# Biological control of invasive species: solution or pollution?

**Russell H Messing* and Mark G Wright**

**Biological control of invasive species using co-evolved natural enemies has long been considered a safe, cost effective, and environmentally benign tool for pest management. However, recent work has questioned the extent to which these imported natural enemies have negative impacts on populations of non-target species. The result has been a vociferous debate about the safety and proper role of biological control, often without convincing evidence on either side. The issues are particularly well focused in Hawaii, with its high numbers of both endemics and invasive pest species. We review the data concerning environmental impacts from past biocontrol projects, discuss the patterns and generalizations that emerge from retrospective analyses, and consider some new techniques for risk assessment. We then emphasize the need for a federal regulatory framework that is rational, efficient, transparent, and ecologically meaningful.**

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Many of the most important insect and mite pests in the US are exotic, invasive species that severely impact agricultural, forest, and urban ecosystems, costing billions of dollars annually and threatening the integrity of natural environments and the viability of endangered species (Perrings *et al.* 2002). The majority of the most invasive weed species in the US are also exotic, as are many nematodes and plant pathogens (Foy and Forney 1985). The US Congress Office of Technology Assessment emphasized the growing pressures that invasive pests are placing on ecosystems (OTA 1993); their role in causing species extinctions is only beginning to be documented (Gurevitch and Padilla 2004). Overall, biotic invasions are very roughly estimated to cost at least $137 billion annually in the US alone (Pimentel *et al.* 2000).

## In a nutshell:

- Classical biological control of invasive pests can be extremely effective, economically invaluable, and environmentally benign
- In some cases, deliberately imported natural enemies have had negative impacts; the extent of these impacts has been stridently debated but seldom quantified
- In Hawaii, large numbers of invasive pest species, a struggling agricultural economy, and high rates of floral and faunal endemism fuel the debate
- Introduced arthropods caused fewer environmental impacts than vertebrates, and specialists fewer than generalists; recent introductions have a better safety record than earlier projects
- Regulations for biocontrol in the US are chaotic, poorly understood, and subject to frequent change, highlighting the need for a streamlined system, for which there are excellent national models

[1]*University of Hawai'i at Manoa, College of Tropical Agriculture and Human Resources, Kaua'i Agricultural Research Center, 7370 Kuamo'o Road, Kapa'a, Hawai'i 96746 *(messing@hawaii.edu)*

Almost all invasive species arrive without their co-evolved predators, parasites (Figure 1), and pathogens (or, in the case of weeds, herbivores). By escaping from these mortality agents, pest populations often increase and spread rapidly in the new environment. Biological control consists of locating natural enemies in the pest's native range and evaluating the results of their importation, quarantine, testing, and release in the new environment. Biocontrol, while long considered environmentally benign, has recently come under fierce criticism for having unintended side effects on non-target organisms.

About one in three attempts at biological control results in the establishment of a new natural enemy (Hall and Ehler 1979); half of these, or 16% of the total, have led to complete control of the target species (Hall *et al.* 1980). Although biocontrol was historically developed against pests in agroecosystems (including rangeland and forests), it has recently gained increased attention for controlling invasive species in natural environments (Hoddle 2002; Louda and Stiling 2004).

In successful biological control, the results can be dramatic (Figure 2). Invasives that threaten entire regional economies or vast areas of natural land can be reduced to a fraction of their previous abundance and sustained at low levels indefinitely, without additional cost or management inputs. Natural enemies are self-sustaining, self-dispersing, and generally adjust their population size in relation to that of the target pests. One example involved control of the cottony cushion scale, *Icerya purchasi*, a pest that almost destroyed the citrus industry in California (Caltagirone and Doutt 1989). Another example is the control of the cassava mealybug, *Phaenococcus manihoti*, a pest species that had previously caused up to 50% crop loss of a staple food for 200 million people in sub-Saharan Africa (Norgaard 1988). The latter project earned the World Food Prize for saving millions of lives and billions of dollars across the African continent.

In the US, insects, plant pathogens, and weeds reduce crop production by about 37% annually (Pimentel 1997), a statistic that hasn't improved over the past 50 years, despite a tremendous increase in pesticide input. From 1945 to 1989, crop losses to insects doubled (from 7% to 13%) in spite of a 10-fold increase in the amount of insecticides used; losses to weeds stayed almost constant, while there was a 100-fold increase in herbicide use (Pimentel 2005). While not all of these losses are due to exotic pests, a large percentage of the crop damage in agricultural states such as Florida (Frank and McCoy 1995) and Hawaii (Funasaki *et al.* 1998) has been shown to be the result of alien, invasive species. In California alone, exotic pest damage to agriculture is estimated to cost $3 billion annually (UC IPM Online).

Applying chemical pesticides has been the primary means of pest control on US farms for over 50 years and the detrimental effects of these chemicals have been amply documented (Carson 1962; Pimentel 2005 and references therein). These effects include 300 000 pesticide poisonings per year (EPA 1992, cited in Pimentel 2005), 10 000–15 000 cases of pesticide-related cancer per year (Pimentel 1997), and health-related costs of about $1 billion per year in the US alone (Pimentel and Greiner 1997). With pesticides ever more restricted due to health effects, environmental impacts, and the development of genetic resistance in pest species, there is an increasing need to implement alternative methods for the management of invasive species (OTA 1995).

As problems with synthetic pesticides became apparent, biocontrol was seen as an ecologically benign replacement technology for pest management. However, when entomologists realized that some introduced predators, parasitoids, and herbivores attacked species other than their intended targets, there were increasing doubts voiced concerning the safety of this strategy. The extent of environmental damage caused by introduced natural enemies, the proper criteria to use in evaluating risks and benefits, and the mechanisms of regulation that are most appropriate have been intensely debated among applied ecologists over the past several years (Follett and Duan 2000; Wajnberg *et al.* 2000; Lockwood *et al.* 2001). Nowhere has the controversy been greater than in the Hawaiian Islands.


Courtesy of MW Johnson

***Figure 1.*** *An introduced Asian parasitoid,* Fopius arisanus, *ovipositing into eggs of the oriental fruit fly,* Bactrocera dorsalis, *in a Hawaiian guava fruit.*

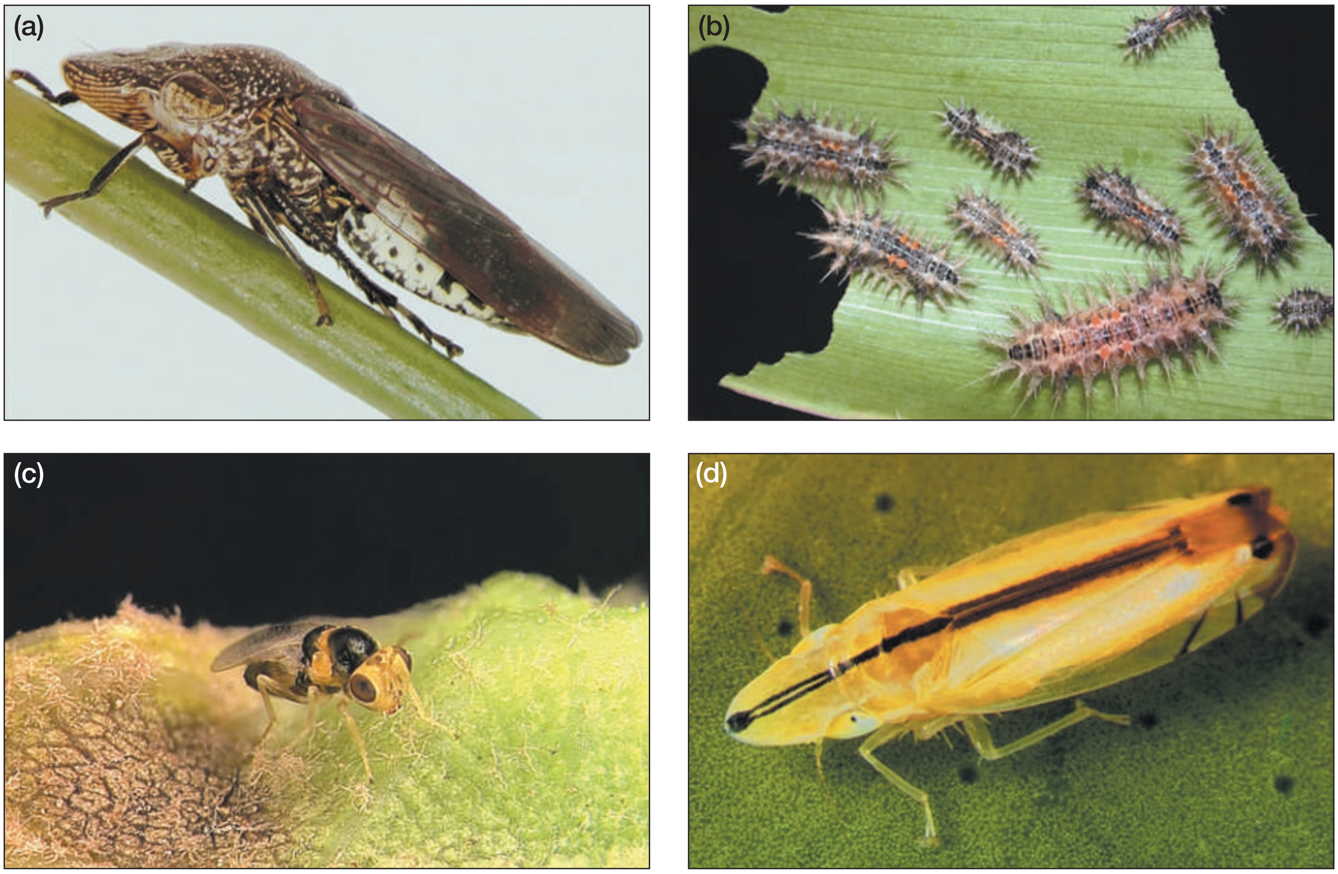
## Hawaiian Islands: crucible of the debate

Hawaii has a unique combination of historical and geographic features that fostered intense controversy regarding the safety of biological control. Agriculture has always played a dominant role in the economy of the Islands, where virtually all arthropod pests are invasive (Crop Knowledge Master 2006), and biological control has been a key tool in the protection of crops and the ability to sustain profitable farming for over a hundred years (Funasaki *et al.* 1988). There have been more biocontrol introductions to Hawaii than almost anywhere else on Earth and a third of the introduced species have become established, contributing to the control of 200 pest species (Funasaki *et*


Courtesy of P Room/CSIRO

***Figure 2.*** *The aquatic weed,* Salvinia molesta, *an invasive pest in Australia, Asia, and Africa, severely interferes with the use of water bodies for boating, irrigation, flood mitigation, and wildlife conservation. A small weevil (*Cyrtobagous salviniae*) from the weed's native range in Brazil rapidly clears the weed mats from affected waterways; it has controlled* Salvinia *in at least 13 tropical countries.*




(a) and (d) courtesy of R Krugner; (b) courtesy of R Heu; (c) courtesy of MN Tremblay

***Figure 3.*** *Hawaii is inundated with invasive species, with over 20 new introductions per year, many of which become serious environmental and economic pests. Recent invasives include: (a) the glassy-winged sharpshooter,* Homalodisca coagulata*; (b) the nettle caterpillar,* Darna pallivitta*; (c) the Erythrina gall wasp,* Quadrastichus erythrinae*; and (d) the two-spotted leafhopper,* Sophonia rufofascia

*al.* 1988). This has saved tens of millions of dollars and reduced pesticide use by many tons annually. The agricultural community relies on this method of pest management, and the State Department of Agriculture is one of the few in the nation to support a full-time exploratory entomologist largely for this purpose.

Hawaii's role as a hub for tourism, trade, and military transport contributes to its continuing assault by foreign species. About 20 new arthropod species invade the Islands each year (Beardsley 1979); many become pests of agriculture and natural ecosystems (Figure 3). A single recent invader, the two-spotted leafhopper from China (Figure 3d), attacks over 300 species of plants in 83 families, of which 68% are crops and 22% are endemic plants, including 14 rare and endangered species.

The need for biocontrol agents to combat these invasive pests is countered by concerns that exotic predators and parasitoids contribute to "biological pollution" (Howarth 1983) of Hawaii's unique, fragile ecosystems (Figure 4). The Islands are one of the most isolated land masses on Earth, and have one of the highest rates of floral and faunal endemism of any region. Many endemic species have lost the defensive adaptations that their ancestors maintain in continental ecosystems, and they are particularly susceptible to competition and exploitation by invasive species (Howarth and Ramsay 1991). There are also more endangered species per square mile in Hawaii than any other place on Earth, and the Islands are home to one-fourth of all endangered species in the entire US (www.fws.gov/endangered/).

Are biological control agents threatening these endangered species, in Hawaii and elsewhere? Do the benefits of invasive species control outweigh the risks of non-target impact? In the two decades since these questions were first widely posed (Howarth 1983, 1991), conservationists, agriculturists, and biological control practitioners have stridently defended disparate points of view, often arguing strongly from narrow perspectives. Only recently have data started to become available for establishing an empirical framework.

## Evidence for non-target impacts: more heat than light

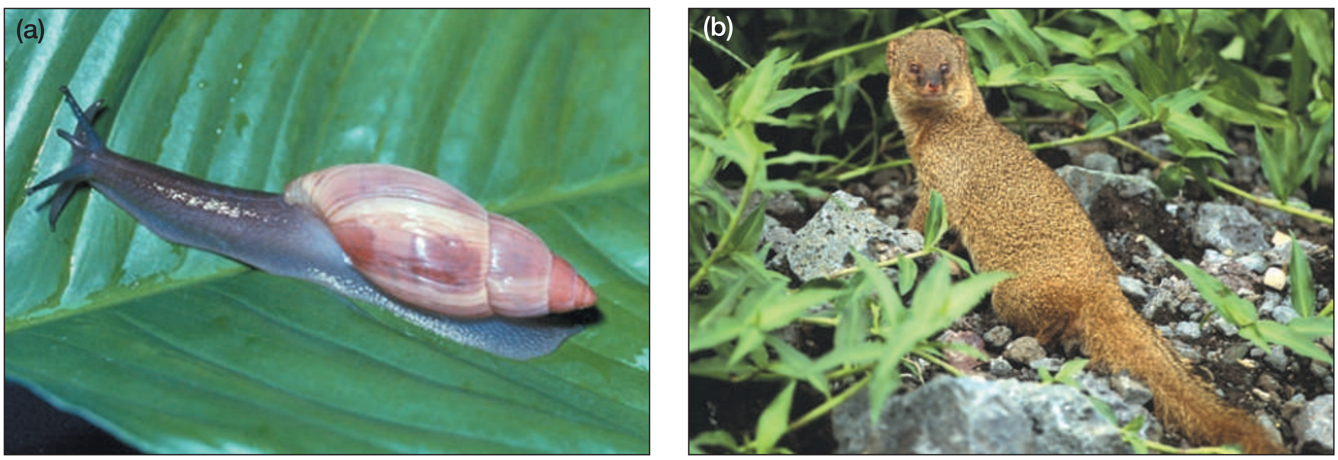
The debate over non-target impacts of biological control began with more conviction than data. Proponents claimed that "no adverse effects on the ecosystem occur from biological control" (DeBach 1974), while critics (Gagne and Howarth 1985) blamed biocontrol for the extinction of Lepidopteran species, including some that were subsequently found extant, with abundant populations (Haines *et al.* 2004).

A substantial number of introduced biocontrol agents do indeed feed on non-target species. In Hawaii, 22% of 243 agents were documented to attack organisms other than their intended targets (Funasaki *et al.* 1988), while across North America, 16% of 313 parasitoid species introduced against holometabolous pests (insects that undergo complete metamorphosis) also attacked native species (Hawkins and Marino 1997). The best-documented and most serious impacts occurred as a result of predaceous vertebrate and snail introductions (Figure 5). The small Indian mongoose (*Herpestes javanicus*), which was brought to Hawaii to control rats in sugarcane, became a serious predator of native birds. The predaceous rosy wolf snail (*Euglandina rosea*), which was introduced to attack the giant African snail (*Achatina fulica*), strongly impacted endemic tree snails in Hawaii and French Polynesia (Cowie 2001).

*Figure 4. Native Hawaiian rainforests are rich in endemic species, many of which are rare or endangered and susceptible to competition and predation from invasive species.*

However, most projects involving vertebrates, snails, and even generalist arthropods occurred before the establishment of government oversight of biological control. A single private individual introduced the mynah bird (*Acridotheres tristis*) to Hawaii in 1865, and a small group of farmers imported the mongoose in 1883, but no regulations were in place until 1890. These poorly considered introductions have thus tarnished the safety record of more recent and carefully regulated arthropod introductions. No biocontrol agent approved for release in Hawaii from 1967 to 1988 was reported to have attacked any native species (Funasaki *et al.* 1988). On the island of Kauai, of the several introduced parasitoids found to attack native moths, there were no non-target impacts for any species released after 1945 (Henneman and Memmot 2001). Thus, the frequency of non-target impacts, while significant overall, has declined dramatically as stricter regulations were put in place. Generalist species that were once routinely released would not be considered under current protocols (Panel 1).

In contrast to frequency, the *strength* of non-target effects is much more difficult to assess. A given record of a predator, parasitoid, or herbivore feeding on a non-target individual may be completely trivial, having absolutely no effect from a population standpoint. In predator–prey population dynamics, density dependence, handling time, satiation, cannibalism, and abiotic factors can all affect the equilibria of the species involved (Holt and Hochberg 2001). Very few studies have gathered sufficient information to address impacts on population density of non-target species (let alone their extinction); comprehensive reviews of the literature conclude only that data "require years of painstaking field work" and are "simply not yet available" (Stiling and Simberloff 2000). Some argue that this absence of evidence




(a) ©J Jeffrey; (b) courtesy of R Heu

*Figure 5. (a) The rosy wolf snail (*Euglandina rosea*) and (b) the small Indian mongoose (*Herpestes javanicus*) are introduced generalist predators that impact native species in Hawaii.*

**Panel 1. Two contrasting biocontrol projects**

In 1934, a wasp in the genus *Eupelmus* (Figure 6) was introduced from Guatemala to Hawaii to help control the pepper weevil, *Anthonomus eugenii*. While we cannot recreate the exact thinking of the time, it is likely that entomologists were focused strictly on the economic aspects of vegetable production and agricultural pest management, and gave little thought to potential environmental impacts. Almost certainly, no non-target host-range testing was conducted.

Since then, it has been discovered that *Eupelmus cushmani* has an extraordinarily broad host range, attacking not only the pepper weevil but also moth larvae, tephritid fruit flies, and even other hymenopterous parasites. The wasp has negative economic and environmental impacts, as it kills beneficial insects such as *Procecidochares alani*, a species that is used to control weeds. A biological control agent with such a wide host range and potential side effects would never receive release permits under today's regulations.

In 2003, we attempted to introduce a different wasp, *Fopius ceratitivorus*, for biological control of the Mediterranean fruit fly, *Ceratitis capitata*. The medfly is one of the most widespread and economically important insect pests in the world; explorations in its native home of sub-Saharan Africa led to the discovery of a parasitic wasp that lays its own eggs inside the eggs of medflies, then devours the fly larvae as the wasp grows inside its host.

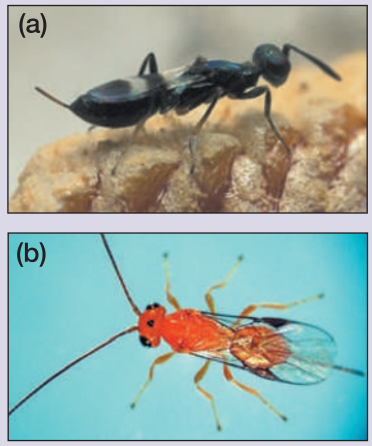



***Figure 6.*** *(a)* Eupelmus *sp and (b)* Fopius ceratitivorus.

In a quarantine laboratory setting, we have shown that this wasp cannot attack any of the other pest tephritids in Hawaii (the melon fly, the Oriental fruit fly, or the solanaceous fruit fly), which is highly unusual among the known braconid fruit-fly parasites from Asia, Africa, and Australia. The data indicate that *F ceratitivorus* is very specialized to attack *Ceratitis*. To go further, we tested *F ceratitivorus* against a beneficial tephritid that is used in biocontrol of weeds (*Procecidochares alani*), and also against an endemic, non-economically important tephritid that occurs in Hawaiian rainforests (*Dubautia raillardiodes*). In not one single case was the parasite able to successfully attack any non-target species. Despite these tests, and over 2 years of investigation into the ecology and behavior of *F ceratitivorus*, we are still unable to obtain release permits from the state of Hawaii.

As the priorities and values of society change, technologies adapt to reflect the goals and principles that form the context of their application. Early in the 20th century, proponents of biological control gave little thought to broader environmental impacts, so that mistakes were made for which we are still paying the ecological price. Under current regulations, however, and largely in reaction to those mistakes, the pendulum has swung so widely in the opposite direction that the timely application of biological pest management has been impeded. Only by improving our risk analysis skills and our ability to predict parasite host range can we arrive at a balanced and well-reasoned regulatory system.

is not evidence of absence, and point to the few well-documented cases of non-target impact as warning flags.

The Eurasian flowerhead weevil *Rhinocyllus conicus*, released for biocontrol of weedy thistles on the Great Plains, went on to attack over 20% of indigenous North American *Cirsium* species, including several rare species, and has been implicated in population declines of native flies feeding on these thistles (Louda *et al*. 2003). The Argentine moth *Cactoblastis cactorum* did an outstanding job of controlling invasive prickly pear cactus in several areas around the world, but after deliberate introduction to the Caribbean it inadvertently jumped to the US mainland, where it threatens the rare semaphore cactus (*Opuntia corallicola*) and other native *Opuntia* species (Louda *et al*. 2003). A tachinid fly, *Compsilura concinnata*, introduced from Europe in 1906 to combat the gypsy moth, has since been recorded attacking over 100 native Lepidopteran species, and is implicated in the decline of giant silk moths in the northeastern US (Boettner *et al*. 2000).

Retrospective analyses of these and other case histories (Follett *et al.* 2000; Louda *et al.* 2003) provide the first real data to begin formulating biocontrol protocols in order to minimize risk. It is now generally accepted that the risk is greatest when non-target species in the new environment are taxonomically related to the target species, and when biocontrol agents are polyphagous. It is also recognized that prediction (and evaluation) of ecological effects requires population dynamics data. Quarantine testing, while necessary, measures only physiological host range and requires complementary data on life history, dispersal, phylogeny, and behavioral ecology in order to predict potential side effects. While the debate is by no means resolved, there has been progress in defining a common vocabulary and delineating research protocols to conduct risk analyses prior to field release (Bigler *et al.* in press).

## Techniques for risk assessment

Imported natural enemies are kept in quarantine until sufficient testing can be done to ensure their safety and to obtain release permits. However, the artificial conditions of a quarantine laboratory severely limit the ecological realism and complexity of interactions that can be assessed (Briese 2005). The primary focus of pre-release testing therefore largely defaults to host specificity screening, which determines the physiological suitability of non-target species for the candidate agent.

Quality quarantine space is extremely expensive, so there is often limited room for any given project. The majority of the work, especially for arthropods, takes place in areas ranging in size from Petri dishes to bench-top cages, where target and non-target species are combined with suitable controls. Natural enemies held in confinement often accept suboptimal hosts or prey, so physiological suitability, as opposed to ecological suitability, leads to an overestimate of the range of non-target species at risk. This results in "false positives" (Wright *et al.* 2005), which may lead us to reject potentially useful biological control agents. While occasional errors have occurred in which host range was underestimated (Briese 2005), the screening process is inherently conservative, which contributes to the good safety record of recent natural enemy importations.

Post-colonization evolution and adaptation to new hosts has been considered a potential risk (Louda *et al.* 2003), but to date there has been only one study specifically designed to test whether a natural enemy imported for biological control has undergone adaptive genetic change following introduction. In fact, this study showed that the agent lost one aspect of virulence in relation to a particular insect/plant host combination (Hufbauer 2002). The evaluation of potential non-target risk due to genetically based host range expansion is considered unfeasible at present, and as such is not currently appraised by regulatory agencies. However, modern genetic tools are beginning to be applied to these questions (Roderick and Navajas 2003).

In determining which non-target species to test in quarantine, weed biocontrol practitioners use a centrifugal phylogeny method (Wapshere 1974), first testing organisms that are most closely related to the target, then expanding to more distantly related species, until the entire host range has been examined. Briese and Walker (2002) underscore the effectiveness of this approach and emphasize that relatedness of hosts overrides other factors often considered in screening (such as the inclusion of economically important plants not related to the target species). In arthropod biocontrol, centrifugal phylogeny is somewhat less useful, being confounded by incomplete systematic knowledge of insect taxa, dissimilar behaviors among closely related species within clades, and parasitoid host selection behaviors that are often based on specific habitat stimuli, rather than on physiological or genetic relatedness of hosts (Messing 2001).

Life history parameters, host range data, and behavioral ecology of biocontrol agents can sometimes be studied in the country of origin, prior to importation. This offers broader ecological realism, but such studies are often constrained by logistical and monetary considerations (particularly in less developed regions lacking solid research infrastructure) and also by the fact that endemic non-target species that are at risk in the target environment do not occur in the region of origin. The expense and difficulty involved in conducting studies abroad must be weighed against the expected gains in data that are of real predictive value, and the consequences of delaying biocontrol efforts must be balanced against the possibility of considerable or even irreparable environmental harm.

Recently, there have been concerted efforts to develop more comprehensive protocols for predicting non-target risks of biocontrol. Van Lenteren *et al.* (2003) proposed a multi-faceted procedure, with variables that can be semi-quantitatively assessed, leading to the development of a robust means of evaluating risks for inundative biocontrol (inundative agents are those reared en masse and released periodically to control pests, rather than the "classical" approach of allowing natural enemies to adjust their own population densities in the field). The authors propose quantifying the possibility of establishment in non-target habitats, dispersal potential, host range, and both direct and indirect effects. Wright *et al.* (2005) go a step further and suggest the use of probabilistic risk assessment techniques in an attempt to provide objective, quantitative analyses of risks posed to non-target species. The use of probabilistic risk assessment is common in disciplines such as medical research, engineering, and finance (Bailes and Nielsen 2001; Murphy 2001; Serrano 2001) and the procedures are readily adapted for biological control. Implementing probabilistic methods requires an understanding of conditional probabilities associated with discrete behaviors (similar to those listed by van Lenteren *et al.* 2003) as central to determining likelihood and magnitude of effects.

Concerns over the potential impacts of biocontrol agents have recently broadened to include not only direct trophic effects but also competition, displacement, and other more subtle secondary ecological interactions. Although it is extremely difficult to predict the outcome of such relationships based on pre-release quarantine testing, regulators increasingly ask for such data, and practitioners must address the issue in order to obtain release permits. To address both top-down and bottom-up effects, historical and phylogenetic considerations should complement descriptive studies and experiments to provide a comprehensive overview of the organism's role in the ecological community (Messing *et al.* 2005)

The estimation of non-target risk should be placed in context: there are also risks associated with the failure to implement biological control and these must be considered in any overall risk/benefit equation (van Lenteren *et al.* 2003). Invasive species, if left unchecked, can severely impact indigenous plant communities (Follett *et al.* 2003) and even entire ecosystems; the consequences of inaction must therefore be weighed against the estimated risk from biological control agents. Difficult though it may be, decisions must be made with imperfect knowledge.

## Regulatory chaos

The US currently has no comprehensive regulatory framework for importing biological control agents. The nominal controlling agency, USDA-APHIS, has statutory authority to regulate plant pests and a fairly well-defined system to screen herbivorous biocontrol agents of weeds that have the potential to feed on desirable plants. Even for weed control agents, however, the agency admits that "the approval process can be very complicated and difficult to

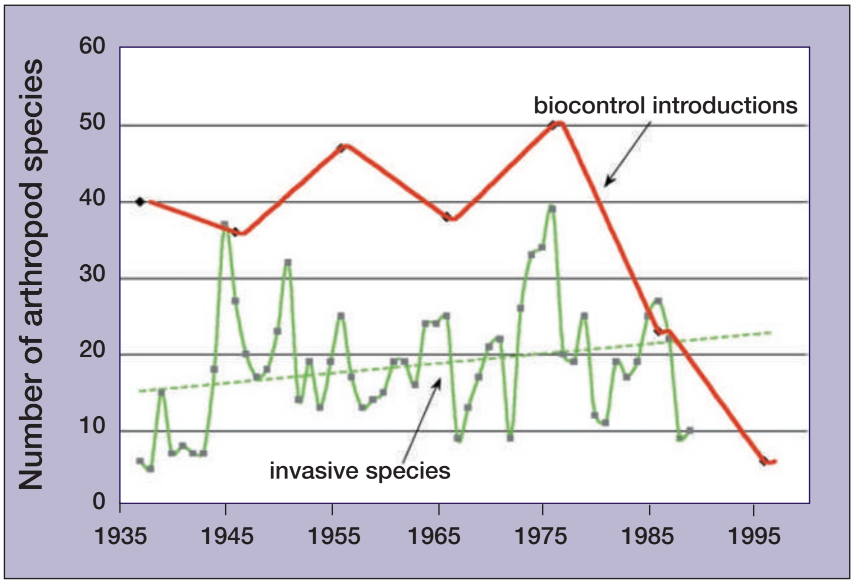



***Figure 7.*** *Introduction of parasitoids into Hawaii for biological control (1900–1998). (Data from Hawaii Dept of Agriculture; biocontrol introductions = 10 year cumulatives.)*

navigate without guidance" (www.aphis.usda.gov/ppq/permits/biological/weedbio.html).

When it comes to arthropods, APHIS has been reluctant to assert its legal authority and implement regulations, because a parasitoid of herbivorous insects is unlikely to be classified as a plant pest. APHIS does, however, issue permits necessary for the introduction of new species from abroad into US quarantine facilities. Before release from quarantine, it requires a second permit, in consultation with state departments of agriculture, the issuance of which depends on evaluation of biological data specified in North American Plant Protection Organization (NAPPO) guidelines. This is a new requirement that has, only within the last year, led to mandatory consultation with counterparts in Canada and Mexico. The National Environmental Policy Act also requires researchers carrying out projects using federal funds to prepare an environmental assessment, while the US Fish and Wildlife Service requests the submission of a biological assessment to satisfy provisions of the Endangered Species Act.

APHIS continues to issue nominal release permits for entomophagous (insectivorous) arthropods, stating that it does not have authority to regulate them. At the same time, it has issued confusing and shifting rule interpretations that leave many biological control practitioners unsettled. It is unclear under what circumstances arthropods can be hand-carried by entomologists across US borders or shipped via licensed freight carriers. It is also not clear whether importations are restricted to certain US entry ports, and whether they must pass through APHIS labs in Maryland for inspection. The ad hoc nature of the federal regulations is at best perplexing, and at its worst inhibits the practice of biological control. The recent division of APHIS into separate Agriculture and Homeland Security divisions has further complicated matters and introduced additional political factors into the permit process as well.

Each state in the US also has its own system to permit biocontrol agents, and state regulations can be more stringent than federal ones. In Hawaii, the uniqueness of flora and fauna and their susceptibility to exploitation have led to the development of a stringent set of rules to control the introduction of beneficial species. While the system is effective at minimizing risk from new importations (Henneman and Memmot 2001), it has become so convoluted and bureaucratic that it hinders, rather than facilitates, timely responses to invasive pest species (Messing 2001). Legal oversight and repeated delays lead to higher costs of conducting biocontrol programs, loss of promising species in quarantine, and reduced funding and support. These burdensome regulations are one of the main factors contributing to a drastic decline in biocontrol introductions in Hawaii over the past 20 years, while the number of introductions of invasive pests keeps rising (Figure 7). There is little doubt that the inefficient regulatory system impedes the ability of entomologists to respond to aggressive new invasive pests, such as the recently discovered *Erythrina* gall wasp, which is threatening both economically important and endemic plant species.

In contrast to the disorganized US system, both Australia and New Zealand have clearly defined and well-integrated regulatory systems for the introduction of both arthropod and weed biocontrol agents (McFayden 1998; Barratt *et al.* 2000). The enabling legislation in both countries was passed in response to a need that is now widely recognized throughout the world; the guiding principles are clearly laid out in documents such as the United Nations Food and Agriculture Organization's Code of Conduct for the import and release of exotic biological control agents (UN-FAO 1997). For both countries, a precautionary approach underlies a process that is based largely upon a risk-cost-benefit (RCB) analysis (Harrison *et al.* 2004). While New Zealand tends to be more risk averse and Australia more risk tolerant, a key issue in both countries involved removing the analysis from an exclusive agricultural purview and instead placing responsibility in whole (New Zealand) or in part (Australia) with a Ministry of the Environment.

Regulatory bodies in the US could contribute substantially to the effective implementation of biocontrol by consulting these guiding principles and harmonizing US regulations with internationally accepted procedures. Although there are obvious differences in physical and economic size, geography, and politics, the Australian and New Zealand regulatory systems could well serve as viable models that, with relatively minor modification, could facilitate a more streamlined and coherent set of protocols in the US.

## Conclusions

Biological control is an important and at times indispensable tool for the management of invasive pest species, not only in agroecosystems but also in natural areas. The importation of exotic predators, pathogens, parasitoids, and herbivores has, at times, led to undesired non-target side effects, but the overall safety record is particularly good in the years since strict quarantine screening and risk/benefit analyses were introduced.

Hawaii has been at the forefront of the debate about the risks and benefits of biological control. The presence of large numbers of endemic and threatened species led to intense scrutiny of natural enemy importation programs. However, with increasing rates of invasive pest species threatening both agriculture and natural ecosystems throughout the islands, biological control remains a keystone of environmentally conscious pest management programs.

Retrospective studies have led to useful rules of thumb that can act as guideposts for both applied programs and the research that supports them. There is broad agreement that a great deal more data are needed in order to make non-target risk analyses more predictive. While a few general principles are beginning to emerge, life histories of arthropods are so diverse and their relationships so idiosyncratic that detailed case-by-case studies will still be needed for most future introductions. Biocontrol introductions are a form of "planned invasion", and detailed follow-up studies can teach us a great deal about invasion biology. A federal regulatory framework should be established that is efficient, rational, transparent, accountable, and ecologically meaningful.

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