Papers in Ecology

Papers in the Biological Sciences

2003

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Nontarget Effects—The Achilles' Heel of Biological Control? Retrospective Analyses to Reduce Risk Associated with Biocontrol Introductions[*]

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Key Words classical biological control, ecological risk, weed control, insect control

■ **Abstract** Controversy exists over ecological risks in classical biological control. We reviewed 10 projects with quantitative data on nontarget effects. Ten patterns emerged: (*a*) Relatives of the pest are most likely to be attacked; (*b*) host-specificity testing defines physiological host range, but not ecological range; (*c*) prediction of ecological consequences requires population data; (*d*) level of impact varied, often in relation to environmental conditions; (*e*) information on magnitude of nontarget impact is sparse; (*f*) attack on rare native species can accelerate their decline; (*g*) nontarget effects can be indirect; (*h*) agents disperse from agroecosystems; (*i*) whole assemblages of species can be perturbed; and (*j*) no evidence on adaptation is available in these cases. The review leads to six recommendations: Avoid using generalists or adventive species; expand host-specificity testing; incorporate more ecological information; consider ecological risk in target selection; prioritize agents; and pursue genetic data on adaptation. We conclude that retrospective analyses suggest clear ways to further increase future safety of biocontrol.

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INTRODUCTION

The risks to native species associated with classical biological control, the introduction of exotic natural enemies to control alien pest species, have been debated (36, 38, 70, 71, 73, 114, 115, 122–124, 129). The issue is not new (1, 60, 61, 96, 97, 111, 113, 125). However, the debate has intensified in light of increasing evidence of nontarget host use by biocontrol agents. In this review we examined 10 cases in detail. These cases were reviewed because nontarget impacts were quantified. They do not constitute a random sample, and so do not estimate the frequency of nontarget effects. Our aims are to summarize the data available, evaluate the patterns, and define further research needed. Our premise is that such retrospective analysis can provide important information on traits associated with environmental risk and suggest protocols or research that would continue to increase the safety of biological control.

Debate over nontarget effects of biocontrol agents has polarized biologists. On the one hand, many practitioners view biological control as a progressive, environmentally benign alternative to chemicals (62, 80, 124). When successful, biological control leads to long-term reduction in pest numbers, potential for wideranging control, elimination of chemical residues, and a low economic cost/benefit ratio. On the other hand, many ecologists view the intentional introductions of alien species into complex biological communities as a threat to their structure and dynamics. Major concerns include the irreversibility of introductions, potential for host switching, dispersal into nonagricultural habitats, lack of research on both efficacy and ecological impacts, possibility of evolutionary adaptation to new hosts, and difficulty of predicting interaction outcomes in complex systems (60, 61, 71–74, 77, 97, 108, 111, 112, 114, 122, 123). In fact, traits viewed as advantageous in biocontrol, such as capacity for self-replication, rapid increase, and high dispersal,

are also traits that enhance the probability of unexpected ecological effects when native species are within the potential host range.

As invasive species proliferate and pressure to control them grows, the need to understand the ecological effects of biological control increases. Environmental protection laws in many countries restrict the introduction of exotic species into natural ecosystems unless there is evidence that such introduction will not have adverse effects on those systems (6, 7, 86). Adverse effects on native species, representing a continuum from small effects to extinctions (31, 37), must be quantified to be evaluated. Thus, there is a real need for increased scientific attention toward the measurement and prediction of impacts on target and nontarget species.

CASE HISTORIES IN BIOLOGICAL CONTROL OF WEEDS

Biological control of weeds has a long recorded history, starting with redistribution in 1832 of *Dactylopius* scales to control weedy prickly pear cacti in South Africa (66). Since then, 153 insects have been released in the continental United States and Hawai'i against 53 target weeds (66). Estimates of success for these weed control projects vary from 41% with evidence of some control (93) to 20% with significant control (136). Nontarget feeding, oviposition, and development are reported on 41 native plants, by 15 of the 112 biocontrol insects (13.4%) established against weeds in Hawai'i, the continental United States, and the Caribbean (99). Plants closely related to the targeted weed were more vulnerable than distantly related species (99). However, neither the quantity of feeding nor the ecological ramifications have been studied in most cases. We review the three cases for which the most quantitative data exist.

Rhinocyllus conicus Against Exotic Thistles

INTRODUCTION   The flower head weevil, *R. conicus* (Curculionidae), indigenous in Eurasia, has been released in Argentina, Australia, New Zealand, and North America against weedy thistles (Asteraceae, Carduinae), especially *Carduus nutans* (41, 141). In the United States, it was redistributed freely until August 2000, when the USDA APHIS Plant Protection and Quarantine removed *R. conicus* from the list of insects preapproved for interstate movement into new areas (T. Horner, personal communication).

EVALUATION   In the field in Europe, hosts included 7 out of 9 *Carduus* spp. (77.8%), 4 out of 17 *Cirsium* spp. (23.5%), plus *Silybum marianum* and *Onopordum acanthium* (141). In the laboratory, no-choice feeding tests found that adults did not feed on cultivated non-Astereae but accepted 12 of 16 European thistles. Leaves of the one North American species tested (*Cirsium undulatum*) were accepted inconsistently. In choice tests, *R. conicus* adults preferred leaves of *C. nutans* over 9 of 11 other thistles (141). Adult oviposition and larval development of *R. conicus* were evaluated in a no-choice cage test using four European

species (*Carduus nutans*, *C. personata*; *Cirsium arvense*, *C. palustre*) but no North American species. All four species received eggs and supported complete development; however, adults emerging from the *Cirsium* spp. were 10% smaller than their parents from *C. nutans*. Although these data suggested nontarget effects could occur, no major impacts were expected because of (*a*) generally lower preference for *Cirsium* spp. than for *Carduus nutans*, (*b*) higher larval mortality and smaller adult size on *Cirsium* spp. than on *Carduus* spp., and (*c*) low population densities of the North American *Cirsium* spp. (141). Side effects, if any, on native thistles were even considered a bonus by some ranchers (D. Schröder, personal communication).

NONTARGET EFFECTS   Use of North American *Cirsium* spp. by *R. conicus* was reported soon after its introduction in 1969. Rees (102) found *R. conicus* developing on *C. undulatum*. Earlier, Maw [reported in (141)] found it developing on *C. flodmanii*. Goeden & Ricker [(42) and references therein] and Turner et al. (126) reported *R. conicus* developed in the flower heads of 17 California *Cirsium* spp. (57% of species sampled), including 3 rare ones. Unexpectedly, weevils from some nontarget *Cirsium* spp. were larger than those from *Carduus* spp. (126). By 2001, *R. conicus* was reported using 22 of the 90+ North American *Cirsium* spp. (99). By 1993, *R. conicus* invaded sand prairie sites in Nebraska where it adopted two well-studied native thistles as hosts in the absence of exotic thistles (68, 70, 74, 77). Prior experiments had shown that native floral insects limited seed, seedlings, population density, and lifetime fitness of one of these, Platte thistle (*Cirsium canescens*) (76). By 1996, the addition of *R. conicus* to the inflorescence guild further reduced seed production by 85.9% (74, 77). The density of Platte thistle in demography plots then declined dramatically (72). In addition, the simultaneous decrease in a native floral-feeding tephritid, *Paracantha culta*, suggested *R. conicus* also may have major indirect ecological effects (73, 74, 77). These outcomes are consistent with the recent theoretical prediction that "shared predation modules" present an indirect risk to nontarget species and their fauna, even at sites away from the area of control (57). The availability of long-term data on interacting populations prior to host range expansion of *R. conicus* onto North American thistles provides unique documentation for ecological aspects of nontarget effects.

IMPLICATIONS   This case illustrates the early lack of concern over potential nontarget effects on noneconomic native species. Additionally, although the host range expansion onto North American thistles is consistent with the host-specificity tests, those tests did not pinpoint the risk to secondary hosts in the absence of the preferred host. Clearly, low native plant densities and lack of habitat overlap with targeted hosts were not sufficient to prevent harm. The influence of variation in availability of the preferred host and potential indirect effects were not evaluated. Finally, as expected, the introduced insect was not restricted to the release sites, but in this case *R. conicus* dispersed into a remote native habitat without the targeted weed.

Larinus planus Against Canada Thistle

INTRODUCTION   This European thistle weevil was first found in the northeast United States in 1971 in fields where *Altica carduorum* (Chrysomelidae) was released against Canada thistle, *Cirsium arvense* (135). In spite of contemporary tests in 1990, which showed that native thistles could be acceptable though less preferred (= "secondary") hosts (82), *L. planus* was distributed by state and federal agencies into six western states and British Columbia in 1990–2000 (75).

EVALUATION   In the 1960s, six species of *Larinus*, including *L. planus* (= *L. carolinae*), were screened as potential biocontrol agents (140). All six European *Cirsium* spp. offered to *L. planus* were acceptable food plants. No North American species were tested. Because *Larinus* spp. had greater diet breadth than *R. conicus*, no official introductions were made into North America. After *L. planus* was found in the northeast United States, it was re-evaluated using contemporary protocols as a prerequisite to deliberate release in Canada (82). Adult preference and larval performance were tested on agronomic plants and native thistles (*Cirsium andrewsii*, *C. flodmanii*, *C. foliosum*, *C. hookerianum*, *C. undulatum*). The average amount of adult feeding in no-choice and choice tests appeared lower on native thistles than on Canada thistle (82), but was not significantly different (75). In no-choice oviposition tests, *Cirsium drummondii* received no eggs in a small test ($n = 4$ female-days), but both *C. flodmanii* and *C. undulatum* were ovipositional and developmental hosts in larger tests (82). However, no emergence of new adults occurred from these native species under the test conditions. McClay (82) concluded in 1990 that *L. planus* was "unlikely to form significant populations on them [native North American thistles]" and that "the redistribution of *L. planus* to Alberta, and other areas of North America where *C. arvense* is a problem, should be considered."

NONTARGET EFFECTS   This weevil was released in the 1990s on state and federal lands in Colorado, a state with many native *Cirsium* spp. (131), at least two of which are considered rare. In 1999, *L. planus* was found feeding on a uncommon native species, Tracy's thistle (*C. undulatum* var. *tracyi*), in western Colorado. A subsequent study found that 75% of the main seed-producing flower heads were destroyed by *L. planus* (75). At the same time, this agent had no effect on Canada thistle nearby (5.2% total seed damaged, with no evidence of *L. planus*). In 2001, *L. planus* also was reared from the flower heads of three native thistles collected in Oregon: *Cirsium brevistylum*, *C. remotifolium*, and *C. undulatum* (128). Apparently, *L. planus* was discovered in Oregon in 1993 and, subsequently, limited redistribution and introduction occurred [(75); E.M. Coombs, personal communication]. Oregon releases have stopped (E.M. Coombs, personal communication).

IMPLICATIONS   This case demonstrates that redistribution of an adventive exotic species for biological control can have undesirable effects. Release into new,

geographically disjunct ecosystems occurred in spite of evidence that native species were acceptable feeding, ovipositional, and possibly developmental hosts. Contemporary host-specificity tests were not sufficient to predict relative use among acceptable hosts in the field. Because permits for interstate transport and release of *L. planus* apparently were issued without formal evaluation by the main scientific advisory group for biological control introductions (USDA, APHIS, Technical Advisory Group), the case suggests that more oversight of movement of adventive exotic species for biological control is warranted.

Cactoblastis cactorum Against *Opuntia* spp. (Prickly Pear)

INTRODUCTION   This Argentine pyralid moth, now used worldwide (66), was introduced first into Australia in 1926 and quickly controlled exotic *Opuntia* spp. (23). *Cactoblastis cactorum* was introduced to Nevis Island in the Caribbean in 1957 against weedy native *Opuntia* spp. (116). By 1960, densities of one native shrub (*O. triancantha*) and several "tall" *Opuntia* spp. were lower (116). This moth is now widespread in the Caribbean, including the Bahamas and Cuba (8); the magnitude of its ecological impact there still needs to be evaluated. Introduction of *C. cactorum* into the continental United States was considered in the 1960s; no release was made out of concern both for economic prickly pears in Mexico (F.J. Bennett, personal communication) and for potential effects on *Opuntia* spp. forage and wildlife support functions (62). The issue arose again in the 1980s, by inclusion of *Opuntia* spp. on a list of rangeland weeds for control (97). Such targeting of native plants for biological control was challenged because both their ecological and economic functions could be irreversibly impaired by the spread of agents beyond areas in which the plants were pests (97).

EVALUATION   Field studies of cactus-feeding insect herbivores in the Western Hemisphere identified host associations (23). *C. cactorum* completed development on all prickly pears, except one (*O. sulphurea*). One exception to the pattern of narrow host specificity defined by genus was a species of *Cleistocactus*, in a different subfamily (Cactoideae) than *Opuntia* (Opuntiioideae), on which feeding but no development was observed (23). No-choice starvation tests indicated that *C. cactorum* could feed but did not develop on plants other than cacti. Potential conservation effects were not considered at the time of introduction into the Caribbean nor studied afterward (F.J. Bennett, personal communication). Retrospective tests of host specificity with six native Florida *Opuntia* spp. indicated that all of these species support complete development (64).

NONTARGET EFFECTS   In 1989, *C. cactorum* was discovered in Florida (8), where it now develops on five of six *Opuntia* spp. (64). Up to 90% of *O. stricta* studied were damaged by *C. cactorum*, and 15% of the monitored plants died (65). The adoption of Florida's *Opuntia* spp. is not surprising because the moth uses almost all *Opuntia* spp. within its native range (23). As with many accidental introductions, how

C. cactorum reached Florida is unclear (98, 139). The quantitative effect of *C. cactorum* on nontarget cacti is unknown. Given its dramatic impact on native *Opuntia* spp. on Nevis Island (116), it is likely that some Caribbean species have been damaged seriously, some possibly driven close to extinction on Nevis and Grand Cayman Islands (8). In Florida, restoration of *Opuntia corallicola* (= *O. spinosissima*), an endemic species already reduced by habitat loss, is hindered by infestation by *C. cactorum* (64). *O. stricta*, one of the cacti under *C. cactorum* control in Australia, is native to Florida and is a common host. Additionally, *O. stricta* occurs all around the Gulf of Mexico, so this plant could serve as a bridge for *C. cactorum* to expand its range, potentially threatening the large complex of native *Opuntia* spp. in the southwestern United States and Mexico (100, 139). By 1999, the moth had spread to southern Georgia (121). Indirect effects of *C. cactorum* on other species also are unknown. Some Caribbean iguanid lizards use *Opuntia* spp. for food (121), and a variety of native insects are associated with *Opuntia* spp. A native moth, *Melitara dentata* (Pyralidae), limited the growth and density of *O. fragilis*, a native of sand prairie in the upper Great Plains (14), suggesting the spread of *C. cactorum* could disrupt such limiting interactions between native *Opuntia* spp. and their associated insects.

IMPLICATIONS   Relatively specialized feeders, such as *C. cactorum*, can still pose an ecological threat. Use of this moth against prickly pear cacti in parts of the world with no native *Opuntia* spp. has caused no known nontarget effects. Yet, use of this moth led to damage of native *Opuntia* spp. in the Caribbean, in close proximity to continental areas with many more native relatives. Thus, the same agent can be either relatively safe or relatively dangerous, depending on geographic region, ecosystem, and number of native relatives in the flora.

CASE HISTORIES IN BIOLOGICAL CONTROL OF INSECTS

Since the 1888 introduction of the vedalia beetle against cottony-cushion scale in California, more than 5000 releases of insects for classical biological control have been documented (49, 79). Establishment frequency is estimated to be 34%–50% (49, 50). Successful control of targeted insects resulted in 3% of introductions, and an additional 11% resulted in partial control (78). Use of native nontarget species has been recorded for 7% of 59 predators and 10% of 115 parasitoids introduced for insect control in Hawai'i (39) and for 16% of 313 parasitoids of holometabolous pests in North America (54). Worldwide, a recent review (79) identified 92 cases (1.7%) of introductions for which nontarget effects were reported. Effects in most cases were minor or minimally documented, but 18 introductions had evidence of significant negative impacts on nontarget populations. Because nontarget feeding by agents for insect biocontrol is greatly under-reported, Lynch & Thomas (79) further estimated that as many as 11% of past introductions for insect biocontrol

may have had serious nontarget effects. We review the seven cases that have received the most detailed quantitative study.

Microctonus spp. Against Forage Weevils in New Zealand

INTRODUCTION   Two braconid parasitoids have been introduced into New Zealand for control of pest weevils on forage. *Microctonus aethiopoides* was released in 1982 against *Sitona discoides* in alfalfa (lucerne), and *M. hyperodae* was released in 1991 against *Listronotus bonariensis* in pasture (6, 7, 43, 44).

EVALUATION   *M. aethiopoides* was released after minimal host testing (7). At the time, it was thought to attack only two genera, *Sitona* and *Hypera* (67). Conversely, extensive host specificity and suitability tests were conducted with *M. hyperodae* before release (43). Of the 24 weevil species tested, 4 native species were physiologically suitable hosts, but the potential nontarget hosts produced only 18.7% as many parasitoids compared to the target. A native minor pest, *Irenimus aequalis*, was the best nontarget host. Earlier, under field conditions in Western Patagonia, *M. hyperodae* was found attacking only *L. bonariensis* and not its three coexisting congeners (67).

NONTARGET EFFECTS   Retrospective analysis was initiated to determine the ability of laboratory host range testing to predict field host range (6). In laboratory tests, *M. aethiopoides* had a broader host range, attacking 12 of 13 species compared to 7 of 30 species attacked by *M. hyperodae*. Among the species attacked by *M. aethiopoides*, mean parasitism was 58% for nontarget species and 62% for targeted species compared to 13% in nontarget species and 61% in targeted species attacked by *M. hyperodae* (5). Cresswell (18) showed that in the laboratory *M. aethiopoides* can complete successive generations on the native weevil *Nicaeana cervina*, and female wasps that first oviposited on *N. cervina* selected this species over the targeted host, *S. discoides*, for subsequent ovipositions. In the field, *M. aethiopoides* parasitized 16 of 48 species of weevils, whereas *M. hyperodae* parasitized only 3. Species attacked by *M. aethiopoides* included four indigenous and four exotic weevil genera, including the thistle biocontrol agent *R. conicus*. Average parasitism among attacked nontarget species was higher by *M. aethiopoides* than by *M. hyperodae* (23% versus 2%), and *M. aethiopoides* attacked nontarget species at more sites (17 versus 2 of 33 sites) [(6); B.I.P. Barratt, personal communication]. In a survey of *M. aethiopoides* parasitism along an elevational gradient, average parasitism of native weevils (Brachycerinae) by *M. aethiopoides* was 64% in alfalfa (450 m), 23% in surrounding pastoral habitats, 4%–10% in overgrown native grasslands (620–780 m), and 2% in a subalpine habitat (850 m) (B.I.P. Barratt, personal communication). Thus, *M. aethiopoides* showed relatively broad host range, and it parasitized multiple nontarget species outside the target host environment, although at lower rates. *M. hyperodae* demonstrated a higher

level of specificity, as predicted, and it parasitized multiple nontarget species only in the target's environment.

IMPLICATIONS   The case shows that prerelease laboratory host-specificity tests can be useful in predicting postrelease specificity in the field ("realized host range"). Also, the introduced biocontrol agents are not restricted to the habitat of the target species where they were released; rather they invaded remote native habitats. Finally, environmental gradients can provide spatial refuges that dampen the impact of the biocontrol agent on some nontarget species, such as in natural habitats at higher elevation.

Introduced Parasitoids Against Tephritid Fruit Flies in Hawai'i

INTRODUCTION   Between 1913 and 1950, over 30 parasitoids were introduced into Hawai'i for control of three exotic pest fruit flies (*Ceratitis capitata*, *Bactrocera dorsalis*, *B. curcurbitae*) (10, 133). Six opiine braconids and a eulophid (*Tetrastichus giffardianus*) became widely established and contributed to pest suppression. For example, the braconid *Fopius arisanus* killed over 90% of oriental fruit fly (*B. dorsalis*) eggs in guava, *Psidium guajava* (88).

EVALUATION   At the time of introduction, host-acceptance tests were conducted with the targeted species, but not with the 33 other tephritids in Hawai'i (26). The other tephritids are gall makers and flower head feeders and include 26 endemic species as well as 5 intentionally and 2 inadvertently introduced weed control agents.

NONTARGET EFFECTS   Nontarget risk to endemic tephritids in Hawai'i was assessed recently. When several introduced fruit fly parasitoids were exposed in cages to flower heads of *Dubautia menziesii* containing the endemic fly *Trupanea dubautiae*, little ovipositional activity occurred (24, 27, 28). In another test, *Diachasmimorpha tryoni* wasps probed galls containing lantana gall fly (*Eutreta xanthochaeta*) less than they probed coffee berries containing *C. capitata*, although learning modified this response (25). In the field, the parasitoid *D. longicaudata*, attracted to decaying fruit infested with fruit fly larvae, visited more nontarget stem galls when decaying fruit was absent (26). In small cages *D. longicaudata* parasitized 54% of the *E. xanthochaeta* larvae in stem galls, whereas in large field cages and in the field <1% of fly larvae in galls were attacked (26). In field surveys, no deliberately introduced parasitoids were recovered from native tephritids (29). However, the adventive opiine braconid *Habrocytus elevatus* as well as the eulophid *Euderus metallicus* were found attacking weed agents (lantana gall fly; Eupatorium gall fly, *Procecidochares utilis*) and native *Trupanea* spp.; *H. elevatus* also was found attacking an adventive tephritid used in weed biocontrol, *Ensina sonchii* (24, 29). A detailed budget of population losses of lantana gall fly

(*E. xanthochaeta*) larvae was conducted to assess the role of fruit fly parasitoids in its population dynamics by using the recruitment method to quantify mortality (30). *D. tryoni* accounted for >86% of total parasitism but caused only a 10% increase in total mortality. Percentage parasitism by *D. tryoni* varied significantly among habitats.

IMPLICATIONS   These studies highlight the importance of microhabitat selection by parasitoids and, therefore, the importance of ecologically relevant host-specificity tests. The difference in vulnerability between gall-forming and flower head-feeding fruit fly species suggests that host testing should include ecologically distinct groups of potential nontarget species. It is also clear that the outcome of host-specificity tests can be influenced strongly by the test conditions (cage size, choice versus no-choice options, starvation, physiological age). Because learning can play a role in host range adaptation in insect parasitoids, simple evaluations of host and habitat preference may underestimate the magnitude of risk to the less preferred native hosts from attack by introduced natural enemies. Finally, detailed life table analysis can play an important part in impact assessment.

Compsilura concinnata Against Gypsy Moth

INTRODUCTION   Beginning in 1906, this tachinid fly, a polyphagous parasitoid of Lepidoptera, was introduced into North America against the gypsy moth (*Lymantria dispar*) and the browntail moth (*Euproctis chrysorrhoea*). *L. dispar* is univoltine, whereas *Compsilura concinnata* is multivoltine. Despite knowledge that this parasitoid depended upon nontarget species to complete multiple generations per year and despite early documentation of nontarget attack on native insects, *C. concinnata* was released repeatedly until 1986 (11, 19, 104, 130).

EVALUATION   *C. concinnata* was poorly studied in Europe before its importation, but it was known to be polyphagous, gregarious, multivoltine, and highly vagile (19).

NONTARGET EFFECTS   The ability of *C. concinnata* to utilize a wide range of species, including over 200 spp. of Lepidoptera and Hymenoptera, became clear soon after initial release (3, 19, 130). However, this polyphagy was considered a bonus, allowing the parasitoid to spread ahead of the gypsy moth and perhaps slow its invasion (130). In 1915, the USDA initiated a 15-year program to determine the native hosts of the introduced parasitoids (104). Over 300,000 field-collected lepidopteran larvae were reared to survey parasitoids. For the macrolepidopterans that were well sampled (n = 164 spp.), 66.9% of the species were attacked by *C. concinnata*. Also, *C. concinnata* was present in 79.6% of the 93 macrolepidopteran species collected >9 years, and in 91.5% of the 59 species that were collected >9 years and had total collections of >200 larvae. Giant silkworm moths (Saturniidae) were among those attacked (104). In fact, the range caterpillar

Hemileuca oliviae, a native saturniid pest of grazing lands in the southwestern United States, was a target of some releases. In the 1950s, some saturniid populations in the northeastern United States appeared to undergo a massive, rapid decline (106). Although populations of most species occupy their precrash range again, reported densities are thought to be lower (106). Three species (*H. maia maia*, *Eacles imperialis*, *Anisota stigma*) have been placed on several state endangered species lists (11), and two *Citheronia* spp. apparently have been extirpated in the northeastern United States (106).

Boettner et al. (11) argued that parasitism by *C. concinnata* likely contributed significantly to the decline in native silk moths. Earlier, Stamp & Bowers (119) suggested that *C. concinnata* could be an important mortality factor for *H. lucina*. Using laboratory-reared cohorts placed as sentinel larvae, Boettner et al. (11) found that *C. concinnata* caused 81% mortality in *Hyalophora cecropia* and 67.5% in *Callosamia promethea* in Massachusetts. In addition, *C. concinnata* was reared from 36% of wild-collected *H. maia maia* (11). Levels of parasitism actually may be higher because these studies did not include late instars. However, other factors also could be involved in the declines, including habitat loss (127), successional change (120), and aerial spraying of *Bacillus thuringiensis* for gypsy moth control (51). In sum, the evidence is clear that *C. concinnata* is a persistent and substantial source of mortality for native Lepidoptera in the northeastern United States, and the recent evidence suggests it could be seriously harming some species. However, further research is needed to quantify nontarget population impacts and to explain mechanisms underlying the persistence of *H. cecropia*, *C. promethea*, and *H. maia maia* populations even after 95 years of nontarget attack by *C. concinnata*. Compensatory and persistence mechanisms for the populations sustaining high levels of parasitism are not known but could include low rates of added mortality from parasitism, life history strategies (127), and the presence of refuges (132).

IMPLICATIONS   This case history shows that polyphagy, combined with multivoltinism and high vagility, represents a risky set of traits for a prospective biocontrol agent in terms of potential for nontarget effects. It also suggests that nontarget effects can continue over time, in this case almost 100 years. With generalists such as *C. concinnata*, there is no opportunity for density-dependent mechanisms to reduce its population level when a specific prey species becomes rare because it can maintain its population on other prey species. This trait, considered advantageous initially, increases the potential for detrimental effects on nontarget species, particularly less common species whose populations can be swamped by large numbers of the biocontrol agent.

Parasitoids Against *Nezara viridula* in Hawai'i

INTRODUCTION   The polyphagous crop pest *Nezara viridula* (Pentatomidae) invaded Hawai'i in 1961 (20). Following unsuccessful attempts at eradication, biocontrol agents used previously in Australia were introduced. Three agents were

established by 1963: the egg parasitoid *Trissolcus basalis* (Scelionidae) and two adult parasitoids, *Trichopoda pilipes* and *T. pennipes* (Tachinidae) (20). Declines in native Hawaiian stink bugs, including the koa bug (*Coleotichus blackburniae*: Scutelleridae), have been attributed to the introduction of these parasitoids (61).

EVALUATION   Laboratory tests and field observations around the time of introduction showed that both the tachinids and the egg parasitoid could locate and develop on *C. blackburniae* (20). Recent studies showed that *T. basalis*, maintained on *N. viridula* in the laboratory, accepted eggs of *N. viridula* and *C. blackburniae* equally in choice and no-choice tests, independent of arena size (M.T. Johnson, unpublished data). Behavioral observations in petri dishes suggested that *T. basalis* used cues for host acceptance similarly in both hosts. However, *C. blackburniae* appeared to be less suitable because many parasitized eggs died without developing parasitoids (M.T. Johnson, unpublished data).

NONTARGET EFFECTS   Examination of museum specimens collected between 1965 and 1995 for attached *Trichopoda* egg shells revealed attacks on *N. viridula* (17%, $n = 302$ specimens), *C. blackburniae* (8%, $n = 107$), and three alien pentatomids, but not on native pentatomids in the genus *Oechalia* ($n = 96$) (37). The low numbers and the haphazard nature of such collections limit these data as a precise historical record of population impacts (37). A recent two-year field study confirmed that *T. basalis* and *T. pilipes* attacked *C. blackburniae* on all four islands surveyed (M.T. Johnson, unpublished data). Parasitism of *C. blackburniae* eggs and sentinel *N. viridula* eggs occurred at levels up to 20% at low elevations on an alien host plant (*Acacia confusa*), but parasitism was low (0%–2%) at higher elevations on the koa bug's two native host plants (*A. koa*, *Dodonaea viscosa*). Contemporary life table analyses indicate that accidentally introduced natural enemies now have a greater impact on *C. blackburniae* populations than do biocontrol agents (M.T. Johnson, unpublished data). The most common egg parasitoid found was an accidentally introduced eupelmid, *Anastatus* sp., not *T. basalis*. Also, egg predation by other accidentally introduced species, primarily ants and the spider *Cheiracanthium mordax*, was a more important source of mortality (10%–80%) than parasitism (M.T. Johnson, unpublished data). Parasitism of adult *C. blackburniae* by *T. pilipes* averaged 7% across sites on Hawai'i, with the highest levels (25%–42%) observed on native host plants ≥ 10 km away from any agricultural areas, levels comparable to those for *N. viridula* adults in agricultural areas. It is not known whether *T. pilipes* persists on *C. blackburniae* at these remote sites or migrates from areas where *N. viridula* is abundant. Although *T. pilipes* uses the male aggregation pheromone in host finding (52), large proportions of *C. blackburniae* females (up to 37%) and fifth instars (up to 26%) were sometimes parasitized. The impact of tachinid parasitism on population growth is potentially more severe for *C. blackburniae* than for *N. viridula* because *C. blackburniae* females produce smaller egg masses (32 versus 70 eggs per mass) and have slower ovarial development (M.T. Johnson & A. Taylor, unpublished data).

IMPLICATIONS   This case illustrates the value of life table analysis in impact assessment. Evaluation of nontarget impacts 30 years after release, however, is difficult because the relative contribution of various mortality sources may have changed. Generalist predators now cause the highest mortality to *C. blackburniae* in all habitats on Hawai'i, but at least one introduced biocontrol agent appears to have a significant impact on populations in one native habitat. Most of the evidence for population decline in *C. blackburniae* to date comes from Oahu, where displacement of native host plants and invasions by alien generalist predators also could be involved in the decline of native insects (37). Because biocontrol agents were shown to attack *C. blackburniae* in the laboratory at the time of introduction, this case study confirms the validity of prerelease testing of native species to predict potential nontarget hosts.

Parasitoids Against *Pieris rapae* in New England

INTRODUCTION   *Pieris rapae*, a pest of crucifers, invaded North America (Canada) from Europe in 1860 (16). The braconid parasitoid, *Cotesia glomerata*, was released against *P. rapae* in the 1880s, although it may have arrived earlier in parasitized hosts (107). *P. napi oleracea*, a native species in northeastern United States and eastern Canada, underwent a range reduction in the late 1800s (107, 109). A recent field study attempted to determine if parasitoids played a role in this decline (R.G. Van Driesche, personal communication).

EVALUATION   Potential nontarget effects of *C. glomerata*, and other parasitoids introduced against *P. rapae* in the United States, on native pierids such as *P. napi* were not evaluated prior to release.

NONTARGET EFFECTS   Artificially placed (sentinel) larvae of *P. napi* and *P. rapae* were used to examine parasitism by *C. glomerata* and another introduced wasp (*C. rubecula*) in Vermont, where *P. napi* persists, and in western Massachusetts, where *P. napi* is now rare or extinct (J. Benson et al., unpublished data). *P. napi* overwinters as a pupa and spends its first generation on *Cardamine* (=*Dentaria*) *diphylla* in wooded habitats and subsequent generations in open fields, whereas *P. rapae* inhabits open fields exclusively. *Cotesia* parasitoids attacked sentinel larvae of both *Pieris* spp. more frequently in fields than in forests; attack by *C. glomerata* was more frequent on *P. napi* than on *P. rapae* when both species were presented in fields (J. Benson et al., unpublished data). Because parasitism rates were similar in Vermont and western Massachusetts, they hypothesized that differences in host diapause and life history accounted for differences in the impact of added parasitism. If the *P. napi* population in Vermont commits a greater percentage of its first generation woodland population to overwintering diapause than does the population in western Massachusetts, then this allocation may buffer the effects in Vermont of heavy second-generation mortality imposed by the acquired parasitoid in open meadows in both locales. Sentinel larvae (*P. rapae*, *P. napi*)

also were used to evaluate the role of *C. glomerata* in the range contraction of another native pierid, *P. virginiensis*, in New York and Ontario (9). Even though both *C. glomerata* and *C. rubecula* parasitize and successfully develop in *P. virginiensis* in the laboratory, no parasitism was detected on sentinel larvae on two host plants, *Brassica oleracea* or *C. diphylla*, within the woodland habitat of *P. virginiensis* (9), suggesting parasitism is not a likely explanation of the observed range contraction.

IMPLICATIONS   Parasitoid foraging behavior and host life history variation in this case appear to have influenced the effect of the introduced parasitoids on native, nontarget species. *Cotesia* parasitoids do not forage in closed woodland, so this habitat provides the strictly woodland species, *P. virginiensis*, with an absolute refuge even though it is an acceptable host in the laboratory. Similarly, woodland provides the first generation of *P. napi* a refuge from parasitism. However, the second generation of *P. napi* suffers significant mortality when it attempts to reproduce in open areas where *Cotesia* parasitoids are active. If life history variation occurs in the portion of the host population so exposed, then the outcome of the added mortality may vary over the range of the nontarget host species, as appears likely for *P. napi*. This case underscores the need for information about agent foraging behavior and host life history variation to supplement physiological host range data.

Coccinella septempunctata (C7) Against Aphids in North America

INTRODUCTION   Roughly 150,000 ladybird beetles of the Palearctic species *Coccinella septempunctata* (C7) were released on aphids in crops in 12 states and Nova Scotia from 1957 to 1971 (103). Despite this effort, establishment of C7 probably occurred accidentally in 1973 in New Jersey and Quebec (2, 21). Over 500,000 beetles were redistributed in 1974–1978 from New Jersey to 20 states (2, 103). Distribution efforts expanded to western states, especially after the 1986 invasion by the Russian wheat aphid, *Diuraphis noxia* (45, 101). Meanwhile, C7 populations increased dramatically in the eastern and central United States (89, 103), fueling concern over possible competitive displacement of native coccinellids (33). Federal programs have stopped dispersing alien coccinellids, but private efforts likely continue (63).

EVALUATION   Early programs paid little attention to potential impacts on nontarget species (123). In the Russian wheat aphid program, prerelease studies were skipped in the interest of responding rapidly to the economic threat (101). Yet, coccinellids were perhaps the least promising agents because their foraging effectiveness is limited by the Russian wheat aphid's habit of feeding within tightly curled leaves (137). Recent studies of nontarget effects of alien coccinellids have focused almost entirely on possible impacts on native coccinellids in agricultural

systems (90). Although impacts on other coccinellids were not predicted explicitly, they are not surprising in light of C7's dominant role among aphidophagous coccinellids in Europe (2, 56). Numerical superiority of C7 in North America was expected to improve pest control (21). Although some coccinellids are broadly polyphagous, C7 population dynamics correlate closely with aphid prey (56). However, Horn (59) argued that C7 could threaten an endangered butterfly in Ohio because it was found in the same habitat and fed on eggs of a congener in the laboratory.

NONTARGET EFFECTS Field evidence for displacement of native coccinellids by C7 is correlative. By the 1990s, C7 had become the dominant coccinellid in a variety of habitats in the United States (2, 13, 45, 87, 134). One of the most severe declines coinciding with a rise of C7 appears to have occurred for *C. novemnotata* in the Northeast. A common species historically, *C. novemnotata* was collected infrequently from 1973–1985 as C7 spread, and only five times after 1985 in spite of extensive searches (134). In eastern South Dakota, populations of two native species (*Adalia bipunctata*, *C. transversoguttata*) declined from historical levels as C7 invaded, but other species appeared unaffected (32). Population growth of C7 did not increase overall coccinellid densities, which suggests that aphid control did not increase (32, 90). Because *A. bipunctata* is better adapted to woodland, negative impacts of C7 on this species are likely to be limited to areas with little forest cover; impacts of C7 on *C. transversoguttata* are more likely to be regional because of broad overlap in habitat and ecological traits (90). Arrival of C7 did not appear to increase competition for prey among coccinellids in Utah because adult body sizes of five native species did not decline (34). Interaction between larvae of C7 and the native *Coleomegilla maculata* in laboratory arenas led to lower survival of *C. maculata*, but only at low prey densities, reflecting either competition for prey or intraguild predation (92). In contrast, no negative interactions were detected between these species in field cages (91). The possibility of indirect impacts by C7 on other biological control agents was investigated in alfalfa (35). Adding C7 to caged field plots reduced numbers of alfalfa weevil larvae slightly, but it also greatly decreased parasitism of the weevil by an introduced ichneumonid parasitoid.

IMPLICATIONS This case study illustrates potential consequences of using predators with relatively broad diets. In addition to C7, five other alien coccinellids established in the United States raise similar concerns over nontarget effects (21). For example, *Harmonia axyridis* can displace competitors, including C7, from some habitats (13, 17). Gaps in knowledge of coccinellid ecology greatly limit our ability to predict the outcome of such complex interactions (90). Ongoing coccinellid invasions present opportunities to measure effects before and after agents arrive in new areas (17). The lack of published studies of nontarget impacts of introduced coccinellids on noneconomic insect species suggests another important avenue for future research.

Parasitoid Infiltration of a Native Food Web in Hawai'i

INTRODUCTION   At least 84 parasitoids of lepidopteran pests have been released in Hawai'i, and 32 became established (39, 53). These parasitoids have been suspected of having severe impacts on native moth populations (40, 138). Although targeted pests were concentrated in agricultural areas at lower elevations (<1000 m), naturalists have worried that biocontrol agents may invade native habitats at higher elevation (60). Henneman & Memmott (55) recently advocated and used a novel food web approach to quantify the penetration of exotic parasitoids, including biological control agents, into the lepidopteran assemblage in a remote native Hawaiian forest.

EVALUATION   Most biocontrol parasitoids against lepidopteran pests in Hawai'i (61 out of 84 species) were released prior to 1960 (53), and they were not screened for host specificity (39). At the time, broad host range was considered advantageous in a parasitoid because it allowed attack on multiple pests and persistence on alternative hosts when targeted pests were rare. Since 1960, the trend in Hawai'i has been to release more specialized parasitoids (39).

NONTARGET EFFECTS   In the high, remote Alaka'i Swamp (1200 m elevation) on the island of Kaua'i, Henneman & Memmott (55) collected leaf-feeding caterpillars from all plant species in two replicate 0.5 ha plots in the native forest over two summer seasons. Moths or parasitoids were reared to adulthood and identified. The collections ($n = 2112$ larvae) contained 58 moth species (93% native) from 60 plant species (85% native). Out of 216 individual parasitoids reared, 83% belonged to one of three species of biocontrol agents, 14% were accidental immigrants (five spp.), and only 3% were native (five spp.). Two braconid parasitoids (*Meteorus laphygmae*, *Cotesia marginiventris*), introduced for biological control in 1942, dominated the guild. They were reared from several native moth species in six and three families. A third biocontrol agent (*Eriborus sinicus*: Ichneumonidae) was reared from three native tortricoid species. Although several of these collections represent new host records, all three agents were known to attack native Lepidoptera (39). Overall, parasitism based on the emergence of adult parasitoids was approximately 10% each year, but parasitism by biocontrol agents reached 28% in some native species. Attack rate on geometrids, determined by dissecting larvae, was 22.6%, nearly twice the 11.6% alien parasitoid emergence rate (M.L. Henneman, personal communication). The potential also exists for indirect effects, via competition with native parasitoids. The native parasitoids were rare. Four species were reared only once from native hosts (M.L. Henneman, personal communication). However, two of five species shared their lepidopteran host species with a biocontrol agent, and three of five shared their host with an accidentally introduced parasitoid (55).

IMPLICATIONS   This study provides some support for the hypothesis that introduced biocontrol agents contributed to the reduction of native Lepidoptera in

Hawai'i, while documenting agent spread from targeted agricultural habitats into native habitats at higher elevations. The measured rates of parasitism (10% average, up to 28%) may substantially underestimate nontarget impacts because some parasitoids killed their host but died before emerging (55). The population effect of these parasitism rates is unknown. The data are insufficient to determine impact on a species-by-species basis. Furthermore, interaction intensities may have changed since the time of introduction and dispersal. Finally, this case demonstrates the insights on community-level impacts of biological control agents available from a food web approach.

EMERGENT PATTERNS

Although the available data are insufficient for a quantitative meta-analysis of specific hypotheses, some clear consistencies emerged from our comparative review of the most intensively quantified cases of nontarget effects reported in weed and insect biocontrol.

1. **Native species most closely related to the targeted species are most likely to be attacked.** Nontarget feeding among our case histories in weed biocontrol was confined to plants in the same tribe or genus as the targeted weed, supporting previous findings (99). Among our case histories in insect biocontrol, nontarget attack occurred over a broader taxonomic range, from subfamily to order (Table 1). A contributing factor is that host specificity and restricted host range have not been the norm until recently in insect biocontrol. Relatedness to a target nevertheless appeared to be a good indicator of potential risk to nontarget insects in most cases. For example, host-specificity tests of weevil parasitoids (*Microctonus* spp.) in New Zealand were consistent at the subfamily level with host utilization realized in the field.

2. **Host-specificity testing determines physiological host range but not ecological range.** Ecologists have been concerned about the power of prerelease evaluations of host specificity to predict nontarget effects (4, 61, 114, 121). Our review supports the current paradigm that field surveys of hosts in the native range plus host-specificity tests provide crucial information on physiological host range, particularly when related native species are included in the testing protocol (Table 1). However, lack of complete larval development on natives (82), considered definitive evidence that the probability of ecological impact is low (81, 83, 108), fell short of predicting host use and impact of *L. planus* in the field (75). Evaluation of larval development necessarily reflects the conditions under which it is done; and, in the case of *L. planus*, test conditions apparently did not simulate field environmental conditions that subsequently allowed complete development of *L. planus* on a native host plant. However, in the case of *P. virginiensis*, while host-specificity tests indicated inclusion in the physiological range of *Cotesia* spp., nonoverlapping habitat use by the native butterfly and the introduced parasitoids

TABLE 1 Synthesis of patterns and information across case histories

Characteristic	Weed control projects			Insect control projects						
	Rhinocyllus	Larinus	Cactoblastis	Microctonus	Tephritids	Compsilura	Nezara	Pieris	Coccinella (C7)	HI Foodweb
Control of target: s = substantial, p = partial, n = negligible	p	n	s	p	p	p	p	p	n	p
Evidence of population-level nontarget effects	x	x	x			x	x		x	x
Host-specificity testing										
Prerelease	x	x	x	x						
Concurrent with releases	x					x	x			
In retrospect	x	x	x	x	x	x	x	x		
Not done									x	x
Native species included in prerelease tests										
Tested intensively		x (late)								
Some/partial testing	x	x (early)		x						
Indirect effects potential also evaluated										
Results of host-specificity tests with native species										
No evidence of acceptance of native species					x					
Small amount of acceptance (no-choice only)				x						
Significant acceptance (choice test use too)	x	x					x	x		
Evidence of larval development on native	x	x	x	x			x	x		x

	tribe	tribe	genus	subfam.	family	2 orders	superfam.	family	class	suborder
Evidence of nontarget feeding/attack:										
Consistent with natural history in native range	x	x	x	x	x	x	x	x	x	x
Consistent with host-specificity data	x	x	x	x	x	x	x		x	
Relative amount/impact greater than expected	x	x						x	x	
No-choice test informative on nontarget use	x	x	x	x	x	x	x			
Ecological factors in nontarget host use										
Habitat not restricted to agronomic release habitat	x	x	x	x	x	x	x		x	x
Attack or impact varies with habitat	x	x		x			x	x	x	
Elevational refuge from attack for some species	x	x	x	x	x	x	x			
Phenological synchrony of agent and nontarget	x	x	x	x				x		
Degree of relatedness of nontarget to target	tribe	tribe	genus	subfam.	family	2 orders	superfam.	family	class	suborder
Low host density did not prevent attack	x	x	x	x	x	x				x
Diet breadth:										
Stenophagous (one genus)			x					x (C.r.)		
Oligophagous (multiple genera in one family)	x	x		x	x	x				
Polyphagous (multiple families, or more)				x	x	x		x (C.g.)	x	x

reduced ecological risk. The case histories illustrate that a variety of factors can influence field host use (Table 1): phenological synchrony (*R. conicus*, *L. planus*), host and agent dispersal (*R. conicus*, stink bug parasitoids, pierid parasitoids), habitat type (*Microctonus* spp., pierid parasitoids), life history variation (pierids), and learning (tephritid parasitoids). Thus, although host-specificity tests in general accurately identified potential host range, insect preference based on those tests failed to predict the magnitude of nontarget risk to native host species in the field.

3. **Prediction of ecological consequences of nontarget attack requires more types of studies.** The case histories suggest that quantification of potential nontarget risk will require better information for agents on the determinants of (*a*) host finding and choice, (*b*) dispersal and dispersal limitation, (*c*) use of alternate host resources in the field, (*d*) insect population growth and stability, (*e*) insect impact on plant population growth and density, and (*f*) environmental effects on the intensity of the interactions. Host finding and host choice often were influenced by environmental conditions that determined the strength of actual versus potential interactions. Information on the conditions under which alternative hosts are used would provide important information relevant for prediction of potential nontarget use in the field. For example for *L. planus*, the earlier flowering phenology of Tracy's thistle, compared to its targeted Canada thistle, at high elevation in Colorado apparently overrode any preference for Canada thistle because the availability of Tracy's thistle flower heads was synchronized better with the weevil's oviposition period. A lack of synchrony in flowering with *R. conicus*'s oviposition periods also may help explain why many native North American *Cirsium* thistles are not significant hosts of the weevil (100). Degree of overlap of host and parasitoid populations helps explain differences in *Cotesia* spp. effects on native pierids (9). More data on the ecological parameters influencing host use and insect population growth, for example from the indigenous region, should provide a stronger basis for evaluation of the probability of major nontarget impacts on native species accepted as secondary hosts in testing. Currently, estimation of this probability largely depends on expert opinion.

4. **Documented impacts on nontarget species vary from negligible to devastating.** The cases we reviewed, those with the most quantitative data, illustrate the range of effects discovered to date. In some cases, the impacts appear minimal, occurring at levels that suggest no effect on host densities in the long run. For example, fruit fly parasitoids intentionally introduced into Hawai'i appear to be insignificant sources of mortality for the native tephritid *T. dubautiae*. On the other hand, impacts on nontargets can be severe, depressing populations of sparse regional plant species (*R. conicus* on Platte thistle) or enhancing extinction risk of a rare species (*C. cactorum* on *O. corallicola* in Florida). Major impacts were associated with redistribution of inadvertently established insects (e.g., *L. planus* for Canada thistle control). Some studies (*R. conicus* on thistles, *Compsilura* on silk moths)

measured attacks on nontarget species reaching levels that could cause long-term population declines and even extirpation from local communities. The only case with quantitative preinvasion data (*R. conicus*) demonstrates that such interactions can cause a severe decline in a native population within its characteristic habitat. In general, however, nontarget effects have been evaluated only after the fact or measured over too short a period to confidently predict the outcomes over time. Long-term monitoring and life table analyses may improve our assessment of the consequences of nontarget use. However, studies conducted decades after introduction, e.g., Hawaiian parasitoids in native forest, will not provide evidence of severe population dynamic effects if those effects occurred near the onset of the invasion into native systems.

5. **Data on magnitude of nontarget impact is sparse.** Use of nontarget species by introduced biocontrol organisms is not by itself evidence of an adverse impact upon a host population. We found that nontarget feeding clearly added to mortality for nontarget insects and decreased growth or reproductive success of nontarget plants. In most cases, however, few of the studies included data with which to estimate the magnitude of the effect of the documented nontarget attack on the population density and growth rate of the native species. A clear exception was the *R. conicus* case, where "before" and "after" data on Platte thistle's vital rates allow estimation of the impact on population parameters. Other cases suggested that life table analyses provide important information with which to initiate assessment of population consequences, e.g., parasitoid impact on the koa bug or on native pierid butterflies. The cases also suggest that population response data are needed to anticipate the quantitative effects of feeding in the field when there is laboratory evidence that native species are within the potential host range (41). Population response data include population growth rates, substitutability among mortality factors, spatial scale of population interactions, variation of life history strategies, compensatory responses, and facultative increases in reproductive rates. Methods by which such information can be acquired include carefully designed experiments in large field cages in which host plant phenology and other environmentally driven traits are varied experimentally, quantitative studies of variable host plant use and impact in the indigenous region (110), and demographic modeling, such as that used in retrospective studies of the tephritid parasitoids in Hawai'i. These data could be used to prioritize candidate agents by maximal likely effectiveness as well as minimal nontarget risk.

6. **Nontarget attack on rare native species can accelerate their decline and enhance their risk of extinction.** High population levels developed by biological control agents may lead to unexpected pressure on uncommon nontarget hosts. Theory indicates that a natural enemy that maintains a high population on its targeted host can extirpate its less common nontarget host species (12, 58). The cases of *Cactoblastis cactorum* and tachinid parasitoids of *Nezara viridula* suggest the potential for this kind of interaction. This risk

is expected to increase if a biocontrol agent causes only a minor reduction in the fitness of its target because then both target and agent can persist at relatively high levels while putting pressure on a rarer nontarget species (94). As an example, *Larinus planus*, which is not a narrow specialist among thistles, is having a minor impact on its targeted host but a major impact on seed production of Tracy's thistle (75). These results support the theoretical arguments for choosing narrow specialists with high virulence against their target as biocontrol agents and rejecting those expected to have relatively minor impacts (84, 85).

7. **Nontarget effects of biocontrol species can be indirect, as well as direct, via food webs and cross-linkages.** Indirect effects are those mediated through effects on another species, such as by competitive resource depletion and by shared hosts or natural enemies. A recent example is the indirect effect of *Urophora* spp., released for knapweed control; it appears to alter plant competitive hierarchies (15), while also augmenting deer mouse populations that subsequently affect the native vegetation (95). Host-specificity testing is designed to detect direct interactions, leaving other less obvious effects to go unevaluated. Some of the case histories demonstrate or suggest ripple effects via indirect interactions. For example, behavior and numbers of the native tephritid fly (*Paracantha culta*), which depends on Platte thistle flower heads in its first generation in sand prairie, have been affected by *R. conicus* [(72); S.M. Louda et al., unpublished data]. Among the insect cases, the effect of exotic introduced coccinellids on native species provides an example of potential indirect effects via competition for shared aphid resources as well as potential direct effects via intraguild predation.

8. **Biocontrol agents can infiltrate natural areas away from targeted agro-ecosystems.** The case studies legitimize the concern of conservation biologists over the ability of biocontrol agents to disperse into native habitats. The study of Henneman & Memmott (55) provides a clear example of the extent of such penetration in a remote native habitat by introduced parasitoids. Similarly, the cases of *R. conicus* on Platte thistle, *C. cactorum* on the rare *O. corallicola*, *M. aethiopoides* on weevils, and *T. pilipes* on koa bug illustrate that biocontrol agents are able to disperse, locate, and reproduce on nontarget hosts at considerable distances from concentrations of their targeted host. Estimation of likely natural dispersal, for example based on habitat range within the indigenous environment, would improve assessment of ecological risk of biological control.

9. **Biocontrol agents have the potential to perturb whole guilds and assemblages of nontarget organisms.** Among our case studies, the most obvious mechanism for community impact appears to be extreme polyphagy. For example, *C. concinnata* in the northeastern United States and generalist parasitoids in Hawai'i are implicated in declines in nontarget lepidopteran populations. Also, the *R. conicus* case demonstrates effects on the feeding

guild into which it penetrated. In most cases, however, without better data on food webs and population sizes prior to nontarget use, the magnitude of the perturbation for interconnected species remains unknown. The *C. cactorum* case suggests that a relatively specialized (genus-level) feeder also can have far-reaching ecological impacts, in this case by its threat to the diverse assemblage of related native North American *Opuntia* spp. and their interacting dependent species. Another possible mechanism for community-level effects involves nontarget impact on a keystone species (105). In theory, this could lead to a cascade of detrimental effects on associated native species (113, 114). Our case studies provided no evidence of keystone effects, reflecting the fact that little information exists on the ecological roles of most native insect species.

10. **Evidence on adaptive change is missing in these case histories.** Although exotic organisms have the potential of evolving to utilize new hosts where introduced (46–48, 113, 117), in none of the cases we reviewed were such adaptations studied directly. The evidence available in these case histories suggests that most host shifts involved preadaptation, rather than newly evolved ability, to utilize nontarget hosts. However, because the population genetic evidence necessary to determine if adaptive change is occurring was absent, this issue presents an opportunity for important future research.

RECOMMENDATIONS BASED ON THE CASE HISTORIES REVIEWED

1. **Avoid the use of exotic generalist predators and parasitoids.** Generalists, such as *Coccinella septempunctata* and *Compsilura concinnata*, utilize a greater number of nontarget species and therefore carry a greater chance of direct and indirect nontarget effects. If the goal is to maximize the predictive power of prerelease studies of candidate agents, then assessment of potential nontarget impacts is greatly simplified by selecting agents with narrow host range.

2. **Expand host-specificity testing.** The case histories provide strong support for the suggestion that host-specificity testing is highly informative on physiological host range, if the tests include potential hosts. This was true for insect cases in which such data were gathered, as well as for the weed cases, supporting the increasing use of such tests in insect control programs. Measures of host specificity across an array of potential hosts that were indicative that nontarget use was possible or likely include feeding preference with no-choice (starvation) tests, in addition to choice tests; oviposition under choice and no-choice conditions; and subsequent larval development and eclosion on an ecologically based set of potential hosts. Because host-specificity preference tests, especially choice tests, did not predict actual host impact in many

cases, these tests need to be supplemented with information on ecological range.

3. **Utilize more ecological information to increase precision of risk assessment for potential host species.** Ecological parameters were significant in many cases in determining the outcome of interactions of introduced agents with potential nontarget species in the field. Thus, the influence of ecological factors on potential nontarget effects needs to be better evaluated for environmental risk assessment. Prerelease field research on candidate biological control agents within their native ranges could provide additional insight into realized host breadth under a range of environmental conditions. Climate matching of the recipient system and the native range may help predict dispersal and potential geographic spread, as was the case for *C. cactorum*. Furthermore, because the cases illustrate that natural dispersal and spread of natural enemies into climatically suitable habitats is likely, more information on habitat preference, host-finding behavior, and limiting conditions for growth would enable better assessment of potential nontarget host attack and spread.

4. **Incorporate population-level measurements of ecological risk.** A consistent theme in the case histories was that environmental conditions influence host utilization and population impact, sometimes contradicting predictions based on host-preference testing. Habitat, phenology, and elevation were critically important predictors of ecological host range and use of native hosts in several cases. Thus, our review suggests that experimental and field research on parameters underlying population growth rates and factors influencing interaction strengths under field conditions would improve prediction of population response when host-specificity tests indicate that native species are potential hosts.

5. **Add ecological risk criteria to target selection.** As pointed out elsewhere (69, 71, 77, 84, 85, 99, 100, 123), not all pest species are appropriate targets for biological control. Some may be associated with high agricultural or ecological risks. For example, targeting weeds with close native relatives, or targeting native weeds with dependent food webs of native species, sharply increases ecological risk. Redistribution of accidentally established insects for biocontrol also appears risky. Furthermore, not all pest populations are likely to be controlled by natural enemies. The possibility that specialist biological control agents that are both effective and safe may not exist needs to be incorporated into target selection and program planning.

6. **Prioritize host-specific agents according to their predicted effectiveness.** It is striking that the pressure assumed to be exerted by the introduced insect often appeared ineffective or only partly effective in providing control (Table 1). Given the accumulating evidence that unanticipated ecological side effects are possible, the benefits to be gained need better quantification. The case histories provide support for further development of protocols, such as

impact studies in candidate agents' native ranges and in large field cages, to evaluate potential effectiveness of agents as well as their potential ecological effects. Such studies would allow for the choice of the most effective agents, allowing intensive screening for those least likely to impose measurable nontarget effects.

ACKNOWLEDGMENTS

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