biodiversity.

Examples

Several examples of hybridization are discussed in the literature for insect biocontrol agents and they are discussed here.

(a) *Chrysoperla* lacewings. Green lacewings are widely mass produced and sold to home gardeners and commercial growers by insectaries. The most commonly sold forms are European or Asian populations of *Chrysoperla carnea* (Stephens) (Figure 21A), which are part of a species complex. Such sales have potential to bring commercialized forms into contact with similar, but locally distinct lacewings. In such cases, there is an opportunity for hybridization. For example, in laboratory studies, the Japanese endemic species *Chrysoperla nipponensis* (Okamoto) (a member of the *C. carnea* complex) (Figure 21B), readily hybridized with the commercially marketed exotic form of *C. carnea* (Naka et al., 2005, 2006). For this reason, regions with rare or endemic green lacewings may want to prohibit importing closely related, exotic green lacewings from commercial sources (see Henry and Wells, 2007).

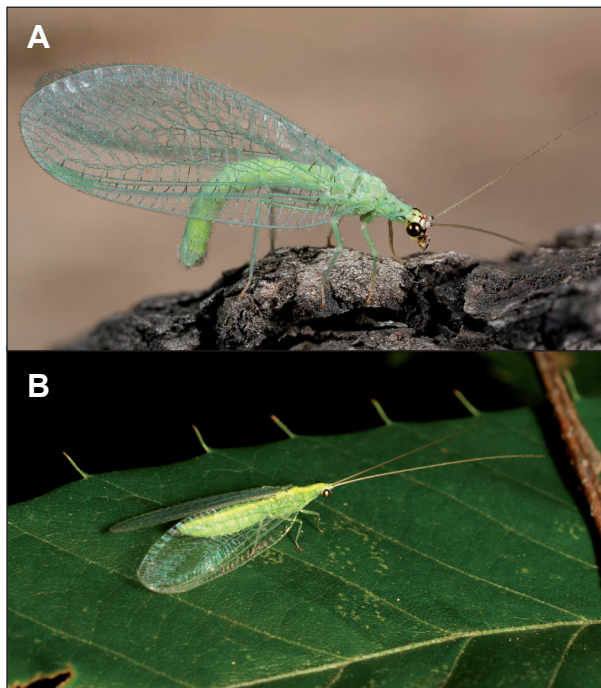


Figure 21. Releases of mass-produced species such as *Chrysoperla carnea* (A) (photo by Joseph Berger, Bugwood.org) may harm closely related native species, such as *Chrysoperla nipponensis* (B) (photo by Nigel Stott, natural-japan.net).

(b) Chestnut gall wasp parasitoids. The Chinese gall wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) (Figure 22B) is a pest of chestnuts (*Castanea* spp.) that has invaded Japan and other areas. The Chinese parasitoid *Torymus sinensis* Kamijo (Hymenoptera: Torymidae) (Figure 22A) was introduced into Japan to suppress *D. kuriphilus*, where it came into contact with a closely related native Japanese species, *Torymus beneficus* Yasumatsu & Kamijo (Hymenoptera: Torymidae), of which two biotypes have been recognized. The introduced parasitoid subsequently hybridized with both of the two native biotypes at rates of about 1% (for the early-spring biotype) and 20% (for the later-spring biotype) (Yara et al., 2010). However, despite this difference in hybridization rates, both biotypes of *T. beneficus* were eliminated in Japanese chestnut orchards (Yara et al., 2007; Yara, 2014), suggesting that the mechanism of elimination was not solely hybridization but more likely due to displacement through competition for hosts.

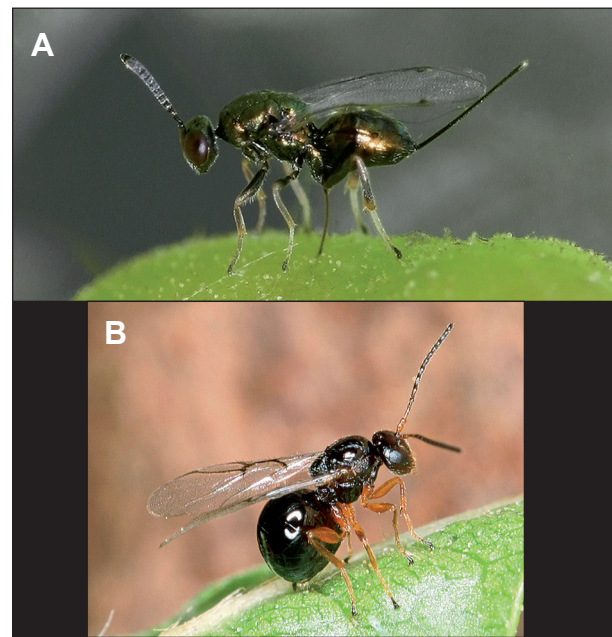


Figure 22. After its release in Japan, *Torymus sinensis* (A) (photo of Ambra Quacchia), a Chinese parasitoid of chestnut gall wasp, *Dryocosmus kuriphilus* (B) (photo credit: Beat Wermelinger, WSL), hybridized with a local Japanese species, *Torymus beneficus*.

(c) ***Laricobius adelgid* predators.** The predatory beetle *Laricobius nigrinus* Fender (Coleoptera: Derodontidae) (Figure 23A) has been moved from its native range in western North America (where it is a specialized predator of hemlock woolly adelgid, *Adelges tsugae* Annand) to the eastern United States for biological control of an invasive population of an invasive population of the same adelgid. Following relocation, *L. nigrinus* has hybridized to a degree with its native congener *Laricobius rubidus* LeConte (Figure 23B), which mainly attacks adelgids on white pine (*Pinus strobus* L.). Hybridization occurs at a stable rate of 10-15% (Havill et al., 2012; Fischer et al., 2015a); hybridization occurs more often on hemlock (*Tsuga canadensis* [L.] Carrière) than on white pine, where *L. rubidus* dominates (Fischer et al., 2015a). Resource partitioning appears to be happening, with *L. nigrinus* increasingly becoming the dominant predator on hemlock, while *L. rubidus* remains dominant on white pine (Fischer et al., 2015a).

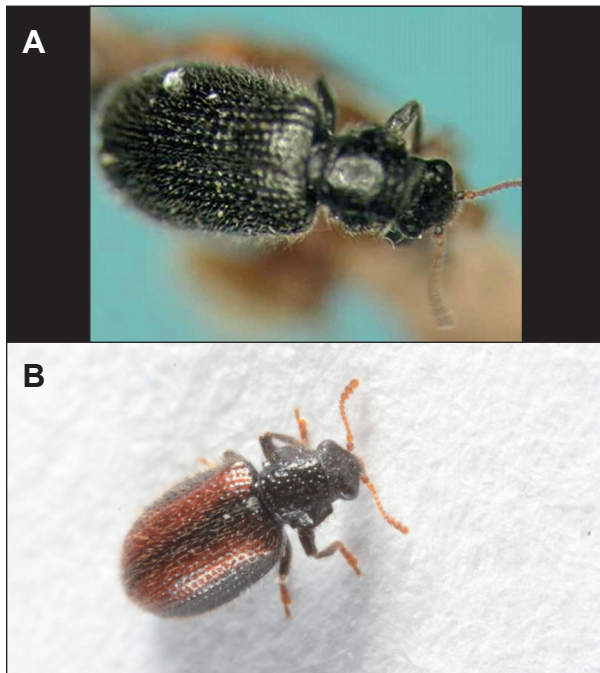


Figure 23. *Laricobius nigrinus* (A) (photo of Ashley Lamb, Virginia Polytechnic Institute and State University, Bugwood.org) was introduced from the western United States to the eastern states, where it hybridized with *Laricobius rubidus* (B) (photo of Tom Murray).

Putting risk in context

Hybridization between an introduced species and a local native congener, as described above, is not uniquely associated with biological control agents. Rather, many species moved by people for recreational or sport purposes have hybridized with closely related species when the two are brought into sympatry, in some cases endangering the native form. Well known examples include the movement of rainbow trout (*Oncorhynchus mykiss* [Walbaum]) throughout the western United States into rivers and lakes where it endangers local trout species through a mix of predation, competition, and hybridization (e.g., Henderson et al., 2000). Similar outcomes have occurred in *Anas* ducks, where the introduction of the common mallard (*Anas platyrhynchos* L.) has led to extensive hybridization with closely related species, such as the grey duck (*Anas superciliosa* Gmelin) in New Zealand (Haddon, 1998).

Mitigation

Tests to detect hybridization potential between species proposed for introduction and congeners living where releases are planned can be run in quarantine. For example, the proposed introduction of *Laricobius osakensis* Montgomery and Shiyake from Japan into the eastern United States was preceded by tests to measure the potential to hybridize with the previously introduced *L. nigrinus*. In this instance, successful interspecific mating was not detected (Fischer et al., 2015b). In contrast, Naka et al. (2005, 2006) found high potential for hybridization between native Japanese green lacewings (*C. nipponensis*) and commercial *C. carnea* and warned against introduction of the commercially available populations.

Type 5. Attack on Weed Biocontrol Agents

The concept

Some insect biological control agents can, depending on their ecology and host ranges, attack weed biological control agents that are similar, taxonomically or ecologically, to the targeted herbivorous pest.

Examples

Three examples of this are discussed below; others almost certainly exist. Examples discussed include an oligophagous weevil parasitoid (*M. aethioides*); braconid parasitoids of tephritid flies, a family that includes both fruit-infesting pests and gall-making weed control agents; and a predaceous mite that attacks spider mites, which mostly are crops pests, but have also been used as weed biological control agents.

(a) The oligophagous weevil parasitoid, *Microctonus aethioides*. This parasitoid has been used successfully to control several pest weevils of forage crops (Barlow and Goldson, 1993; Kingsley et al., 1993) and is known to attack some native weevils in New Zealand (Barratt et al., 2007) (see earlier discussion of this case). Among the nontarget weevils attacked is the introduced weed biocontrol agent *Rhinocyllus conicus* Froelich, which has controlled nodding thistle (*Carduus nutans* L.) in parts of the United States and New Zealand (Kok and Surles, 1975; Jessep, 1990). In New Zealand, this weevil has been found to be parasitized by *M. aethioides* at rates up to 17% (Murray et al., 2002).

(b) Parasitoids of frugivorous tephritid flies. Several species of parasitoids, including *Diachasmimorpha longicaudata* (Ashmead) (Figure 24A), *D. tryoni*, and *Psytalia fletcheri* (Silvestri) (Figure 24C) (all Hymenoptera: Braconidae), have been introduced to Hawaii to attack invasive frugivorous tephritid flies. Investigations were later undertaken to determine if these species attacked the gall fly *E. xanthochaeta* (Figure 24B), introduced to

suppress invasive lantana. In the laboratory, the level of attack on *E. xanthochaeta* larvae by *D. longicaudata* or *P. fletcheri* was reduced but not eliminated if gall wasp larvae were presented naturally inside their galls. If attack did occur, *D. longicaudata* developed successfully but *P. fletcheri* did not (Duan and Messing, 1996). In contrast, both *D. tryoni* and *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae)

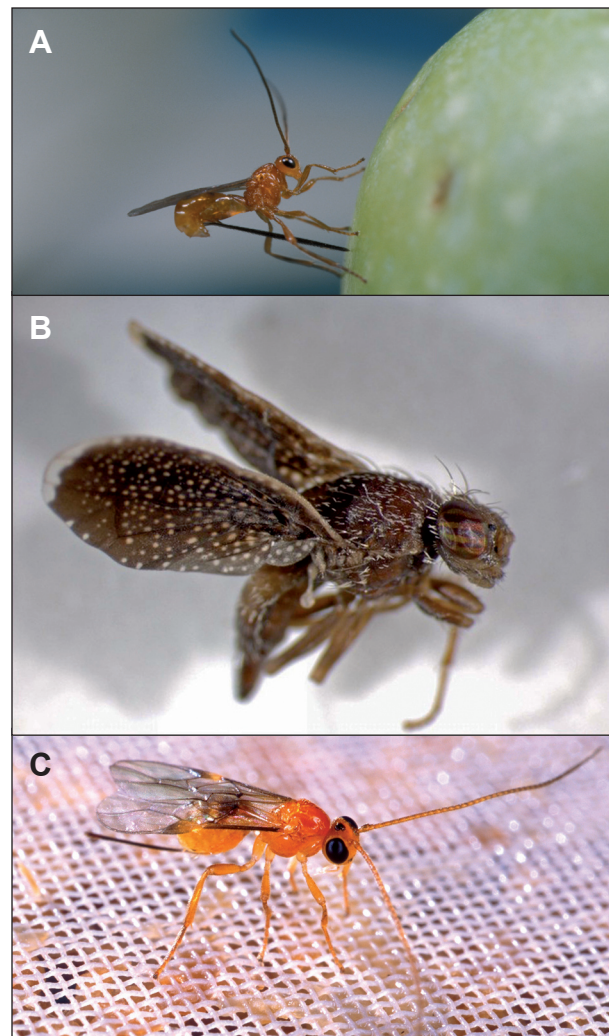


Figure 24. Different host range widths among parasitoids imported to control fruit flies in Hawaii: *Diachasmimorpha longicaudata* (A) (photo of Kent Daane), an older introduction, attacked a gall-forming tephritid, *Eutreta xanthochaeta* (B) (photo of Jared Bernard), while *Psytalia fletcheri* (C), a more recent introduction, did not (photo of Scott Bauer, USDA Agricultural Research Service, Bugwood.org).

did attack some lantana gall fly larvae in laboratory trials (Duan et al., 2000; Duan and Messing, 2000a,b, respectively). In the field, however, <1% of lantana gall flies were parasitized by *D. longicaudata* at sites where 37% of this parasitoid's normal host (*Bactrocera dorsalis* [Hendel] [Diptera: Tephritidae]) were attacked (Duan et al., 1997). Field attack rates, however, are not reported for the other parasitoids.

(c) Predatory phytoseiids attacking spider mites. The gorse spider mite, *Tetranychus lintearius* (Dufor) (Acari: Tetranychidae) (Figure 25A), has been released in New Zealand and the USA for control of gorse (*Ulex europaeus* L.) (Figure 25B). This spider mite, however, has failed to have any persistent, significant effect on gorse. Field studies in Oregon (USA) showed this was likely due to feeding on the spider mite by predatory phytoseiid mites, including *Phytoseiulus persimilis* Athias-Henriot (Figure 25C), a non-native phytoseiid that established in Oregon after being released for control of pest spider mites in agricultural fields (Pratt et al. 2003).

Putting risk in context

Attacks on weed biocontrol agents by locally existing parasitoids, while potentially damaging from a practical point of view, is a common phenomenon, occurring, for example, in about 40% of all weed biological control agents established in South Africa (Hill and Hulley, 1995). Such use of introduced herbivores by native parasitoids may or may not affect their population levels. Attack by *Mesopolobus* sp. (Hymenoptera: Pteromalidae) on rush skeletonweed gall midge (*Cystiphora schmidtii*) (Diptera: Cecidomyiidae), for example, in Washington state (USA) did not prevent development of damaging levels of galls on the target weed (Wehling and Piper, 1988), and rates of parasitism by native parasitoids on a biological control agent may vary greatly among locations or plant species (Dowd and Kok, 1982). Similarly, native predators may attack herbivores introduced for weed biological control (e.g.,

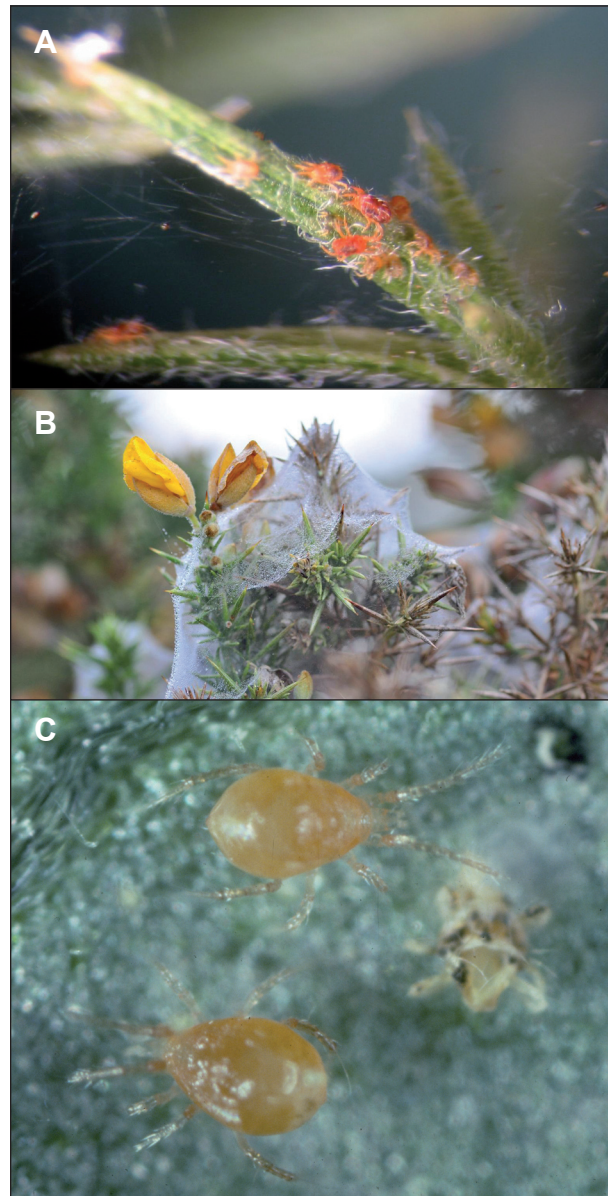


Figure 25. The spider mite *Tetranychus lintearius* (A) (photo of Eric Coombs, Oregon Department of Agriculture, Bugwood.org) was released for control of the introduced plant gorse, shown here covered with the mite's webbing (B) (photo of Steven Conaway, Penn State University, Bugwood.org) but failed to have significant impact in Oregon because of predation from an introduced predatory mite, *Phytoseiulus persimilis* (C) (photo of Jack Kelly Clark from UC Davis and Lance Osborne University of Florida at Gainesville).

Nechols et al., 1996; Hunt-Joshi et al., 2005), reducing their efficacy in some cases (Hunt-Joshi et al., 2005).

Mitigation

Safety of new insect biocontrol agents to previously released weed biocontrol agents can be determined during host range testing for the new agent. What cannot be avoided is potential future conflict with unspecified weed biocontrol agents whose release might later be desired, unless their possible use is foreseen at the time of the insect biocontrol agent's proposed introduction. For example, Nadel et al. (2009), when estimating the host range of *Bracon celer* Szépligeti

(Hymenoptera: Braconidae) for potential introduction to California against olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae: Dacinae), found the parasitoid could attack and successfully develop in *Parafreutreta regalis* Munro (Tephritidae: Tephritinae), a gall making fly of interest as a potential weed control agent for Cape ivy, *Delairea odorata* Lem. Consequently, *B. celer* was rejected for introduction into California, at least until it is clarified if *P. regalis* is going to be introduced.

HOW COMMON HAVE POPULATION-LEVEL NONTARGET EFFECTS BEEN?

Deciding how best to assess the risk of biological control introductions has become an important focus of classical biological control of arthropods. New knowledge gained from in-depth studies of particular cases over the last 30 years has improved our ability to assess risk and determine how it can be lowered (Barratt, 2011). However, a comprehensive review of results of all parasitoid and predator releases for insect biological control has not been done and is not likely to be done because of the constraints of resources and scientific expertise. Consequently, any attempt to determine the frequency of such impacts devolves into collecting all the cases for which an attempt to obtain such information has been made (on the basis that cases with no data do not tell us there are no impacts, but only that the case has not been evaluated). It is less likely than for weed biocontrol agents that the impacts of insect biocontrol agents would be observed outside of deliberate scientific studies.

Cases where data exist, however, are not a random sample of all introductions, but rather seem to fall into three groups, each with strong but different biases. One group consists of cases in which preliminary knowledge suggested that nontarget effects had or were likely to have occurred and the researcher was interested in finding such cases because they could produce positive, publishable results that fit into a trending area of emphasis in the science. A second group of studies consists of work by biological control scientists who investigated historical cases where nontarget impacts were asserted but data were lacking. Such studies were often carried out either because the scientist was located in the affected region or had a personal interest in the

system. The third group of cases consists of more recent projects carried out by biological control scientists who developed extensive pre-release information (subject to stricter regulations for new projects) or investigated consequences of previous projects. The purpose of this work was to test hypotheses developed during host specificity testing in quarantine after agents were established in the field (i.e., were agents as host specific as predicted).

This scarcity of well developed studies on insect biocontrol agents contrasts with weed biocontrol whose herbivorous agents are generally large, visible, and reasonably easy to collect and identify. As a consequence, the number of recorded cases of nontarget impacts by weed biocontrol agents actually reflects the real number of cases, and in this instance, it is probably reasonable to infer that no information of nontarget impacts means that no impacts occurred. This strong difference between nontarget impact assessments for insect and weed biocontrol agents is not likely to change because it is caused, in part, by the small size and taxonomic complexity of insect biocontrol agents and the often poorly understood native insect fauna in the receiving environment.

Therefore our ability to assess the level of nontarget impacts for insect biocontrol agents (parasitoids and predators) will be imperfect and will consist of collecting and analyzing published peer-reviewed information. We should expect knowledge to increase as more effort in this research area is made. However, these types of field studies, reviews, or metastudies may be subjected to the biases because of the research motivations listed above. Here, we discuss the literature as of 2016

to the best of our knowledge, grouping studies as (1) no impact on nontarget species, (2) population-level impacts through attack, or (3) indirect population-level impacts through mechanisms such as apparent competition or displacement through competition for hosts or prey. For the third case, we exclude displacement from an anthropogenic system (such as a native parasitoid being displaced from attacking an invasive pest on a crop); such evidence by itself does not mean significant ecological impact because the native natural enemy must have had a native host and its displacement in this native habitat by an introduced agent(s) is, in our opinion, the critical issue of most concern. At this point, displacement of native natural enemies in native habitat as opposed to agroecosystems has been inadequately addressed in previous studies assessing nontarget impacts of introduced biological control agents.

Below we discuss 22 past cases, selected by us for purposes of this discussion, in which efforts were made to detect nontarget impacts. We grouped 12 of these as showing no convincing evidence of significant impact, four showing direct impact, and six showing alleged indirect impacts via displacement, of which in four cases we argue that displacement of native parasitoids from their native hosts has not been shown.

Group 1. No Impact

Bessa remota and levuana moth

The introduction to Fiji of the tachinid fly *B. remota* (originally given as *Ptychomyia remota*) (Figure 26A) successfully controlled a devastating pest of coconut, the defoliating moth *Levuana iridescens* Beth.-Bak. (Lepidoptera: Zygaenidae) (Figure 26B) (Tothill, 1926, Tothill et al., 1930; DeBach, 1974). This case is portrayed by Howarth (1991) as the cause of extinction for two moths, the target *L. iridescens* (asserted by Howarth to be native to Fiji) and another, certainly native, zygaenid called *Heteropan dolens* Druce. If both statements were well substantiated, this would be a case of great importance. However, neither

assertion is supported by adequate evidence (Hoddle, 2006). The parasitoid is native to the East Indies region (Simmonds, 1930) and is clearly polyphagous. Host range testing done 50 years later, when its introduction to India was being considered, found parasitism rates in the laboratory of 4 to 20% in larvae of eight Lepidoptera in various families (Jayanth and Nagarkatti, 1984). However, the target pest on Fiji was considered invasive at the time of the original work (Simmonds, 1930; Tothill et al., 1930) and in later analyses (Kuris, 2003; Hoddle, 2006). As for *H. dolens*, there are no records of this moth being attacked by *B. remota*, and this species may continue to exist on Fiji (Hoddle, 2006). Consequently, there are no data to support claims that *B. remota* has caused the extinction of either *L. iridescens* or *H. dolens*. Thus, we can only say that further study is needed.

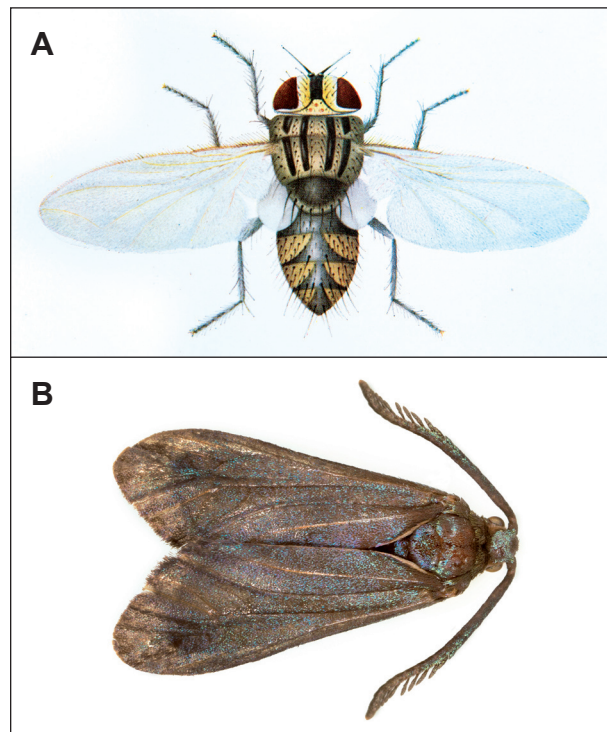


Figure 26. The tachinid *Bessa remota* (A) (photo of Mark Hoddle of illustration in Tothill et al. 1930) was released in Fiji for control of the coconut pest *Levuana iridescens* (B) (photo of Mike Lewis, Center for Invasive Species Research, University of California Riverside).

Australian mealybug parasitoids in New Zealand

A post-release monitoring program in New Zealand found that four species of Australian parasitoids (*Tetracnemoidea sydneyensis* [Timberlake], *Anagyrus fusciventris* [Girault], *Gyranusoidea advena* Beardsley, and *Parectromoides varipes* [Girault]) (all Hymenoptera: Encyrtidae) of longtailed mealybug (*Pseudococcus longispinus* [TargioniTozzetti]) that were accidentally introduced by commerce do not affect native mealybugs in New Zealand, which occur in native forest. Longtailed mealybugs placed in native forest on potted citrus were always unparasitized, in contrast to similarly deployed longtail mealybugs placed in orchards, which were consistently parasitized. The native mealybugs *Paracoccus glaucus* (Maskell) and *Paracoccus zealandicus* (Ezzat & McConnell) placed in orchards on potted pigeonwood plants, *Hedycarya arborea* J.R. Forst. et G. Forst., a native plant host of these mealybugs, were unparasitized by the exotic parasitoids. Collections of native mealybugs from native forest were parasitized by only native parasitoids. Collectively, these experiments and surveys show high specificity of these exotic parasitoids, a probable aversion by them to forage in forest habitats, and no change in the host ranges of any of the introduced parasitoids 14 to 47 years after their self-introduction (Charles et al., 2015).

Citrus blackfly parasitoids on the island of Dominica

A survey of 51 sites in the Caribbean Island of Dominica by Lopez et al. (2009) found a high degree of suppression of the target citrus blackfly, *Aleurocanthus woglumi* Ashby (Hemiptera: Aleyrodidae), and no instances of parasitism on other whiteflies (six species, a mix of native and introduced) by either of the two released parasitoids, *Amitus hesperidum* Silvestri (Hymenoptera: Platygasteridae) and *Encarsia perplexa* Huang and Polaszek (Hymenoptera: Aphelinidae).

Neotropical phytoseiid, *Typhlodromalus aripo*, in Africa

In Malawi and Mozambique, native mite communities on the introduced crop cassava (*Manihot esculenta* Crantz) were monitored for two years following the introduction of the phytoseiid predatory mite *Typhlodromus aripo* De Leon for control of cassava green mite, *Mononychellus tanajoa* (Bondar) (Zannoua et al., 2007). In Mozambique, densities of all the common phytoseiids on cassava—*Euseius baetae* (Meyer & Rodrigues), *Euseius bwende* (Pritchard & Baker), and *Ueckermannseius saltus* (Denmark & Matthyse)—remained stable during the study, despite establishment of *T. aripo* and its suppression of the target pest mite. In Malawi, two of the most common native cassava phytoseiids—*Euseius fustis* (Pritchard and Baker) and *Iphiseius degenerans* (Berlese)—increased in abundance, while that of the third species, *U. saltus*, was not affected.

Parasitoids attacking the endemic Hawaiian moth *Udea stellata*

Udea stellata (Butler) (Lepidoptera: Crambidae) is a common, non-threatened, endemic Hawaiian moth. Kaufman (2008) examined sources of mortality affecting life stages of this moth and found seven polyphagous endoparasitoids attacking it: a) three species likely moved accidentally in commerce: *Casinaria infesta* (Cresson), *Trathala flavoorbitalis* (Cameron), and *Triclistus* nr. *aitkeni* (all Hymenoptera: Ichneumonidae); b) two species introduced for biological control: *Meteorus laphygmae* (Viereck) and *Cotesia marginiventris* (Cresson) (both Hymenoptera: Braconidae); and c) two likely endemic species: *Diadegma blackburni* (Cameron) and *Pristomerus hawaiiensis* (Perkins) (both Hymenoptera: Ichneumonidae). The two biocontrol agents were introduced to Hawaii in 1942 to control the sugarcane pest *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). Highest rates of apparent field parasitism were from the accidentally moved species

T. flavoorbitalis and occurred mainly below 850 m elevation. The parasitoids introduced as biocontrol agents were detected in the target moth only above this elevation (Kaufman, 2008; Kaufman and Wright, 2010). Kaufman and Wright (2009) explored these relationships more thoroughly, using demographic techniques such as life tables and marginal rate analyses. They found that the impact of parasitoids on *U. stellata* larvae was much lower than apparent parasitism had suggested, only about a 5% population reduction. The large difference between this finding and their earlier study was caused by a high rate of predation on larvae, which had not been accounted for previously. Furthermore, Kaufman and Wright (2009) found that it was the accidentally introduced parasitoid *T. nr. aitkeni* that dominated the parasitoid guild (48.5% of all parasitoids reared in this study), not the accidentally introduced species *T. flavoorbitalis*, as reported earlier. This study clearly illustrates the ease with which field data drawn from simple samples, unaided by a demographic analysis framework, can be misleading. It also suggests that accidentally introduced parasitoids (never subjected to selection criteria) can be more damaging to local native species than biological control agents. We suggest that these two types of invasions, deliberate (i.e., intentional release of biological control agents) and accidental (i.e., self-introduction or via the live plant trade), should be distinguished during assessments of impact on nontarget species.

***Peristenus digoneutis* Loan (Hymenoptera: Braconidae)**

This European parasitoid (Figure 27) of certain species of *Lygus* mirid bugs was introduced into eastern North America to suppress a native species, *Lygus lineolaris* (Palisot de Beauvois). Before this introduction, the target pest was parasitized by a presumed native euphorine braconid, *Peristenus pallipes* (Curtis) at a low level (9%) (Day, 2005). However, it may be that *P. pallipes* is itself invasive, as it parasitizes at a high rate only two invasive European mirids (Day, 1999).

After its introduction into the eastern United States, *P. digoneutis*' effects on mirids and their parasitoids were assessed over a 19-year period by Day (2005), who found that parasitism of *L. lineolaris*, the target pest of the biocontrol program, increased to 64% and its density dropped by two-thirds. The parasitoid *P. pallipes* remained present in the system throughout the study. Some individuals of the mirid *Adelphocoris lineolatus* (Goeze) were parasitized, but its density was not reduced. *Leptopterna dolabrata* (L.), a European grass-feeding species, was not attacked by *P. digoneutis*. These observations suggest that the introduced parasitoid reduced the target host's density without damaging populations of either its native parasitoid or those of other mirids found in the same habitat.

For this same system, Haye et al. (2005) assessed the value of laboratory host range test results as a predictor of field events. They did this by first assessing rates of *P. digoneutis* parasitism in the laboratory for a range of European mirids and then measuring parasitism of the same species collected from their native habitats in Europe. They reared *P. digoneutis* from ten field-collected hosts—three species of *Lygus* and seven non-*Lygus* species in the subfamily Mirinae. These



Figure 27. The braconid *Peristenus digoneutis* was released in the eastern United State for control of the native mirid *Lygus lineolaris* (photo of Scott Bauer, USDA Agricultural Research Service, Bugwood.org).

findings were consistent with laboratory testing, showing that all seven nontarget species that were parasitized in the laboratory were also attacked and successfully parasitized in the field. However, rates of parasitism observed in the field were low (<1% for 8 of 10 species), in contrast to laboratory parasitism (11-100%, by species). Haye et al. (2005) suggested that such native range host surveys can help interpret quarantine data on parasitism, given that in small cages there is no need to find host habitats or hosts, as would be necessary in the field. So, while negative data in small cage laboratory studies probably indicate a high degree of safety to rejected species, the meaning of acceptance of species for parasitism under confined laboratory conditions is more ambiguous. In summary, the introduction of *P. digoneutis* into the eastern United States for Lygus bug control appears to have achieved its goals without population-level nontarget impacts. *Peristenus digoneutis*, however, has also been released (since 1998) into the western United States (Pickett et al., 2007), where there is a larger set of potential nontarget mirids. Mason et al. (2011), considering the possible effects of *P. digoneutis*, concluded from laboratory testing that native *Lygus* spp. in the region were at risk of being parasitized, but other regional nontarget mirids were not. Information on actual field outcomes in western North America is not yet available and is needed.

***Torymus sinensis* Kamijo (Hymenoptera: Torymidae) in Italy**

This parasitoid of the chestnut gall wasp, *D. kuriphilus*, has successfully controlled the target pest in Japan (Moriya et al., 1989) and more recently has been released in other countries invaded by *D. kuriphilus*. Following its release in Italy, instances of nontarget attack were sought by collection of a total of 1,371 nontarget galls (nine species of gall makers) in north-central Italy over a two-year period from four species of oak and one of wild rose (Ferracini et al., 2015). Five native torymid parasitoids were reared from the collected

galls but *T. sinensis* was recorded from only one nontarget gall wasp, *Biorhiza pallida* Galle (Hymenoptera: Cynipidae), from which two males of *T. sinensis* were reared. These field records are consistent with the fact that in the laboratory all the nontarget galls tested were unsuitable for *T. sinensis* oviposition, except for the cynipid *Andricus curvator* Milan Zubrik.

***Rodolia cardinalis* in the Galápagos**

Seven years after this lady beetle's release in the Galápagos, Hoddle et al. (2013) evaluated the effects of *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae) (Figure 28), released for control of the cottony cushion scale, *Icerya purchasi* Maskell (Hemiptera: Monophlebidae), on native insects on the islands to compare observed outcomes with quarantine predictions. Before release, up to 60 native or endemic species of plants on the islands were affected by the scale, causing population declines of some critically endangered plants and associated specialized insects (Causton, 2001, 2003). The assessment (2009-2011) found the project to have been safe and effective (Hoddle et al. 2013). On evaluated plant species, scale densities were reduced by ~60-98% compared to pre-release surveys. Most



Figure 28. The ladybird beetle *Rodolia cardinalis* was released in the Galápagos where it successfully controlled the cottony cushion scale, *Icerya purchasi* (photo of Mark Hoddle, UC Riverside, CA).

native plants surveyed were no longer heavily infested by the scale, with the exception of the dune-inhabiting *Scaevola plumieri* (L.) Vahl., which still supported substantial, but fluctuating scale populations. Also, in urban areas, scale-tending by invasive ants kept scale populations high. During 22 h of field-cage observations, *R. cardinalis* adults were offered five nontarget arthropod species. A total of 351 predator/prey encounters were observed, 166 with *I. purchasi* and 185 with nontarget prey. Encounters with cottony cushion scale resulted in 53 attacks (32% rate) but none of the 185 encounters with nontarget species resulted in attacks (Hoddle et al., 2013). Collectively these studies demonstrated that this introduced natural enemy was beneficial to the biota of the Galápagos Islands and was without observable negative consequences.

***Pteromalus puparum* on *Bassaris* butterflies in New Zealand**

The yellow admiral (*Vanessa itea* [F.] [Lepidoptera: Nymphalidae]) (Figure 29A) was listed by Lynch and Thomas (2000) as having been significantly affected by the pupal parasitoid *Pteromalus puparum* (L.) (Hymenoptera: Pteromalidae) (Figure 29C), a parasitoid released against *Pieris rapae* (L.). This listing was based on

a personal communication by George Gibbs. Field studies assessing the impact of *P. puparum* on *V. itea* showed that in natural habitats parasitism rates by this species were low, ~7 percent, but they increased to ~73 percent if study populations were in close proximity to *P. rapae* populations (Hicks, 1997). Despite this, Hicks (1997) concluded that the most important factor depressing populations of *V. itea* was loss of its larval food plant, a stinging nettle (*Urtica* sp.), and Patrick and Dugdale (2000) do not list *V. itea* in their summary of threatened New Zealand Lepidoptera.

Impacts of this same parasitoid on another New Zealand butterfly, the red admiral (*Vanessa gonerilla* [F.] (Lepidoptera: Nymphalidae) (Figure 29B) is not mentioned by Lynch and Thomas (2000), but an impact was similarly presumed to have been caused by *P. puparum* (Barron et al., 2003). Further analysis, however, using field data and a population growth model (Barron, 2007) found that *P. puparum*'s impact (5%) was minor compared to another generalist pupal parasitoid, *Echthromorpha intricatoria* (F.) (Hymenoptera: Ichneumonidae), an accidentally introduced species. This ichneumonid parasitoid reduced the butterfly's density in the same modeling analysis by an estimated 30 percent.

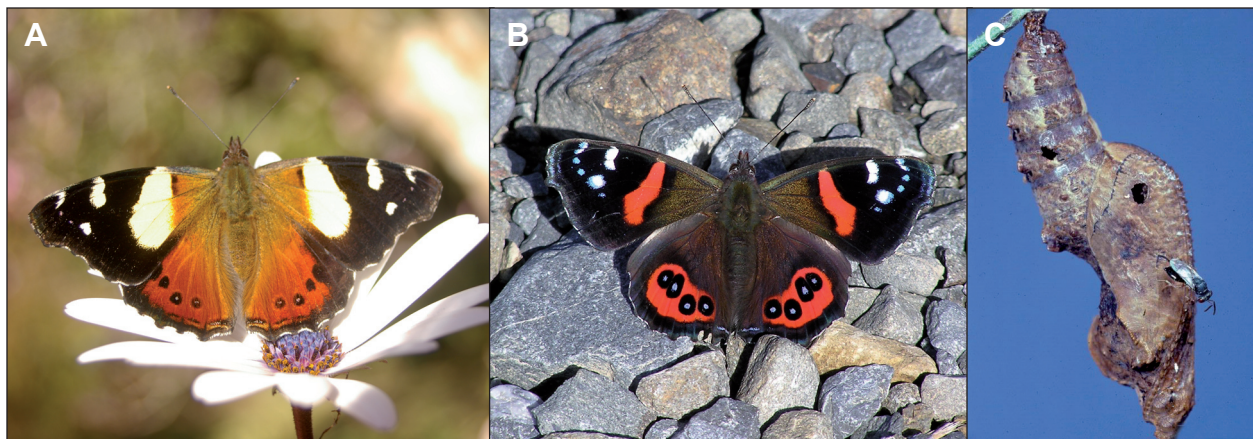


Figure 29. In New Zealand, pupae of both the yellow admiral, *Vanessa itea* (A) (photo by Carol and Trevor Deane, www.butterfliesdorrigo.weebly.com) and the red admiral, *Vanessa gonerilla* (B) (photo by Tony Wills, from [https://commons.wikimedia.org/wiki/File:NZ_Red_Admiral_\(Vanessa_gonerilla\)-2.jpg](https://commons.wikimedia.org/wiki/File:NZ_Red_Admiral_(Vanessa_gonerilla)-2.jpg)) are both attacked by the introduced parasitoid *Pteromalus puparum* (C) (photo of Sturgis McKeever, Georgia Southern University, Bugwood.org).

***Trigonospila brevifacies* in New Zealand**

The tachinid *Trigonospila brevifacies* (Hardy) was introduced into New Zealand against light-brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae). It was later found attacking several native tortricids (Munro and Henderson, 2002). Of all parasitoids individuals reared from the sampled tortricids, *T. brevifacies* comprised 15.6 to 79.5% of the total. However, rates of parasitism by *T. brevifacies* on individual host species were not given, but rather it was stated that the whole parasitoid guild caused 13 to 26.5% parasitism (by host species) (Munro and Henderson, 2002). Without rates of attack by *T. brevifacies* on individual host species and without a life-table-based understanding of their meaning, we conclude that there is as yet no evidence of population level impacts by this parasitoid on nontarget tortricids in New Zealand.

***Trichopoda giacomelli* (Diptera: Tachinidae)**

The tachinid *Trichopoda giacomelli* (Blanchard) (Figure 30A) was introduced into Australia in 1996 for control of the stink bug *Nezara viridula* (L.) (Figure 30B) following study of its likely host range (Sands and Coombs, 1999). Initial laboratory studies found that three nontarget bugs were attacked and supported tachinid development: *Plautia affinis* Dallas, *Alciphron glaucus* (F.), and *Glaucias amyoti* (White) (Figure 30C) (all Hemiptera: Pentatomidae).

After establishment of the tachinid, field studies in New South Wales were conducted in 1999-2000 to measure its relationships with nontarget pentatomids and scutellerids. Information was collected from 11 plant species, which collectively supported nine pentatomid species and two scutellerids. Some 1,686 host individuals, summed over all species, were examined. Of the eleven bug species collected, nine were not attacked at all, one species had one parasitized individual

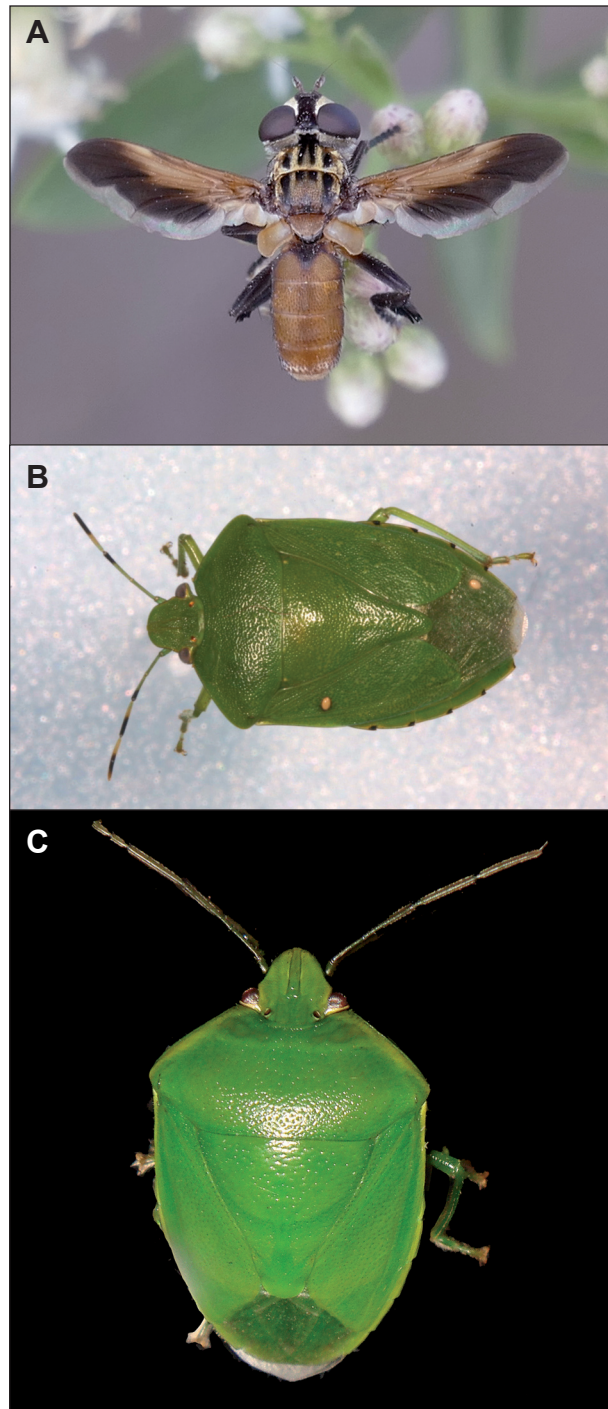


Figure 30. *Trichopoda giacomelli* (A) (photo of Gustavo Duran), from Argentina was released in Australia for control of *Nezara viridula*; host with parasitoid eggs (B) (photo of Russ Ottens, University of Georgia, Bugwood.org); it also attack three native species, including *Glaucias amyoti* (C) (photo of Phil Bendle).

out of 369 (0.03%), and one, *P. affinis*, had an overall parasitism rate of 4.8% (21/441), although at individual collecting sites, rates of parasitism ranged from 0.5 to 50%, effects likely mediated by attraction to the host plant. Only attack on *P. affinis* might rise to the level of population-level impacts, but only in selected locations (Coombs, 2003).

Parasitoids of frugivorous and native gall making tephritids in Hawaii

Efforts to control pest tephritids in Hawaii that attack fruits or coffee berries have included screening for attack by parasitoids of these pests on native tephritid gall makers. This was done either during consideration of new parasitoids for release or, for species released in the past, as later follow-up studies. The effort examined the propensity of seven parasitoids to probe or attack larvae of *Trupanea dubautiae* (Bryan), a native gall-making tephritid that infests flowerheads of the native composite shrub *Dubautia raillardioides* Hillebrand. Studies included laboratory studies and, for previously released species, field surveys. Duan and Messing (1997) found that neither *D. longicaudata* nor *P. fletcheri* attacked *T. dubautiae* larvae in intact galls in laboratory tests. In a further study, Duan and Messing (1998) found no attack on this same gall maker by another parasitoid, *Tetrastichus giffardianus* Silvestri (Hymenoptera: Eulophidae), under laboratory conditions, nor in a field survey on Kauai. Similarly, for a fourth parasitoid, *D. kraussi*, there was no attack on this gall maker in laboratory tests (Duan and Messing, 2000). Wang et al. (2004) also found no attack in laboratory tests of this same gall maker by any of three additional parasitoids: *Fopius caudatus* (Szépligeti), *Fopius ceratitivorus* Wharton, and *F. arisanus* (all Hymenoptera: Braconidae). Collectively, these studies indicate no risk to this native gall maker from any of these seven introduced parasitoids.

Group 2. Direct Trophic Impact

***Tamarixia* (formerly *Tetrastichus*) *dryi* in La Réunion**

On the island of La Réunion in the Indian Ocean, the parasitoid *Tamarixia dryi* (Waterston) (Hymenoptera: Eulophidae) was introduced during a successful program to control two introduced psyllids that vector bacteria causing citrus greening disease. This case is listed in a review of nontarget impacts by van Lenteren et al. (2006a) as causing “reductions in population levels” of a local psyllid whose name was given as *Trioza eastopi* Orian (Aubert and Quilici, 1983), but which is a junior synonym of *Trioza litseae* Bordage. This psyllid is known only from two islands: La Réunion, where it is a pest of vanilla cultivation (Chalot and Bernard, 1918) and Mauritius (Diana Percy, pers. comm.). On La Réunion, populations were high on a widely planted, introduced shrub, *Litsea chinensis* Jacq., which is a traditional medicinal plant from the Andhra Pradesh region of India. While this psyllid may be native and endemic to La Réunion, it is possible that it may not be, and it could have arrived on *L. chinensis* from India. Uncertainty over the area of origin for *T. litseae*, and its abundance on La Réunion, need to be clarified. Until *T. litseae* is confirmed to be a native species and to be endangered by *T. dryi*, the ecological importance of its reduction in density remains unclear and somewhat doubtful.

***Brachymeria lasus* and two native butterflies on Guam**

In Guam, native butterflies have experienced considerable decline. To understand if this was linked to species introduced for biological control, Nafus (1993b) measured apparent mortality rates for life stages of two native nymphalid butterflies on Guam: *Hypolimnas anomala* (Wallace) and *Hypolimnas bolina* (L.). For the egg stage, native ants were the dominant source of mortality for both species. In neither case did an introduced

biological control agent cause important levels of egg parasitism. For larvae, a pathogen was an important source of mortality and larval parasitoids were not found. Only in the pupal stage did a biological control agent, *Brachymeria lasus* (Walker) (Hymenoptera: Chalcididae), cause significant levels of mortality, but only for *H. bolina* (25%). These findings demonstrate use of this species as a host in the field by *B. lasus*. However, since data were not placed in a life-table context so that marginal attack rates could be calculated from apparent mortality rates, the actual population-level significance of this mortality estimate and the subsequent importance of parasitism by *B. lasus* are unclear.

***Cotesia glomerata* in the Canary Islands**

Lozan et al. (2008) detected *C. glomerata* on the island of La Palma in the western Canary Islands, where it was found parasitizing an island endemic pierid butterfly, *Pieris cheiranthi* (Hübner). While rates of attack are not documented, it appears that the butterfly, a forest species, is principally in contact with the parasitoid at forest edges and not inside intact forests. This observation is consistent with evaluations in Massachusetts, which found that *Pieris virginiensis* (Edwards), also a forest species, was not attacked by *C. glomerata* inside forests (Benson et al., 2003b). In the Canary Islands, *C. glomerata* was not introduced as a biocontrol agent, having likely hitchhiked on traded goods.

***Peristenus relictus* Loan (= *P. stygicus*) and the western tarnished plant bug**

This parasitoid, introduced into the western United States against the native western tarnished plant bug (*Lygus hesperus* Knight) (Hemiptera: Miridae), is an oligophagous parasitoid of mirid bugs, including *L. hesperus*, *L. lineolaris*, *Polymerus basalis* (Reut.), *Labopidicola geminatus* (Johnston), and *Psallus seriatus* (Reut.) (= *Pseudatomoscelis seriatus*) (Condit and Cate, 1982). In northern Germany, part of the native area of *P. relictus*, the ecological host range of this parasitoid includes at least 16 mirids in the

subfamilies Mirinae, Phylinae, or Bryocorinae (Haye et al., 2006). These data suggest that *P. relictus* is a generalist mirid parasitoid. However, it was not the primary source of parasitism of most of its hosts (Haye et al., 2006) and appears to have only minor population-level effects on those it attacks. In laboratory tests in western North America, *P. relictus* was found to attack and develop in a number of non-*Lygus* mirids, including *Amblytylus nasutus* (Kirsch.), *Leptopterna dolabrata* (L.), and *Melanotrichus coagulatus* (Uhler) (Mason et al., 2011). Post-release field studies are needed to determine if *P. relictus* has population-level effects on native nontarget mirids in its introduced North American range (Mason et al., 2011).

Group 3. Displacement or Other Indirect Impacts

Several cases of displacement of native parasitoids by introduced parasitoids are listed by Bennett (1993), Lynch and Thomas (2000), and van Lenteren et al. (2006a). But a close examination suggests some of these reports may not be ecologically important. Of the 17 cases listed in Table 2 of Lynch and Thomas (2000) as having significant effects on nontarget species, four (*C. concinnata*, *M. aethiopoulos*, *T. pallipes*, *C. septempunctata*) seem likely or possible cases of important impact on nontarget native species, and these have been discussed in earlier sections. Another six cases of presumed displacement (two for *C. flavipes*, two for *A. holoxanthus*, and *C. noacki* and *T. brevifacies*) seem to be cases with no ecological importance for native species (for several differing reasons, as discussed below), and their inclusion in Table 2 of Lynch and Thomas (2000) may be misleading. The problem here lies with labeling a case as one of impact or displacement as it invites further repetitive citation without consideration of relevant underlying details. One further case in Lynch and Thomas (2000), that of *P. puparum* and the yellow admiral in New Zealand, has been discussed above under no impacts, as the impacts of this introduced

parasitoid were demonstrated to be unimportant at the population level (Hicks, 1997). Here below we provide details for additional cases where displacement is claimed by Bennett (1993) or Lynch and Thomas (2000).

***Cotesia flavipes* Cameron in Trinidad and Brazil**

This Asian braconid parasitoid was introduced from India and Pakistan into the Caribbean and, later, throughout the sugarcane-producing regions of Latin America against the sugarcane borer *Diatraea saccharalis* (F.) (Lepidoptera: Crambidae). This and three other economically important species in the genus *Diatraea* are considered native to the Americas, and historically they supported several native parasitoids. One of these borers, *Diatraea lineolata* (Walker), is a maize stock borer attacked by the native braconid *Apanteles diatraeae* Muesebeck, typically at about the 10% level (Kevan, 1945).

In Trinidad, after the build-up of *C. flavipes*, parasitism of *D. lineolata* by *A. diatraeae* was undetectable in a 1984-1985 survey (Bennett, 1993), suggesting this species had been displaced by the newly introduced parasitoid. However, the time period over which surveys were conducted was relatively short and Trinidad is only a small part of the range of this parasitoid, which also includes Mexico. In Mexico, Rodríguez-del-Bosque and Smith (1991) detected *A. diatraeae* at a low level on another borer, *Diatraea muellerella* Dyar & Heinrich, in Guerrero, Mexico, and noted that it was a common parasitoid of several species of *Diatraea* throughout Mexico. Similarly, Tejada and Luna (1986) found it to be the dominant parasitoid of *Diatraea* spp. larvae in the state of Nuevo Leon in northern Mexico. These records, while in need of greater amplification (and possibly molecular level work to confirm species identities), demonstrate that the introduction of *A. flavipes* has not caused widespread displacement of *A. diatraeae* in Latin America but rather may have displaced it only locally (in Trinidad) or from only one of its hosts. The

current status of *A. diatraeae* in Trinidad should be reassessed.

Bennett (1993) also reported effects of *C. flavipes* in Brazil (following its 1978 introduction from Pakistan) on the abundance of two native tachinids. These effects were characterized as “The native tachinid parasitoids *Metagonistylum minense* and *P. claripalpis* have become scarce. While they are no longer represented in survey collections in many fields, they occur sporadically in collections from other fields.” Also, Trejos et al. (1986) recorded the presence of both of these tachinids in the Cauca Valley in Colombia. These survey results suggest strongly that there are likely important temporal and spatial effects on the abundance of native and introduced parasitoids and the hosts that they share. Surveys should be of sufficient duration and across many study sites so that robust conclusions can be drawn about population-level impacts from natural enemy introductions.

***Aphytis holoxanthus* DeBach (Hymenoptera: Aphelinidae)**

This parasitoid has controlled the armored scale *Chrysomphalus aonidum* (L.), which is native to Asia, but is widely invasive in several citrus-producing regions around the world. It is listed by Bennett (1993) and Lynch and Thomas (2000) as being responsible for displacing two native parasitoids: one in Florida, *Pseudhomalopoda prima* Girault (Hymenoptera: Encyrtidae), and one in Brazil, *Aphytis costalimai* (Gomes) (Hymenoptera: Aphelinidae). However, in both cases, the same sequence of events seemed to have happened. First, a native parasitoid moved from native hosts and habitats into citrus groves (an artificial habitat created by people with an introduced tree) where it attacked an introduced Asian scale (*C. aonidum*) and became common on that host. Later, because control by native parasitoids was insufficient, the specialized parasitoid *A. holoxanthus* was introduced (into Florida in 1960 and Brazil in 1962). *Aphytis holoxanthus* became the dominant parasitoid on

C. aonidum, removing it as an available high-density resource for local native parasitoids that had been opportunistically exploiting the uncontrolled scale populations. This replacement does not mean, however, that native parasitoids suffered a negative ecological impact. Rather, they lost a previous gain due to the proliferation of a pest species in a man-made ecosystem, the citrus crop. In the case of *P. prima* in Florida, Bennett (1993) recorded that this parasitoid remained the dominant parasitoid of the diaspidid scale *Acutaspis morrisonorum* Kosztarab on southern red cedar, *Juniperus virginiana* var. *silicicola* (Small) Bailey. This same scale occurs on several native pines in the southern United States, including *Pinus taeda* L. and *Pinus echinata* Mill. (Anon., 1978). More recently, Ceballos et al. (2011) reported collection of *P. prima* from *Aspidiotus destructor* Signoret on coconut (*Cocos nucifera* L.) in Cuba. As for the parasitoid in Brazil, Terán et al. (1985) reported *A. costalimai* from scales on citrus in northern Argentina 23 years after the introduction of *A. holoxanthus* to the region. These records suggest that both of these native parasitoids remain present on various native scales infesting non-crop plants and rarely being collected unless they attack a pest scale on an economically important crop.

***Cales noacki* Howard
(Hymenoptera: Aphelinidae)**

This parasitoid (Figure 31A) was introduced into Europe to control the whitely *Aleurothrixus floccosus* Maskell (Figure 31B), and Lynch and Thomas (2000) list Viggiani (1994) (also repeated by van Lenteren et al. [2006a]) as recording it as displacing *Encarsia margaritiventris* Mercet (Hymenoptera: Aphelinidae) from the viburnum whitefly, *Aleruotuba jelinekii* (Frauenf.), a native species in Europe. Little is known about the host range of *E. margaritiventris* as there are few published records, but it is likely not monospecific, as Malumphy et al. (2009) recorded it as being reared from the whitefly *Aleurochiton aceris* (Modeer) in Lithuania. More data from field surveys are needed to evaluate this case.

***Trigonospila brevifacies* (Hardy)
(Diptera: Tachinidae)**

This tachinid, introduced into New Zealand to control light-brown apple moth (*E. postvittana*), is recorded by Lynch and Thomas (2000) through Roberts (1986) as significantly harming the parasitoid *Xanthopimpla rhopaloceros* Kreiger (Hymenoptera: Ichneumonidae). This latter parasitoid, however, is not native to New Zealand, having been introduced from Australia as part of the same biocontrol program targeting *E. postvittana* (Munro, 1998). These parasitoids exist in sympatry in New Zealand where they attack light-brown apple moth (Munro and Henderson, 2002).

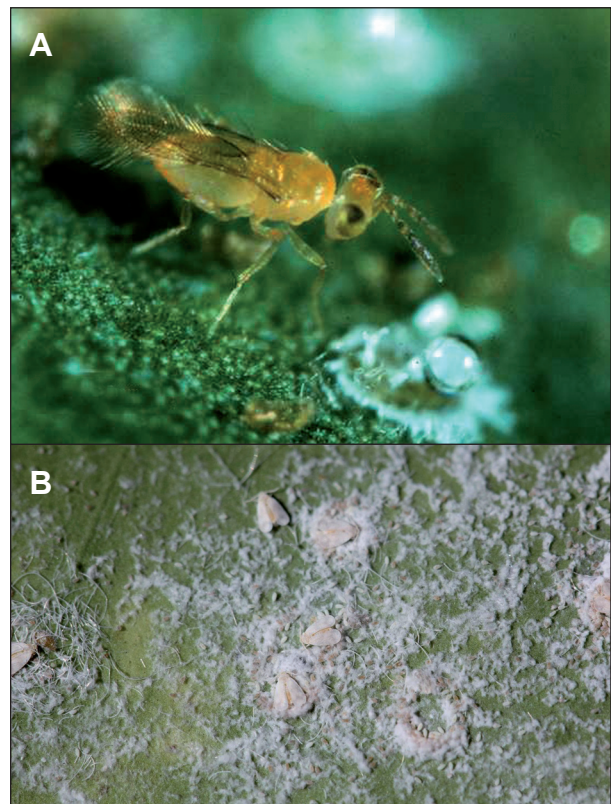


Figure 31. *Cales noacki* (A) (photo by Mike Rose) was used for control of citrus whitefly, *Aleurothrixus floccosus* (B) in Europe.

Diadegma semiclausum
(Hymenoptera: Ichneumonidae)

Two additional cases of apparent displacement not reported by Bennett (1993) or Lynch and Thomas (2000) were noted in this review of the literature: the ichneumonid *Diadegma semiclausum* (Hellén) in Africa and various parasitoids introduced into the United States against the tobacco whitefly, *Bemisia tabaci* (Gennadius) strain B (also known as *B. argentifolii*) (discussed below).

Diadegma semiclausum (Figure 32A) (was released in Kenya in 2002 to control a cabbage pest, the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Figure 32B). This release increased parasitism of diamondback moth larvae from 14 to 53% and consequently lowered crop damage. At the same time, rates of attack on the pest by several native parasitoids decreased. Attack rates on the pest by *Diadegma mollipla* (Holmgren) (Hymenoptera: Ichneumonidae) (Figure 32C) and *Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae) (Figure 32D) on cabbage in Kenya decreased from 5.4 to 2.8% and 9.0 to 2.2%, respectively (Löhra et al., 2007). Is such an impact significant to populations of these native parasitoids? In addition to attacking diamondback moth in cabbage fields, these native parasitoids also attack it on a variety of wild crucifers (weeds or native plants), where they were found co-existing with the introduced parasitoid 3-4 years after its release (Kahuthia-Gathu et al., 2009). Also, these native parasitoids remained present, in lower numbers, 3-4 years post release on diamondback moth in cabbage fields (Kahuthia-Gathu, 2013). These native parasitoids are known to be widely distributed in southern Africa, having been recovered from diamondback moth, for example, in South Africa (Nofemela and Kfir, 2005). *Diadegma mollipla* has also been recorded in the literature from the potato tuberworm (*Phthorimaea operculella* [Zeller]) (Lepidoptera: Gelechiidae) in Egypt (Abbas and Abdel-Samad, 2006). Since this record is of a host in a different family, it should be confirmed.

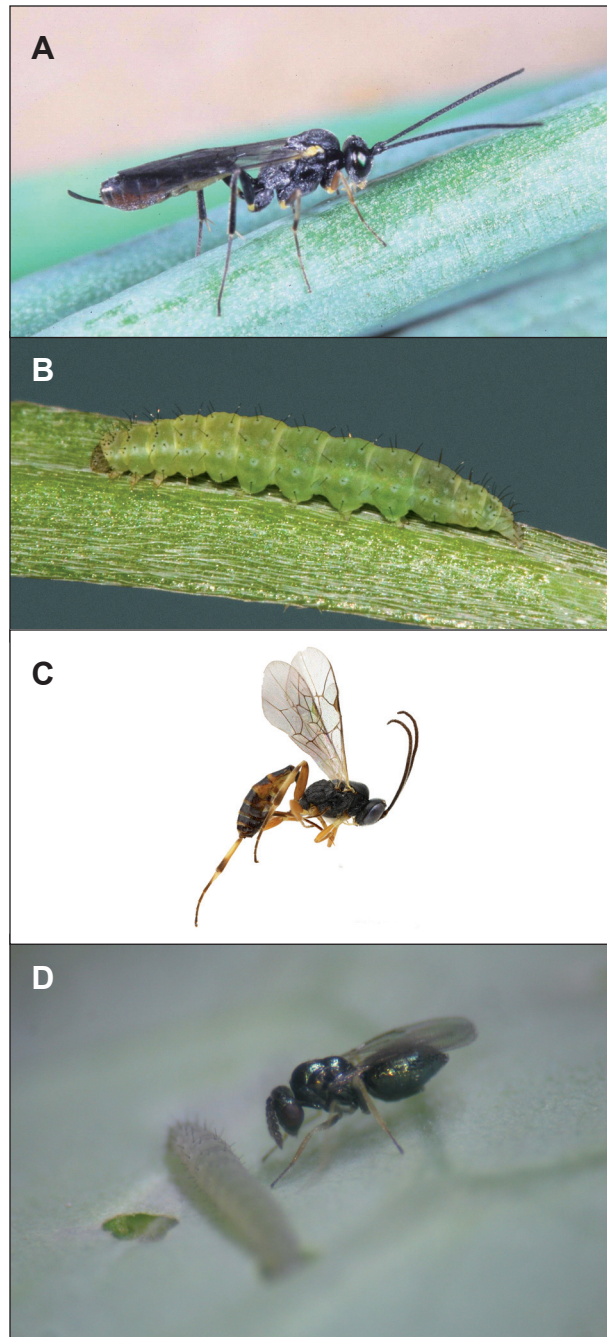


Figure 32. *Diadegma semiclausum* (A) was released in South Africa (photo of Merle Shepard, Gerald R. Carner, and P.A.C Ooi, *Insects and their Natural Enemies Associated with Vegetables and Soybean in Southeast Asia*, Bugwood.org) for control of *Plutella xylostella* (B) (photo of David Cappaert, Bugwood.org), where it competed for larvae of this invasive species with several native parasitoids, including *Diadegma mollipla* (C) (photo of Agnièle Touret-Alby © MNHN) and *Oomyzus sokolowskii* (D) (photo of Alex Gumovsky).

While much is not known about the native hosts and habitats of these nontarget parasitoids, these records from crop studies suggest both that their densities have been lowered in cabbage fields in some areas, but also that they are widespread geographically, found on many host plants, and several insect species, which likely ensures their continued population-level well being. Such instances of displacement, in the view of the authors, do not represent loss of biodiversity because of introduced natural enemies.

Parasitoids introduced into the United States against tobacco whitefly

In response to large financial losses in cotton, winter vegetables, melons, and greenhouse crops from the invasion of the B strain of the tobacco whitefly (*B. tabaci*), some 20 parasitoid populations were collected from this species in many countries and introduced into the southwestern United States (Goolsby et al., 1998). Prominent among 11 released parasitoid populations (species x country combinations) was *Eretmocerus mundus* (Mercet) (Hymenoptera: Aphelinidae) from Spain (Kirk et al., 2000). Of five species released in California, *E. mundus* later was found in a ten-year survey to have become the dominant parasitoid on *B. tabaci* on cotton in California and to have displaced the native *Eretmocerus* species formerly attacking *B. tabaci* on that crop (Pickett et al., 2013). However, when non-cotton host plants were

surveyed for whiteflies and their parasitoids, it was found that *E. mundus* did not attack either of two likely native whiteflies—the banded-wing whitefly (*Trialeurodes abutiloneus* [Haldeman]) on sunflower (*Helianthus annuus* L.) or mulberry whitefly (*Tetraleurodes mori* Quaintance) on mulberry (*Morus* sp.) (Pickett et al., 2013). Furthermore, the native parasitoids formerly attacking *B. tabaci* on cotton, *Eretmocerus eremicus* Rose and Zolnerowitch and *Eretmocerus joeballi* Rose and Zolnerowitch, were found attacking banded-wing whitefly and mulberry whitefly on their respective host plants, indicating that displacement of these parasitoids by *E. mundus* was primarily from the introduced *B. tabaci* on cotton and not from other whitefly hosts on different plants (Pickett et al., 2013).

As part of the same program, introductions into Arizona of the same suite of parasitoids resulted in the displacement (from *B. tabaci* on cotton) of two native species—*E. eremicus* and *Encarsia meritoria* (Gahan)—by the exotic parasitoids *Eretmocerus* sp. (Ethiopia) and *Encarsia sophia* (Gahan) in the early 2000s (Naranjo and Li, 2016). Information has not been published, however, concerning the status of these native parasitoids in Arizona on other species of whiteflies on other plants. It is quite possible that niche division, rather than general displacement, is also at work in Arizona, and this possibility needs to be resolved.

LOOKING AHEAD: WHAT IMPACTS WILL NEW PARASITOID/ PREDATOR INTRODUCTIONS HAVE ON NONTARGET SPECIES?

Forecasting Likely Host Use

Avoidance of nontarget effects from new introductions of parasitoids or predaceous arthropods is based on estimating fundamental host or prey ranges and releasing only species that are adequately specific for where they will be released, where they might naturally spread, and where they have a high risk of being accidentally transported (Babendreier et al., 2005, 2006; van Lenteren et al., 2006b). Part of the selection process is correct species-level recognition of the candidate natural enemy, as candidate natural enemies may be collected from a species complex whose aggregate host range is larger than that of some of its member species (e.g., Smith et al., 2006a,b; Zhang et al., 2011). Estimating host ranges of parasitoids and predators was considered unimportant until about 1990 because nontarget insects are generally of little economic importance and were mostly considered unimportant as species for conservation (Van Driesche and Hoddle, 1997). Methods for estimating parasitoid and predator host ranges were developed as extensions of methods used earlier for weed biocontrol agents and are reviewed by Van Driesche and Reardon (2004) and discussed by van Lenteren et al. (2005) and Babendreier et al. (2005). Here, framed around some key ideas, we discuss more recent contributions to methods for determination of host ranges.

Herbivore host range estimation, for weed biocontrol, seeks to understand the taxonomic limits of what an agent's offspring can eat, if given the opportunity. The assumption is strongly and correctly made that if plants are closer taxonomically to the target weed, they will be

inherently at greater risk of being eaten by the agent (Pemberton, 2000). Tests assess what adult and immature stages will eat, what host species the agents can feed on to maturity, and what plants adult agents will lay eggs on when given access to test species in small cages. Trials are either run one plant species at a time or in pairs (or larger groupings), where one species is the target pest. Alternatively, agents may be offered target and nontarget plants in various sequences over time. Small-cage tests in quarantine cannot assess the ability of natural enemies to orient to a plant from a distance, distinguish it upon contact, and chose a preferred plant among locally available hosts.

Given this history, one should ask whether estimating parasitoid and predator host/prey ranges would be a simple extension of methods developed for herbivorous natural enemies. Consider the following: First, plants frequently defend themselves against herbivores with secondary plant compounds, which, once developed by a lineage of plants, tend to be conserved. These specialized compounds tend to deter generalist-feeding insects that lack an ability to survive possible intoxication following consumption, but these same compounds often are specific attractants for the specialists associated with the plant lineage (Bernays and Chapman, 1987). Insects, in contrast, generally do not generally produce specialized chemical defenses, although some species sequester toxins from their host plants, such as the cardiac glycosides obtained by larvae of monarchs, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), from milkweeds (*Asclepias* spp.). The correlation between herbivore host ranges and plant taxonomy is a

core theoretical tenant for screening weed control agents. This approach, however, is weak when applied as the basis to determine the host ranges of insect control agents (Sands, 2000). Specialized secondary compounds do not have a large influence on parasitoid and predator host ranges, but host taxonomy still functions as a partial predictor of risk for nontarget species based on (1) the general morphology of potential host insects, (2) the manner in which nontarget species feed on host plants, and (3) where nontarget species live in the physical environment. Beyond host taxonomic position, several other important factors must be considered when attempting to assess the host range of entomphagous natural enemies.

The first of these factors is that host odors and odors from the insect's host plant are important attractants for many parasitoids and predators, which orient from a distance toward the plants on which their hosts or prey are feeding (Bouchard and Cloutier, 1985; Vet and Dicke, 1992; Wajnberg et al., 2008). Such plant volatiles also play an important role in host finding by herbivorous insects, but this factor has not been widely used in estimating herbivore host ranges because it requires use of olfactometers or wind tunnels to assess long distance responses to odors from different plants, and the use of these devices in quarantine may be difficult due to space limitations. For herbivores, it has been possible to generally ignore the need to assess "attraction from a distance" because the secondary plant compound signal is strong and its effects are easier to measure in the laboratory. But for parasitoids and predators, the absence of a strong signal analogous to that provided to herbivores by secondary plant compounds makes the "attraction from a distance" factor more important to assess.

Second, plant tissues, unlike those of insects, usually do not have mechanisms (other than plant chemistry) that actively attempt to kill attackers. In contrast, insects have blood cell-based immune systems that attempt to defeat parasitism through

mechanisms such as encapsulation, and if successful, such measures limit the host ranges of internal parasitoids (Blumberg, 1997). In response, parasitoids have developed countermeasures to defeat encapsulation, such as the use of polydnviruses by braconids and ichneumonids (Gundersen-Rindal et al., 2013).

Third, parasitoid and predator host/prey ranges are typically less specialized than those of specialized herbivores used as weed biocontrol agents. The challenge, then, is how are we to estimate the range of hosts whose populations are likely to be reduced by a parasitoid (population-level impact) based on results from laboratory testing, given that this strongly affected group will be some subset of all hosts that the parasitoid can attack. Minor levels of attack on some nontarget species by parasitoids is likely to occur during quarantine testing. However, such attacks may not translate into significant population level impacts in the field, and this possibility needs consideration when data from quarantine tests are being analyzed and interpreted.

This distinction between host use under quarantine conditions and population-level impacts in the field was clearly stated by van Lenteren et al. (2006b) and re-emphasized by Blossey (2016). How, therefore, are predictions about population-level impact to be made from laboratory data designed to measure host use? Several alternative methods of investigation have potential to do so, including literature surveys (Nardo and Hopper 2004), field surveys in the agents' native range (Kuhlmann and Mason, 2002), post-release monitoring in the area of release (Nardo and Hopper 2004), and population modeling (Barron 2007). What is currently needed is to expand the inventory of well studied cases that allow us to examine the strength of such methods for assessing risks of significant nontarget impacts and identify reasons for exceptions to anticipated outcomes.

Moving from Host Use to Population-level Effects

Post-release, estimates of population-level effects on nontarget species caused by deliberately introduced biological control agents can be made with life table studies (Kaufman and Wright, 2009), studies of impact using cohorts deployed on host plants or over physical gradients (Johnson et al., 2005; Barratt et al., 2007), or through the application of population models that use field-collected demographic data (Barron, 2007; Barratt et al., 2010).

Pre-release prediction of likely nontarget impact, however, cannot use the above methods because the agent is not yet present in the field in the country of intended release. Paynter et al. (2015) proposes a pre-release method for predicting host use by weed biocontrol agents on nontarget plants based on the ratio, in quarantine tests, of attacks on the nontarget vs. target plants. This method, however, only predicts host use, not population-level impact and the approach may not be applicable to entomophagous natural enemies. Wright et al. (2005) presented a method for assessing risk of use of a nontarget species from augmentative release of an egg parasitoid (*Trichogramma ostrinae* Pang and Chen, Hymenoptera: Trichogrammatidae) that assessed risk as the cumulative probability over a series of links in a decision tree (e.g., probability of dispersing to nontarget species' habitat x probability of attacking nontarget species, etc.). In principle, this system could be applied to classical biological control agents provided necessary information on habitat use, density in habitat, and attack rate on nontarget species could be developed. Risk of introductions, particularly for augmentative biocontrol agents, has also been discussed in terms of the product of risk of establishment x dispersal x host range, making it possible to estimate effects on native species. This was done, for example, for eight species of

predatory mites introduced into Japan (Sato et al., 2012). Such schemes, however, while using knowledge and judgment, are fundamentally forecasts, not facts.

What is needed to improve understanding of the potential impacts of insect biocontrol agents is to conduct replicated (across sites and over time) longitudinal studies that are designed to assess population-level impacts in the field and compare those estimates to rates of attack on nontarget species in pre-release tests. For new agents undergoing release consideration, this would mean conducting impact studies on nontarget species of interest. For agents released without host range testing, such studies would require carrying out both field impact studies and after-the-fact laboratory host-specificity tests.

From Host Impact to Determination of a Project's Risks and Benefits

A final evaluation that regulatory agencies have to make regarding biological control projects is to compare potential benefits to program costs, including monetary costs and ecological damage to nontarget species. Predictions of nontarget impacts made before releases are largely educated guesses, based on some sense of the likely host range of the agent as determined from quarantine studies or literature reviews, how attack might translate into population-level impacts, and the value of the nontarget species likely to be affected. These negative effects then have to be compared to the ecological damage or economic costs that might reasonably be expected if the pest is not controlled, together with an estimate of the chances of successfully controlling the pest. While most of the above quantities are rarely precisely known, the benefits and losses of such actions are easiest to compare if they are in the same currency (either both ecological damage or both economic losses). When targets are agricultural pests that do not affect natural areas, benefits to nature are

indirect in the form of reduced use of pesticides and lower levels of environmental contamination. Direct economic benefits to farmers (e.g., Jetter et al., 1997; Bangsund et al., 1999; Hill and Greathead, 2000) are part of the “benefits ledger” and are not required as part of these analyses, but can be very important for justifying programs.

Risk analysis is complicated, and factors that will need to be taken into account will vary by project. Hoelmer and Kirk (2005) discuss how several lines of information can be combined to improve selection of biological control agents. Some risk modeling suggests that even nontarget species that are low on the agent’s preference scale may be harmed if the agent builds quickly to very high densities when the host is still abundant and if during this period the agent spills over on a small nontarget population (i.e., apparent competition; Lynch et al., 2002). This possibility is not yet part of main stream risk analysis and would likely be very difficult to estimate accurately, but it should receive further investigation, especially if the suspected impact is not going to be transitory.

Summing up the risks for an agent’s introduction was attempted by Wyckhuys et al. (2009) for *Binodoxys communis* (Gahan) (Hymenoptera: Braconidae) released against soybean aphid, *Aphis glycines* Matsumura, in North America. This summation was based on information about host suitability (as seen in laboratory tests), seasonal overlap of the parasitoid with susceptible hosts, and protection of native aphids by physical refuges or ant-tending. Ultimately such risk assessments describe probable risks, and it remains the job of regulators to decide on behalf of society if the risks to nontarget species posed by introductions of natural enemies are warranted.

Another factor bearing on accuracy of risk prediction is selecting appropriate native species for nontarget testing in quarantine. Barratt et al. (2016) describes a new tool (PRONTI) that is intended to strengthen this process. As a test

case, they applied the tool, as an after-the-fact exercise to *M. aethiopoulos*’ 1982 introduction to New Zealand, since a great deal is known about its subsequent relationships with native species of nontarget weevils. The exercise concluded that if PRONTI had been used, many of the species subsequently attacked would have been chosen for host-range testing, and thus use of this system would have provided a much clearer assessment of the agent’s likely host use. Population level impacts (as opposed to predicting possible nontarget use), however, are not predictable using PRONTI.

Recent Practice (1985-2016) as Predictor of Future Nontarget Impacts

A question of interest for this article, in addition to compiling and analyzing records of past impacts, is whether safety practices used by biological control practitioners are improving and reducing risk to nontarget species. Improving practice is based on better science (e.g., technical aspects of host range and risk estimation) and policy (e.g., societal goals and institutions that determine what risks are acceptable or even recognized). To address this issue of improved practice, we compiled information on cases of parasitoid or predator introductions over the last 30 years (1985-2015) that spans the historical period when the goal of estimating host ranges for insect control agents was adopted and gradually implemented in the United States. In Appendix 1, we list 158 parasitoid species introduced during this period (94 in the first decade, 41 in the second and 23 in the third; also included in Appendix 1 are 7 species that were studied but not released). While not a complete list of parasitoids introduced over this 30 year period, Appendix 1’s entries are, we believe, unbiased with regard to the level of host specificity exhibited by the natural enemies of interest. Entries were drawn from the senior author’s personal files (assembled over the period 1976-2015), reading of additional articles on

species mentioned tangentially in the first group of articles, and from the BIOCAT database records for North America (Canada, Mexico, and the US, including its overseas territories). In Appendix 2, we list 23 species of predacious arthropods introduced over the same period (1985-2015), compiled in a similar manner as species in Appendix 1.

For each record, the senior author read the primary literature on the biocontrol agent to understand its likely host range and then used that information to choose a taxonomic rank (order, family, subfamily, tribe, genus, or species) most likely to encompass all of the agent's known hosts or prey. This does not imply that all the members of that taxonomic unit are actual hosts, but only that no smaller unit contains all the known hosts. This classification system should be treated as an index of the host range (based on hosts known from the literature and other available data), rather than a true estimate of the fundamental host range based on appropriate quarantine studies, which often were not done.

In most cases in Appendix 1, the parasitoid's host range was not known and was not estimated by the researchers before the agent's introduction. In the first and second decades (with some exceptions in the second decade), agents were introduced if, based on available information, they were considered to be primary parasitoids of the target pest and likely to be efficacious. Host range was generally not estimated, although some information was usually available in the form of records of attacks on other hosts, or from studies

designed to investigate whether species related to the target pest could be used as alternative hosts. This approach was largely replaced in the third decade by checking the host status of a list of more or less taxonomically (or ecologically) related nontarget species, limited to those species that could be obtained for testing. The transition to formal estimation of the fundamental host range (van Klinken and Heard, 2000) of entomophagous natural enemies based on experimentation, as is done for weed biocontrol agents, is gaining momentum in several countries (e.g., New Zealand and the United States). While continued momentum towards an increased requirement for host range and host specificity data is expected, strong differences exist in the biological factors structuring host ranges of parasitoids/predators vs. herbivorous insects that may limit progress towards this goal.

In general, analysis of trends found in Appendix 1 (see Figure 33 on next page) showed a shift in the third decade (2005-2015) toward a preponderance of agents showing an index of genus-level (60%) or species-level (8%) specificity (with only 12% being assigned a family-level or above index of specificity) compared to the first and second decades, when 50% and 40% of introductions had family level or above categorizations of specificity and only 21-27 (1985-1994, and 1995-2004, respectively) with genus, or 1-11% (1985-1994 and 1995-2004, respectively) with species level specificity. In all three decades, 11-12% of introductions could not be classified in this manner due to lack of information.

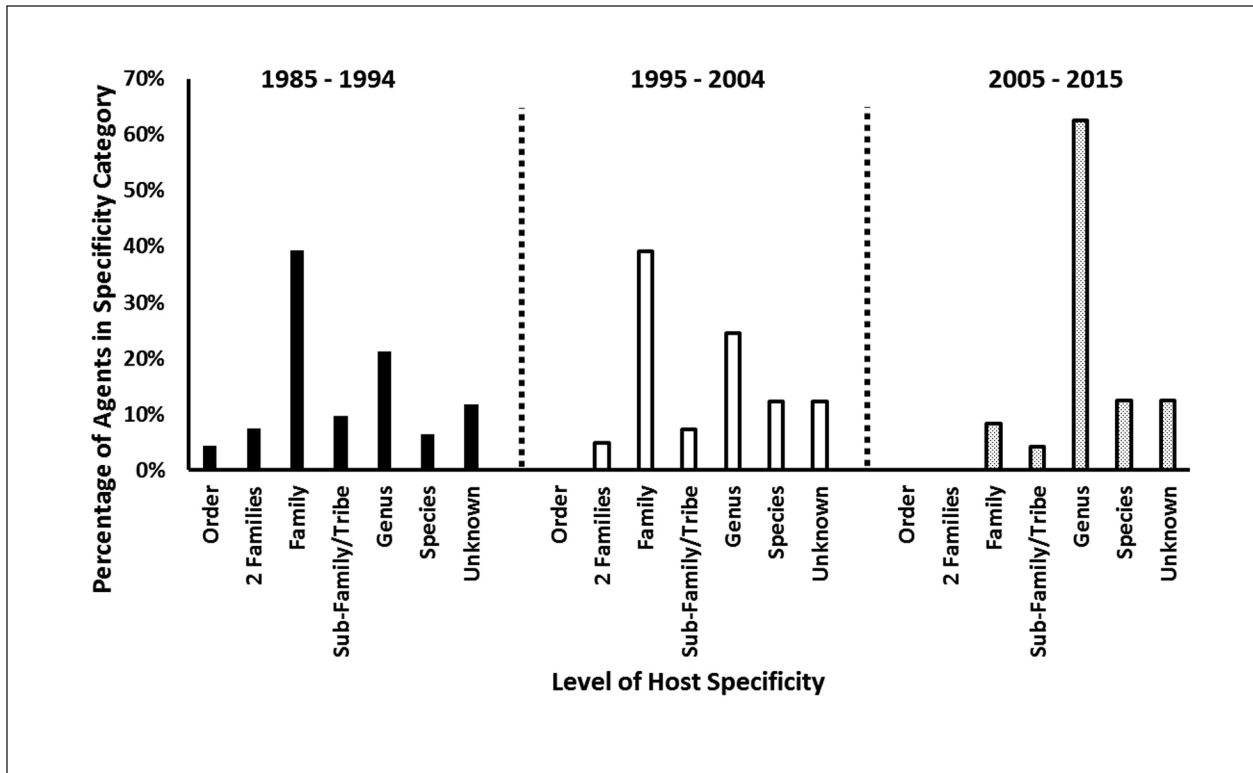


Figure 33. Trends in levels of host specificity of parasitoids released for insect biocontrol over three decades, indicating a shift toward genus-level specificity and a reduction in use of agents with family-level specificity. See Appendix I for details of cases used to compile Figure 33.

CONCLUDING REMARKS

Caveats and Clarifications

Evaluate original evidence; do not just repeat past claims.

It is important that summaries do more than just repeat conclusions of earlier studies. Summaries should consider the evidence past studies contain and make critical judgments on the strength of what is being claimed. Otherwise, errors of either pessimism or optimism cannot be expunged and replaced with data-supported conclusions. A good example of the need for this process is that of *B. remota* and whether or not it caused the extinction of either its host (*L. iridescens*) or a second species (*H. dolens*) on Fiji, as claimed by Howarth (1991), disputed by Kuris (2003) and Hoddle (2006), but not supported by adequate evidence.

Distinguish biological control agents from adventive parasitoids and predators.

Adventive (self-introduced) parasitoids and parasitoids should not be included in analyses assessing nontarget impacts by biological control agents. Invasions by polyphagous natural enemies occur naturally or because of commercial movement of plants and other goods. The impacts of accidentally introduced species, even if they are classified as biological control agents elsewhere, are not an indictment of sound biological control practice.

Critical need for good taxonomy BEFORE releasing new species.

Many biological control agents turn out to be species new to science. They are often described as part of the process of exploration related to actual or potential biological control projects (e.g., Japoshvili et al., 2013). Such descriptions and clarifications of any cryptic species that may mask the identity of potential agents should be done before agents are released (see Paterson et al., [2016] for an example of molecular identification of cryptic species, supported by mating studies).

Prioritize agents and begin by releasing the likely best species first.

Thoughtful programs should not operate on the principle that release of all species (sometime referred to as the lottery or shotgun approach) found to be primary parasitoids of the target pest is justified (e.g., as against Russian wheat aphid [Tanigoshi et al., 1995; Kazmer et al., 1996; Bernal et al., 2001] and sweetpotato whitefly strain B [Goolsby et al., 1998]). Rapid release of many species with little time to evaluate impacts of any is may be a sign of poor conduct and is likely to draw criticism (Strong and Pemberton, 2001).

Displacement of native species from a non-native host on a crop is not evidence of actual ecological harm.

Denying a native species the opportunity to use an exotic pest on an exotic plant (e.g., agricultural crops) by introducing an effective biological control agent of the pest should not be considered as a nontarget impact. Rather, displacement is an impact only when the native species is displaced from its native host in its usual ecological niche.

Guides for Future Thinking

Distinguish host use from population-level impact.

Feeding on or parasitizing a native species at levels that do not significantly lower its long term density should be considered “use” but not “impact” and should not be considered as ecologically damaging. While exact numbers are not known, we suggest that, in the absence of data, we should assume that rates of attack <10% are likely to have little impact, while rates of >50%, if widespread and sustained over time, may reduce populations of affected nontarget species.

Develop country-level on-line summaries of relevant information.

All countries making releases of biological control agents should develop and maintain web-accessible databases where lists of released agents, by year and target, can be viewed, as well as references or links to sources of information about the estimated host ranges of the agents.

Plan biological control projects with conservation partners.

Collaborative studies with conservation biologists are recommended as an effective way to build bridges and maximize use of existing expertise. See Van Driesche et al. (2016b) for discussion of potential joint efforts.

Conduct post-release comparisons of actual impact to predicted risk based on quarantine studies.

Post-release activities are central to improving our understanding of the level of accuracy of quarantine predictions in forecasting field nontarget impacts. Post-release studies, either retroactively for past projects or as part of current programs, should improve understanding of the ecological consequences of natural enemy releases and model insect life-systems to link observable levels of attack to population-level impacts (which is what matters).

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APPENDIX 1

The following table contains parasitoids introduced between 1985 and 2015, with notes on the level of specificity of each, drawn from literature records (worldwide) and BIOCAT (for North America, including Canada, Mexico, the United States, and U.S. overseas territories, 1985-2010 [end of available records]). Records for North America are relatively complete but for other regions are partial but not selective. Introductions were

only excluded if (1) species were unidentified (e.g., *Aphytis* sp.), (2) had also been released in the country before 1985), (3) were duplicative (i.e., release of the same agent in more than one country was not generally tracked unless there were important differences the current authors wished to capture, which was done only in a few cases), or (4) no published information could be located on the release of the species.

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
1985-1994							
1	1985 USA (Hawaii) from Pakistan	<i>Diadegma semiclausum</i> Hellén Ichneumonidae	<i>Plutella xylostella</i> (L.) Xylostellidae	0	No laboratory host range estimation done	Species? No other hosts are reported in the literature and the species show a strong response to cabbage odor, particularly when infested by <i>P. xylostella</i> (Rossbach et al., 2005)	R+/E? 1985 Funasaki et al., 1988; Rossbach et al., 2005
2	1985 USA	<i>Doryctobracon</i> (formerly <i>Opius</i>) <i>trinidadensis</i> (Gahan) Braconidae	<i>Anastrepha suspensa</i> (Loew) Tephritidae	0	No laboratory host range estimation done	Genus? Known only from original description, which lists two hosts, <i>Anastrepha serpentina</i> (Wiedemann) and <i>Anastrepha striata</i> Schiner	R+/E? 1985 Wharton and Marsh, 1978
3	1985 USA (Guam)	<i>Ganaspidium utilis</i> Beardsley (now <i>Banacuniculus utilis</i>) (Buffington, 2010) Eucosmidae	<i>Liriomyza trifolii</i> (Burgess) Agromyzidae	0	No laboratory host range estimation done	Family? All species in <i>Ganaspidium</i> are parasitoids of Agromyzidae (Diptera) (Buffington, 2004).	R+/E+ 1985 Beardsley, 1988; Johnson, 1993; Buffington, 2004, 2010
4	1985 USA (Texas) from Mexico	<i>Mallochia pyralidis</i> Wharton Ichneumonidae	<i>Eoreuma loftini</i> (Dyar) Crambidae	0	No laboratory host range estimation done	Unknown	R+/E? 1985 Wharton, 1985

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
5 1985 USA (Northern Mariana Is.)	<i>Pediobius foveolatus</i> (Crawford) Eulophidae	<i>Epilachna philippinensis</i> Dieke Coccinellidae	0	No laboratory host range estimation done	Subfamily? (Epilachninae) Literature hosts include principally various epilachnine coccinellids, e.g., <i>Epilachna varivestis</i> Mulsant (Nakamura and Shiratori, 2010) and <i>Henosepilachna vigintioctopunctata</i> (F.) (Varma and Anandhi, 2008); unusual records that need confirmation include the skipper <i>Borbo cinnara</i> (Wallace) (Gupta and Kalesh, 2012) and a braconid wasp (<i>Cotesia</i> sp.) (Paulraj and Ignacimuthu, 2007)	R+/E+ 1985	Chiu and Moore, 1993; Paulraj and Ignacimuthu, 2007; Varma and Anandhi, 2008; Gupta and Kalesh, 2012
6 1985-91 Canada from Europe	<i>Phygadeuon wiesmanni</i> Sachtleben Ichneumonidae	<i>Rhagoletis pomonella</i> (Walsh) Tephritidae	0	No laboratory host range estimation done	Genus? Literature records include other species of <i>Rhagoletis</i> , such as <i>R. cerasi</i> L. (Weismann, 1933), <i>R. alternata</i> Fallén (Rygg, 1979)	R+/E-	Weismann, 1933; Rygg, 1979; Hoffmeister, 2001
7 1985-91 Canada	<i>Psytalia carinata</i> (Thompson) senior synonym of <i>P. (Opius) rhagoleticola</i> (Sachtleben) Braconidae	<i>Rhagoletis pomonella</i> (Walsh) and/or <i>Rhagoletis cerasi</i> Tephritidae	0	No laboratory host range estimation done	Unknown Other species in the genus are parasitoids of tephritids	R+/E- 1985	Hoffmeister, 2001
8 1985-87 USA from Mexico	<i>Trichogramma atopovirilia</i> Oatman & Platner Trichogrammatidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	No laboratory host range estimation done	Two Families (Noctuidae and Crambidae) Literature records include eggs of noctuids (e.g., <i>Helicoverpa zea</i> [Boddie] [Tejada and Pablo, 1988] and <i>Anticarsia gemmatalis</i> Hübner [Foerster and Avanci, 1999]) and crambids (e.g., <i>Diatraea grandiosella</i> Dyar [Rodríguez-del-Bosque et al., 1989])	R+/E- 1985	Tejada and Pablo, 1988 Rodríguez-del-Bosque et al., 1989; Overholt and Smith, 1990

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
9	Ca 1985 Israel (from USA)	<i>Trichogramma platneri</i> Nagarkatti Trichogrammatidae	<i>Ascotis selenaria</i> Denis & Schiffermüller (= <i>Boarmia selenaria</i>) Geometridae; <i>Cryptoblabes gnidiella</i> (Milliere) Pyralidae	0	No laboratory host range estimation done	Order or multiple families At the time of introduction, it was known to attack eggs of moths in Tortricidae (<i>Cydia pomonella</i> [L.]; <i>Amorbia cuneana</i> [Wlsm.]), Geometridae (<i>Sabulodes aegrotata</i> [Gn.] (Oatman et al., 1983); <i>Boarmia selenaria</i> Schiff.), and Pyralidae (<i>Cryptoblabes gnidiella</i> Milliere)	R+/E- (Blumberg, pers. comm.) Ca 1985	Nagarkatti et al., 1975; Wysoki and Renneh, 1985; Oatman et al., 1983; Wysoki et al., 1988
10	1985 New Zealand	<i>Aphidius rhopalosiphi</i> De Stephani-Perez Braconidae	<i>Metopolophium dirhodum</i> (Walker) Aphididae	4-6?	Several (4-6?) exotic aphids were examined as hosts, but no native species were tested at the time. In addition host records from the literature were considered.	Tribes Aphidini and Macroshiphini This information was determined ~30 yrs after the introduction by Cameron et al., 2013	R+/E+ 1985	Farrell and Stufkens, 1990; Teulon et al., 2009; Cameron et al., 2013; David Teulon, pers. comm.
11	1985-1987 USA (northern Texas, from Indo-Australian region)	<i>Cotesia flavipes</i> Cameron Braconidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	No laboratory host range estimation done	Two Families (Noctuidae and Crambidae) Known to attack many noctuid and crambid stemborers in grasses (Rutledge and Wiedenmann, 1999)	R+/E- This species was released in south Texas, Rio Grande Valley, earlier (Fuchs et al., 1979) and established there. It failed to establish in 1985 in more northern Texas	Fuchs et al., 1979; Overholt and Smith, 1990; Polaszek and Walker, 1991; Overholt et al., 1994; Rodríguez-del-Bosque and Smith, 1997; Rutledge and Wiedenmann, 1999

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
12	1985-1987 USA (northern Texas, from Mexico)	<i>Trichogramma atopovorilia</i> Oatman and Platner Trichogrammatidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	Laboratory host testing was done to determine if certain pest borers were susceptible, including various crambids (formerly part of Pyralidae): <i>Diatraea considerata</i> Heinrich, <i>D. saccharalis</i> (F.), <i>D. grandiosella</i> Dyar, and <i>Eoreuma loftini</i> (Dyar)	Unknown	R+/E-	Browning and Melton, 1987; Overholt and Smith, 1990
13	1985-1987 USA (northern Texas, from Mexico)	<i>Allorhogas pyralophagus</i> Marsh Braconidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	Laboratory host testing was done to determine if certain pest borers were susceptible.	Two Families Grass stem borers in Crambidae and Noctuidae; known hosts include <i>Diatraea saccharalis</i> , <i>Emmalocera depressella</i> (Swinhoe), several species of <i>Chilo</i> , and the noctuid <i>Acigona steniellus</i> (Hampson), among others	R+/E- 1985-1987	Bennett et al., 1983; Marsh, 1984; Varma et al., 1987; Hawkins et al., 1987; Smith et al., 1987; Overholt and Smith, 1990
14	1985-1987 USA (northern Texas, from Mexico)	<i>Macrocentrus prolificus</i> Wharton Braconidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	No laboratory host range estimation done	Family? Known hosts include several species of <i>Diatraea</i> (<i>D. considerata</i> Heinrich, <i>D. grandiosella</i> Dyar, <i>D. saccharalis</i> [F.])	R+/E- 1985-1987	Wharton, 1984; Overholt and Smith, 1990
15	1985-1987 USA (northern Texas, from Mexico)	<i>Digonogastra kimballi</i> Kirkland Braconidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	No laboratory host range estimation done	Two Families Known hosts are <i>Eoreuma loftini</i> and 5 species of <i>Diatraea</i> (all Crambidae or Pyralidae)	R+/E- 1985-1987	Wharton et al., 1989; Overholt and Smith, 1990
16	1985-1987 USA (northern Texas, from Mexico)	<i>Pediobius furvus</i> (Gahan) Eulophidae	<i>Diatraea grandiosella</i> Dyar Crambidae	0	No laboratory host range estimation done	Two Families Grass stem borers in Pyralidae and Noctuidae	R+/E- 1985-1987	Overholt and Smith, 1990; Vignes, 1991; Oloo, 1992; Pfannenstiel et al., 1992; Yitaferu and Gebre-Amlak, 1994
17	1986-1989 USA (Texas and Florida) (Browning, 1994)	<i>Aphytis yanonensis</i> DeBach & Rosen Aphelinidae	<i>Parlatoria pergandii</i> Comstock (Texas) <i>Unaspis citri</i> (Florida) Diaspididae	0	No laboratory host range estimation done	Family Literature records include diaspidid scales such as <i>Unaspis yanonensis</i> Kuwana (Tanaka and Inoue, 1977).	R+/E-	Tanaka and Inoue, 1977; DeBach and Rosen, 1982; Browning, 1994

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
18	1986-1987 Canada	<i>Eurithia</i> (formerly <i>Ernestia consobrina</i>) (Meigen) Tachinidae	<i>Mamestra configurata</i> Walker Noctuidae	5	Of 5 nontarget (NT) noctuid species tested by placing a fly maggot on the test larva, 4 supported maggot development to pupation (Turnock and Carl, 1995)	Subfamily (Hadenine)	R+/E-	Turnock and Carl, 1995; Erlandson, 2013
19	1986-1990 USA	<i>Peristenus conradi</i> Marsh Braconidae	<i>Adelphocoris lineolatus</i> (Goeze) Miridae	0	No laboratory host range estimation done	Species? Post release surveys in two US states found parasitism in only the target mirid, of 7 species surveyed.	R+/E+	Day et al., 1992; Day, 1999, 2005
20	1986 USA (Hawaii)	<i>Tetrastichus brontispae</i> Ferrière Eulophidae	<i>Brontispa chalybeipennis</i> (Zacher) Chrysomelidae	0	No laboratory host range estimation done	Family? (coconut-feeding chrysomelid beetles) Field host records include <i>Brontispa froggatti</i> [<i>Brontispa longissima</i>] var. <i>selebensis</i> Gestro (Lever, 1936), <i>Brontispa mariana</i> Spaeth (Lange, 1950), <i>Gestronella centrolineata</i> (Fairm.) and <i>G. lugubris</i> (Fairm.), (Appert, 1974), <i>Octodonta nipae</i> (Maulik) (Chrysomelidae) (Tang et al., 2014)	R+/E?	Lever, 1936; Lange, 1950; Appert, 1974; Funasaki et al., 1988; Tang et al., 2014
21	1986-89 USA	<i>Thripobius javae</i> (Girault) (= <i>T. semiluteus</i> Boucek) Eulophidae	<i>Heliothrips haemorrhoidalis</i> (Bouché) Thripidae	0	No laboratory host range estimation done	Subfamily (Panchaetothripinae) This estimation was made by Froud et al. (1996) based on literature records.	R+/E+	McMurtry, 1988; McMurtry et al., 1991; Froud et al., 1996; Froud and Stevens, 2003
22	1986 USA (Guam)	<i>Trichogramma platneri</i> Nagarkatti Trichogrammatidae	<i>Penicillaria jocosatrix</i> Guenée Noctuidae	0	No laboratory host range estimation done	Order or multiple families At the time of introduction, it was known to attack eggs of moths in Tortricidae (<i>Cydia pomonella</i> [L.]; <i>Amorbia cuneana</i> [Wism.]), Geometridae (<i>Sabulodes aegrotata</i> [Gn.]; <i>Boarmia selenaria</i> Schiff.) (Oatman et al., 1983), and Pyralidae (<i>Cryptoblabes gnidiella</i> Millière)	R+/E?	Nagarkatti et al., 1975; Oatman et al., 1983; Wysoki and Renneh, 1985; Wysoki et al., 1988

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
23	1986-1987 Guam (from India)	<i>Aleiodes</i> nr. <i>circumscriptus</i> (Nees) Braconidae	<i>Penicillaria jocosatrix</i> Guenée Noctuidae	0	No laboratory host range estimation done	Unknown	R+/E- 1986-1987	Nafus, 1991
24	1986-1987 Guam (from India)	<i>Blepharella lateralis</i> Macquart Tachinidae	<i>Penicillaria jocosatrix</i> Guenée Noctuidae	0	No laboratory host range estimation done	Order Recorded from Noctuidae, Arctiidae, and Lymantriinae	R+/E+ 1986-1987	Battu and Dhaliwal, 1977; Kumar and Yadav, 1987; Nafus, 1991
25	1986-1987 Guam (from India)	<i>Euplectrus</i> nr. <i>parulus</i> Ferriere Eulophidae	<i>Penicillaria jocosatrix</i> Guenée Noctuidae	0	No laboratory host range estimation done	Unknown	R+/E+ 1986-1987	Nafus, 1991
26	1986 Turkey (from California)	<i>Eretmocerus debachi</i> Rose and Rosen Aphelinidae	<i>Parabemisia myricae</i> (Kuwana) Aleyrodidae	0	No laboratory host range estimation done	Species? Known only from target host	R+/E+ 1986	Sengonca et al., 1993
27	1987 Cyprus (from France)	<i>Metaphycus bartletti</i> (Annecke and Mynhardt) Encyrtidae	<i>Saissetia oleae</i> (Olivier) Coccidae	0	No laboratory host range estimation done	Genus (<i>Saissetia</i> and closely related Coccidae)	R+/E+ 1988-1989	Annecke and Mynhardt, 1972; Blumberg and Swirski, 1982; Orphanides, 1993
28	1987 Togo and later other parts of West Africa (from India by CABI)	<i>Gyranusoidea tebygi</i> Noyes Encyrtidae	<i>Rastrococcus invadens</i> Williams Pseudococcidae	3	One species each of <i>Pseudococcus</i> , <i>Planococcus</i> , and <i>Phenacoccus</i> were tested but none were parasitized	Species Did not parasitize either <i>R. iceryoides</i> (Green) or <i>R. mangiferae</i> (Green) in laboratory tests (Narasimham and Chacko, 1988)	R+/E+ 1988	Narasimham and Chacko, 1988; Agricola et al., 1989; Moore, 2004
29	1991 West Africa (from India by CABI)	<i>Anagyrus mangicola</i> Noyes Encyrtidae	<i>Rastrococcus invadens</i> Williams Pseudococcidae	3	One species each of <i>Pseudococcus</i> , <i>Planococcus</i> , and <i>Phenacoccus</i> were tested but none were parasitized	Species Did not parasitize either <i>R. iceryoides</i> (Green) or <i>R. mangiferae</i> (Green) in laboratory tests (Narasimham and Chacko, 1988)	R+/E+ 1991	Narasimham and Chacko, 1988; Moore, 2004
30	1987 USA (Hawaii)	<i>Psyllaephagus yaseeni</i> Noyes Encyrtidae	<i>Heteropsylla cubana</i> Crawford Psyllidae	0	No laboratory host range estimation done	Family (Psyllidae) No other hosts are recorded but there are few studies on this species	R+/E+	Beardsley and Uchida, 1990; Noyes, 1990

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
31	1987-1989 USA	<i>Trissolcus basalis</i> (Wollaston) (formerly <i>Microphanurus basalis</i> and <i>Asolcus basalis</i>) Scelionidae	<i>Nezara viridula</i> L. Pentatomidae	0	No laboratory host range estimation done	Family (Pentatomidae) Hosts recorded in the literature include various pentatomids, including <i>Euschistus servus</i> Say and the predator <i>Euthyrkynchus floridanus</i> L. (Miller, 1928), <i>Eurygaster integriceps</i> Put. (Shapiro et al., 1975); <i>Aelia rostrata</i> Boheman (Gallego et al., 1979), <i>Acrosternum</i> sp. and <i>Thyanta perditor</i> (F.) (Corrêa-Ferreira, 1986), among others.	R+/E+	Miller, 1928; Shapiro et al., 1975; Gallego et al., 1979; Corrêa-Ferreira, 1986
32	1987 Hawaii (from Tobago)	<i>Psyllaephagus rotundifolius</i> (Howard) (first identified as <i>Psyllaephagus</i> sp. near <i>rotundiformis</i>) (Howard) Encyrtidae	<i>Heteropsylla cubana</i> Crawford Psyllidae	2	Two other NT species in the same genus were accepted as hosts (Nakahara and Funasaki, 1987)	Genus? Recorded hosts include target plus 2 other species in same genus: <i>H. huasachae</i> Caldwell and <i>H. fusca</i> Crawford (Nakahara and Funasaki, 1987)	R+/E? 1988	Nakahara et al., 1987; Nakahara and Funasaki, 1987
33	1988-1989 USA (Guam)	<i>Adelencyrtus oceanicus</i> Doutt Encyrtidae	<i>Furcaspis oceanica</i> (Lindinger) Diaspididae	0	No laboratory host range estimation done	Unknown No other host records in literature	R+/E+	Muniappan and Marutani, 1989; Muniappan et al., 2003
34	1988 USA	<i>Ageniaspis</i> (formerly <i>Holcothorax</i>) <i>testaceipes</i> (Ratzburg) Encyrtidae	<i>Phyllonorycter</i> (formerly <i>Lithocolletis</i>) <i>crataegella</i> (Clemens) Gracillariidae	0	No laboratory host range estimation done	Genus? Limited to ecological niche of leafminers on deciduous trees? Most literature records are gracillariid (Lep.) leafminers in the genus <i>Phyllonorycter</i> including <i>P. blancardella</i> (F.) (Kadubowski, 1981), <i>P. ringoniella</i> (Matsumura) (Sun et al., 1987), and <i>Phyllonorycter pyrifoliella</i> (Gerasimov) (Kharchenko and Ryabchinskaya, 1995). However, one record is of the gelichiid (Lep.) leafminer <i>Recurvaria syrtictis</i> Meyrick (Cao and Guo, 1987) (needs verification)	R+/E+ (in Connecticut [Maier, 1990])	Kadubowski, 1981; Sun et al., 1987; Cao and Guo, 1987; Maier, 1990; Kharchenko and Ryabchinskaya, 1995
35	1988-1989 USA	<i>Aphidius rhopalosiphi</i> De Stefani-Perez Braconidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory host range estimation done	Tribes Aphidini and Macroshiphini Biotypes of this species may exist that have different host ranges (Höller, 1991)	R+/E-	Höller, 1991; Tanigoshi et al., 1995; Cameron et al., 2013

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
36	1988 USA Florida, from Bolivia	<i>Larra godmani</i> Cameron Sphecidae	<i>Scapteriscus</i> spp.(now <i>Neoscapteriscus</i>). This was an accidental contaminant in a shipment of <i>Larra</i> <i>bicolor</i> from Bolivia (Frank et al., 1995) Gryllotalpidae	0	No laboratory host range estimation done	Genus (<i>Neoscapteriscus</i>)	R+/E-? 1988	Menke, 1992; Frank et al., 1995
37	1988 USA Florida, from Bolivia	<i>Larra bicolor</i> F. Sphecidae	<i>Scapteriscus</i> <i>vicinus</i> Scudder (now <i>Neoscapteriscus</i>) Gryllotalpidae	1	No successfull attack observed on 1 native NT species, <i>Neocurtilla</i> <i>hexadactyla</i> (Perty), the only native cricket in the family in the region (Frank et al., 1995)	Genus (<i>Neoscapteriscus</i>) This parasitoid is functionally specific to the genus level in the US because it does not successfully attack the only native mole cricket in the region, <i>Neocurtilla</i> <i>hexadactyla</i> (Perty) (Frank et al., 1995)	R+/E+ 1988	Frank et al., 1995; Frank and Walker, 2006
38	1988-1989 USA	<i>Telenomus remus</i> Nixon Scelionidae	<i>Spodoptera</i> <i>frugiperda</i> (J. E. Smith) Noctuidae	39	Of 39 NT spp tested, of those not in the Noctuidae, there were 7 Arctiidae, 1 Ctenuchidae, 5 Geometridae, 1 Mimallonidae, 2 Notodontidae, and 2 Pyralidae. Of these, only 1 pyralid was parasitized. Of the 21 noctuids tested, 11 spp. in 11 genera were parasitized	Family (Noctuidae) From <i>Spodoptera</i> <i>mauritica</i> Boisd., in Malaysia (Nixon 1937), <i>Prodenia</i> (<i>Spodoptera</i> ?) <i>litura</i> F. (Lever, 1943) and 11 other noctuids and 1 pyralid (Wojcik et al., 1976)	R+/E-	Nixon, 1937; Lever, 1943; Wojcik et al., 1976
39	1988 Israel (from USA- CA; from Australia originally)	<i>Cryptochaetum</i> <i>iceryae</i> (Williston) Cryptochaetidae	<i>Icerya purchasi</i> Maskell Monophlebidae	0	No laboratory host range estimation done	Family (<i>Monophlebidae</i>) (or perhaps just the genus <i>Icerya</i> or even only the target pest)	R+/E+ 1988	Blumberg et al., 1989
40	Australia, from United States ca 1986	<i>Roptrocerus</i> <i>xylophagorum</i> (Ratzeburg) Pteromalidae	<i>Ips grandicollis</i> (Eichh.) Curculionidae, Scolytinae	0	No laboratory host range estimation done	Subfamily (Scolytinae) Attacks species of <i>Ips</i> (Mokrzecki, 1923), <i>Dendroctonus</i> (Bedard, 1937), <i>Hylurgops</i> (Lovaszy, 1943); <i>Pityogenes</i> (Galoux, 1947)	R+/E+ ca 1986	Mokrzecki, 1923; Bedard, 1937; Lovaszy, 1941; Galoux, 1947; Samson and Smibert, 1986; Berisford, 1991

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
41	1988 USA Florida	<i>Ormia (Euphasiopteryx) depleta</i> (Wiedemann) Tachinidae	<i>Scapteriscus vicinus</i> Scudder (now <i>Neoscapteriscus</i>) Gryllotalpidae	5	<i>Ormia depleta</i> was attracted to 3 of 5 <i>Scapteriscus</i> species tested, two of which were program targets and one a non-target invasive (Fowler 1987)	Genus That North American <i>Anurogrillus</i> species would not be attacked was determined (Walker, 1993) based on song characteristics, which determine parasitoid attraction.	R+/E+ 1988	Fowler and Mesa, 1987; Fowler, 1987, 1988; Walker, 1993; Frank et al., 1996; Frank and Walker, 2006
42	1988-1991 USA (from both France and Korea)	<i>Ageniaspis fuscicollis</i> (Dalman) Encyrtidae	<i>Yponomeuta malinellus</i> (Zeller) Yponomeutidae	0	No laboratory-based host range testing prior to release	Genus? At least five species in the target species' genus known to be parasitized in the field (Slavgorodskaya-Kurpieva, 1986)	R+/E+ 1988	Slavgorodskaya-Kurpieva, 1986; Hérard and Prévost, 1997; Unruh et al., 2003
43	1989-1990 USA	<i>Binodoxys</i> (formely in <i>Trioxys</i>) <i>brevicornis</i> (Haliday)	<i>Brachycorynella asparagi</i> (Mordv.)	0	No laboratory-based host range testing prior to release	Family? A polyphagus aphid parasitoid known from at least three genera in addition to that of the target: <i>Myzus cerasi</i> (F.) (Wimshurst, 1925), <i>Cavariella</i> spp. (Tremblay, 1975) <i>Hyadaphis coriandri</i> (Das) (Mescheloff and Rosen, 1993)	R+/E+	Wimshurst, 1925; Tremblay, 1975; Starý, 1990; Daane et al., 1992; Mescheloff and Rosen, 1993
44	1989-1991 USA	<i>Eurystheae scutellaris</i> (Robineau-Desvoidy) Braconidae, Aphidiinae	<i>Yponomeuta malinellus</i> (Zeller) Yponomeutidae	0	No laboratory-based host range testing prior to release	Order (Three moth families) Hosts recorded in the literature, include species in three families: the pyralid <i>Acrobasis consociella</i> (Hübner) (Lerer and Plugar, 1962), various yponomeutids including <i>Yponomeuta padellus</i> (L.) (Heusinger, 1981), and the geometrid <i>Abraxas pantaria</i> (L.) (Pernek et al., 2015)	R+/E-	Lerer and Plugar, 1962; Heusinger, 1981; Unruh et al., 2003; Pernek et al., 2015
45	1989 New Zealand (from Argentina)	<i>Microctonus hyperodae</i> Loan Braconidae, Euphorinae	<i>Listronotus bonariensis</i> (Kuschel) Curculionidae	24	Of 24 NT weevils tested, 1 NT supported complete development	Tribe? or Subfamily? The one NT that supported developed was in new genus	R+/E+ 1992	Goldson et al., 1992; Barker and Addison, 2006
46	1989 Australia (from Europe via New Zealand)	<i>Sphecoptera vesparum</i> (Curtis) Ichneumonidae	<i>Vespula germanica</i> (F.) and <i>Vespula vulgaris</i> (L.) Vespidae	8	No NT species tested were regularly attacked (3 instances observed)	Subfamily Hosts appear to be restricted to the Vespinae	R+/E+? 1989	Field and Darby, 1991

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
47	1989-1991 USA (from both France and Korea)	<i>Diadegma</i> (formerly <i>Nythobia armillata</i> (also <i>armillatum</i>) (Gravenhorst) (perhaps now in <i>Angitia</i>) Ichneumonidae	<i>Yponomeuta malinellus</i> (Zeller) Yponomeutidae	7	4 NT species in the genus were suitable hosts, while 3 others were not, due to encapsulation	Family? Known from species in two genera of Yponomeutidae, including <i>Yponomeuta rorellus</i> (Hb.) (Koehler and Kolk, 1971), <i>Y. evonymella</i> L. (Bartninkaite, 1996), and <i>Prays oleae</i> (Bernard) (Agrò et al., 2009)	R+/E-? Koehler and Kolk, 1971; Dijkerman, 1990; Bartninkaite, 1996; Hérard and Prévost, 1997; Unruh et al., 2003; (see also Wagener et al., 2006 for notes on phylogeny of parasitoid genus); Agrò et al., 2009
48	1989-1991 USA (from France, Korea, and Japan)	<i>Herpestomus brunnicornis</i> (Gravenhorst) Ichneumonidae	<i>Yponomeuta malinellus</i> (Zeller) Yponomeutidae	3	3 NT hosts in the same genus in the native range were suitable hosts	Genus?	R+/E? Fischer. 1987; Unruh et al., 2003
49	1989-1996 Samoa, Tonga, Fiji, and the Cook Islands	<i>Telenomus lucullus</i> (Nixon) Scelionidae	<i>Eudocima fullonia</i> (Clerck) Noctuidae	11	All 3 NT in same genus were attacked; 0 of 8 NT noctuids in other genera were attacked	Genus Considered adequate for island fauna.	R+/E+ 1989-1996 Sands and Liebrechts, 2005
50	1989-1996 considered for use in Australia; Not released	<i>Telenomus lucullus</i> (Nixon) Scelionidae	<i>Eudocima fullonia</i> (Clerck) Noctuidae	11	All 3 NT in same genus were attacked; 0 of 8 NT noctuids in other genera were attacked; The rare native species <i>Eudocima iridescens</i> (T.P. Lucas) could not be found for testing	Genus Considered insufficiently specific in view of known rare congeneric species in Australia	R- Not released Sands and Liebrechts, 2005
51	1989-1996 Samoa, Tonga, Fiji, and the Cook Islands	<i>Ooencyrtus</i> sp. in <i>papilionis</i> group Encyrtidae	<i>Eudocima fullonia</i> (Clerck) Noctuidae		All 3 NT in same genus and 8 of 8 NT noctuids in other genera were attacked.	Family Considered adequate for island fauna.	R+/E+ 1989-1996 Sands and Liebrechts, 2005
52	1989-1996 considered for use in Australia; Not released	<i>Ooencyrtus</i> sp. in <i>papilionis</i> group Encyrtidae	<i>Eudocima fullonia</i> (Clerck) Noctuidae		All 3 NT in same genus and 8 of 8 NT noctuids in other genera were attacked; The rare native species <i>Eudocima iridescens</i> (T.P. Lucas) could not be found for testing	Family Considered insufficiently specific.	R- Not released Sands and Liebrechts, 2005

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
53	1989-1990 USA	<i>Encarsia inaron</i> (Walker) Aphelinidae	Ash whitefly, <i>Siphoninus phillyreae</i> (Haliday) Aleyrodidae	0	No formal host range testing was done before release. The parasitoid is known to attack species of whiteflies in several genera, including <i>Siphoninus</i> , <i>Bemisia</i> , <i>Trialeurodes</i> , and <i>Pealius</i> .	Family Not reported from non-pest, native U.S. whiteflies.	R+/E+ 1990	Mohyuddin et al., 1989; Bene, 1990; Bene et al., 1991
54	1990 Canada	<i>Apanteles murinanae</i> Čapek and Zwölfer Braconidae	<i>Choristoneura fumiferana</i> (Clemens) Tortricidae	0	No laboratory host range estimation done. This species was collected in Europe from the closely related species <i>Choristoneura murinana</i> (Hübner) and, after confirming its ability to develop in the target host, released in Canada as single release.	Family? The only other known field host is <i>Eucosma nigricana</i> (H.-S.), another tortricid of similar biology as <i>C. murinana</i> , with which it shares a common host and habitat (Čapek, 1961)	R+/E-	Čapek, 1961; Smith et al., 2002
55	1990-1994 USA, Florida, from Hong Kong	<i>Eretmocerus rui</i> Zolnerowich and Rose Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family? No other host records from field or laboratory studies were located.	R+/E-	Zolnerowich and Rose, 2004
56	1990-1995 (USA from China)	<i>Coccobius</i> nr. <i>fulvus</i> Aphelinidae	<i>Unaspis euonymi</i> (Comstock) Diaspididae	0	No laboratory host range estimation done	Genus? <i>C. fulvus</i> is known only from two species of <i>Unaspis</i> scales (Drea and Carlson, 1987; Takagi, 1991; Van Driesche et al., 1998; O'Reilly and Van Driesche, 2009), assuming that <i>C. fulvus</i> and <i>C. nr fulvus</i> are the same, which was never determined	R+/E+ 1984/ 1990-1995	Drea and Carlson, 1987; Takagi, 1991; Van Driesche et al., 1998; O'Reilly and Van Driesche, 2009

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References	
57	1990-1995 USA (from China)	<i>Encarsia</i> (formerly <i>Prospatella</i>) nr. <i>diaspidicola</i> Silvestri Aphelinidae	<i>Unaspis euonymi</i> (Comstock) Diaspididae	0	No laboratory host range estimation done	Family? Assuming this is the same as <i>E. diaspidicola</i> and that it is not a species complex, then several diaspidid scales (including <i>Pseudaulacaspis</i> <i>pentagona</i> [Targioni- Tozzetti] and <i>Quadraspidiotus</i> <i>perniciosus</i> [Comstock]) are known hosts, but others are not hosts (Neumann et al., 2010)	R+/E-? 1990-1995	Drea and Carlson, 1987; Van Driesche et al., 1998; Sands et al., 1990; Matadha et al., 2003, 2005; O'Reilly and Van Driesche, 2009; Neumann et al., 2010
58	1990-1995 USA (from China)	<i>Aphytis proclia</i> (Walker) Aphelinidae	<i>Unaspis euonymi</i> (Comstock) Diaspididae	0	No laboratory host range estimation done	Family? Several diaspidid scales (including <i>Pseudaulacaspis</i> <i>pentagona</i> [Targioni- Tozzetti] and <i>Quadraspidiotus</i> <i>perniciosus</i> [Comstock]) among others) are known hosts. Note, however, that <i>A. proclia</i> as a name may refer to more than one species.	R+/E-? 1990-1995	Drea and Carlson, 1987; Van Driesche et al., 1998; Matadha et al., 2003, 2005; Graora and Spasic, 2008
59	1992 USA, Colorado, Washington and others (from Morroco and the Middle East)	<i>Ephedrus plagiator</i> (Nees) Braconidae, Aphidiinae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory host range estimation done	Family? Several aphids are recorded as hosts, including <i>Aphis pomi</i> de Geer (Cierniewska, 1973), <i>Schizaphis</i> <i>graminum</i> (Rondani), <i>Rhopalosiphum padi</i> (L.), <i>Macrosiphum</i> (<i>Sitobion</i>) <i>avenae</i> (F.) (Rakhshani et al., 2008), <i>Aulacorthum solani</i> (Kaltenbach) (Ji et al., 2014), among others.	R+/E-	Cierniewska, 1973; Elliott et al., 1995; Tanigoshi et al., 1995; Rakhshani et al., 2008; Ji et al., 2014
60	1992 USA	<i>Aphelinus atriplicis</i> Kurdjumov Aphelinidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	Limited to Aphididae; species identity misunderstood initially but sorted out after introduction	Family Safe to non-aphids; parasitizes many NT aphids; but population impacts are unknown	R+/E+ 1992	Tanigoshi et al., 1995; Kazmer et al., 1996; Bernal et al., 2001; Burd et al., 2001; Noma et al., 2005; Hopper et al., 2005; Heraty et al., 2007

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
61	About 1990 Mexico (from Africa)	<i>Prorops nasuta</i> Waterson Bethyridae	<i>Hypothenemus hampei</i> (Ferrari) Curculionidae, Scolytinae	2	Both NT species were used successfully as hosts	Family? Several genera of weevils are known to support oviposition and development. Boundaries of host range are not known.	R+/E+ 1988	Barrera et al., 1990; Pérez-Lachaud and Hardy, 2001
62	1988 Mexico (from Africa)	<i>Cephalonomia stephanoderis</i> Betrem Bethyridae	<i>Hypothenemus hampei</i> (Ferrari) Curculionidae, Scolytinae	2	Both NT species were used successfully as hosts	Family? Several genera of weevils are known to support oviposition and development. Boundaries of host range are not known.	R+/E+ 1989	Barrera et al., 1990; Pérez-Lachaud and Hardy, 2001
63	ca 1990 Guatemala (from Africa)	<i>Phymastichus coffea</i> (LaSalle) Eulophidae	<i>Hypothenemus hampei</i> (Ferrari) Curculionidae, Scolytinae	5	2 NT <i>Hypothenemus</i> sp. were attacked; 1 <i>Hypothenemus</i> sp. was not and 2 species in other bark beetle genera were not.	Genus?	R+/E+? 1990?	Gálvez, 1992
64	1991 Canada (from Europe)	<i>Aphantorhaphopsis (Ceranthis) samarensis</i> (Villeneuve) Tachinidae	<i>Lymantria dispar</i> (L.) Erebidae, Lymantriinae	11	Of 11 North America species (in 5 families) tested, only one species, <i>Orgyia leucostigma</i> (J. E. Smith) (Lymantriinae) was a suitable host	Subfamily (Lymantriinae)	R+/E? 1991	Mills and Nealis, 1992; Nealis and Quednau, 1996; Fuester et al., 2014
65	1992 USA	<i>Aphelinus nr asychis</i> Aphelinidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	Limited to Aphididae; species identity misunderstood initially but sorted out after introduction	Family Safe to non-aphids; certainty of "use" of many NT aphids; uncertainty about population impacts	R+/E+ 1992	Tanigoshi et al., 1995; Kazmer et al., 1996; Bernal et al., 2001; Burd et al., 2001; Noma et al., 2005; Hopper et al., 2005; Heraty et al., 2007
66	1992 Australia	<i>Citrostichus phyllocnistoides</i> (Naryanin) Eulophidae	<i>Phyllocnistis citrella</i> Stainton Gracillariidae	17 ^b	0 NT species attacked (including 1 leafminer in same genus, 5 leafminers in other genera and 11 other foliovores, leafminers, or gall makers in other families and gall makers)	Genus? relative to Australia biota	R+/E- 1992	Neale et al., 1995

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
67	1992 Australia	<i>Ageniaspis citricola</i> (Longvinovskaya) Encyrtidae	<i>Phyllocnistis citrella</i> Stainton Gracillariidae	17 ^b	0 NT species attacked (including 1 leafminer in same genus, 5 leafminers in other genera and 11 other foliovores, leafminers, or gall makers in other families and gall makers)	Genus? relative to Australia biota	R+/E+ 1992	Neale et al., 1995
68	1992 Australia	<i>Cirrospilus ingenuus</i> (= <i>quadristriatus</i>) Gahan Eulophidae	<i>Phyllocnistis citrella</i> Stainton Gracillariidae	17 ^b	0 NT species attacked (including 1 leafminer in same genus, 5 leafminers in other genera and 11 other foliovores, leafminers, or gall makers in other families and gall makers)	Genus? relative to Australia biota	R+/E+ 1992	Neale et al., 1995
69	1992 Italy (from USA)	<i>Neodryinus typhlocybae</i> (Ashmead) Dryinidae	<i>Metcalfa pruinosa</i> (Say) Flatidae	8	8 NT – no attack, but no tested species were other flatids	Family?	R+/E+	Villani and Zandigiacomo 2000; Strauss, 2009
70	1993 USA, California (from Turkmenistan)	<i>Aphelinoidea turanica</i> Trjapitzin Trichogrammatidae	<i>Circulifer tenellus</i> (Baker) (sometimes given as <i>Neoaliturus tenellus</i>) Cicadellidae	0	No formal host range testing done	Family (Cicadellidae) No information found in CAB on hosts, field or laboratory, apart from its success in attacking the target species after release	R+/E+	Trjapitzin, 1994
71	1993-2000 USA, California and Washington (from Kazakstan)	<i>Lytopylus rufipes</i> (Nees von Esenbeck) (previous generic assignments include <i>Agathis</i> , <i>Microdus</i> , <i>Bassus</i>) Braconidae	<i>Cydia pomonella</i> (L.) Tortricidae	0	No formal host range testing done	Two Families A number of tortricids and pyralids (Mills, pers. comm.; Simbolotti and van Achterberg, 1992)	R+/E-	Simbolotti and van Achterberg, 1992; Mills, 2005a,b; Stevens et al., 2011
72	1993-2000 USA California and Washington (from Kazakstan)	<i>Liotryphon caudatus</i> (Ratzburg) (former generic placements were <i>Apistephialtes</i> , <i>Calliephialtes</i> , and <i>Ephialtes</i>) Ichneumonidae	<i>Cydia pomonella</i> (L.) Tortricidae	0	No formal host range testing done	Family? (Tortricidae) Attacks various fruit-boring and cocoon-forming tortricids such as <i>Cydia molesta</i> (Busck) and <i>Grapholita funebrana</i> (Treitschke) (Mills, pers. comm.)	R+/E+? (temporarily established)	Mills, 2005a,b

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
73	1993 USA, California (from Australia)	<i>Avetianella longoi</i> Siscaro Mymaridae	<i>Phoracantha semipunctata</i> F. Cerambycidae	0	No formal host range testing done	Unknown Likely restricted to hosts on eucalypts due to attraction to host plant odors	R+/E+ Ca 1993	Hanks et al., 1996; Luhning et al., 2000
74	1993 USA, California (from Australia)	<i>Syngaster lepidus</i> Brulé Braconidae	<i>Phoracantha semipunctata</i> F. and <i>P. recurva</i> Newman Cerambycidae	0	No formal host range testing done	Unknown Likely restricted to hosts on eucalypts due to attraction to host plant odors	R+/E+ Ca 1993	Paine et al., 1995
75	1993 USA, California (from Australia)	<i>Jarra phoracantha</i> Austin, Quicke, and Marsh Braconidae	<i>Phoracantha semipunctata</i> F. Cerambycidae	0	No laboratory host range estimation done	Unknown Likely restricted to hosts on eucalypts due to attraction to host plant odors	R+/E?	Paine and Millar, 2003
76	1993 Kenya (from Pakistan)	<i>Cotesia flavipes</i> Cameron Braconidae	<i>Chilo partellus</i> Swinhoe Crambidae	3	2 NT pest hosts (both noctuids, one in same genus) were suitable hosts; 1 was not (noctuid, non- <i>Chilo</i>)	Two Families Known to attack some noctuid and some crambid stemborers in grasses	R+/E+ 1993	Overholt et al., 1994; 1997
77	1993 California (from Australia); 1994 Britain 1997 France and Ireland; 2001 Chile	<i>Psyllaephagus pilosus</i> Noyes Encyrtidae	<i>Ctenarytaina eucalypti</i> (Maskell) Psyllidae	0	No formal host range testing done but this is likely a eucalypt specialist (Withers, 2001), conferring high host specificity in the invaded range via the influence of the host plant	Family High specificity in invaded ranges due to attraction to eucalyptus	R+/E+ 1993-1997	Malaus and Girardet, 1997; Dahlsten et al., 1998; Hodkinson, 1999; Withers, 2001
78	1993-1999 USA (from United Arab Emirates)	<i>Eretmocerus emiratus</i> Zolnerowich & Rose Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done. Plans to test <i>Trialeurodes vaporariorum</i> (Westwood), <i>T. abutilonia</i> (Haldeman), and <i>Bemisia berbericola</i> (Cockerell) were made but not carried out.	Family (Aleyrodidae) No field hosts recorded other than <i>Bemisia</i>	R+/E+ (in southern CA) <2000	Zolnerowich and Rose, 1998; Goolsby et al., 1998; Roltsch, 2000; Hoelmer and Goolsby, 2003; Goolsby et al., 2005
79	1993-1999 USA (from Ethiopia)	<i>Eretmocerus</i> nr <i>emiratus</i> Zolnerowich and Rose Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) Known from <i>Aleyrodes loniceræ</i> Walker in China (Yu, 2015)	R+/E+ (in Arizona) <2000	Goolsby et al., 1998; Roltsch, 2000; Hoelmer and Goolsby, 2003; Goolsby et al., 2005; Yu, 2015

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
80	1993-1999 USA (from Pakistan)	<i>Eretmocerus hayati</i> Zolnerowich and Rose Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) No field hosts recorded other than <i>Bemisia</i>	R+/E+ (in Texas and Mexico) <2000	Goolsby et al., 1998; Zolnerowich and Rose, 1998; Hoelmer and Goolsby, 2003; Goolsby et al., 2005
81	1993-1999 USA (from Thailand, Taiwan)	<i>Eretmocerus melanoscutus</i> Zolnerowich and Rose Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) No field hosts recorded other than <i>Bemisia</i>	R+/E+ (in Florida) <2000	Goolsby et al., 1998; Zolnerowich and Rose, 1998; Hoelmer and Goolsby, 2003; Goolsby et al., 2005
82	1993-1999 USA (from Taiwan)	<i>Eretmocerus</i> nr. <i>furuhashii</i> Rose and Zolnerowich Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) No field hosts recorded other than <i>Bemisia</i>	R+/E- <2000	Goolsby et al., 1998; Hoelmer and Goolsby, 2003; Goolsby et al., 2005
83	1993-1999 USA (from Spain, Israel)	<i>Eretmocerus mundus</i> Mercet Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) Field surveys in California found <i>E. mundus</i> only from <i>B. tabaci</i> , not non-target whiteflies (Pickett et al., 2013). In the laboratory two species of <i>Trialeurodes</i> were attacked (<i>T. abutilonea</i> [Haldeman] and <i>T. vaporariorum</i> [Westwood]) (Greenberg et al., 2009).	R+/E+ (in California) <2000	Goolsby et al., 1998; Roltsch, 2000; Hoelmer and Goolsby, 2003; Goolsby et al., 2005; Greenberg et al., 2009; Pickett et al., 2013
84	1993-1999 USA (from Puerto Rico)	<i>Amitus bennetti</i> Viggiani & Evans Platygasteridae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) No field hosts recorded other than <i>Bemisia</i>	R+/E? <2000	Hoelmer and Goolsby, 2003

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
85	1993-1999 USA (from Israel)	<i>Encarsia lutea</i> (Masi) Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) Females: (Aleyrodidae) Males: Lepidoptera Known to attack several genera of whiteflies, including <i>Trialeurodes abutilonea</i> (Hald.) and <i>T. vaporariorum</i> (Westw.) and for males to emerge from eggs of noctuid moths (Stoner and Butler, 1965), and <i>Acaudaleyrodes citri</i> (Priesn. & Hosni) (Rosen, 1966); <i>Parabemisia myricae</i> (Kuwana) (Longo et al., 1990); <i>Aleurolobus</i> spp. (Abd-Rabou, 1997).	R+/E- <2000	Stoner and Butler, 1965; Rosen, 1966; Longo et al., 1990; Abd-Rabou, 1997; Goolsby et al., 1998; Hoelmer and Goolsby, 2003; Goolsby et al., 2005
86	1993-1999 USA (from Pakistan)	<i>Encarsia sophia</i> (= <i>E. transvena</i>) (Girault & Dodd) Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) Known to attack <i>T. vaporariorum</i> (Westw.) (Kumar and Gupta, 2006) and <i>Bemisia tuberculata</i> Bondar (Vásquez-Ordóñez et al., 2015)	R+/E+ <2000 (Established in California [Gould et al., 2008]) and Texas [Goolsby et al., 2009])	Goolsby et al., 1998; Roltsch, 2000; Hoelmer and Goolsby, 2003; Kumar and Gupta, 2006; Gould et al., 2008; Goolsby et al., 2005, 2009; Vásquez-Ordóñez et al., 2015
87	1993-1999 USA (from Brazil)	<i>Encarsia</i> nr <i>pergandiella</i> Howard Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) Females: Aleyrodidae or below Males: Aphelinid parasitoids Males develop as hyperparasitoids on whitefly parasitoids, including <i>E. mundus</i> (Zhang et al., 2015)	R+/E- <2000	Goolsby et al., 1998; Hoelmer and Goolsby, 2003; Goolsby et al., 2005; Zhang et al., 2015
88	1993-1999 USA (from Brazil)	<i>Encarsia</i> nr <i>hispida</i> De Santis Aphelinidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory host range estimation done	Family (Aleyrodidae) Known to attack <i>T. vaporariorum</i> (Westw.) (Maignet and Onillon, 1997), <i>Trialeurodes variabilis</i> (Quaintance) (Lourenção et al., 2007), <i>Paraleyrodes minei</i> Iaccarino (Telli and Yigit, 2012), and <i>Aleurotrachelus socialis</i> Bondar (Vásquez-Ordóñez et al., 2015)	R+/E- <2000	Maignet and Onillon, 1997; Goolsby et al., 1998; Hoelmer and Goolsby, 2003; Goolsby et al., 2005; Lourenção et al., 2007; Telli and Yigit, 2012; Vásquez-Ordóñez et al., 2015

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
89	1993-2000 USA (from Central Asia [Kazakstan])	<i>Mastrus ridens</i> Horstmann (formerly <i>M. ridibundus</i>) Ichneumonidae	<i>Cydia pomonella</i> L. Tortricidae	0	No laboratory host range estimation done at the time of the introduction to USA. Later, in New Zealand (Charles et al., 2013), some post facto host range testing showed that of 5 species tested, 1 NT <i>Cydia</i> species and 4 others in the target's family (Tortricidae) were attacked, but offspring were small and mostly male; known in native range only from target; but little sampling other than of the target	Genus? Other tortricids could be killed by this parasitoid but seem unlikely themselves to support <i>M. ridens</i> populations due to a too rapid death from the paralyzing venom of the parasitoid.	R+/E+ 1993-2000	Mills, 2005a; Charles et al., 2013
90	1994 USA, California	<i>Anaphes nitens</i> (Girault) (other generic placements include <i>Patasson</i> and <i>Anaphoidea</i>) Mymaridae	<i>Gonipterus scutellatus</i> Gyllenhal. See Mapondera et al. (2012) for notes on cryptic species in genus. Curculionidae	0	No laboratory host range estimation done	Genus? Field records include <i>Gonipterus gibberus</i> Boisduval (Sanches, 2000)	R+/E+	Hanks et al., 2000; Sanches, 2000; Mapondera et al., 2012
91	1994 Spain (from South Africa??)	<i>Anaphes nitens</i> (Girault) (other generic placements include <i>Patasson</i> and <i>Anaphoidea</i>) (Mymaridae)	<i>Gonipterus platensis</i> (Marelli) (see Mapondera et al., 2012 for notes on cryptic species in genus) (Curculionidae)	0	No laboratory host range estimation done	Genus? Field records include <i>Gonipterus gibberus</i> Boisduval (Sanches, 2000)	R+/E+ ca 1994	Rivera et al., 1999; Sanches, 2000; Mapondera et al., 2012
92	1994 Brazil, Bahia (from Colombia or Venezuela)	<i>Apoanagyrus diversicornis</i> (Howard) Encyrtidae	<i>Phenacoccus herreni</i> Cox and Williams Pseudococcidae	0	No laboratory host range estimation done	Genus? Known only from species of <i>Phenacoccus</i>	R+/E+ 1994-1995	Van Driesche et al., 1986, 1987; Bento et al., 2000

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
93	1994 Brazil, Bahia (from Colombia or Venezuela)	<i>Aenasius vexans</i> (Kerrich) Encyrtidae	<i>Phenacoccus herreni</i> Cox and Williams Pseudococcidae	7 (six yrs post release)	No laboratory host range estimation done before release in Brazil, but subsequent studies of 7 mealybug species found that <i>A. vexans</i> did not attack any of the nontarget mealybugs tested.	Species? No attack in laboratory tests and no other known field hosts.	R+/E+ 1994-1995	Bento et al., 2000; Dorn et al., 2001
94	1994 Brazil, Bahia (from Colombia or Venezuela)	<i>Acerophagus coccois</i> Smith Encyrtidae	<i>Phenacoccus herreni</i> Cox and Williams Pseudococcidae	7 (six yrs post release)	No laboratory host range estimation done before release in Brazil, but subsequent studies of 7 mealybug species found that <i>A. coccois</i> attacked 3 (two species of <i>Phenacoccus</i> and <i>Ferrisia virgata</i> [Cockerell])	Family (Pseudococcidae) Known from <i>Oracella acuta</i> (Lodbell) (Clarke et al. 1987), <i>Ferrisia virgata</i> (Cockerell) (Dorn et al., 2001) and several species of <i>Phenacoccus</i>	R+/E+ 1994-1995	Van Driesche et al., 1986, 1987; Clarke et al., 1990; Bento et al., 2000; Dorn et al., 2001
95	1994 USA/Florida (via Australia from Thailand)	<i>Ageniaspis citricola</i> Longvinovskaya Encyrtidae	<i>Phyllocnistis citrella</i> Stainton Gracillariidae	0	No laboratory host range estimation done relative to US <i>Phyllocnistis</i> species; specificity assumed based on testing in Australia ^b	Unknown relative to North American fauna	R+/E+ 1994	Smith and Hoy, 1995; Pomerinke and Stansly, 1998; Xiao et al., 2007
96	1994 USA/Florida (via Australia from Thailand)	<i>Cirrospilus ingenuus</i> (= <i>quadristriatus</i>) Gahan Eulophidae	<i>Phyllocnistis citrella</i> Stainton Gracillariidae	0	No laboratory host range estimation done relative to US <i>Phyllocnistis</i> species; specificity assumed based on testing in Australia ^b	Unknown relative to North American fauna	R+/E-? 1994	Smith and Hoy, 1995; LaSalle et al., 1992

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
1995-2004							
1	1995 USA, California	<i>Aphelinoidea anatolica</i> Nowicki Mymaridae	<i>Circulifer tenellus</i> (Baker) (sometimes given as <i>Neoaliturus tenellus</i>) Cicadellidae	0	No laboratory host range estimation done	Family (Cicadellidae) No information found in CAB on hosts, field or laboratory.	R+/E+ Huffaker et al., 1954; Walker et al., 1997; Bayoun et al., 2008
2	1995-1999 Canada (from Europe)	<i>Lathrolestes ensator</i> (Brauns) Ichneumonidae	<i>Hoplocampa testudinea</i> (Klug) Tenthredinidae	0	No laboratory host range estimation done	Species? This species is known only from one host, but this does not exclude its existence on hosts not sampled.	R+/E+ Vincent et al., 2001a,b; Vincent et al., 2016
3	1995-1997 USA, Texas (1995), Florida (1997) (from South America)	<i>Pseudacteon tricuspis</i> Borgmeier Phoridae	<i>Solenopsis invicta</i> , <i>S. richteri</i> , and hybrids Formicidae	13 +1	0 NT attack on 13 NT ants not in <i>Solenopsis</i> ; 0 NT attack on 1 NT in <i>Solenopsis</i> ; Post-release, 0 NT attacks on 15 NT ants including 1 native NT congener	Species Group level within Genus	R+/E+ 1997 Gilbert & Morrison, 1997; Porter, 1998; Porter & Alonso, 1999; Morrison & Porter, 2006; Callcott et al., 2011
4	1995-1997 USA, Texas (1995), Florida (1997) (from South America)	<i>Pseudacteon litoralis</i> Borgmeier Phoridae	<i>Solenopsis invicta</i> , <i>S. richteri</i> , and hybrids Formicidae	27 +1	0 NT attack on 27 NT ants not in <i>Solenopsis</i> ; 1 NT <i>Solenopsis</i> (<i>S. geminata</i>) attacked (at 9% of target rate), but no successful development	Species Group level within Genus	R+/E+ 2003 Porter et al, 1995; Gilbert and Morrison, 1997; Porter 1998; Porter and Alonso, 1999; Porter et al., 2011
5	USA Not petitioned for release	<i>Pseudacteon wasmanni</i> Schmitz ^c Phoridae	<i>Solenopsis invicta</i> , <i>S. richteri</i> , and hybrids Formicidae	27 +2	0 NT attack on 27 NT ants not in <i>Solenopsis</i> ; 2 NT <i>Solenopsis</i> attacked (<i>S. geminata</i> , <i>S. saevissima</i> , <i>S. geminata</i> at 11% target rate)	Genus level or better	R- Porter et al, 1995; Gilbert and Morrison, 1997; Porter and Alonso, 1999

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
6	1996 Australia (from Argentina)	<i>Trichopoda giacomellii</i> (Blanchard) Tachinidae	<i>Nezara viridula</i> (L.) Pentatomidae	14	Of 10 NT pentatomids, 6 attracted oviposition, but only 3 supported complete development, 2 at levels equal to target and 1 at 1/3 level of target. Species in other families were rejected.	Family Including target, acceptable hosts were found in four genera of pentatomids	R+/E+ Ca 1997	Sands and Coombs, 1999; Coombs and Sands, 2000
7	1996-1999 Spain	<i>Citrostichus phyllocnistoides</i> (Naryanin) Eulophidae	<i>Phyllocnistis citrella</i> Stainton (note, about 8 other parasitoids were introduced into Spain for this pest that are not listed here) Gracillariidae	0	Unknown. No testing done relative to European leafminers. Post-release attack observed on an unidentified Nepticulidae on <i>Pistacia lentiscus</i> L. and <i>Stigmella</i> sp. on <i>Rubus ulmifolius</i> Schott in Sicily and Jordan respectively (Massa et al., 2001), and in Sicily this parasitoid parasitized <i>Cosmopterix pulcherimella</i> , Chambers (Cosmopterigidae), on <i>Parietaria diffusa</i> Mert. & W.D.J. Koch and <i>Liriomyza</i> sp. (Agromyzidae) on <i>Mercurialis annua</i> L. (Rizzo et al., 2006). See Karamaouna et al. (2009) for details on displaced parasitoids	Unknown relative to European fauna	R+/E+ 1996-1999	Massa et al., 2001; Vercher et al., 2000, 2003; Garcia-Marí et al., 2004; Rizzo et al., 2006; Karamaouna et al., 2009
8	1996-2004 China (from USA)	<i>Allotropa oracellae</i> Masner Platygastridae	<i>Oracella acuta</i> (Lodbell) Pseudococcidae	0	No laboratory host range estimation done	Unknown No other hosts records in literature	R+/E- 1996-2004	Clarke et al., 2010

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
9	1996-2004 China (from USA)	<i>Acerophagus coccois</i> E. Smith Encyrtidae	<i>Oracella acuta</i> (Lodbell) Pseudococcidae	0	No laboratory host range estimation done	Family? Records exist of use of several mealybugs, including <i>Phenacoccus herreni</i> Cox & Williams (Bellotti, 1983), <i>P. gossypii</i> Ben-Dov (Van Driesche et al., 1986), <i>P. madeirensis</i> , and <i>Ferrisia virgata</i> (Cockerell) (Dorn et al., 2001)	R+/E- 1996-2004	Bellotti, 1983; Van Driesche et al., 1986; Dorn et al., 2001; Clarke et al., 2010
10	1996-2004 China (from USA)	<i>Zarhopalus debarri</i> Sun Encyrtidae	<i>Oracella acuta</i> (Lodbell) Pseudococcidae	0	No laboratory host range estimation done	Unknown No other hosts records in literature	R+/E- 1996-2004	Sun et al., 1998; Clarke et al., 2010
11	1997-1998 USA	<i>Coccobius fulvus</i> (Compere and Annecke) (also given as <i>Physcus fulvus</i>) Aphelinidae	<i>Aulacaspis yasumatsui</i> Takagi Diaspididae	0	No laboratory host range estimation done	Two Families Literature records include use of scales in the Coccidae (one record: <i>Parthenolecanium corni</i> Bouché [Basheer et al., 2011]) and Diaspididae (many records of this host: <i>Unaspis yanonensis</i> Kuwana [Matsumoto et al., 2004])	R+/E+	Howard and Weissling, 1999; Matsumoto et al., 2004; Basheer et al., 2011; Wang et al., 2014 (for taxonomy of <i>Coccobius</i>)
12	1997-2000 USA, California (from Mexico)	<i>Encarsiella noyesi</i> Hayat Aphelinidae	<i>Aleurodicus dugesii</i> Cockerell Aleyrodidae	0	No laboratory host range estimation done	Genus? The only other recorded host is <i>Aleurodicus dispersus</i> Russell (Blanco-Metzler and Laprade, 1998)	R+/E+	Blanco-Metzler and Laprade, 1998; Bellows and Meisenbacher, 2000
13	1997 US Virgin Islands (from Egypt or Pakistan); also, 1998 Puerto Rico; 1999-2000 continental USA; and 2004 Mexico	<i>Gyranusoidea indica</i> Shafee, Alam and Agarwal Encyrtidae	<i>Maconellicoccus hirsutus</i> (Green) Pseudococcidae	0	No laboratory host range estimation done	Family? No other information on other hosts was found. Post-hoc sampling of other mealybugs in California following release of the parasitoid and its establishment there on the target did not detect any parasitism of either <i>Phenacoccus solenopsis</i> Tinsley or <i>Ferrisia</i> species (Roltsch et al., 2006)	R+/E+	Roltsch et al., 2006
14	1997 USA, Florida	<i>Ceratogramma etiennei</i> Delvare Trichogrammatidae	<i>Diaprepes abbreviatus</i> (L.) Curculionidae	8	No parasitism of 7 NT species of Lepidopteran eggs or those of 1 NT species of weevil	Family? Attacks eggs of weevils concealed in plant tissues	R+/E- 1994	Delvare, 1988; Hall et al., 2001; Peña et al., 2004, 2010

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
15	1998-1999 USA, Guam (from India)	<i>Euplectrus maternus</i> Bhatnagar Eulophidae	<i>Eudocima</i> (<i>Othreis</i>) <i>fullonia</i> (Clerck) Noctuidae	0	No host range testing reported	Genus? Two additional species of underwing moths in the genus <i>Eudocima</i> are known to be parasitized: <i>E. materna</i> L. and <i>E. homaena</i> (Hübner) (Bhumannavar and Viraktamath, 2000)	R+/E-	Bhumannavar and Viraktamath, 2000; Muniappan et al., 2004
16	1998-2000 USA (from Central America)	<i>Idioporus affinis</i> LaSalle et Polaszek Pteromalidae	<i>Aleurodicus dugesii</i> Cockerell Aleyrodidae	0	No host range testing reported	Family? No other hosts reported but little literature of any kind	R+/E+	Bellows and Meisenbacher, 2000
17	1998 USA, Florida	<i>Quadrastichus haitiensis</i> (Gahan) Eulophidae	<i>Diaprepes abbreviatus</i> (L.) Curculionidae	0	No host range testing reported	Family? Attacks eggs of weevils concealed in plant tissues	R+/E+ 1998	Peña et al., 2004, 2010
18	1998 USA, New England	<i>Tetrastichus sertifer</i> Thomson Eulophidae	<i>Lilloceris lili</i> Scopoli Chrysomelidae	10	2 NT European species of <i>Lilloceris</i> tested and both were attacked; 8 species of North American non- <i>Lilloceris</i> (6 same family; 2 other families) and none were attacked	Genus High safety as there are no native congeners in North America	R+/E+ 1999	Gold, 2003; Casagrande and Kenis, 2004; Tewksbury et al., 2005; Tewksbury, 2014
19	1999 USA	<i>Pseudacteon curvatus</i> Borgmeier Phoridae	<i>Solenopsis invicta</i> Buren, <i>S. richteri</i> Forel, and hybrids Formicidae	19 +2 ^d	0 NT attack on 19 NT ants not in <i>Solenopsis</i> ; attack of 2 NT <i>Solenopsis</i> , but at lower rates than on target; no significant attack on two NT <i>Solenopsis</i> in field in post-release evaluation	Genus	R+/E+ 1999/2000	Gilbert and Morrison, 1997; Porter, 2000; Vazquez and Porter, 2005; Vazquez et al., 2004; Callcott et al., 2011
20	ca 1999 USA, Florida (from Japan?)	<i>Lysiphlebia japonica</i> Ashmead Braconidae	<i>Toxoptera citricida</i> (Kirkaldy) Aphididae	0	No laboratory host range estimation done	Unknown	R+/E-	Takanashi, 1990; Michaud, 2002a
21	2000-2003 Mexico; and USA, 2002 Guam	<i>Acerophagus papayae</i> Noyes and Schauff Encyrtidae	<i>Paracoccus marginatus</i> Williams and Granara DeWillink Pseudococcidae	0	No laboratory host range estimation done	Family?	R+/E+	Noyes and Schauff, 2003

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References	
22	2000 USA, Florida (from Guam)	<i>Lipolexis oregmae</i> Gahan (introduced as <i>L. scutellaris</i> Mackauer) Braconidae, Aphidiinae	<i>Toxoptera citricida</i> Kirkaldy Aphididae	0	No laboratory host range estimation done.	Family? Post release field studies found parasitism of two black citrus aphid species (<i>Toxoptera citricidus</i> [Kirkaldy] and <i>T. aurantii</i> [Boyer de Fonscolombe]), cowpea aphid (<i>Aphis craccivora</i> Koch), spirea aphid (<i>Aphis spiraeicola</i> Patch) and melon aphid (<i>Aphis gossypii</i> Glover) (Persad et al., 2007)	R+/E+ 2001-2002	Persad et al., 2007
23	2000 USA, Florida and Caribbean (from China)	<i>Anagyrus kamali</i> Moursi Encyrtidae	<i>Maconellicoccus hirsutus</i> Green Pseudococcidae	8	2 NT species of <i>Planococcus</i> were attacked but failed to support complete development	Species In the context of the the Caribbean, the target species was the only suitable host. In a larger geographic context, the host range is likely greater.	R+/E+ 2000	Kairo et al., 2000; Sagarra et al., 2001
24	2000 USA, California (from Australia)	<i>Psyllaephagus bliteus</i> Riek Encyrtidae	<i>Glycaspis brimblecombei</i> Moore Psyllidae	3	None of the 3 NT eucalyptus- feeding psyllids (<i>Trioza eugeniae</i> Froggatt, <i>Ctenarytaina eucalypti</i> [Maskell], <i>Boreioglycaspis melaleucaae</i> Moore) tested were attacked	Unknown Other species in target genus were not tested	R+/E+ 2000	Dahlsten et al., 2003
25	2000 Trinidad	<i>Amitus hesperidum</i> Silvestri Platygasteridae	<i>Aleurocanthus woglumi</i> Ashby Aleyrodidae	0	No host range testing reported	Family This parasitoid controlled citrus blackfly in other locations earlier, before host range testing was begun. Reuse in other areas later did not do host range testing, but a post release survey in Dominica (Lopez et al., 2009) did not detect attacks on non-target whiteflies there	R+/E+ 2000	Dowell et al., 1979; White et al., 2005; Lopez et al., 2009
26	2000 USA, Florida	<i>Aprostocetus vaquitarum</i> Wolcott Eulophidae	<i>Diaprepes abbreviatus</i> (L.) Curculionidae	0	No host range testing reported	Family? Likely within-family (Curculionidae) of eggs concealed in plant tissue	R+/E+ 2000	Peña et al., 2004, 2010

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
27	2001 Mexico <i>Phymastichus coffea</i> (LaSalle) Eulophidae	<i>Hypothenemus hampei</i> (Ferrari) Curculionidae: Scolytinae	5	Of 3 NT species in same genus as target ^a , 2 were successfully parasitized and 1 was not. Two other species in other weevil genera were not parasitized. Attack on two <i>Hypothenemus</i> species were at levels of 14 and 6 percent.	Genus?	2001	Castillo et al., 2004
28	2001 Kenya (via South Africa, via Mauritius, but originally from Sri Lanka) <i>Xanthopimpla stemmator</i> Thunberg Ichneumonidae	<i>Chilo partellus</i> (Swinhoe) Crambidae; <i>Busseola fusca</i> Fuller Noctuidae	2	1 NT was as suitable as target hosts; 1 NT was inferior with a low proportion of accepted hosts producing parasitoid progeny	Two families (Noctuidae, Crambidae) Known to attack several noctuid and crambid stemborers in its native range. Complete list of known hosts in Gitau et al., 2007.	R+/E+ 2002 established in Mozambique, later in Malawi, Tanzania, Zimbabwe, Ethiopia, Eritrea and Kenya	Gitau et al., 2005, 2007
29	2001 New Zealand <i>Thripobius javae</i> (Girault) (= <i>T. semiluteus</i> Boucek) Eulophidae	<i>Heliothrips haemorrhoidalis</i> (Bouché) Thripidae	2	Two NT Panchaetothripinae thrips were exposed – the native <i>Sigmothrips aotearoana</i> (Ward) and the African thrips <i>Hercinothrips bicinctus</i> Bagnall (adventive in NZ). Both were successfully parasitized.	Subfamily (Panchaetothripinae) This estimation by Froud et al. (1996) was made based on literature host records.	R+/E+	McMurtry, 1988; McMurtry et al., 1991; Froud et al., 1996; Froud and Stevens, 2003
30	2002 USA, Guam <i>Anagyrus loecki</i> Noyes Encyrtidae	<i>Paracoccus marginatus</i> Williams and Granara DeWillink Pseudococcidae	0	No host range testing reported	Family?	R+/E?	Meyerdirk et al., 2004
31	2002 USA, Guam <i>Pseudleptomastix mexicana</i> Noyes and Schauff Encyrtidae	<i>Paracoccus marginatus</i> Williams and Granara DeWillink Pseudococcidae	0	No host range testing reported	Family?	R+/E?	Meyerdirk et al., 2004

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
32	2002 USA	<i>Diaparsis jucunda</i> (Holmgren) Ichneumonidae	<i>Lilloceris lili</i> Scopoli Chrysomelidae	10	2 NT European species of <i>Lilloceris</i> were tested and both were attacked; 8 species of North American non- <i>Lilloceris</i> (6 same family; 2 other families) were tested and none were attacked	Genus There are no native congeners in North America	R+/E+ 2003	Gold, 2003; Casagrande and Kenis, 2004; Tewksbury, 2014
33	2002 USA	<i>Lemophagus errabundus</i> Gravenhorst Ichneumonidae	<i>Lilloceris lili</i> Scopoli Chrysomelidae	10	2 NT European species of <i>Lilloceris</i> were tested and both were attacked; 8 species of North American non- <i>Lilloceris</i> (6 same family; 2 other families) were tested and none were attacked	Genus There are no native congeners in North America	R+/E+ 2003	Tewksbury, 2014
34	2002 USA; never petitioned	<i>Lemophagus pulcher</i> Szepligetii Ichneumonidae	<i>Lilloceris lili</i> Scopoli Chrysomelidae	10	2 NT European species of <i>Lilloceris</i> tested and both were attacked; 8 species of North American non- <i>Lilloceris</i> (6 same family; 2 other families) and were 2 were attacked	Subfamily level: Criocerinae ^f	Not released	Gold, 2003; Casagrande and Kenis, 2004
35	2002 USA, California (from Egypt)	<i>Allotropa nr mecrida</i> (Walker)	<i>Maconellicoccus hirsutus</i> (Green)	4	4 NT – no parasitism in four mealybugs from 3 other genera (<i>Pseudococcus</i> , <i>Paracoccus</i> , and <i>Phenacoccus</i>); 1 NT species affected by host feeding	Genus?	R+/E- Released in 2003-2004	Roltsch et al., 2006, 2007
36	2004 USA; not petitioned for release	<i>Bracon celer</i> Szépligetii Braconidae	<i>Bactrocera oleae</i> Gmelin Tephritidae	3	No attack on 1 NT gall-making tephritid, but successful parasitism occurred on another fly species, <i>Parafreutreta regalis</i> Munro, and host deaths without successful parasitism on another	Family? Hosts included valuable weed biocontrol gall-making tephritids and so rejected by scientists in charge	R-	Nadel et al., 2009

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established^a (yr if given equals of first release)	References
37	2005 Tahiti (USA)	<i>Gonatocerus ashmeadi</i> Girault Mymaridae	<i>Homalodisca vitripennis</i> (Germar) Cicadellidae	3	1 of three NT species was an acceptable host, another <i>Homalodisca</i> species	Tribe Hosts are in the Proconiini, especially species in the same genus as target and with similar egg size and deposition pattern	R+/E+ 2005	Grandgirard et al., 2007, 2009
38	2002 California (from southeastern USA)	<i>Gonatocerus fasciatus</i> Girault Mymaridae	<i>Homalodisca vitripennis</i> (Germar) Cicadellidae	3	1 of three NT species was an acceptable host, another <i>Homalodisca</i> species	Tribe Hosts are in the Proconiini, especially species in the same genus as target and with similar egg size and deposition pattern	R+/E+ 2002	Pilkington and Hoddle, 2006; Boyd and Hoddle, 2007
39	2005 New Zealand (from Ireland)	<i>Microctonus aethiopoulos</i> Loan (all female strain) Braconidae: Euphorinae	<i>Sitona Lepidus</i> Gyllenhal Curculionidae	9	5 NT native species were parasitized at rates from 2-28%; risk perceived to be lower than the already established Moroccan strain of this species	Family? Several genera of Curculionidae	R+/E+ 2006	Goldson et al., 2005; Gerard et al., 2007
40	2005 USA	<i>Haeckeliana sperata</i> Pinto Trichogrammatidae	<i>Diaprepes abbreviatus</i> (L.) Curculionidae	4	No attack on eggs of 2 NT Lepidoptera or 2 NT Coleoptera (1 Coccinellidae and 1 a non- <i>Diaprepes</i> Curculionidae)	Family? Likely within-family (Curculionidae) specificity on eggs concealed in plant tissue	R+/E+ 2006	Peña et al., 2010
41	2005 USA	<i>Fidiobia dominica</i> Evans and Peña Platygasteridae	<i>Diaprepes abbreviatus</i> (L.) Curculionidae	0?	No host range testing reported	Family? Likely within-family (Curculionidae) specificity on eggs concealed in plant tissue Assumed to have low to medium specificity, given records of other species' hosts in genus	R+/E+ 2006	Evans and Peña, 2005
42	2005 USA	<i>Psytalia lounsburyi</i> Sylvestri	<i>Bactrocera oleae</i> Gmelin	3	No attack on 3 NT tephritids tested	Genus?	R+/E+ 2005	Daane et al., 2008
43	2005-2007 USA, Texas (2005) and Florida (2007)	<i>Pseudacteon obtusus</i> Borgmeier Phoridae	<i>Solenopsis invicta</i> , <i>S. richteri</i> , and hybrids Formicidae	1	1 NT species in <i>Solenopsis</i> tested (<i>S. geminata</i>) and found not to be attacked	Species	R+/E+ 2006/2008	Morrison and Gilbert, 1999; Estrada et al., 2006; Porter and Calcaterra, 2013
44	2005 USA	<i>Pseudacteon nocens</i> Borgmeier Phoridae	<i>Solenopsis invicta</i> , <i>S. richteri</i> , and hybrids Formicidae	1	Low attack rates with 1 NT native <i>Solenopsis</i>	Genus	R+/E+ 2006	Estrada et al. 2006

Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References	
2005-present (mid 2016)								
1	2006 USA, Florida	<i>Citrostichus phyllocnistoides</i> (Naryanin) Eulophidae	<i>Phyllocnistis citrella</i> Stainton Gracillariidae	0	No testing done relative to North American leafminers	Unknown relative to North American fauna But see Massa et al. (2001) relative to European leafminers	R+/E+ Ca 2006	P. Stansly (pers. comm.)
2	2006 USA, Minnesota	<i>Binodoxys communis</i> (Gahan) Braconidae, Aphidiinae	<i>Aphis glycines</i> Matsumura Aphididae	19	6 of 8 NT <i>Aphis</i> species were highly suitable, while 2 were either not or only marginally so. For 11 NT non- <i>Aphis</i> species, 1 was suitable while 3 were marginally so and 7 were not.	Genus Of native <i>Aphis</i> spp, risk modeling based on ant-tending and phenological overlap suggest high exposure for <i>Aphis asclepiades</i> Fitch but low exposure to <i>Aphis oestlundii</i> Gillette; ant tending suggests medium exposure to <i>Aphis monardae</i> Oestlund	R+/E- 2007	Wyckhuys et al., 2007; 2009; Desneux et al., 2012
3	2006 Israel (from Australia) (thereafter, many other countries)	<i>Closterocerus chamaeleon</i> (Girault) Eulophidae	<i>Ophelimus maskelli</i> (Ashmead) Eulophidae	0	No testing done relative to Mediterranean gall makers	Unknown Assumed to be safe to nontarget insects outside the native range of the pest's host-plant group	R+/E+ 2006	Mendel et al., 2007; Protasov et al., 2007
4	2007 Israel (from Australia)	<i>Stethynium ophelimi</i> Huber Mymaridae	<i>Ophelimus maskelli</i> (Ashmead) Eulophidae	0	No testing done relative to Mediterranean gall makers. It may develop on other unidentified <i>Ophelimus</i> species (Zvi Mendel, pers. comm.)	Genus?	R+/E+ 2007	Huber et al., 2006; Mendel et al., 2007
5	2007 Comoros Islands, Indian Ocean (from La Réunion)	<i>Eretmocerus cocois</i> Delvare Aphelinidae	<i>Aleurotrachelus atratus</i> Hempel Aleyrodidae	# unpub.	Tested against native whiteflies of Comoros Islands and none were attacked	Unknown Names of nontarget species tested not published	R+/E+ 2007	Borowiec et al., 2008, 2010
6	2007 USA, Hawaii	<i>Binodoxys communis</i> (Gahan) Braconidae, Aphidiinae	<i>Aphis gossypii</i> Glover Aphididae	6	3 NT, non-native <i>Aphis</i> species were highly suitable, while 3 NT, non-native non- <i>Aphis</i> species were either not suitable (1 sp.) or marginally so (2 spp.)	Largely Genus specific but not entirely Safe because there are no native aphids or biocontrol aphids in Hawaii	R+/E+ 2010	Acebes and Messing, 2013

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
7	2006 USA. Not petitioned for release	<i>Fopius arisanus</i> (Sonan) Braconidae	<i>Bactrocera oleae</i> Gmelin Tephritidae	2	Known from the literature to develop on many fruit-feeding tephritids, including over 20 <i>Bactrocera</i> species and various species of <i>Anastrepha</i> , <i>Carpomya</i> , <i>Ceratitis</i> , <i>Dacus</i> , and <i>Euphranta</i> (at least 30 hosts). Did not attack two species of weed biocontrol gall-making tephritids tested	Family level, for fruit-feeders Given extensive list of host genera attacked, it was rejected by scientists in charge.	R-	Sime et al., 2008
8	2006 La Réunion (from Hawaii)	<i>Fopius arisanus</i> (Sonan) Braconidae	Various pest frugivorous tephritids (no single target)	8	All 8 local tephritids tested were attacked. This was seen as desirable	Family Known to attack at least 20 species of tephritids	R+/E+ 2006	Rousse et al., 2006; Deguine et al., 2011
9	2006 Not petitioned for release	<i>Trichomalus perfectus</i> (Walker) Pteromalidae	<i>Ceutorhynchus obstrictus</i> (Marsham) Curculionidae	16 ^a	4 NT attacked equal to target; 5 NT attacked <target; 7 NT not attacked	Genus level Not pursued, as species-level specificity would be required to protect weed biocontrol agents	R-	Kuhlmann et al., 2006; Muller et al., 2011; Haye et al., 2015
10	2007 USA	<i>Spathius agrili</i> Yang Braconidae	<i>Agrilus planipennis</i> (Fairmaire) Buprestidae	17 (field) + 9 (lab)	Of 17 NT wood-boring species collected in the field in China, 0 were attacked. Of 9 NT <i>Agrilus</i> species tested in the laboratory, 3 were attacked and 6 not attacked	Genus	R+/E+ 2007	Gould, 2007; Yang et al., 2008; Van Driesche et al., 2016b
11	2007 USA	<i>Oobius agrili</i> Zhang and Huang Encyrtidae	<i>Agrilus planipennis</i> (Fairmaire) Buprestidae	12	In the laboratory, of 6 NT <i>Agrilus</i> , 3 were attacked and of 6 NT, non- <i>Agrilus</i> , none were attacked	Genus	R+/E+ 2007	Gould, 2007; Van Driesche et al., 2016b
12	2007 USA	<i>Tetrastichus planipennisi</i> Yang Eulophidae	<i>Agrilus planipennis</i> (Fairmaire) Buprestidae	6 (field) + 11 (lab)	Of 6 NT <i>Agrilus</i> species collected in the field in China, 0 were attacked. Of 5 NT <i>Agrilus</i> and 6 other buprestids, 0 were attacked in laboratory tests	Species?	R+/E+ 2007	Gould, 2007; Van Driesche et al., 2016b

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
13	2007 USA	<i>Lixadmontia franki</i> Wood Tachinidae	<i>Metamasius callizona</i> (Chevrolat) ^b Curculionidae	1	1 NT native Floridian congenera, <i>Metamasius mosieri</i> Barber, was tested and found to be attacked at significant rates in choice and no-choice tests	Genus Limited host range testing done	R+/E- 2007	Frank, unpub.
14	2007 USA, Hawaii	<i>Eurytoma erythrinae</i> Gates Eurytomidae	<i>Quadrastichus erythrinae</i> Kim Eulophidae	7	None of the 7 NT gall-makers tested (1 native, 4 bicontrol agents, 2 adventive) were attacked.	Genus	R+/E+ 2008	HDOA, 2008
15	2008 Australia	<i>Diaeretus essigellae</i> Starý and Zuparko Braconidae, Aphidiinae	<i>Essigella californica</i> (Essig) Aphididae	8	8 NT – no parasitism on any tested species	Genus?	R+/E+ 2009	Kimber et al., 2010
16	2008 USA, Hawaii	<i>Aroplectrus dimerus</i> L. Eulophidae	<i>Darna pallivitta</i> (Moore) Limacodidae	25	Of the 25 NT gall-makers tested, none were attacked. There are no native limacodid species in Hawaii. The host range tests used species from other 13 families, 2 of which were endemic, and 19 were immigrant pests.	Family level, same as species level In Hawaii, there are no con-familial natives	R+/E+ 2010	HDOA, 2007
17	2008 USA, California	<i>Tamarixia radiata</i> (Waterson) Eulophidae	<i>Diaphorina citri</i> Kuwayama Liviidae (formerly Psyllidae)	7	6 NT – no parasitism. One invasive pest attacked at a low rate (5%).	Genus?	R+/E+ 2010	Hoddle and Pandey, 2014
18	2008 Canada (from Europe, but never released)	<i>Aleochara bipustulata</i> L. Staphylinidae	<i>Delia radicum</i> (L.) Anthomyiidae	18	11 NT species supported parasitoid development; most frequently attacked species had small pupae or were in families related to target	Order level Species in 8 families supported attack and development	Never released	Andreassen et al., 2009
19	2009 Switzerland (from Mexico, but never released)	<i>Celatoria compressa</i> (Wulp) Tachinidae	<i>Diabrotica virgifera virgifera</i> Leconte Chrysomelidae	9	Of 9 NT species tested, the agent developed, at low rates, in only 1 test species	Two Subtribes Fundamental host range restricted to subtribes Diabroticina and Aulacophorina	Never released (hard to rear)	Toepfer et al., 2009

	Year Released	Agent	Target	# Test spp.	Test outcomes	Smallest taxon including all likely hosts	Released/ Established ^a (yr if given equals of first release)	References
20	2010 USA, Florida	<i>Pseudacteon cultellatus</i> Borgmeier Phoridae	<i>Solenopsis invicta</i> , <i>S. richteri</i> , and hybrids Formicidae	1	1 NT species in <i>Solenopsis</i> tested (<i>S. geminata</i>) and found to be attacked in a few cases, at about 10% of the rate on the target host	Genus More host specific than <i>P. curvatus</i> or <i>P. nocens</i> , but less than other <i>Pseudacteon</i> species released	R+/E+ 2010	Estrada et al., 2006; Porter et al., 2013
21	2010 USA	<i>Aphelinus glycinis</i> Wooley and Hopper Aphelinidae	<i>Aphis glycines</i> Matsumura Aphididae	12	No NT attacks on aphids outside of genus <i>Aphis</i> . Of 7 NT <i>Aphis</i> species, 4 were suitable for parasitism, while 3 were not	Genus	R+/E? 2013	Hopper, 2010; USDA APHIS, 2012
22	2011 New Zealand (from Tasmania, Australia)	<i>Cotesia urabae</i> (Austin & Allen) Braconidae	<i>Uraba lugens</i> Walker Nolidae	2	1 NT-substitute not attacked in native range. 1 NT attacked but no development	Species Given limited New Zealand fauna and nature of host plant of target pest, <i>C. urabae</i> is expected to be nearly host specific.	R+/E+	Berndt et al., 2009; Avila and Berndt, 2011; Rowbottom et al., 2013; Avila et al., 2015
23	2013 USA, California	<i>Diaphorencyrtus aligarhensis</i> (Shafee, Alam & Agarwal) Encyrtidae	<i>Diaphorina citri</i> Kuwayama Liviidae (formerly Psyllidae)	7	6 NT – no parasitism; 1 invasive pest psyllid attacked (at 14% rate)	Genus?	+/-?	Bistline-East et al., 2015
24	2013 USA	<i>Spathius galinae</i> Belokobylskij and Strazanac Braconidae	<i>Agrilus planipennis</i> Fairmaire Buprestidae	15	14 NT – no attack. 1 pest NT – attacked ^d	Genus	R+/E+ 2015	Duan et al., 2015; USDA APHIS, 2015
25	2013 USA, Hawaii	<i>Encarsia diaspidicola</i> (Silvestri) Aphelinidae	<i>Pseudaulacaspis pentagona</i> (Targioni) Diaspididae	7	None of the 7 NT were parasitized or killed	Family? Several diaspidid scales (including <i>Pseudaulacaspis pentagona</i> [Targioni-Tozzetti] and <i>Quadraspidiotus perniciosus</i> [Comstock]) are known hosts, but others are not hosts (Neumann et al., 2010)	R+/E+	Neumann et al., 2010; Follett et al., 2015
26	Not yet petitioned for release but under study for release in the USA (from Argentina)	<i>Apanteles opuntiarum</i> Martínez and Berta Braconidae	<i>Cactoblastis cactorum</i> Berg <i>Pyrallidae</i>	6	6 NT – 5 spp in native range were not attacked; 1 sp. attacked	Genus While laboratory tests have not yet been run, field surveys in the native range (Argentina) found this species attacking only the target pest and one other species in the target's genus. One other species in the target's genus was not attacked.	Laboratory testing of this newly recognized species has yet to be done	Martínez et al., 2012; Varone et al., 2015

^aOutcomes: R- (not released), R+/E+ (released and established), R+/E- (released but not established).

^bSpecies tested in Australia included a range of other leafminers (one in target genus, three others in target family, 7 more in 4 other families), as well as 4 gall makers and 2 less related weed biocontrol agents.

^cResearch group concluded this was primarily a parasitoid of *S. saevissima* and did not petition for release.

^dNineteen ants in genera other than that of the target (*Solenopsis*) and two in *Solenopsis*; same format used in following additional species of *Pseudacteon*.

^eAssessments of coffee berry borer parasitoid host range was done after release had already occurred.

^fAttack in laboratory was found on *Lema trilineata* White (Criocerinae), a native North American insect (Casagrande and Kenis, 2004); also, for all parasitoids of lily leaf beetle, potential conflict exists with use of *Lilioceris* beetles as future weed biological control agents of various invasive plants.

^gAll non-target species were in the same genus as the target pest.

^hIn Florida, there are three *Metamasius* weevils, two of which (including the target pest) attack bromeliads and one not. The nontarget species in bromeliads was attacked by the tachinid, but the NT species not in a bromeliad host was not. No other weevils outside of *Metamasius* attack bromeliads in Florida.

ⁱAttack in field on *Agrilus auroguttatus* Shaeffer unlikely because of extremely thick bark of oak hosts, but would be beneficial if it occurred, as this is highly damaging and invasive in California.

APPENDIX 2

The following table contains predacious insects (23 species) introduced between 1985 and 2015, with notes on the level of specificity of each, drawn from literature

records (worldwide) and BIOCAT (for North America, including Mexico and the US overseas territories, 1985-2010 [end of available records]).

Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
1 1984 USA (from Korea) and 1990-1995 (from China)	<i>Chilocorus kuwanae</i> (Silvestri) Coccinellidae	<i>Unaspis euonymi</i> (Comstock) (Diaspididae)	0	No laboratory prey range estimation done	Order (Multiple families in the Coccoidea) Known field prey of this species include various diaspidid scales, e.g, <i>Unaspis yanonenis</i> (Kuwana) (Nohara et al., 1962), <i>Quadraspidiotus perniciosus</i> (Comstock) (Chumakova, 1967), <i>Quadraspidiotus macroporanus</i> Takagi (Tachikawa, 1974); more broadly it is known to feed on at least 28 scale species in five scale families (Xia et al., 1986), including the mealybug <i>Pseudococcus citriculus</i> Green (Itioka and Inoue, 1996), the coccid <i>Protopulvinaria mangiferae</i> (Green) (Kim and Morimoto, 1998), and the eriococcid <i>Eriococcus lagerstroemiae</i> Kuwanae (Luo et al., 2000); see also Bull et al., 1993.	R+/E+ 1984/ 1990-1995	Nohara et al., 1962; Chumakova, 1967; Tachikawa, 1974; Xia et al., 1986; Drea and Carlson, 1987; Bull et al., 1993; Itioka and Inoue, 1996; Van Driesche et al., 1998; Kim and Morimoto, 1998; Luo et al., 2000

Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
2 1984 USA (from Korea) and 1990-95 (from China)	<i>Cybocephalus</i> nr <i>nipponicus</i> Enrody-Younga (for this analysis we conflate <i>C. nipponicus</i> and <i>C. nr nipponicus</i>) Nitidulidae	<i>Unaspis euonymi</i> (Comstock) Diaspididae	0	No laboratory prey range estimation done. No host range testing done before the introduction, but see Song et al. (2012) for results of such tests done several decades later.	Family (Diaspididae) Known field prey of this species include various diaspidid scales, e.g. <i>Quadraspidiotus macroporanus</i> Takagi (Tachikawa, 1974), <i>Unaspis yanonensis</i> Kuwana (Huang et al., 1981), as well as (for adult feeding) eggs of the tetranychid <i>Panonychus citri</i> (McGregor) (Tanaka and Inoue, 1980); while adult feeding ranges include multiple families, oviposition and development only occurred in diaspidid scales, with reproduction on 6 of 9 species tested (Song et al., 2012), as reproduction is more similar to that of a parasitoid than predator.	R+/E+ 1984/ 1990-1995	Tachikawa, 1974; Tanaka and Inoue, 1980; Huang et al., 1981; Drea and Carlson, 1987; Van Driesche et al., 1998; Song et al., 2012
3 1985 Oman (from India)	<i>Chilocorus nigritus</i> (F.) Coccinellidae	<i>Aspidiotus destructor</i> Sign. Diaspididae	0	No laboratory prey range estimation done	Order (Hemiptera) An effective biocontrol agent of diaspidid scales (Hutson, 1933; Samways, 1984; Kinawy, 1991), some species of Coccidae and Asterolecaniidae (Ponsonby, 2009). Also recorded feeding on some aphids (Omkar and Bind, 1995) and whiteflies (Kapur, 1942)	R+/E+ 1985	Hutson, 1933; Kapur, 1942; Samways, 1984; Kinawy, 1991; Omkar and Bind, 1995; Ponsonby, 2009
4 1986 Guam and Mariana Islands (from Hawaii)	<i>Curinus coeruleus</i> (Mulsant) Coccinellidae	<i>Heteropsylla cubana</i> Crawford Psyllidae	0	No laboratory prey range estimation done	Order (Hemiptera) Known prey include aphids, e.g., <i>Rhopalosiphum maidis</i> (Fitch) (Nawanich et al., 2013); whiteflies e.g., <i>Aleurodicus dispersus</i> Russell (Villacarlos and Robin, 1992); and liviids, e.g., <i>Diaphorina citri</i> Kuwayama (Michaud, 2002b)	R+/E+	Nafus and Schreiner, 1989; Villacarlos and Robin, 1992; Michaud, 2002b; Nawanich et al., 2013

Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
5 1980-1990	<i>Clitostethus arcuatus</i> (Rossi) Coccinellidae	<i>Siphoninus phillyreae</i> (Haliday) Aleyrodidae	0	No laboratory prey range estimation done	Family (Aleyrodidae) Known field prey of this species are whiteflies, including <i>Dialeurodes citri</i> (Ashmead) (Priore, 1969), <i>Aleurodes proletella</i> L. (Bathon and Pietrzik, 1986), <i>Aleurothrixus floccosus</i> Maskell (Katsoyannos et al., 1997), among others.	R+/E+	Priore, 1969; Bathon and Pietrzik, 1986; Bellows et al., 1990; Katsoyannos et al., 1997
6 1988 USA (from Europe)	<i>Rhizophagus grandis</i> Gyllenhal Rhizophagidae	<i>Dendroctonus terebrans</i> (Olivier) Curculionidae, Scolytinae	0	No laboratory prey range estimation done	Genus Known field prey of this species are bark beetles in the genus <i>Dendroctonus</i> , including <i>D. micans</i> Kugelmann (Gregoire, 1976) and <i>Dendroctonus valens</i> LeConte (Wei et al., 2010)	R+/E+	Gregoire, 1976; Wei et al., 2010
7 1989 USA	<i>Hippodamia undecimnotata</i> (Schneider) (other generic placements include <i>Semiadalia</i> and <i>Adonia</i> ; also known as <i>Hippodamia oculata</i>). Note: this species apparently invaded North America on its own about the same time it was being introduced into other parts of the continent (Day et al. 1994). Coccinellidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory prey range estimation done	Family (Aphididae) Adults feed on various aphids. Larvae develop on <i>Aphis fabae</i> Scopoli in the French lower Alps (Ipert, 1965), on <i>Myzus persicae</i> (Sulzer) in France (Ferran and Larroque, 1977), and <i>Toxoptera aurantii</i> (Boyer de Fonscolombe) in the country of Georgia (Sikharulidze, 1986).	R+/E?	Ipert, 1965; Ferran and Larroque, 1977; Sikharulidze, 1986; Gordon and Vandenberg, 1991; Day et al., 1994
8 1989 USA	<i>Propylea quatuordecimpunctata</i> (L.). Note: this species apparently invaded North America on its own about the same time it was being introduced into other parts of the continent (Wheeler, 1990; Day et al. 1994) Coccinellidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory prey range estimation done	Family (Aphididae) Field prey include <i>Aphis fabae</i> Scopoli (Čamprag et al., 1990); larvae can develop on <i>Acyrtosiphon pisum</i> Harris and <i>Rhopalosiphum maidis</i> (Fitch) (Obrycki and Orr, 1990) and <i>Schizaphis graminum</i> (Rondani) (Michels and Flanders, 1992)	R+/E+	Čamprag et al., 1990; Obrycki and Orr, 1990; Wheeler, 1990; Gordon and Vandenberg, 1991; Michels and Flanders, 1992; Day et al., 1994

Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
9 1990 USA	<i>Scymnus frontalis</i> (F.) Coccinellidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory prey range estimation done	Family (Aphididae) Larvae develop well on several aphids, including <i>Schizaphis graminum</i> (Rondani), <i>Macrosiphum (Sitobion) avenae</i> (F.), and <i>Acyrtosiphon pisum</i> Harris (Gibson et al., 1992)	R+/E?	Gordon and Vandenberg, 1991; Gibson et al., 1992
10 1990 USA	<i>Oenopia (Synharmonia) conglobata</i> (L.) Coccinellidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory prey range estimation done	Two or most Orders. Feeds on several families, including Monophlebidae, Coccidae, Chrysomelidae, and Aphididae. Field prey records include a monophlebid scale (<i>Matsucoccus josephi</i> Bodenheimer et Harpaz) (Bodenheimer and Neumark, 1955), a coccid scale, <i>Ceroplastes rusci</i> (L.) (Özsemerci and Aksit, 2003), and various aphids, e.g., <i>Aphis craccivora</i> Koch (Kesten, 1975), and <i>Hyadaphis tataricae</i> (Aizenberg) (Toros, 1986), and eggs of flea beetles (Chrysomelidae) (Chen, 1982), the psyllid <i>Euphyllura straminea</i> Loginova (Baki and Ahemed, 1985).	R+/E?	Bodenheimer and Neumark, 1955; Kesten, 1975; Chen, 1982; Baki and Ahemed, 1985; Toros, 1986; Gordon and Vandenberg, 1991; Özsemerci and Aksit, 2003
11 1991 Canada	<i>Leucopis ninae</i> Tanasijtshuk Chamaemyiidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory prey range estimation done	Family (Aphididae) Recorded prey include aphids, i.e., <i>Aphis nerii</i> Boyer de Fonscolombe (Abdul-Satar, 1988) and <i>Rhopalosiphum padi</i> (L.) (Dabiré et al., 1997)	R+/E-	Abdul-Satar, 1988; Dabiré et al., 1997
12 1991 Canada	<i>Leucopis atritaris</i> Tanasijtshuk Chamaemyiidae	<i>Diuraphis noxia</i> (Kurdjumov) Aphididae	0	No laboratory prey range estimation done	Family? or Unknown No other prey records were found.	R+/E-	Olfert et al., 2001
13 1991-1992 Togo, Benin, Kenya (from Central America)	<i>Teretrius (Teretriosoma) nigrescens</i> (Lewis) Histeridae	<i>Prostephanus truncatus</i> (Horn) Bostrichidae	0	No laboratory prey range estimation done	Species? Predator is attracted to the sex pheromone of the target pest (Boeye et al., 1992). No other field hosts have been reported.	R+/E+ 1991-Togo and Benin 1992-Kenya	Boeye et al., 1992; Borgemeister et al., 1997; Hill et al., 2003; Schneider et al., 2004

	Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
14	1993-1999 USA, including Puerto Rico	<i>Serangium parcesetosum</i> Sicard (formerly <i>Catana parcesetososa</i>) Coccinellidae	<i>Bemisia tabaci</i> (Gennadius) strain B Aleyrodidae	0	No laboratory prey range estimation done	Family (Aleyrodidae) Prey records include various other whiteflies, e.g., <i>Dialeurodes citri</i> (Ashmead) (Antadze and Timofeeva, 1976), but not lepidopteran eggs (Legaspi et al., 1996); the predator appears to be limited to whitefly species as prey for both larvae and adults (Al-Zyoud, 2007)	R+/E?	Antadze and Timofeeva, 1976; Legaspi et al., 1996; Al-Zyoud, 2007
15	1995 USA, Hawaii	<i>Rodolia blackburni</i> Ukrainsky; formerly <i>Rodolia limbata</i> (Blackburn) Coccinellidae	<i>Icerya aegyptiaca</i> (Douglas) Monophlebidae	0	No laboratory prey range estimation done	Two Families (Monophlebidae and Diaspididae) Known from the monophlebid <i>Drosicha contrahens</i> Walker (Chu, 1933) and <i>Icerya</i> sp. (Lethane, 1998) and the diaspidid <i>Comstockaspis macroporanus</i> Normark, Morse, Krewinski & Okusu (Choi et al., 1995)	R+/E+	Chu, 1933; Choi et al., 1995; Lethane, 1998
16	1997-98 USA, Florida (from Thailand)	<i>Cybocephalus binotatus</i> Grouvelle Nitidulidae	<i>Aulacaspis yasumatsui</i> Takagi Diaspididae	0	No laboratory prey range estimation done	Family? (Diaspididae) Host records include several diaspids, including <i>Aonidiella aurantii</i> (Maskell) and <i>Chrysomphalus aonidum</i> (L.) but not <i>Aspidiotus nerii</i> Bch. and attempts to rear the species on spider mites or moth eggs failed (Blumberg and Swirski, 1974a,b)	R+/E+	Blumberg and Swirski, 1974a,b; Howard and Weissling, 1999
17	1997 US Virgin Islands and 2004, Mexico	<i>Cryptolaemus montrouzieri</i> (Mulsant) Coccinellidae	mealybugs and other Hemiptera	0	No laboratory prey range estimation done	Order level >8 families of Hemiptera known as prey	Past releases in many locations	Kairo et al., 2013

	Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
18	2000 Caribbean (from India)	<i>Scymnus coccivora</i> Ram. Ayyar Coccinellidae	<i>Maconellicoccus hirsutus</i> Green Pseudococcidae	0	No laboratory prey range estimation done	Order, several families (Pseudococcidae, Coccidae, Aphididae) Recorded prey are predominately mealybugs in a variety of genera, including <i>Pseudococcus saccharifolii</i> (Green) (Mohammad, 1963) and <i>Ferrisia virgata</i> (Cockerell) (Rawat and Modi, 1968), with some records of other families, such as the coccid <i>Saissetia privigna</i> De Lotto (Muzaffar and Ahmad, 1977) and the aphid <i>Aphis punicae</i> Shinji (Karuppuchamy et al., 1998)	R+/E? Ca 2000	Mohammad, 1963; Rawat and Modi, 1968; Muzaffar and Ahmad, 1977; Karuppuchamy et al., 1998; Gautam, 2003
19	2002 Ecuador	<i>Rodolia cardinalis</i> (Mulsant) Coccinellidae	<i>Icerya purchasi</i> Maskell Monophlebidae	16 (L) 8 (A)	Of 16 species tested, larvae fed on only one NT species (same genus); none supported development. Adults did not fed on any of the 8 NT species.	Genus level or better Functionally monophagous under conditions of use in the Galapagos	R+/E+	Causton et al., 2004; Causton, 2005; Hoddle et al., 2013
20	1994 USA (from Japan)	<i>Sasajiscymnus (Pseudoscymnus) tsugae</i> Sasaji and McClure Coccinellidae	<i>Adelges tsugae</i> Annand Adelgidae	4	3 NT adelgids and 1 NT aphid were fed on by adult beetles but at low rates compared to target; no non-adelgid prey was able to support development (Butin et al., 2004)	Family level for adults Genus level or lower for larvae Other suitable prey include <i>Adelges piceae</i> Ratzeburg (Jetton et al., 2011)	R+/E+	Butin et al., 2004; Jetton et al., 2011
21	2003 USA, Virginia (from Washington state)	<i>Laricobius nigrinus</i> Fender Derodontidae	<i>Adelges tsugae</i> Annand Adelgidae	6	All three NT adelgids tested received eggs, but none supported full development (Zilahi-Balogh et al., 2002)	Species No other field prey are known	R+/E+ 2005	Zilahi-Balogh et al., 2002; Lamb et al., 2006; Mausel et al., 2008, 2010

	Year of petition for release	Agent	Target	# Test spp.	Test outcomes	Likely safety	Reg. dec. ^a	References
22	2005 USA (from China)	<i>Scymnus ningshanensis</i> Yu and Yao Coccinellidae	<i>Adelges tsugae</i> Annand Adelgidae	4	2 of the 3 NT adelgids and the NT aphid were fed on by adult beetles but at low rates compared to the target pest; development was assessed only on the aphid, which did not support development (Butin et al., 2004)	Family level Both <i>Pineus strobi</i> (Hartig) and <i>Adelges cooleyi</i> (Gillette) were accepted as prey.	R+/E+	Butin et al., 2004
23	2009 (from Japan)	<i>Laricobius osakensis</i> Montgomery and Shiyake Derodontidae	<i>Adelges tsugae</i> Annand Adelgidae	6	No oviposition and no development on 6 NT species; some feeding by adults on 3 adelgids and 1 aphid, but not 2 scales (Vieira et al., 2011).	Species level for larvae Family level for adults	R+/E+ 2010	Vieira et al., 2011

^aOutcomes: R- (not released), R+/E+ (released and established), R+/E- (released but not established).

