

Risks of biological control for conservation purposes

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Abstract Striking successes in classical biological control in agriculture and rangelands engender great interest in using this technology for wildlands conservation and environmental purposes. However, well known unintended consequences of several biological control projects have led to concern that possible environmental benefits do not warrant inherent risks. Four risks demand attention: (1) direct attack on non-targets; (2) indirect effects on non-targets; (3) dispersal of a biocontrol agent to a new area, either autonomously or with deliberate or inadvertent human assistance; (4) changed relationships between a control agent and a native species, particularly as generated by global climate change. Procedures for assessing risk of direct attack on non-targets by phytophagous biological control agents have steadily improved and an expanded centrifugal phylogenetic approach appears to provide adequate insight. Direct non-target impacts by entomophages are more difficult to predict. Myriad possible indirect effects, some subtle but nonetheless important, present a far greater challenge, and techniques of assessing such risks are in their earliest infancy and not as closely regulated. Despite prominent examples in both the general invasion literature

and that for biological control, the risk that a species, once introduced, will spread beyond its intended range, and the consequences of such spread, are not routinely treated by risk assessors. This phenomenon deserves far more attention. Global changes—especially climate change—can lead to modified ranges and efficacies of introduced biological control agents and their targets. Although many examples show that climatic niches are often not conserved, an important first routine step would be to combine climatic envelopes with general circulation models for predicted future climates. Finally, actions based on a risk assessment are always implemented in a framework of predicted costs and benefits, which are inevitably asymmetric, so it is critically important that all stakeholders, including conservationists, participate in the decision-making process.

Keywords Climate change · Dispersal · Ecosystem impact · Indirect effect · Non-target host · Risk assessment

Introduction

The impetus for the growth of classical biological control to deal with introduced species arose from famous successful campaigns in the United States in the late 19th and early 20th centuries aimed at eliminating pests of agriculture or ranching. For

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instance, cottony cushion scale (*Icerya purchasi*) was controlled on citrus in California by the Australian vedalia ladybeetle, *Rodolia cardinalis* (Caltagirone and Doutt 1989), and *Chrysolina* beetles from Australia suppressed Klamath weed (*Hypericum perforatum*), which was poisoning cattle and sheep in California (Huffaker and Kennett 1959). Striking successes such as these, in which seemingly intractable, expensive problems were solved in perpetuity and with minor cost, were subsequently matched by other successful projects, some of which achieved international recognition—for example, control of pest *Opuntia* cactus species in Australia by the South American cactus moth *Cactoblastis cactorum* (Dodd 1940). It is primarily this record of successful projects in the service of agriculture and ranching that earned the technology a reputation as a “green” alternative to chemical pesticides, particularly as the various non-target impacts of the latter were heralded by Rachel Carson in *Silent Spring* (1962) and by many in the environmental movement triggered by that book.

However, there were early biocontrol debacles as well. The small Indian mongoose (*Herpestes auro-punctatus*), introduced in 1872 primarily for rat control from the vicinity of Calcutta to Jamaica, then carried from Jamaica to other islands in the West Indies (occasionally to control snakes as well as rats) and to Hawaii, and independently from Asia to a number of other islands around the world, has combined with introduced rats and cats to cause several extinctions of endemic mammal and bird species and subspecies and threatens a number of other taxa (Hays and Conant 2007). Beginning in 1955, the rosy wolf snail, *Euglandina rosea* was introduced widely, first from Florida to Hawaii, then to various island groups primarily in the Pacific, to control the previously introduced giant African snail *Lissachatina fulica*. *Euglandina rosea* has globally extinguished over 50 island endemic snail species, such as species of *Partula* in French Polynesia and *Achatinella* in Hawaii (Civeyrel and Simberloff 1998; Cowie 2002, 2011). Both the mongoose and the rosy wolf snail are regarded by the World Conservation Union (IUCN) as among the 100 worst global invaders (Lowe et al. 2001), as are at least five other species introduced for biological control: the flatworm *Platydemus manokwari*, the cane toad (*Rhinella marinus*), the western mosquitofish (*Gambusia affinis*), the Indian myna (*Acridotheres tristis*), and the stoat (*Mustela erminea*).

These two projects were old ones, the snail, the mongoose, and four of the five other “worst” invaders (all but the myna) are generalized predators, and they are not insects. A common response among modern practitioners of biological control is that such projects would not be undertaken today, as the dangers of such non-target impacts are well recognized by professional entomologists, and generalized feeders are shunned (e.g., Murphy and Evans 2009). Nevertheless, some more recent instances of insects introduced for biological control have had troubling non-target impacts. The case of the weevil *Rhinocyllus conicus* is particularly well known (van Driesche et al. 2008). First introduced from France to North America in 1968 by Agriculture Canada to control invasive musk thistle (*Carduus nutans*), then widely distributed in the United States by federal and state agencies, this seed predator attacks at least 22 native species of *Cirsium* in North America, including some species of conservation concern that have been shown to be seed-limited (Louda et al. 1997, 2003; Pemberton 2000), among 88 native species and 29 subspecies and varieties (NatureServe 2010). It is even the primary cause of endangerment of the federally listed Suisun thistle *Cirsium hydrophilum* var. *hydrophilum* (United States Department of the Interior 1997). The project leaders responsible for the initial testing, from Agriculture Canada and the Commonwealth Institute of Biological Control, recognized the possibility of important non-target impacts (Zwölfer and Harris 1971, 1984) but conducted tests on only one native species of *Cirsium* plus five European species introduced to North America and concluded, incorrectly, that the facts that the weevil chose to oviposit and feed on the target musk thistle, that larval mortality was relatively high on the few *Cirsium* tested, and that adults that do mature on these *Cirsium* were smaller than those maturing on *Carduus nutans* meant that impact on non-target species would be minimal (Zwölfer and Harris 1984).

Another increasingly well-known example is that of the multicolored Asian lady beetle *Harmonia axyridis*, a generalist predator of soft-bodied insects. First introduced as a biocontrol agent to North America in 1916, it was frequently released in large numbers in the United States and Canada in the 1980s (Koch et al. 2006; Koch and Galvan 2008). It was widely established in North America by 2000,

although controversy surrounds the source(s) of the established population (Koch and Galvan 2008). The beetle was quickly recognized as having non-target impacts on native insects, including both native coccinellids and phytophagous insects, and also harmed fruit production and became a household pest (Koch and Galvan 2008). It has recently spread to South America and northwest Europe, and its introduction for biological control is now widely regarded as a mistake (Roy and Wajnberg 2008).

Although biocontrol began as a technique for pest control in agriculture and rangelands, it has increasingly been used for ecological or conservation purposes, in some instances generating great benefits. For instance, in Florida, the South American alligatorweed (*Alternanthera phytolaxoides*) has been well controlled by the alligatorweed flea beetle, *Agasicles hygrophila*, plus a moth and a thrips (Center et al. 1997). On the island of St. Helena, a tropical American scale insect (*Orthezia insignis*) had threatened the endemic gumwood tree (*Commidendrum robustum*) but is now controlled by the South American lady beetle *Hyperaspis pantherina* (Booth et al. 2001). The floating fern giant salvinia (*Salvinia molesta*) from Brazil was widely transported as an aquarium plant and escaped to become an invasive pest of waterbodies in many tropical and subtropical countries. The Brazilian weevil *Cyrtobagous salviniae*, first released in Australia in 1980 and subsequently in many other nations (e.g., Papua New Guinea, Sri Lanka) including the United States (Texas and Louisiana), has dramatically suppressed giant salvinia in many locations (Room et al. 1984; Julien et al. 2002).

However, the well-known cases of serious non-target impacts, such as those of *Cactoblastis cactorum* (discussed below) and *Rhinocyllus conicus*, give conservationists and refuge managers much pause and lead them to ask what separates the successes from the disasters, and can risk assessment procedures used to evaluate proposed biocontrol projects be sufficiently well-informed and comprehensive to reduce the probability of such cases to near zero when biological control is employed in wildlands? Barratt et al. (2010) perceived great progress in such risk assessments over the last decade, but they focused only on increased attention to determining host range, improved procedures for host-range testing, and better methods of predicting and assessing population impact rather than simply attack rate.

In fact, at least four types of risks are apparent: (1) direct attack on non-targets; (2) indirect effects on non-targets; (3) dispersal of the biocontrol agent to a new area; (4) changed relationships between a control agent and a native species, including change generated by global climate change.

Direct effects on non-targets

Variants of the centrifugal phylogeny method (Wapshere 1974) have become the modus operandi for biological control of plants. As a safeguard, Wapshere suggested adding several economically important plants to the list, and nowadays often other plants are added based on phytochemical or morphological similarity or other reasonable concerns. The key is to use no-choice tests, because preference alone is not always a good indicator of population impact in the field, which may vary greatly depending on various other factors. Svata Louda and her colleagues showed that two weevils introduced to North America—*Rhinocyllus conicus* introduced primarily for musk thistle (Louda et al. 1997, 2003) and *Larinus planus* introduced for Canada thistle (*Cirsium arvense*) (Louda and O'Brien 2002; Louda et al. 2003)—affect native thistles of some conservation concern in the field even though these are less preferred than the targets in laboratory choice tests. However, with a large enough potential host list and no-choice tests, the centrifugal approach should usually delineate the host range accurately, and an impressive number of plant biological control projects have applied it rigorously. There will be mistakes, of course—some species not on the host test list might turn out to be attacked with subsequent population impact. For thistles, with 88 native *Cirsium* species in North America it is not reasonable to demand a test of all of them for a proposed introduction of a thistle insect, but neither is it acceptable to test just one native species, especially if one suspects that several non-native congeners may be attacked, as in the *Rhinocyllus conicus* example.

For biocontrol candidates for insect control, the centrifugal phylogeny method seems presently insufficient for several reasons (Messing 2001). First, the systematics of many insect groups are not well known, so that arranging a centrifugal array of hosts with increasing phylogenetic distance from the target

would often involve much guesswork. This situation will improve, of course, as modern systematics methods are applied to an increasing number of taxa. Second, some parasitoids attack distantly related hosts that are ecologically similar (see, e.g., Whitfield and Wagner 1988)—for instance, sharing the same host plant. Third, many non-target potential hosts are so poorly studied that we are far from being able to judge whether there is a risk that they could be competent hosts. Even if it should turn out in a specific case that the systematics and other problems of insufficient knowledge are resolved and a suitable host-test list is compiled—following procedures such as those outlined by Kuhlmann et al. (2006)—the difficulty of rearing all those insects is much greater than that of rearing plants on a host test list. For instance, it may include rearing the host plants of all the potential targets. In light of the difficulties of applying a centrifugal phylogeny approach to entomophages, Babendreier et al. (2006) suggest consideration of entirely different approaches, such as studying the habitat-specificity of proposed agents. However, for all the difficulties, centrifugal phylogeny methods still provide valuable information relating to risk, and a more reasoned approach would be to improve them and to supplement them with other procedures as these prove useful.

Aside from the difficulty of testing for potential direct non-target impacts of entomophages, there is the issue of public concern. Plants—even thistles—nowadays engender both public and scientific concern. Of about 6,000 species in the United States designated as at substantial risk of extinction by The Nature Conservancy, about 5,000 are plants (Master et al. 2000). The authors conceded that most insect groups are so poorly studied that they could not even be included in the survey. Surely part of the reason status is so poorly known for most insects is that most of the public does not care about them nearly as much as they do about vertebrates and plants. Except for a few “charismatic” groups, such as lepidopterans, tiger beetles, and odonates, for much of the public insects are, unfortunately, not very interesting. In the United States, whereas host range testing is legally required for proposed phytophagous biocontrol agents, there is no such requirement for entomophages (van Driesche et al. 2008). Of course, insects are also far more diverse than vertebrates and even plants, and their habits and small size make surveys and ecological studies particularly challenging.

Does the difficulty of performing adequate host-testing for entomophagous insects mean that use of such species for biological control should be greatly curtailed? Should more extensive host testing and risk assessment be mandated? Doubtless many conservationists would answer at least the second question in the affirmative. The rigor of such tests will vary. For example, the stakes are sometimes so high that land managers and other affected parties might be inclined to allow a greater risk of attack on non-targets. Two prominent current North American cases bring this issue to the fore: invasions by the hemlock woolly adelgid (*Adelges tsugae*) and the emerald ash borer (*Agrilus planipennis*). In each instance a common and beloved tree species is in the process of quickly becoming “ecologically extirpated” (so scarce as to be unable to fulfill its former ecological role) from a large part of its range. The specter of the near total loss of dominant American chestnut (*Castanea dentata*) in the first half of the twentieth century (Freinkel 2007) hovers over these invasions and considerations of how to respond to them. In each instance, a number of other species are specialized to use either the tree species itself or the habitat created by forests in which the tree species is dominant.

To control the hemlock woolly adelgid, two beetles have been widely released. The coccinellid *Sasijiscymnus tsugae* is known to complete development also on the balsam woolly adelgid (*Adelges piceae*) and pine bark adelgid (*Pineus strobi*), which are introduced pests, and the native Cooley spruce gall adelgid (*Adelges cooleyi*) (Cheah et al. 2004). Perhaps as a testimony to the perceived urgency of the problem, 100,000 of these beetles were released in Connecticut, USA while the species was still undergoing laboratory and field evaluation as a potential biocontrol agent (Cheah and McClure 2000). The derodontid *Laricobius nigrinus* was tested for oviposition on three other adelgids, two aphids, and pine needle scale (*Chionaspis pinifoliae*) and for feeding just on the adelgids. In a nutshell, it ate eggs of all the other prey presented and oviposited on the other adelgids but showed a preference for the hemlock woolly adelgid (except with respect to eating pine bark adelgid eggs), and it completed its life cycle only on hemlock woolly adelgid (Zilahi-Balogh et al. 2002).

Thus, not many host species were tested, but it is unlikely that an army of homopteran-lovers will

complain about the relative dearth of host-testing, particularly with hemlock disappearing rapidly from many forest types. Eastern hemlock (*Tsuga canadensis*) is a dominant tree in parts of the Northeast and forms ecologically distinctive glades in the southern Appalachians, and enormous publicity in the lay press surrounds its decline in the face of adelgid attack. Individual trees can be treated by occasional drenching with insecticidal soaps or horticultural oils, or by injecting the soil or trunk with imidacloprid (Cheah et al. 2004), but these approaches are not feasible in the long term for extensive stands of trees, hence the great attraction of biological control.

Evidence that either of these newly introduced beetles has significantly stemmed the spread and impact of the hemlock woolly adelgid is scant, although Cheah et al. (2004) observe that data from Connecticut show some promise for *Sasijiscymnus tsugae* in particular field conditions. They suggest that substantial control might yet be achieved by a combination of predators and fungi, although they would restrict candidate species to those having a host range limited to that of the hemlock woolly adelgid “or similar pests,” a requirement that was not met in the limited host-testing for *Sasijiscymnus tsugae*. However, the decline of hemlock has been so widely lamented and adelgids are so little loved that such an attempt would not likely be criticized on the grounds of inadequate host-testing.

The situation for the emerald ash borer seems not so clearcut. The emerald ash borer has at least 175 native congeners in the United States (H. Hespeneide, personal communication, 2010) and 624 congeners in Mexico (Hespeneide 1996). Three parasitoids have been widely released. Of nine species of *Agrilus* used in no-choice, host-specificity tests by Yang et al. (2008), *Spathius agrili* attacked three: the emerald ash borer was parasitized significantly more frequently than the other species, but two of the latter suffered parasitism rates of over 25%. In olfactometer tests, leaves and twigs of two ash (*Fraxinus*) species and 12 other plant species were tested against control chambers without plant volatiles. Yang et al. (2008) found the number of wasps selecting each of the ash species over the controls to be highly significant, while two non-ash species were selected against, and no other species showed significant results. However, Yang et al. (2008) used the overly conservative χ^2 test for a simple binomial choice test. The binomial test

shows *Salix babylonica* to be selected over the control at $P < 0.05$ and an additional species (*Euonymus japonica*) selected against at $P < 0.05$. In short, the conclusion of Yang et al. (2008) that the emerald ash borer is attracted only by ash leaves is incorrect, and the fact that percent parasitism of other *Agrilus* species was lower than that of the emerald ash borer does not mean that other species will necessarily be immune to population impact of this parasitoid.

The egg parasitoid *Oobius agrili* was found in no-choice tests to oviposit in three of six native North American species of *Agrilus*, though it preferred the emerald ash borer in choice tests of the latter on ash against the former three species on their respective host plants (Bauer and Liu 2007; Bauer et al. 2008). *Tetrastichus planipennisi* was presented with larvae of eight buprestid species in no-choice tests and rejected all except for the emerald ash borer implanted in ash branches (Liu and Bauer 2007; Bauer et al. 2008).

This case is more worrisome than that of the hemlock woolly adelgid. Ash is a component of 146 distinct plant associations in the United States (as opposed to 225 for hemlock; NatureServe 2010), but it does not dominate vast forest stretches as hemlock does. Further, although at least some native *Agrilus* are considered pests, there are hundreds of native species, and these are buprestids, not aphids and adelgids. Buprestids are prized by collectors, nature photographers, and others as “jewel beetles.” At least two buprestids were even proposed for protection under the United States Endangered Species Act (1973), although these were subsequently taxonomically resolved to belong to more widely distributed species. Many native species of *Agrilus* are rare, or at least rarely seen. If some were to become rarer, or even to disappear, it is not clear that anyone would be able to detect this change, at least for decades. How should the risk of this prospect be weighed against the loss of most ash trees? It is unlikely that any species of *Fraxinus* will be extinguished by the emerald ash borer, though some may become ecologically extinct, as did the American chestnut in the wake of the chestnut blight.

Indirect effects

One of the most prominent developments in recent ecological research is the recognition of the variety

and importance of indirect effects of species on one another and on communities and ecosystems (Strauss 1991; Wootton 1994). The most frequently demonstrated types are apparent competition, trophic cascades, and indirect mutualism, but many other indirect effects occur, some of them highly idiosyncratic and subtle but nonetheless consequential, even at the level of entire ecosystems.

For example, Callaway et al. (1999) have shown that the root moth species *Agapeta zoegana*, introduced for biological control of introduced spotted knapweed (*Centaurea maculosa*) in North America, surprisingly decreased reproduction by native *Festuca idahoensis*. The result was clear, even though the mechanism by which *Agapeta* affects *Festuca* remains undetermined. Callaway et al. (1999) suggest as possibilities the production of secondary metabolites that may be allelopathic, or root exudates that change microbe–plant or plant–plant relations, or simple compensatory growth by the knapweed. This is just one of several surprising findings of indirect effects involving spotted knapweed that may affect entire ecosystems. For instance, spotted knapweed can be facilitated by soil microbes in the presence of native plant species (Callaway et al. 2004), and in certain soils, spotted knapweed increases phosphorus availability to other plants (Thorpe et al. 2006), suggesting that it may facilitate other invaders. Two tephritid gall flies (*Urophora affinis* and *U. quadrifasciata*) introduced to control spotted knapweed, though failing to do so, have established in enormous numbers and have generated a substantial indirect effect by subsidized populations of the deer mouse *Peromyscus maniculatus*, comprising 85% of deer mouse winter diet in knapweed-infected areas and elevating deer mouse populations two- to threefold (Pearson and Callaway 2003; Ortega et al. 2004). The full impact of increased populations of deer mice, a generalist predator, are unknown but could include seed predation of native plants, competition with other small mammals, predation on and competition with insects, and even increased transmission of the hantavirus to humans (Pearson and Callaway 2003).

The problem of indirect ecological effects is a key reason that choice tests do not suffice and no-choice tests are needed. If a target host is attacked by a biocontrol agent but still maintains a substantial population, the target may subsidize the population of the agent, and the result may be a sufficient attack

rate on a non-target to threaten extinction, or at least ecological extinction. This is a classic version of “apparent competition.” and it may well have happened with *Rhinocyllus conicus* introduced for musk thistle control—not only did *Rhinocyllus* attack non-targets, but many populations of musk thistle have remained so large that, even as a preferred host, it subsidizes the weevil population to the extent that it attacks less common native thistles. With the target pest still present in sufficient numbers, the population of an introduced control agent can never reach a homeostatic relationship with a population of the non-target, and the non-target population could decline or even in principle be driven to extinction. Conversely, Karban et al. (1994) showed how apparent competition could aid a biological control effort. Predatory mites (*Metaseiulus occidentalis*) by themselves failed to control Pacific mites (*Tetranychus pacificus*), an economic pest of grapevines. Addition of the folivorous Willamette mite (*Eotetranychus willamettei*), which feeds on grape but is not an economic problem, led to a significant reduction in populations of the Pacific mite and damage caused by them, apparently because the alternate prey allowed for larger predator populations with concomitant increased predation on the target species.

However, apparent competition is but one of several kinds of indirect effects that ecologists are increasingly interested in, and, in invasion biology in general, many of the surprising things that have happened fall under the category of indirect effects. *Rhinocyllus conicus* was likely involved in another indirect effect on a native species—exploitative competition with native picture-wing flies whose populations declined when seeds of their native thistle hosts were consumed by *Rhinocyllus* (Louda et al. 1997, 2003). Trophic cascades, a type of indirect effect, are the goal of any biological project that targets a phytophagous insect to reduce damage to a native plant—for example, the insects released to attack the emerald ash borer and the hemlock woolly adelgid. Holt and Hochberg (2001) listed the main indirect effects generated by chains of concatenated species-on-species interactions as they might arise in biocontrol and explored theoretical implications. Predicting the kinds of indirect effects that might arise from a biological control introduction is vastly more difficult than predicting direct effects on non-targets because of the myriad possible concatenations

of species-on-species interactions, and it is even difficult to imagine straightforward laboratory tests, such as those used in the centrifugal phylogeny method, that would allow acceptably reliable prediction of indirect impacts at the population level. Field tests would also be immeasurably more difficult, though the example of Karban et al. (1994) cited above suggests that such tests might not be impossible if one had some way of picking out particularly likely indirect effects from the huge number of possible ones. Thus risk assessment even of these relatively straightforward indirect effects is in its early infancy (Messing et al. 2006).

However, an entirely different sort of indirect, non-target impact can be even greater and is even harder to predict. This occurs when an introduced species greatly affects ecosystem processes, such as nutrient or fire cycles, or ecosystem physical structure, in turn affecting large fractions of the native species community. As knowledge accrues about the variety, frequency, and subtlety of such impacts (Ehrenfeld 2010; Simberloff 2011), it becomes incumbent to take the possibility of such impacts into account in consideration of biological control introductions, yet assessing risk seems enormously challenging.

Consider, for example, the case of *Morella faya* in Hawaii. This nitrogen-fixing Atlantic shrub has invaded young, nitrogen-poor areas on the volcanic island of Hawaii and is increasing nitrogen concentrations in the soil and canopy (Vitousek 1986; Vitousek et al. 1987; Vitousek and Walker 1989). As Hawaii lacks native nitrogen-fixers, native plant species have evolved adaptations to nitrogen-poor soil. The dominant tree on much of island, the endemic *Metrosideros polymorpha*, is gradually being replaced in many areas by *Morella faya*. Nitrogen and water content of the canopy have doubled where *Morella faya* has replaced native forest (Asner and Vitousek 2005). The ramifications for the entire system have not yet been elaborated, but at least one consequence is that many non-native plant species brought to Hawaii, previously hampered by poor soil nutrients, are now spreading. At least three moth species and two fungal species have been introduced as biological controls, but with little effect on *M. faya* (Smith 2002; Hawaiian Ecosystems at Risk 2010). Two more recent major invaders on Hawaii are the exotic grasses *Melinis minutiflora* and

Schizachyrium condensatum. Because they are fire-prone, they are turning much of Hawaiian dry forest into grasslands (D'Antonio and Vitousek 1992). Substantial discussion about how to control them has not yet, to my knowledge, led to a biocontrol program for either of these species. A potential problem is that *Schizachyrium condensatum* slows the invasion of *Morella faya* by reducing light at the soil surface, thereby reducing germination and early seedling growth of *Morella faya* (D'Antonio and Mack 2001). In addition, just the presence of these two grasses greatly affects nitrogen dynamics, often in ways opposite to the effect of *Morella faya* (Mack et al. 2001; Mack and D'Antonio 2003). Any assessment of the likely impact of a biocontrol agent on either the grasses or *Morella faya* therefore will have to take account of the full impacts of the target species on ecosystems, and this has not been a consideration of risk to non-targets in the past.

Movement to new areas

The spread of *Cactoblastis cactorum* from Nevis through the West Indies to Florida and beyond (Zimmermann et al. 2000) exemplifies a risk that often receives insufficient consideration. The moth was introduced in 1957 to Nevis by the Commonwealth Institute of Biological Control (CIBC) to control pest native *Opuntia*, and CIBC did not account for the possibility of autonomous or unauthorized human-assisted island-hopping (Simmonds and Bennett 1966). It makes little difference whether, as I think is most likely, the moth flew or was blown from Cuba to the Florida Keys, or, as Pemberton (1995) suggests, it arrived in Miami in cut flowers from the Dominican Republic, then somehow reached the Florida Keys, where it was first discovered in the United States. This was a disaster waiting to happen by one means or another once the moth was brought to the West Indies. It similarly spread through the Hawaiian archipelago in seven years once introduced to the island of Hawaii (Tuduri et al. 1971). From Florida, the moth has now spread as far west as Louisiana and north to South Carolina (Marsico et al. 2011). North America not counting Mexico has 68 native species and 54 varieties of *Opuntia*, several of which are imperiled to some degree (NatureServe 2010), and Mexico has many

more. Some of these species are commercially important as food or ornamental plants. Zimmermann et al. (2000) believe that 79 species are at risk as suitable hosts for *C. cactorum*, so non-target impacts of this unintended spread could be substantial.

The release of the chrysomelid beetle *Diorhabda carinulata* to control Asian salt cedar (*Tamarisk* spp.) in the southwestern United States is currently garnering newspaper headlines. Salt cedar, introduced in the early nineteenth century for ornamental purposes, was subsequently deliberately distributed in many areas of the Southwest beginning in the late nineteenth century to control erosion (Chew 2009). By the 1930s, it was recognized as invasive, replacing native plants, using great amounts of water, and even drying up springs (DiTomaso 1998). Major projects to remove salt cedar were launched in the 1950s, but none were very successful, and non-target impacts of chemical and mechanical approaches were substantial (DiTomaso 1998). This state of affairs led in the 1990s to calls to study biological control (DeLoach 1990). The *Diorhabda* beetle was quickly discovered, imported from China and Kazakhstan, tested for host-specificity, and released in 2001 (DeLoach et al. 2007). However, by this time another problem had arisen. Several native bird species, including the southwestern willow flycatcher, *Empidonax traillii*, listed under the U.S. Endangered Species Act, were nesting in salt cedar, and it was feared that destruction of salt cedar by the biocontrol beetle would lead to lowered nesting success. Thus, the U.S. Department of Agriculture (USDA) restricted its releases to sites more than 200 miles from known nests of the flycatcher in salt cedar. However, the USDA lacks jurisdiction over the transport and release of biocontrol insects within a state, and, in the wake of campaigns by Utah and local government agencies to release the beetle more widely, weed control workers from Washington County, Utah, moved *Diorhabda* much further south (Dark 2009; T. Dudley, personal communication, 2010), within range of the flycatcher, leading the USDA to cancel the entire release program (United States Department of Agriculture 2010).

The importance of this case resides not in whether the beetle poses a real threat to the flycatcher. I believe this is unlikely: as salt cedar is replaced by native willow, the flycatcher will likely have ample nesting habitat. Rather, the lesson is that, once a

species is released, there is some probability that it will be transported inadvertently to a new site, or that an individual will simply decide to release it in a rogue introduction, legal or not. Such actions have occurred with other introductions, such as the northern snakehead, *Channa argus*, in Maryland (Orrell and Weigt 2005), and species being tested or locally released for biological control are not immune from such activities. For instance, rabbit calicivirus (RCD), undergoing testing as a biocontrol for the European rabbit (*Oryctolagus cuniculus*) on Wardang Island off the coast of South Australia, mysteriously appeared on nearby coastal mainland Australia as well as hundreds of kilometers inland (Mead et al. 1996). In 1997 it was illegally introduced to New Zealand and deliberately spread by farmers (New Zealand Parliamentary Commissioner for the Environment 1998).

To me, the focus on host range, though essential, does not seem nearly matched by attention to the possibility of dispersal. Once a species is well established, propagule pressure generated by natural reproduction and dispersal, or inadvertent or deliberate transport by humans, can sometimes take it to distant sites, and the extent and risk of such dispersal, especially the latter type, will be extremely difficult to quantify and predict. Possibly this is why it has drawn insufficient attention in formal risk assessments.

Changed relationships and climate change

The problem of predicting geographic range change becomes more urgent in the face of climate change. Prediction of ranges of newly introduced species and spread of previously established introduced species is a major growth area of invasion biology, with climatic envelope and various other sorts of models being combined with general circulation models of global climate change (Guisan and Thuiller 2005; Fitzpatrick et al. 2007; Bradley et al. 2010). Although much of the early literature is based on a claim that physical niches are highly conserved (e.g., Peterson et al. 1999), several recent examples show that the niche of introduced species in fact often changes substantially and quickly (e.g., Broennimann et al. 2007; Fitzpatrick et al. 2007; Loo et al. 2007; Broennimann and Guisan 2008; Beaumont et al. 2009; Rödder and Lötters 2009; Medley 2010). Many

such studies predict dramatic geographic range shifts, and an abundance of evidence already exists for geographic range shifts in many native species that are best explained by climate change (Parmesan 2006). Similarly, many phenological shifts associated with anthropogenic climate change have also now been documented in both animals and plants (Parmesan 2006), and such shifts can dramatically change relationships between biological control agents, their targets, and non-target species. One might even expect that insects, because of their great fecundity and short generation times, might be particularly prone to rapid niche evolution under the influence of natural selection. Thomson et al. (2010) discuss several implications of climate change for natural enemies of agricultural pests, and many similar issues arise with respect to biocontrol for conservation purposes.

One can ask about effects on both efficacy and non-target impacts of biocontrol introductions in the light of anticipated climate change. Most obviously, will the geographic range of a biocontrol agent shift so as to overlap that of a potential non-target host species whose geographic range it would not be expected to reach under current climatic conditions? Or will the geographic range of some non-target host change and bring it in contact with the expected geographic range of the biocontrol agent? Several studies on potential biocontrol agents, especially phytophagous insects to attack pest plants, begin with an examination of which native congeners of the target weed co-occur with the target. An exemplary study by Pemberton (1984) mapped the distribution of North American spurge species to determine if any of them would likely be threatened by phytophages introduced to control leafy spurge (*Euphorbia esula*). This meticulous project looked not only for overlap of ranges of rare native spurges with leafy spurge but even at whether a rare spurge allopatric with leafy spurge could be threatened by sympatry with another spurge, sympatric with leafy spurge, that might act as a “bridge species.” But if either an insect or a plant species is predicted to shift its geographic range by 1000 km over a fairly short time, how predictive will such examinations of current geographic ranges really be?

Moreover, this is just one of several sorts of changes in interactions between a species and its natural enemy that could be produced by climate

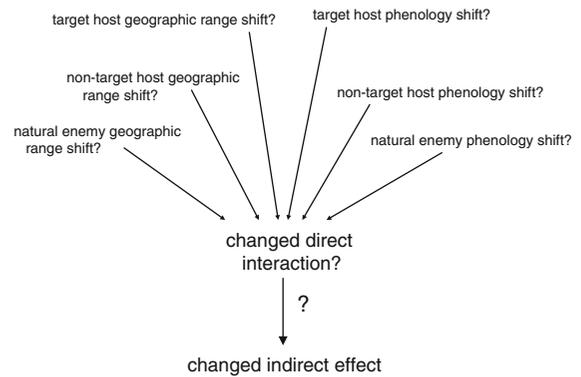


Fig. 1 Some possible changes in geographic range and phenology of biological control agents and potential hosts, with potential subsequent impacts

change (Fig. 1). For example, the life cycles of a host and its parasitoid could be desynchronized because of a climatic shift (Goldson 2007), as was shown elegantly with the native Glanville fritillary (*Melitaea cinxia*) and its native braconid parasitoid *Cotesia melitaeorum* in Finland (van Nouhuys and Lei 2004). In cooler temperatures, the wasp cocoons develop so slowly that adults emerge after host caterpillars have pupated and are no longer available. One can easily imagine an asynchronous relationship becoming synchronous or vice versa as climate changes. In fact, many phytophagous insects are restricted to only part of the geographic range of their host plants, and for at least some of these, experiments show that this range restriction is because of some sort of developmental asynchrony. A good example is use by the psyllid *Cacopsylla moscovita* of creeping willow, *Salix repens* (Hill and Hodkinson 1992). Of course, as climate change generates asynchrony one might expect natural selection to counteract this effect, but the degree to which this happens and the rate of evolution of synchrony are not predictable at present.

It is not only increased temperature that could drastically effect interactions between biocontrol insects and targets. For instance, increased carbon dioxide generally leads to decreased leaf nitrogen and increased leaf phenolics (Bezemer and Jones 1998). What effect will these changes have on the interactions of phytophagous biocontrol agents with their target host or with non-targets?

These changes in range and in phenology might facilitate biological control. For example, as noted above, the alligatorweed flea beetle controls alligatorweed

in Florida. However, it cannot tolerate the colder weather further north, where the plant is still a substantial nuisance. Climate change may well allow the beetle to spread northward. Of course, alligatorweed itself might spread further north also. I am not suggesting that, on balance, global climate change and the associated increase in CO₂ will create more problems for biological control than they will solve. Rather, the important point is that global change is not routinely taken into account in biological control risk assessments and that it could lead to greatly changed ecological impacts in many ways. For instance, Rafter et al. (2008), seeking to prioritize areas for exploration of biocontrol agents of cat's claw creeper (*Macfadyena unguis-cati*) in Latin America and release in Australia and South Africa, used CLIMEX software (Sutherst et al. 2004) to match climates in the current native and introduced ranges but not the predicted ones. Dhileepan et al. (2010) subsequently examined the thermal tolerance of one such potential agent, *Carvalhotingis visenda*, to determine its potential distribution in Australia while considering only current temperature regimes and extremes.

It would be unreasonable for conservationists to demand that risk assessments for biological control—or indeed for any species introduction—account for every aspect of predicted global climate change and associated changes. The entire field of global change ecology is not nearly sophisticated enough yet to support such an effort (cf. Buisson et al. 2010). However, at least the general circulation models should be employed much more frequently, just as some invasion biologists are using them.

Discussion

Much progress has been made in assessing certain types of risks associated with biological control, particularly non-target impacts of herbivores (Barratt et al. 2010). Similarly, the realization that attack, even substantial rates of attack, need not imply a population impact on either targets or non-targets is increasingly understood and population impact addressed in risk assessment (Barratt et al. 2010). However, it remains difficult to assess a variety of risks, and the range of concerns associated with biological control for conservation would be expected

to exceed that associated with biological control in agroecosystems. Difficulties of host-range testing for entomophages are widely acknowledged in the biological control community, but improvements have been slow and incremental at best. These efforts should be accelerated and could include increased systematic work and improved methods of insect-rearing associated with enhanced centrifugal phylogeny methods. Although recognition of the possibility of indirect effects in biological control followed quite quickly on the heels of the explosion of interest in such effects in the ecological literature, the variety and complexity of possible indirect effects are probably still not well grasped. Useful estimates of risks of certain kinds of indirect effects, particularly those involving trophic interactions, can perhaps be derived. It is interesting that scientists attempting eradication for conservation purposes have raised this issue to a greater extent than biological control scientists (see, e.g., Zavaleta 2002), and they have even conducted simple risk assessments of simple indirect effects for particular projects (e.g., Courchamps et al. 1999; Caut et al. 2007).

Risks associated with dispersal and range shift are not routinely accounted for, at least in formal risk assessments. Rogue introduction of a biocontrol agent is probably intractable to model, at least to model fruitfully. Likelihood of inadvertent introduction by hitchhiking on cargo is probably more tractable. Invasion biologists, especially those working in the marine and aquatic literatures, have had some success associating invasion rates with shipping routes and other correlates of volume of movement of goods: numbers of nursery catalogs and other indications of horticultural activity (Mulvaney 2001), area and dates of plantings (Krivánek et al. 2006), aquarium trade figures (Semmens et al. 2004), boat and shipping traffic (Schneider et al. 1998; Colautti et al. 2003; Semmens et al. 2004). Range shifts associated with climate change could be profitably assessed by linking general circulation models to climatic envelope or other range prediction models that are already employed by both invasion biologists and biological control scientists. However, the likelihood of impacts associated with phenological shifts, and perhaps even the nature of such shifts, would currently be extremely difficult to predict.

Finally, a worry among conservation biologists regards the linkage of risk assessment with cost-benefit

analysis for introduced species in general and biological control introductions in particular. Basing decisions on risk makes sense only in the context of cost (van Lenteren et al. 2003; Bigler and K lliker-Ott 2006). Thus, even if one accepted the validity of a particular risk assessment, any decision based on that risk assessment will rest on the value judgments with respect to cost and benefit of whoever is making the decision. Many costs that concern conservationists cannot be transformed satisfactorily into monetary costs, in spite of the best efforts of many economists (Simberloff 1992; Simberloff and Stiling 1996), and benefits and costs of species introductions, including those for biological control, are unequally shared by different stakeholders (Simberloff 2005). Further, entities charged with determining costs and benefits in the context of risk assessment do not routinely contain conservationists and conservation biologists. Until this community is represented at the highest level in decision-making with respect to biological control for conservation purposes, the suspicion will linger that the interests of nature are not being best served.

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