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Beyond Pandora's Box: quantitatively evaluating non-target effects of parasitoids in classical biological control

Dylan Parry

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Abstract A seminal paper by Howarth (Proc Hawaii Entomol Soc 24:239–244, 1983) entitled "Classical biological control: Panacea or Pandora's Box" ignited a sometimes acrimonious debate over the relative safety of introductions for classical biological control. Extolled for years as environmentally benign, the litany of negative non-target effects profiled by Howarth heightened awareness of this issue. Several factors have muddied this debate including the conflation of frequency of effects with their strength, grouping the effects of disparate biological control agents together, and the lack of quantitative data on either side of the argument. Here, I examine the potential for non-target effects among insect parasitoids, the most common group used for biological control of arthropods. In response to calls for better quantitative studies, I highlight three different techniques, quantitative food webs, life table analysis, and experimental populations, respectively, to quantitatively assess or reassess non-target effects in different systems. I also explore three methodological approaches employed to ascertain the strength of competitive interactions between native and introduced parasitoids, a potential non-target effect that has received little attention in the literature. These types of studies may greatly increase our understanding of the nature of non-target interactions with introduced parasitoids and bring more rigor to a debate often dominated by rhetoric.

Keywords Parasitoid drift · Non-target · Competition · Biological control · Invasive · Native · Lepidoptera

Abbreviation
CBC Classic biological control

Introduction

Classic biological control (hereafter CBC), the deliberate introduction of the natural enemies of a non-indigenous species, was long considered the most environmentally desirable method for controlling the proliferation of exotic organisms (McEvoy and Coombs 2000). Francis Howarth (1983) published *Panacea or Pandora's Box*, a paper that provocatively challenged the long-standing paradigm of biological control as a safe alternative to chemical pesticides. His article documented a litany of non-target effects and unintended consequences of organisms released in CBC programs. The paper launched a heated and sometimes acrimonious debate often dominated by rhetoric rather than science. Despite bold pronouncements extolling the safety of CBC (e.g., Funasaki et al. 1988; Lai 1988; DeLoach 1991;

D. Parry (✉)
College of Environmental Science & Forestry,
State University of New York, 246 Illick Hall,
1 Forestry Drive, Syracuse, NY 13082, USA
e-mail: dparry@esf.edu

Frank 1998; Headrick and Goeden 2001), or its catastrophic consequences (Lockwood 1993; Howarth 1991) quantitative studies validating either viewpoint are few (Thomas and Willis 1998).

There is little debate that some species introduced for CBC have had or are having detrimental impacts on non-target native species (Simberloff and Stiling 1996; Follett and Duan 2000; Strong and Pemberton 2000). Certainly, some early CBC programs, especially those where vertebrate predators were introduced to islands, had devastating consequences for non-target organisms (Smith and Remington 1996; Simberloff and Stiling 1996). Modern practitioners of CBC point out that none of these introductions would be considered today, while critics rejoin that some organisms introduced within the last 30 years have also had undesirable effects on non-target species despite extensive screening (Strong and Pemberton 2000; Louda and Stiling 2004). While less polarized in recent years, the debate about the risk posed by CBC continues (see Hoddle 2004 and Louda and Stiling 2004).

The arguments about the safety of CBC and its non-target effects may be confounded by sweeping generalizations across diverse groups of organisms. For example, while the introduction of mammalian predators and freshwater fish often results in severe non-target consequences (Simberloff and Stiling 1996), fewer non-target effects have been documented for the biological control of plants and even fewer for efforts aimed at arthropods. However, non-target effects from CBC programs against arthropods may be greater than has been recognized because only a few systems have been extensively studied (e.g., Lynch and Thomas 2000). To move beyond polarization, we need finer scale analyses that scrutinize specific groups of biological control organisms. Secondly, we must evaluate the effects on non-target species in a more quantitative manner using realistic in situ field studies.

Parasitoids in classical biological control

Insect parasitoids, primarily from the orders Diptera and Hymenoptera, are the most common organisms used for the CBC of other arthropods. In the Hymenoptera, several large super-families are exclusively parasitic or nearly so (Pennacchio and Strand 2006), whereas the majority of dipteran parasitoids are in the family Tachinidae (Stireman et al. 2006), although this life-history strategy does occur in numerous other dipteran families.

Parasitoid biology

Parasitoids can be broadly divided into idiobionts and koinobionts based on life-history (Hawkins 1994). Idiobiont parasitoids kill their host at or shortly after parasitism, then feed externally on the host, a life history strategy that precludes interaction with the intact immune system of the host. Koinobionts on the other hand, complete most or all of their larval development in a living host, necessitating evasion or manipulation of host defenses in order to survive and complete development. This dichotomy has led to speculation that idiobionts should have larger host ranges than koinobionts although the evidence is equivocal (Hawkins and Marino 1997).

Parasitoid drift

The acquisition of novel non-target hosts by introduced parasitoids or 'drift' incorporates several processes, including host shifts, host range expansion, and host switching (Follett et al. 2000). Studies suggest that parasitoid drift may be extensive. For example, of 313 exotic parasitoids released in North America for CBC of holometabolous insects prior to 1990, 51 were recorded from native non-target insects (Hawkins and Marino 1997). While the acquisition of non-target species by so many introduced parasitoids is alarming, it is not particularly surprising. Few parasitoids are truly monophagous (Shaw 1994; Sheehan and Hawkins 1991) and drift has long been recognized (e.g., Webber and Schaffner 1926; Nishida 1956; Davis 1964; Duan et al. 1996; Follett et al. 2000). In fact, the expansion of host range by introduced parasitoids through the acquisition of native species was historically viewed as beneficial (e.g., Culver 1919; Webber and Schaffner 1926). Until recently, parasitoids introduced for CBC were thought to have little or no effect on populations of most native species (Coulson et al. 1991; Godfray 1994; Onstad and McManus 1996).

The debate over non-target utilization by parasitoids has been significantly hampered by the conflation of *frequency* of occurrence with the *strength* of their effects. Most reviews have concentrated on the former, which is relatively easy to assess. However, estimating the frequency of non-target utilization without assessing impact on their population density may lead to exaggerated claims of risk or, conversely, underestimate their importance. While dramatic effects on non-target species and even extinctions have been proposed (e.g., Gagne and Howarth 1985), these claims have often not withstood scrutiny (Lynch and Thomas 2000). Despite increased attention to this issue, the greatest impediment to understanding non-target issues is the absence of quantitative data on the actual impact or strength of the effect. With few exceptions, non-target species were not routinely surveyed, and we often have no knowledge about their population dynamics prior to introductions of biological control agents. Thus, implicating an introduced parasitoid in the decline of a native insect will always be difficult and has been shown with confidence in only a few cases.

Quantitatively evaluating non-target effects

As the debate over the relative safety of parasitoids in CBC has matured, some researchers have attempted to bring a more quantitative approach to assessing non-target effects. Lynch and Thomas (2000) developed a hierarchical ranking for non-target effects that would allow comparison among different systems. Using a severity index, they ranked different systems from 0 to 9 based on the known effects on non-target species. The most severe non-target effects attributable to a parasitoid were those of *Bessa remota* (Ald.), a tachinid introduced to control a native pest of coconut, *Levuana iridescens* Betheune-Baker (Zygaenidae), which it may have ultimately extirpated (Table 1) along with other native lepidopterans (Kuris 2003). While one may quibble with their criteria, and the likelihood that data are inherently too incomplete for accurate ranking, the authors should be commended for advancing a methodology for assessing non-target impacts.

Several recent studies have experimentally investigated non-target effects using more quantitatively rigorous methods than in the past. While this is certainly not an exhaustive list of potential experimental approaches, I illustrate three different methodologies used in these studies to assess the non-target effects of exotic parasitoids and resolve longstanding issues about the nature and consequences of parasitoid drift.

Quantitative food webs

As early as 1958, the loss of lepidopteran biodiversity in Hawaii had been attributed to parasitism by exotic biological control agents (Gagne and Howarth 1985; Howarth 1983). While some have argued that evidence for this outcome is scant (Lynch and Thomas 2000), there is no doubt that Hawaii has been the recipient of a large number of CBC introductions (Funasaki et al. 1988; Messing and Wright 2006) and that a significant number of these attack Lepidoptera.

To quantitatively assess the effects of introduced parasitoids on native Hawaiian Lepidoptera, Henneman and Memmott (2001) focused on community interactions among plants, lepidopteran herbivores, and their parasitoids. The study was conducted in the remote Alakai swamp, a relatively pristine Hawaiian forest. In the study, 58 species of Lepidoptera were systematically collected and reared from 60 plant species. The parasitoids reared from the collection were used to construct quantitative food webs (e.g., Memmott 2000). Despite the remote forested location, 83% of the parasitoids recovered were species introduced for biological control of primarily agricultural pests. An additional 14% were exotics introduced accidentally and only 3% of the complex was represented by native species. This type of study does not lend itself to directly assessing the role of parasitism in the population dynamics of a particular species. The parasitism rates recorded in several species ($\sim$25%) could have significant impact at the population level, but determination would require more detailed study of individual species. Trophic web studies are an excellent starting point for investigating non-target effects of parasitoids in the context of community structure.

Life table analysis

The decline of the koa bug, *Coleotichus blackburniae* White (Scutelleriidae), an endemic Hawaiian heteropteran, has been used as the poster-child for parasitoid drift by numerous authors including

Table 1 The severity ranking of selected non-target effects caused by parasitoids introduced for biological control (adapted from Lynch and Thomas 2000)

Introduced parasitoid	Family	Region/Country	Number of non-target species affected	Severity
Bessa remota	Tachinidae	Fiji	1	7
Cotesia flavipes	Braconidae	Mexico & Brazil	1	6
Aphytis holoxanthus	Aphelinidae	Florida, Texas & Brazil	2	6
Copidosoma floridanum	Encyrtidae	New Zealand	Several	5
Tetrastichus dryi	Eulophidae	La Réunion	1	5
Cales noacki	Aphelinidae	Italy	4	5
Trigonospila brevifacies	Tachinidae	New Zealand	1 +	5
Compsilura concinnata	Tachinidae	New England, USA	Several	3
Microctonus aethiopoides	Braconidae	New Zealand	3	3
Pteromalus puparum	Pteromalidae	New Zealand	1	3
Trichopoda pilipes	Tachinidae	Hawaii	1	3
Trissolcus basalis	Scelionidae	Hawaii	1	3

The ranking (0–9, with 9 being most severe) was based on a severity index that incorporates varying degrees of mortality, population reduction, and extinction

Howarth himself (Howarth 1983, 1991). This insect is attacked by several species of introduced parasitoids, most notably *Trichopoda pilipes* (F.), a tachinid originally introduced to control the southern green stink bug, *Nezara viridula* (L.) (Pentatomidae), an exotic agricultural pest. Post-release museum collections indicated that more than 17% of koa bug specimens had *T. pilipes* eggs attached to their bodies (Follett et al. 2000), although sample sizes were small and possibly biased. Thus, speculation about non-target effects on koa bugs is based on limited qualitative data.

To determine the actual effect of *T. pilipes* on koa bugs relative to other sources of mortality, Johnson et al. (2005) used life table analysis. They determined that, although *T. pilipes* responded to koa bugs in a density-dependent fashion and could extirpate localized populations, it appeared to play a minor role in koa bug mortality at many sites. In this case, quantitative assessment of parasitism suggests that the general decline of the koa bug is unlikely to have been caused by *T. pilipes* alone, and that general predators and habitat loss should also be considered.

Experimental populations

Populations of several species of native giant silk moth (Saturniidae) have declined or been extirpated in parts of Northeastern North America (Schweitzer 1988; Tuskes et al. 1996). Several hypotheses have been advanced to explain this decline, but Boettner et al. (2000) proposed that an exotic parasitoid introduced for control of gypsy moth a century ago may be at least partially responsible. Borrowing a technique used in studies of forest pest insects (e.g., Gould et al. 1990; Parry et al. 1997), Boettner et al. (2000) established experimental populations of two native giant silk moths, *Hyalophora cecropia* (L.) and *Callosamia promethea* (Drury) (Saturniidae), in western Massachusetts. Laboratory reared sentinel larvae were deployed in the field from 6 to 8 days before being retrieved and reared in captivity. In turn, these larvae were replaced in the field by another cohort at the same stage of development as the ones collected. Mortality within each time interval is then combined to estimate cumulative parasitism (Boettner et al. 2000; Kellogg et al. 2003; Elkinton et al. 2006). This sequential rear, release, and retrieve technique is very labor intensive but can be a powerful tool in estimating the impact of parasitoids on populations.

The dominant source of mortality in the experimental silk moth populations was parasitism from the exotic tachinid, *Compsilura concinnata* Meig., confirming the authors' original hypothesis. First released in 1906, *C. concinnata* is abundant and widely distributed throughout eastern and mid-western North American forests. In Massachusetts, the staggeringly high rates of parasitism (69–81%) by this tachinid in cecropia (*H. cecropia*) and promethea (*C. promethea* provides a plausible explanation for the well-documented decline in saturniids in this region. Subsequent studies have validated these results for some species, but have also indicated that *C. concinnata* may not be the only or even the most important reason for region-wide declines in other saturniid populations. For example, Kellogg et al. (2003) conducted similar research in Virginia using the saturniids *Actias luna* (L.), *H. cecropia* and *C. promethea.* Although mortality from *C. concinnata* was high (80%) in first generation *A. luna*, parasitism was much lower in the second generation (20%) as well as in the other species studied. However, Kellogg et al. (2003) found native hyperparasitoids in the majority of *C. concinnata* recovered in Virginia, which may be limiting the impact of this parasitoid in some regions. A comprehensive study by Selfridge et al. (2007) found much lower parasitism (<10%) of *Hemileuca maia* (Drury) on Cape Cod, MA, than described from a small sample of this species elsewhere on the Cape (36%, Boettner et al. 2000) and from the closely related *H. lucina* in mainland Massachusetts (26–53%, Stamp and Bowers 1990).

Comparison among these studies is difficult because of differences in methodology, density, species used, and experimental habitats. To address this issue, I have conducted experiments in New York and Massachusetts using several species of saturniids and compared parasitism by *C. concinnata* (Fig. 1). The results suggest that for two of the species, *C. promethia* and *Antheraea polyphemus* (Cramer), *C. concinnata* has significantly greater impact in Massachusetts than it does in New York. Two other saturniids, *Anisota senatoria* (J.E. Smith) and *H. maia*, appear to be little affected by *C. concinnata* in either region. These studies suggest that *C. concinnata* has had and continues to have significant impacts on non-target species, but reveals large differences over a regional scale that will not be easy to explain. Some saturniids, especially in the sub-family Ceratocampinae, have declined (e.g., Schweitzer 1988) in the apparent absence of high mortality from *C. concinnata*, although quantitative studies validating this observation are lacking.

Competitive interactions between introduced and native parasitoids

The focus of research on non-target effects of parasitoids released for biological control has been on their potential to attack indigenous host species. Relatively little attention has been paid to possible detrimental effects to native parasitoids with which they may directly or indirectly compete. Many native insect herbivores are associated with a community of indigenous parasitoids made up of both specialist and generalist species (Schaffner and Griswold 1934;

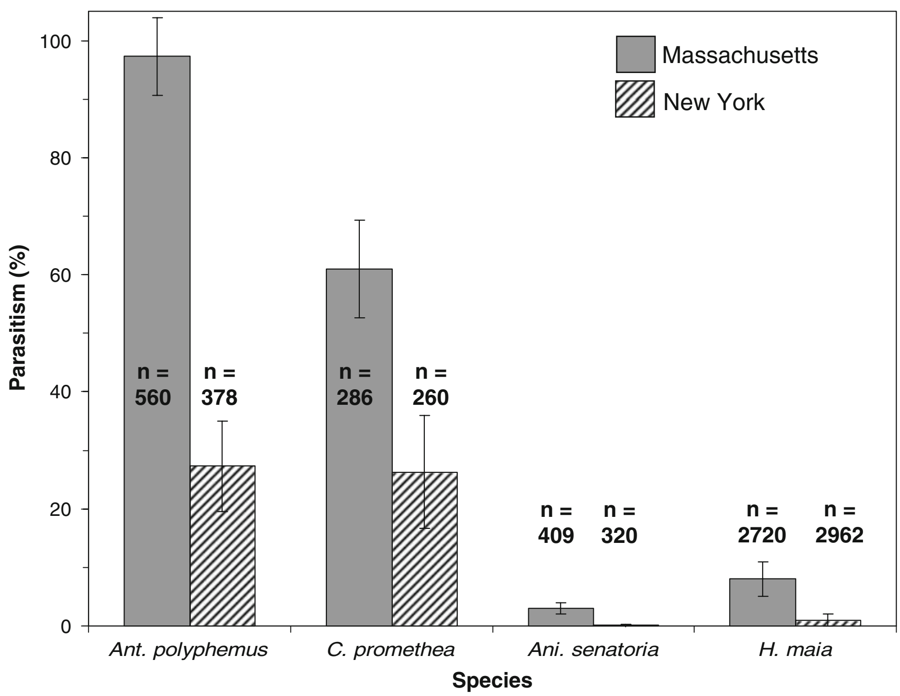

Fig. 1 Parasitism (mean ± SE) of four species of giant silk moth (Saturniidae) in Massachusetts and New York by *Compsilura concinnata.* Data for *A. polyphemus* from D. Parry, G. Boettner, and G. Tuttle (unpublished manuscript), *C. promethea* from Boettner et al. (2000) and Parry (2007), *H. maia* from Selfridge et al. (2007) and B. Hoven (unpublished), and *A. senatoria*, D. Parry (unpublished data). The number of sentinel larvae deployed for each species within a region are provided on each bar

Hochberg and Hawkins 1992; Hawkins and Mills 1996; Marino et al. 2006). The insertion of an exotic parasitoid into these communities will inevitably change host-parasitoid relationships. One outcome may be competitive displacement, as has been seen with introduced arthropod predators such as lady beetles (e.g., Evans 2004). Such effects may be confined to one or a few native species in many systems, but for highly polyphagous species such as *C. concinnata*, negative interactions could conceivably extend to hundreds of native parasitoids.

The role of competition in structuring parasitoid communities has long been debated (Hawkins 2000). Competitive exclusion has been shown for hymenopteran parasitoids introduced for CBC, although the excluded species have been other introduced parasitoids rather than native species (Luck and Podoler 1985; Bennett 1993; Murdoch et al. 1996). To my knowledge, the extirpation of a native parasitoid by an introduced parasitoid has not been documented. Determining that competition has occurred is difficult because studies of native parasitoid fauna are rarely conducted prior to introduction of species for CBC, thus limiting the utility of any post-hoc analyses (Bennett 1993). Even where exotic species have become a significant component of a host's parasitoid load, determining if they are simply exploiting an unoccupied niche or if they have out-competed and replaced native species is difficult. Despite these hurdles, there are cases where the preponderance of evidence suggests that exotic parasitoids have displaced native parasitoids.

Competition among parasitoids can take several forms, including hyper- and klepto-parasitism (Mills 2003). For the purposes of this paper, I will restrict discussion to exploitative and interference competition among obligate parasitoids. In exploitative competition, an exotic parasitoid reduces the density of native host species required by indigenous parasitoids. Interference competition results when one species uses physical combat, physiological suppression, or more rapid development to usurp host resources from a competitor (Mills 2003). Priority effects can be important in governing the outcome of competition among parasitoids, with the first arriving parasitoid species often intrinsically superior to later arriving species (Reitz 1996).

One of the first studies to examine competition between introduced and native parasitoids was conducted in New Zealand. Following the introduction of the tachinid *Trigonospila brevifacies* (Hardy) in the 1960s for control of tortricid pests of fruit trees, researchers were surprised to find that the species adopted multiple species of native tortricids as hosts even though they occurred in natural forests rather than orchard environments. Using connectance and quantitative food webs, Munro and Henderson (2002) identified the host species utilized by *T. brevifacies*, quantified their parasitoid load, and attempted to determine if this species has become dominant in native hosts at the expense of indigenous parasitoids. Remarkably, within 30 years of introduction, *T. brevifacies* had become the dominant parasitoid of all but one of the tortricid species, and contributed from 16% to 80% of the total parasitism, the most of any parasitoid in the system. The host range of *T. brevifacies* overlaps in part or completely with that of 13 native parasitoids. The numerical dominance and degree of overlap with native parasitoids strongly suggests that this species is displacing native parasitoids of tortricids, although refugia in contiguous forest may prevent their complete loss.

Perhaps our most detailed understanding of competitive interactions between introduced and native parasitoids comes from research on the braconid *Aphidius ervi* (Haliday). This wasp was introduced to the continental United States in 1959 to control the pea aphid, *Acyrthosiphon pisum* Harris (Homoptera: Aphidae), an important pest of a variety of leguminous crops (Angalet and Fuester 1977). This parasitoid is a good competitor and had displaced another introduced braconid, *A. smithi* (Sharma and Subba Rao) by the 1970s (Reitz and Trumble 2002). Until the introduction of *A. ervi*, the dominant parasitoid of pea aphids was the native *Praon pequadorum* Viereck (Braconidae), which accounted for as much as 42% of the parasitism (Schellhorn et al. 2002). The percentage of parasitism attributable to *A. ervi* is now 90–100% and parasitism by *P. pequadorum* has fallen to very low levels (Danyk 1993).

To determine if the decline of the native *P. pequadorum* was caused by the exotic *A. ervi*, Schellhorn et al. (2002) coupled experimental manipulation with modeling. Competition was first addressed using population level manipulations of host density and subsequently by quantifying foraging ability on individual plants. In an apparent paradox, *P. pequadorum* was superior to *A. ervi* in larval–larval competition within a host, an effect most pronounced when aphid populations were manipulated to create high parasitism levels by both braconids. This conundrum was resolved when the foraging efficiency of each braconid species was examined. The introduced species, *A. ervi*, was significantly more efficient and parasitized more aphids per unit time than its native competitor. The model developed by Schellhorn et al. (2002) showed that the superior foraging ability of *A. ervi* could overcome the superiority of *P. pequadorum* as a larval competitor. Anthropogenic factors tilt the scales further toward *A. ervi* because the harvesting practices used in crops like alfalfa create frequent, catastrophic disturbance in this host-parasitoid system. In the low density aphid populations following harvest, the superior foraging abilities of *A. ervi* enable it to dominate its native competitor.

Identifying a mechanistic basis for competitive effects between native and introduced parasitoids as Schellhorn et al. (2002) did in an agroecosystem will be more challenging in unmanipulated natural environments. In many systems, parasitoids were released without any knowledge of existing host–parasitoid relationships. There are, however, a few natural systems where sufficient data were recorded to evaluate the effects of an introduced parasitoid on native parasitoid complexes. In eastern North America, we are fortunate to have information quantifying the native parasitoid complexes of Lepidoptera shortly after the introduction of *C. concinnata.* Coupling this historical data with contemporary field studies has allowed insight into the effects of a dominant introduced parasitoid on native competitors.

The prevalence of *C. concinnata* in forest lepidopteran communities in Northeastern North America suggests that this species has had a long and extensive interaction with native parasitoids. In an extraordinarily prescient study, Schaffner and Griswold (1934) undertook one of the most ambitious systematic collections of hosts and parasitoids ever conducted, with more than 300,000 individual Lepidoptera from 164 species reared from 1915 to 1929. Most importantly, the project encompassed a 15-year period following the release of *C. concinnata* in New England. This study serves as a benchmark that can be used to retroactively assess the effects of this introduction on native parasitoid communities.

Given the wealth of data in Schaffner and Griswold's (1934) landmark compendium, it is surprising that few ecologists have taken advantage of it. To illustrate the utility of this data set in retrospective studies, I examined changes in the abundance of a native generalist tachinid, *Lespesia frenchii* (Williston), one of the most polyphagous native tachinids attacking forest Lepidoptera in North America (Arnaud 1978). This species was historically prevalent in several saturniids that are now heavily parasitized by *C. concinnata* and was not recovered from 2000 saturniid sentinel larvae deployed in central Massachusetts (Boettner et al. 2000). To assess the abundance of *L. frenchii* and *C. concinnata*, I utilized experimental populations of two lepidopterans in Massachusetts and northern New York State. One of the host species, *C. promethea*, is heavily parasitized by *C. concinnata* and has precipitously declined in Massachusetts. In New York, *C. concinnata* parasitism is significantly lower in *C. promethea*, which is still common across central and western parts of the state. The other species, eastern tent caterpillar (*Malacosoma americanum* F.), serves as a control because it has remained abundant in both regions, utilizes a host tree (*Prunus serotina* Ehrh.) shared with Promethea, yet is rarely attacked by *C. concinnata.* In this case study, the potential confounding effect of historical change in land use was minimized by comparing regions (MA and NY) that underwent a similar conversion from forest to agriculture followed by succession back to forest.

Data from Schaffner and Griswold (1934) indicate that *Lespesia frenchii* was the most common parasitoid recovered from *C. promethea* from 1915 to 1929 (Table 2). Promethea larvae deployed in two experimental populations in western Massachusetts did not yield *L. frenchii* in 2004 (Parry 2007) nor did Boettner et al. (2000) recover it from their sentinel populations (Table 2). In contrast, *L. frenchii* was reared from three experimental populations in New York where *C. concinnata* parasitism was much lower (see Fig. 1). Given that *L. frenchii* is highly polyphagous, it is possible that it has shifted to alternative host species less favored by *C. concinnata.* To investigate this possibility, I quantified parasitism in eastern tent caterpillar, a species favored by *L. frenchii* and seldom used by *C. concinnata.* When the parasitoid complex of *M. americanum* in present day Massachusetts was examined, oligophagous tachinid species (*L. exul* and *C. malacosomae*) occurred in the same rank order as Schaffner and Griswald had found 70 years earlier, but

Table 2 A comparison of historical and present-day tachinid complexes for two species of Lepidoptera

Species	Location (dates)	Sample size	Rank abundance of Tachinid species
C. promethea	New England (1915–1929)[a]	$n = 4644$ (multiple sites)	1. *Lespesia frenchii* (p)
			2. *Compsilura concinnata* (p)
			3. *Chetogena* sp. (p)
	Massachussets (1999–2004)[b,c,d]	$n = 1607$ (4 sites)	1. *C. concinnata*
			No *L. frenchii* collected
	New York (2003–2004)[c,d]	$n = 239$ (4 sites)	1. *C. concinnata*
			2. *L. frenchii*
M. americanum	New England (1915–1929)[a]	$n = 60031$ (multiple sites)	1. *Carcelia malacosomae* (o)
			2. *Leschenaultia exul* (o)
			3. *L. frenchii* (p)
			4. *Chetogena* sp. (p)
			5. *Exorista mella* (p)
	Massachussets (2001–2005)[d]	$n = 1246$ (12 sites)	1. *C. malacosomae* (o)
			2. *L. exul* (o)
			3. *Chetogena* sp. (p)
			No *L. frenchii* collected
	Michigan (2003)[d]	$n = 840$ (8 sites)	1. *L. exul* (o)
			2. *C. malacosomae* (o)
			3. *L. frenchii* (p)
			4. *Chetogena* sp.

Polyphagous species are denoted by (p) and oligophagous species by (o). Promethea (*C. promethea*) is heavily parasitized by *C. concinnata* (see Fig. 1) whereas eastern tent caterpillar, *Malacosoma americanum*, is seldom attacked. Schaffner and Griswold (1934) collected *C. promethea* and *M. americanum* in New England shortly after the release of *C. concinnata.* I collected promethea and eastern tent caterpillar from experimental populations in Massachusetts nearly 100 years later. Additional populations of Promethea and eastern tent caterpillar were collected in New York where parasitism by *C. concinnata* is much lower. In addition, a collection of eastern tent caterpillar was made in Michigan where *C. concinnata* is a relatively recent arrival. All tachinids are native to eastern North America except *C. concinnata*

[a] Schaffner and Griswold (1934)

[b] Boettner et al. (2000)

[c] Parry (2007)

[d] Parry (unpublished)

the polyphagous *L. frenchii* was completely missing (Table 2). In northern New York and in Michigan, where non-target parasitism from *C. concinnata* is much lower, *L. frenchii* resumed its rank (3rd most abundant) in the *M. americanum* parasitoid complex.

While these data are not conclusive evidence for competitive displacement, they are certainly suggestive of it. In the absence of further experimentation, we can only speculate as to the actual mechanism(s) underlying the disappearance of *L. frenchii.* One possibility is that the multivoltine *L. frenchii* is dependent on saturniid silk moths as overwintering hosts. Even though alternative hosts are readily available to *L. frenchii* at other points in the season, it may be that the loss or severe reduction of hosts at a critical point in the season can limit its population density. The effects of high *C. concinnata* attack rates on specialist parasitoids may be even greater. Collections of silk moth larvae from both wild and experimental populations in Massachusetts have failed to yield a number of specialists such as tachinids in the genus *Belvosia*, recorded by Schaffner and Griswold (1934) and others (Arnaud 1978). Intriguingly, native parasitoids have been recovered from saturniids on Martha's Vineyard, an island off the coast of Massachusetts where *C. conncinata* is thought to be absent (G.H. Boettner, personal communication). While admittedly an extreme example, the *C. concinnata* system does illustrate that going beyond simple host-parasitoid interactions is important when evaluating the ecological impact of CBC introductions.

Future directions in research and regulation

Practitioners of biological control have suggested that the introductions responsible for the most severe effects on non-target species were conducted in earlier, less enlightened times, and that modern criteria for release would have prevented the occurrence of many of these effects (e.g., Hoddle 2004; Messing and Wright 2006). Indeed, the studies highlighted in this manuscript illustrate this point well. In Henneman and Memmott (2001), exotic parasitoids found attacking native Lepidoptera were all released prior to 1945, the species' attacking the koa bug in Hawaii were introduced in the early 1960s (Johnson et al. 2005), and the first releases of *Compsilura* were in 1906 (Culver 1919).

One recent introduction does cast doubt on the frequent assertion that generalist parasitoids would not be used in CBC today. In the late 1970s, a hymenopteran parasitoid from Asia, *Pimpla disparis* Vierick, was released for gypsy moth control. This was done despite existing knowledge about the highly polyphagous nature of this ichneumonid. Although originally released in Delaware, the state of Minnesota (MDNR 1997, 1999) acquired and released large numbers and a separate introduction occurred in Illinois (Ellis et al. 2005). I have collected *P. disparis* from eastern tent caterpillar and the exotic lymantriid *Euproctis chrysorrhoea* (L.) in Massachusetts (Elkinton et al. 2006; D. Parry, unpublished), indicating substantive movement from release sites. In retrospect, it is puzzling why a highly polyphagous, multivoltine parasitoid (Schaefer et al. 1989) was considered a candidate for release, especially given its low rate of attack on the target species (Fuester et al. 1997). Not only was the original release ill-conceived, but a state agency continued to release this species recently despite increased attention given to non-target concerns in recent years.

This example highlights some pressing concerns regarding parasitoid introduction. Clearly, significant regulatory changes coupled with the development of better host-range testing protocols are long overdue. A review by Messing and Wright (2006) highlights 'regulatory chaos' in the United States. They contrast the tangled web of sometimes contradictory rules and regulations regarding the introduction of arthropod natural enemies with the system developed by Australia and New Zealand where well-defined legislative frameworks have been implemented.

Host-range testing protocols specifically for parasitoids have lagged behind those developed for CBC of plants (Sands and Van Driesche 2004). The range of behaviors and interactions exhibited by parasitoids in natural environments may be impossible to replicate in captivity rendering interpretation of results difficult (Briese 2005). The development of better risk assessment protocols for evaluating candidate species would be a significant step in assuring ecologists, conservation biologists and other stakeholders that biological control is an effective tool against invasive species rather than a source of additional problems.

Insect parasitoids will continue to be the most widely used group for the biological control of arthropods. In contrast to introductions for the biological control of plants, parasitoids were not subjected historically to host-range testing. The slew of recent review and synthesis articles by biological control practitioners, ecologists, and conservation biologists suggest an increasing awareness that a *laissez-faire* approach to non-target effects is no longer acceptable in arthropod control programs. Although classical biological control is not the Pandora's Box premised by Howarth, it certainly has not been a Panacea either. While catastrophic non-target effects have been identified in relatively few systems and generally have been restricted to parasitoids that would not be considered candidates today, it is disconcerting that we know so little about the interaction with native species for most releases. Recognition that less dramatic non-target effects can still have fundamental effects on the integrity and function of ecosystems through more subtle mechanisms such as competition or interactions with anthropogenic stressors should provide researchers with alternative avenues to fully assess the non-target effects of parasitoids released for classical biological control.

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