

# RISKS OF SPECIES INTRODUCED FOR BIOLOGICAL CONTROL

Daniel Simberloff

*Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA*

&

Peter Stiling

*Department of Biology, University of South Florida, Tampa, FL 33620, USA*

## Abstract

*Numerous biological control introductions have adversely affected non-target native species. Although many of these problems occurred in the early days of biological control, some are recent. Because of how little monitoring is done on species, communities, and ecosystems that might be affected by biological control agents, it is quite possible that known problems are the tip of an iceberg. Regulations for officially sanctioned releases for biological control are insufficient, and there are also freelance unregulated releases undertaken by private citizens. Cost-benefit analyses for conservation issues, including those associated with biological control, are exceedingly difficult because it is hard to assign values to the loss of species or ecosystem functions. Risk assessment for biological control is difficult because of how hard it is to predict community- and ecosystem-wide impacts of introduced species and because introduced species disperse and evolve. Nevertheless, cost-benefit analyses and risk assessments for biological control introductions would have the salubrious effect of forcing consideration of myriad factors that now often receive cursory attention and of broadening public understanding of the issues. Copyright © 1996 Published by Elsevier Science Limited*

**Keywords:** biological control, biological introduction, monitoring, neo-classical control.

## INTRODUCTION

A recent report of the National Academy of Sciences argued that biological control should become the primary pest control method in the United States (NAS, 1987). Simultaneously, conservationists began to worry that non-indigenous species introduced for pest control can extinguish native species and devastate native ecosystems. Howarth (1983, 1985, 1991) first raised this

alarm, pointing to probable extinctions that had already occurred and inadequate protocols to prevent future damage. Other examples soon surfaced in which potential problems from non-indigenous control agents had been insufficiently considered (e.g. Ehler, 1991; Nafus, 1992; Simberloff, 1992; Lockwood, 1993a,b).

Biological control practitioners have rebutted these warnings, arguing that they rest on unproven cases and hyperbole, that biological control need not be risky, and that current procedures minimize the already low likelihood of unforeseen disasters (e.g. Funasaki *et al.*, 1988; Lai, 1988; Gonzalez & Gilstrap, 1992; Messing, 1992; Carruthers & Onsager, 1993). These advocates of biological control admit that early projects, especially those using generalized vertebrate predators, had unexpected consequences but contend that such projects were primitive by today's standards. According to DeLoach (1991), current practices in the United States insure against damage to non-target species. The strong reaction is not surprising. Biological control has long been touted as an environmentally friendly alternative to chemical control, and many workers in the field see themselves as conservationists (Center, 1995). But the vehemence of the response does not mean the critics are unnecessarily worried, and their arguments deserve detailed assessment.

This paper will focus primarily on problems in the United States, but we have chosen examples that we feel are broadly relevant. Of course, as living organisms do not respect international borders, these problems are international. For example, below we describe how a biological control introduction to Nevis in the West Indies by the Commonwealth Institute of Biological Control has led to a threat of extinction of an endemic non-target plant in the United States.

## TWO-SPECIES INTERACTIONS

Many early biological control projects used generalized predators that subsequently attacked non-target species (Simberloff, 1992). For example, the fish *Gambusia*

Correspondence to: D. Simberloff. Tel.: (904) 644 6739; Fax: (904) 644 9829; e-mail: Simberloff@bio.fsu.edu

*affinis* and *G. holbrooki*, introduced in many regions to control mosquitoes, have decreased populations of numerous native fish species through predation, extinguishing some in the process (Lloyd, 1990; references in Simberloff, 1992). Similarly, polyphagous herbivores introduced to control weeds have affected non-target native species. Among the most damaging of such introductions are those of freshwater fishes to attack introduced aquatic weeds, and some of these have been recent (Moyle *et al.*, 1986; Courtenay & Williams, 1992; Courtenay, 1993). Some of these fishes have so greatly reduced vegetation that native fish community structure was highly modified, but other possible effects of these fishes are often unstudied. In every such instance in which research has been detailed, however effective the biological control agent was on its target organism, there was substantial harm to non-target native species.

Groves (1989) and DeLoach (1991) claim that insects introduced for control of terrestrial weeds have never eliminated non-target native species, but there are certainly examples in which they have at least come close. The weevil *Rhinocyllus conicus* was introduced to Canada in 1968 and Virginia in 1969 to control weedy, non-indigenous thistles (Ehler, 1991). It was then released in many other regions of North America (Schroder, 1980). In the 1980s it was discovered feeding on several native thistle species (*Cirsium* spp.) (Turner *et al.*, 1987), of which three species are classified as category 2 species under the Endangered Species Act. In North Carolina, a curculionid introduced in 1990 for control on non-indigenous pasture thistles may threaten the host-specific little metalmark butterfly *Calephelis virginensis* by reducing its food plant *Cirsium horridulum* and also threatens two rare native thistles (S. Hall, pers. comm.). In Hawaii, the native plant *Tribulus cistoides* has become rare owing to herbivory by seed weevils *Microlarinus* spp. introduced to control puncture vine *T. terrestris* (Howarth, 1991). The cactus moth *Cactoblastis cactorum* introduced in 1957 to the Lesser Antilles to control *Opuntia* spp., arrived in the Florida Keys by 1989 and has severely threatened a category 2 species in the wild, the semaphore cactus *Opuntia spinosissima* (Habeck & Bennett, 1990; Simberloff, 1992). In each of these cases, the presence of a common alternative host maintains high numbers of the introduced phytophage, so that density-dependence does not operate between the insect and the native non-target host as populations of the latter decline.

Funasaki *et al.* (1988) reject the contention of Gagné and Howarth (1985) and Howarth (1985) that parasitoids brought to Hawaii for biological control have eliminated native lepidopterans. They contend that virtually all non-indigenous parasitoids recorded from native moth species between 1890 and 1985 reached the Hawaiian islands on their own, although Howarth (1991) suggests that many of these 'autonomous' arrivals may in fact have been unrecorded deliberate

introductions, either in early government-sponsored projects or by private interests (see below). Funasaki *et al.* (1988) believe that current procedures are so greatly improved over those of early practitioners that environmental concern is unwarranted.

Although Howarth (1991) cites other examples of introduced biological control agents threatening or eliminating non-target native hosts, biological control practitioners (e.g. Center, 1995) see these as unproven. However, it is notoriously difficult to determine the causes of particular extinctions (Simberloff, 1994) and, even if a biological control agent actually caused an extinction, it might not be too surprising if this cause could not be demonstrated, given the paltry amount of monitoring that might be expected; we discuss this point below.

Resource competition is even more difficult to demonstrate than predation and parasitism, so one cannot discount the possibility that introduced biological control agents compete with native species simply because very few cases have been documented. The Palearctic seven-spot lady beetle *Coccinella septempunctata* is strongly suspected of replacing native coccinellids in South Dakota (Elliott *et al.*, in press) and Washington (P. Kareiva, pers. comm.), based on precipitous declines in populations of some native species exactly when the seven-spot invaded. Exactly how the decline in native coccinellids will affect other species, such as their prey, is unknown.

## COMMUNITY AND ECOSYSTEM EFFECTS

The effects of non-indigenous species, including biological control agents, can be much more byzantine than the one-on-one trophic or competitive interactions we have described so far. Consider the coconut leaf-mining beetle *Promecotheca reichei* on Fiji, originally controlled by two native parasitoids (DeBach, 1974). A mite (*Pediculoides ventricosus*) accidentally introduced there attacked beetle larvae and pupae, but not eggs or adults. In the dry season it locally destroyed all larvae and pupae, then laid eggs and died. Thus a beetle population with overlapping generations had been converted to a synchronous population. Now that there were no beetle larvae and pupae, the mite population crashed. Worse, the synchronous nature of the beetle population virtually eliminated the native parasitoids, adapted to the presence of all stages of the beetle at all times, and with generation lengths too short for them to survive the intervals between occurrences of the particular host stages in which they oviposit. Neither the mite nor the native parasitoid could prevent a subsequent beetle population explosion. The beetle was eventually controlled by the introduction of a parasitoid that was not so fussy about the developmental stage of the host when it oviposits (Taylor, 1937). The implications of this case are clear: the precise phenologies of host and native natural enemies are often not

well-studied, especially if the host species is of no great economic or conservation significance. It would be quite easy for an introduced entomophage to disrupt this phenology, and this statement would be as true for non-target as for target hosts.

At first blush, it might seem that as complicated an effect as that of *Pediculoides* could not have been predicted with the sorts of information that could reasonably be made available. The concept of the keystone species (Paine, 1966, 1969) may be useful here. Classically, a keystone is an herbivore or predator whose impact on the proportions of species in the next lower trophic level substantially modifies the physical structure of the entire community, and thus affects many of its species. The concept has more recently been broadened to include any species that affects, directly or indirectly, many species in the community, these effects often being out of proportion to the numbers or biomass of the keystone species itself (references in Simberloff, 1991). And an entire group of related species may be termed a 'keystone taxon'. Although Mills *et al.* (1993) suggest that this expansion has rendered the entire keystone concept useless, we are not so sure. For example, perhaps any potential invader that would attack a numerically dominant species or group of related species should raise a flag, because one should consider the potential impacts on other species that interact with the dominant species.

The planned USDA introduction of a scelionid wasp (*Scelio parvicornis*) and fungus (*Entomophaga praxibuli*) from Australia to control native grasshoppers in western rangeland (Carruthers & Onsager, 1993) may be an example in which ecological ripple effects might be predicted because the target organisms constitute a keystone taxon (Lockwood, 1993a,b). There are no non-indigenous grasshoppers in this habitat, and most of the native ones are not known to be harmful. Although there is no full study of their myriad ecological roles, some species are known to benefit the native community. It is difficult to believe that a change in such a numerically dominant taxon would not generate many other effects elsewhere in the community.

### NEOCLASSICAL CONTROL AND NEW HOSTS

The proposal just described to control grasshoppers is termed 'neoclassical biological control' (Lockwood, 1993a) because a non-indigenous enemy is introduced to attack a native species, while classical biological control entails introducing enemies of non-indigenous pests (Nechols & Kauffman, 1992). Because neoclassical control cannot count on exquisitely coevolved adaptations between pest and enemy to keep the enemy from inflicting unexpected damage on non-target species, it seems particularly dangerous. Why should the enemy limit itself to the target, when the target is as novel as non-targets? Neoclassical control rests on the new association hypothesis of Hokkanen and Pimentel (1984,

1989), which predicts that new associations will probably lead to more effective control of the target pest because the pest has not coevolved with its enemies. The analogy to the evolution of benignity in pathogen-host relationships (Ewald, 1983) is patent. Successive epizootics of a newly introduced disease are often of decreasing virulence, because natural selection produces hosts that are more resistant and pathogens that do not destroy the host. In biological control, the effect of myxoma virus on rabbits in Australia (Williamson, 1992) is a good example.

The claims of Hokkanen and Pimentel (1984, 1989) that a majority of effective biological control programs involve new associations between host and enemy, and that often they involve host-range expansion by a species that had been considered monophagous or oligophagous, has been rejected (e.g. Waage & Greathead, 1988). However, the rejection is not on the grounds that new associations and host-range expansions do not occur, but rather on the basis of the definition of 'effective' and the precise fractions of projects that constituted new associations. Probably the species that are especially likely to constitute successful neoclassical biological control introductions are those that are preadapted to attack, survive, and reproduce on new hosts — in short, the very species that would be most likely to affect non-target species (Roderick, 1992).

### COSTS, BENEFITS, AND RISKS

Conservation issues do not lend themselves very well to cost-benefit analyses because the value of a population or species is extremely difficult to assess, in economic or other terms (Simberloff, 1992). The economic cost of losses to a plant pest can be measured, and so can the cost of pesticides and manpower. For biological control, the cost of collecting trips and testing for efficacy and specificity are also straightforward. On the other hand, even if we could predict that events such as extinction of a population or species or change in community composition or perturbation of an ecosystem process would occur, it is not obvious how to assign costs to them. Beyond the fact that we usually cannot predict very well the subsequent ripple effects of these events on other populations, species, communities, and ecosystems, how much is the very existence of these entities worth? Economists and philosophers who have grappled with this matter have yet to reach consensus (Norton, 1987; Rolston, 1991). This problem is particularly acute for biological control because an established population can almost certainly not be eradicated.

Advocates of biological control can argue that, from the standpoint of ecological costs to nature, particular invasions are so devastating that it is inconceivable that unintended consequences of a biological control introduction could be worse (e.g. Center, 1995). For example, the catastrophic effects of purple loosestrife *Lythrum*

*salicaria* on native plant communities of the midwestern and northeastern US and adjacent Canada and the insufficiency of mechanical and chemical control are seen as justifying a biological control program (Malecki *et al.*, 1993); in this instance, host-specificity testing is mandated, but the implication is that entire communities will be lost anyway if something is not done. For the imported fire ant *Solenopsis invicta* in the southeastern US, Buren (1983) suggested importing 20–30 ant species from South America and constructing an ‘artificial’ ant fauna on the grounds that the fire ant is destroying most of the native ant fauna anyway and no other control is working.

These are powerful arguments. When an invasion affects an entire community, is spreading rapidly, and appears to be producing irreversible effects, even the most cautious observers would suggest that biological control be considered (e.g. Howarth, 1991; Simberloff, 1992). However, it is still important to attempt to list the suspected ecological costs of the invasion and the potential problems that a control agent might cause. Further, the fact that living organisms need not stay in the habitat or region to which they are introduced must be considered. Introductions of the New World carnivorous snail *Euglandina rosea* to control the giant African snail *Achatina fulica* were made in agricultural communities because *Achatina* was seen as an agricultural pest; however, the snail has extinguished populations and entire species of endemic snails of forested habitats in the Tahitian and Hawaiian islands (references in Civeyrel & Simberloff, 1995). Similarly, the cactus moth discussed above dispersed from its initial site of introduction, where it is not known to have caused ecological damage, to other islands where it threatens at least one endemic species with extinction. So a risk assessment for a biological control introduction must consider dispersal.

The fact that living organisms disperse is but one complication in risk assessment for living organisms. Equally problematic is the fact that living organisms evolve. Species evolve to acquire new hosts (e.g. Prokopy *et al.*, 1988), to tolerate a greater range of physical factors (e.g. pesticides), and, for pathogens, to be more virulent (e.g. Brasier, 1979) or less virulent (Ewald, 1983). A single gene mutation can modify host specificity (Williamson, 1992). Any of these changes could turn an innocuous species into a harmful one. Hopper *et al.* (1993) provide several examples of changes in biological control organisms after introduction, including all the sorts of modifications just suggested. However, in no instance do they find strong evidence that the change is actually genetic. Thus they conclude that demographic barriers (such as difficulty finding mates at low population densities) may be more important in preventing establishment, but they do not address the likelihood that evolution of an established biological control population will cause an ecological problem.

## DOES THE ABSENCE OF CONFIRMED DISASTERS IMPLY LITTLE RISK?

The absence of conclusive evidence that problematic evolution of biological control agents has occurred is perhaps unsurprising when one considers the depth of research that had to be conducted to determine that, for example, a host-shift was genetically determined (e.g. Bush, 1975; Prokopy *et al.*, 1988; Feder & Bush, 1989). It is no mean undertaking to demonstrate that many traits, especially behavioral ones, are genetically determined, much less that changes in such traits are caused by genetic changes. Even the ranges and population densities of most insect species are very inadequately monitored (Center *et al.*, 1994). Just to have detected that a trait changed would be remarkable in this context. To show that the change is genetic would be astounding. In other words, it is possible that such changes are commonplace even though we have no ironclad examples.

Lai (1988), Funasaki *et al.* (1988), and Center (1995) view the paucity of known ecological damage from biological control introductions in comparison to the numerous projects as proof that biological control is generally safe. If one considers the remarkable circumstances surrounding discovery of some of the known problems, this argument is unconvincing (Simberloff, 1992).

Consider, for example, the extinction of seven endemic land snails of the genus *Partula* on the Tahitian island of Moorea caused by the introduction of the predatory snail *Euglandina rosea* for biological control, discussed above (Clarke *et al.*, 1984; Murray *et al.*, 1988; Murray 1993). As it happens, the Moorean *Partula* have long been recognized as a superb system for studying aspects of evolution, particularly divergence. Thus a team of researchers were closely studying the genetics and evolution of *Partula* on Moorea just as *Euglandina* was spreading. Had these *Partula* not been the subject of intense long-term biological research, we might not have known that all those species existed. Had a team not been working there at precisely the right time, we might not know they had gone extinct, much less why they had gone extinct. Also, the *Partula* on Moorea and Tahiti are culturally and economically important to the indigenous people, a fact that would also predispose us to know of a drastic change in their status. For how many invertebrates and plants are there long-term studies underway and cultural interest in the species?

Only a small fraction of all taxa are observed more than casually even by scientists. Snails, butterflies, and birds are beautiful, and large groups of amateurs collect them or their sightings. Few species receive this attention. Thus the argument of Funasaki *et al.* (1988) that few harmful effects are known for biological control introductions should not comfort us (Simberloff, 1992). Surely the post-release effort to study non-target

hosts and community and ecosystem properties was extremely limited, especially in pristine habitats, which are often remote. Lack of close study often prevents us from understanding the decline and disappearance of a species (Simberloff, 1994). Many known extinctions of animals since 1600 are not even assigned a 'possible cause' (Groombridge, 1992), and of those where a guess is made, in the majority of cases it is truly a guess. This is especially true for invertebrates. Thus, the fact that, except for a few cases like that of the *Partula* snails, few extinctions are known to have been caused by biological control agents should not make us complacent.

Disruption of community or ecosystem processes is even less likely to be observed than is extinction. At a few intensive research locations like the NSF-funded Long Term Ecological Research sites, nutrient flows, decomposition, and other processes are routinely monitored. Even here, a minority of ecosystem traits and processes are studied; myriad others are possible (Noss, 1990). Outside these sites, it would be remarkable if any unexpected community- or ecosystem-level effect of a biological control agent were noticed, even if such effects were common.

### CAN BIOLOGICAL CONTROL BE SAFE?

We have described several harmful effects of biological control agents, some of them indirect and perhaps unpredictable, and we have argued that these cases are probably the tip of an iceberg. One might reasonably ask whether, given the inherent unpredictability and usual irreversibility of biological introductions (Simberloff, 1991), biological control is categorically unsafe. Could any procedures ensure against ecologically harmful impacts? No, but this fact does not mean that no biological control should be practiced. Occasionally individuals react strongly and even fatally to a pharmaceutical that generally has no side-effects and is enormously useful. The unpredictability and irreversibility do suggest, however, that we must view biological control as risky and that specific projects should not be assumed to be innocuous until substantial effort has been expended to support this assumption.

We are skeptical of the merit of pleas that more rigorous testing and research on biological control agents will cost so much as to sound the death knell for the entire approach. Testing of pharmaceuticals is very expensive, and doubtless some pharmaceuticals that would otherwise have been developed and might have been useful were never produced because of regulatory costs. Nevertheless, the pharmaceutical industry is extremely profitable. One can also argue that some technologies that might be of great use are so risky that they should not be developed—some critics would put nuclear power in this category.

So long as professional biological control advocates tout the power and safety of this practice and down-

play its risks, there will be problematic projects no matter how carefully conducted and regulated officially sanctioned programs are. This is because freelance projects will inevitably be mounted by a public blithely unconcerned with risks, especially risks to non-commercial species, and eager to solve perceived pest problems cheaply. This is not a new problem, of course. In the 19th century, the small Indian mongoose *Herpestes auropunctatus* was privately introduced for rat control by sugarcane growers in both the West Indies and the Hawaiian islands (Tomich, 1986), causing much subsequent harm to native species (Simberloff, 1992); similar private actions brought stoats *Mustela erminea* and weasels *Mustela nivalis* from Britain to New Zealand in the 19th century for rabbit control (King, 1984). In the 1930s, a private citizen introduced feral hogs *Sus domesticus* onto Santa Catalina Island, California, solely to attempt to control rattlesnakes (Mayer & Brisbin, 1991).

However, some freelance projects are recent. For example, in Florida homeowner associations and individual citizens have released the goldenhorn marisa or wheeled apple snail *Marisa cornuarietis* in attempts to control hydrilla *Hydrilla verticillata* and water hyacinth *Eichhornia crassipes*, in spite of the fact that it feeds indiscriminately on many desirable native plant species and causes severe damage to aquatic animals whose habitat is native macrophytes (Warren, 1994). These releases are encouraged in popular shell guides (e.g. Emerson & Jacobson, 1976). Blue tilapia *Oreochromis aureus* was brought to Florida in 1961 for experiments in aquatic plant control, then hijacked, apparently by fisherman, and released in several areas (Courtenay *et al.*, 1974); it has negatively impacted native vegetation and fishes (Courtenay & Robins, 1973; Courtenay, 1994). Even the nutria *Myocastor coypus* was released privately three times in Florida for aquatic plant control (Griffo, 1957; Layne, 1994); this mammal has not established substantial populations in Florida, which is fortunate as it has been extremely problematic in England (Gosling, 1989) and Louisiana.

Although recently published safety-testing protocols for phytophages (e.g. that for the purple loosestrife project [Malecki *et al.*, 1993]) appear to be substantial, those for entomophages are often minimal. In many countries, such testing is restricted to possible effects on the few insects that have commercial value, such as bees. Historically, legal regulation of most classical biological control has been virtually non-existent (Miller & Aplet, 1993); this is part of the larger issue of inadequate regulation of biological introductions (Campbell, 1993). In the US (Coulson *et al.*, 1991), Congress has never specifically addressed biological control, and no federal statute specifically requires review of biological control agents before introduction (Abrams, 1990). For biological control of weeds, there is a federal review following guidelines suggested by a low-level advisory

group, and even these guidelines mandate consideration only of plants of 'value'. Further, the focus is only on species, not on ecosystem features, so that approval for an initial introduction is construed as approval for repeated introductions of the same species, even into different communities and ecosystems. There is little concern for introductions from one part of the United States to another, despite enormous regional differences at the community and ecosystem levels. Crucially, there are no formal, enforceable requirements for research and subsequent monitoring to assess impact. For entomophages in the US, The Biological Assessment and Taxonomic Support group of the USDA reviews proposals for release, but their concern for non-target organisms of no commercial value seems quite cursory.

Most state laws in the US encourage the use of biological control and constrain it minimally (Abrams, 1990; Miller & Aplet, 1993). For example, California has no provision for damage to ecosystems while Florida limits biological control agents to those that do not have 'an unreasonable effect on the environment', with 'unreasonable' undefined. The Wisconsin law appears strongest because it requires a permit for any biological control agent, even for intrastate movement, and expresses concern for safety and injury to 'useful' plants and animals, but there is no mention of biodiversity or natural ecosystems.

Australia is the only nation with a specific law for classical biological control, the Australian Biological Control Act of 1984. Its primary purpose is to bring concerns into public view, and it approves an introduction only upon a finding of no significant harm to any person or to the environment, although 'significant' is undefined and variously interpreted. This law arose because of a conflict between beekeepers and ranchers (Delfosse, 1985) that could not be resolved by a mechanism, similar to the current US procedures, in force at the time. The proposal to introduce insects to control Paterson's curse *Echium plantagineum* a range pest, elicited opposition from apiarists who prized the same plant for its high pollen: nectar ratio. Thus, concern for non-target organisms or ecosystems as a whole was secondary, although the Act is certainly a vehicle for airing such concerns.

Can one conceive of a broad, carefully crafted statute that would be proof against the potential problems we have outlined above? As noted above, no law can allow biological control and yet completely eliminate the possibility of collateral damage. However, Campbell (1993) and Miller and Aplet (1993) believe that, at least in the US, laws could be constructed that would be far superior to the current patchwork of regulations and would allow biological control while greatly lowering the risk of unintended harmful consequences.

## ACKNOWLEDGEMENTS

We thank P. Kareiva, D. F. Schweitzer, and S. Hall for unpublished information on several cases.

## REFERENCES

- Abrams, J. C. (1990). Biological control agents in integrated pest management: Are they regulated? *Pace Environmental Law Rev.*, **8**, 89–115.
- Brasier, C. M. (1979). Dual origin of recent Dutch elm disease outbreaks in Europe. *Nature Lond.*, **281**, 78–80.
- Buren, W. F. (1983). Artificial faunal replacement for imported fire ant control. *Fl. Entomol.*, **66**, 93–100.
- Bush, G. L. (1975). Sympatric speciation in phytophagous parasitic insects. In *Evolutionary strategies of parasitic insects and mites*, ed. P. W. Price. Plenum, New York, pp. 187–206.
- Campbell, F. C. (1993). Legal avenues for controlling exotics. In *Biological pollution: the control and impact of invasive exotic species*, ed. B. N. McKnight. Indiana Academy of Sciences, Indianapolis, pp. 243–50.
- Carruthers, R. I. & Onsager, J. A. (1993). Perspective on the use of exotic natural enemies for biological control of pest grasshoppers (Orthoptera: Acrididae). *Environ. Entomol.*, **22**, 885–903.
- Center, T. D. (1995). Selection criteria and ecological consequences of importing natural enemies (book review). *Biodiversity & Conserv.*, **4**, 524–6.
- Center, T. D., Frank, J. H. & Dray, F. A., Jr (1994). Scientific methods for managing invasive non-indigenous species—biological control. In *An assessment of invasive non-indigenous species in Florida's public lands*, ed. D. C. Schmitz & T. C. Brown. Florida Dept. of Environmental Protection, Tallahassee, pp. 209–47.
- Civeyrel, L. & Simberloff, D. (in press). A tale of two snails: Is the cure worse than the disease? *Biodiversity and Conserv.*
- Clarke, B., Murray, J. & Johnson, M. S. (1984). The extinction of endemic species by a program of biological control. *Pacif. Sci.*, **38**, 97–104.
- Coulson, J. R., Soper, R. S. & Williams, D. W. (eds). (1991). *Biological control quarantine: needs and procedures, proceedings of a workshop*. USDA – Agricultural Research Service, Beltsville, Maryland.
- Courtenay, W. R., Jr (1993). Biological pollution through fish introductions. In *Biological pollution: the control and impact of invasive exotic species*, ed. B. N. McKnight. Indiana Academy of Science, Indianapolis, pp. 35–61.
- Courtenay, W. R., Jr (1994). Non-indigenous fishes in Florida. In *An assessment of invasive non-indigenous species in Florida's public lands*, ed. D. C. Schmitz & T. C. Brown. Florida Dept. of Environmental Protection, Tallahassee, pp. 57–63.
- Courtenay, W. R., Jr & Robins, C. R. (1973). Exotic aquatic organisms in Florida with emphasis on fishes: a review and recommendations. *Trans. Amer. Fish. Soc.*, **102**, 1–12.
- Courtenay, W. R., Jr, Sahlman, H. H., Miley, W. W. II & Herrema D. J. (1974). Exotic fishes in fresh and brackish waters of Florida. *Biol. Conserv.*, **6**, 292–302.
- Courtenay, W. R., Jr & Williams, J. D. (1992). Dispersal of exotic species from aquaculture sources, with emphasis on freshwater fishes. In *Dispersal of living organisms into aquatic systems*, ed. A. Rosenfield & R. Mann. Maryland Sea Grant College, College Park, pp. 49–81.
- DeBach, P. (1974). *Biological control by natural enemies*. Cambridge University Press, London.
- Delfosse, E. S. (1985). *Echium plantagineum* in Australia: effects of a major conflict of interest. In *Proceedings of the VI International Symposium on Biological Control of Weeds*, ed. E. S. Delfosse. Agriculture Canada, Ottawa, pp. 293–8.
- DeLoach, C. J. (1991). Past successes and current prospects in biological control of weeds in the United States and Canada. *Natural Areas J.*, **11**, 129–42.

- Ehler, L. E. (1991). Planned introductions in biological control. In *Assessing ecological risks of biotechnology*, ed. L. R. Ginzburg. Butterworth-Heinemann, Boston, pp. 21–39.
- Elliott, N. C., Kieckhefer, R. W. & Kauffman, W. C. (in press). Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia, Berl.*
- Emerson, W. K. & Jacobson, M. K. (1976). *Guide to shells*. Knopf, New York.
- Ewald, P. W. (1983). Host–parasite relations, vectors, and the evolution of disease severity. *Annu. Rev. Ecol. Syst.*, **14**, 465–85.
- Feder, J. L. & Bush, G. L. (1989). Gene frequency clines for host races of *Rhagoletis pomonella* (Diptera: Tephritidae) in the midwestern United States. *Heredity*, **63**, 245–66.
- Funasaki, G. Y., Lai, P. Y., Nakahara, L. M., Beardsley, J. W. & Ota, A. K. (1988). A review of biological control introductions in Hawaii: 1890 to 1985. *Proc. Hawaiian Entomol. Soc.*, **28**, 105–60.
- Gagné, W. C. & Howarth, F. G. (1985). Conservation status of endemic Hawaiian Lepidoptera. In *Proceedings of the 3rd congress on European Lepidoptera* (1982, Cambridge), pp. 74–84.
- Gonzalez, D. & Gilstrap, F. E. (1992). Foreign exploration: Assessing and prioritizing natural enemies and consequences of preintroduction studies. In *Selection criteria and ecological consequences of importing natural enemies*, ed. W. C. Kauffman & J. E. Nechols. Entomological Society of America, Lanham, Maryland, pp. 51–70.
- Gosling, M. (1989). Extinction to order. *New Scientist*, **121**, 44–9.
- Griffo, J. V., Jr (1957). The status of nutria in Florida. *Quart. J. Fla. Acad. Sci.*, **20**, 209–15.
- Groombridge, B. (ed.). (1992). *Global biodiversity*. Chapman and Hall, London.
- Groves, R. H. (1989). Ecological control of invasive terrestrial plants. In *Biological invasions: a global perspective*, ed. J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson. Wiley, Chichester, pp. 437–61.
- Habeck, D. H. & Bennett, F. D. (1990). *Cactoblastis cactorum* Berg. (Lepidoptera: Pyralidae), a phycitine new to Florida. Florida Dept. of Agric. and Consumer Services, Div. of Plant Industry, Entomol. Circ. No. 333.
- Hokkanen, H. & Pimentel, D. (1984). New approach for selecting biological control agents. *Can. Entomol.*, **116**, 1109–21.
- Hokkanen, H. & Pimentel, D. (1989). New associations in biological control: theory and practice. *Can. Entomol.*, **121**, 829–40.
- Hopper, K. R., Roush, R. T. & Powell W. (1993). Management of genetics of biological-control introductions. *Annu. Rev. Entomol.*, **38**, 27–51.
- Howarth, F. G. (1983). Classical biological control: Panacea or Pandora's Box? *Proc. Hawaiian Entomol. Soc.*, **24**, 239–44.
- Howarth, F. G. (1985). Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. In *Hawaii's terrestrial ecosystems: preservation and management*, ed. C. P. Stone & J. M. Scott. University of Hawaii Cooperative National Park Resources Study Unit, Honolulu, pp. 149–78.
- Howarth, F. G. (1991). Environmental impacts of classical biological control. *Annu. Rev. Entomol.*, **36**, 485–509.
- King, C. (1984). *Immigrant killers*. Oxford University Press, Auckland.
- Lai, P.-Y. (1988). Biological control: A positive point of view. *Proc. Hawaiian Entomol. Soc.*, **28**, 179–91.
- Layne, J. N. (1994). Non-indigenous mammals in Florida. In *An assessment of invasive non-indigenous species in Florida's public lands*, ed. D. C. Schmitz & T. C. Brown. Florida Dept. of Environmental Protection, Tallahassee, pp. 79–95.
- Lloyd, L. (1990). Native fishes as alternatives to the exotic fish, *Gambusia*, for insect control. In *Introduced and translocated fishes and their ecological effects*, ed. D. A. Pollard. Department of Primary Industries and Energy, Bureau of Rural Resources, Canberra, pp. 115–22.
- Lockwood, J. A. (1993a). Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environ. Entomol.*, **22**, 503–18.
- Lockwood, J. A. (1993b). Benefits and costs of controlling rangeland grasshoppers (Orthoptera: Acrididae) with exotic organisms: Search for a null hypothesis and regulatory compromise. *Environ. Entomol.*, **22**, 904–14.
- Malecki, R. A., B. Blossy, B., Hight, S. D., Schroeder, D., Kok, L. T. & Coulson, J. R. (1993). Biological control of purple loosestrife. *BioScience*, **43**, 680–6.
- Mayer, J. J. & Brisbin, I. L. Jr (1991). *Wild pigs in the United States*. University of Georgia Press, Athens, GA.
- Messing, R. H. (1992). Biological control in island ecosystems: Cornerstone of sustainable agriculture or threat to biological diversity? *Pacif. Sci.*, **46**, 387–8.
- Miller, M. & Aplet, G. (1993). Biological control: a little knowledge is a dangerous thing. *Rutgers Law Rev.*, **45**, 285–334.
- Mills, L. S., Soule, M. E. & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience*, **43**, 219–24.
- Moyle, P. B., Li, H. W. & Barton, B. A. (1986). The Frankenstein effect: impact of introduced fishes on native fishes in North America. In *Fish culture in fisheries management*, ed. R. H. Stround. American Fisheries Society, Bethesda, Maryland, pp. 415–26.
- Murray, E. (1993). The sinister snail. *Endeavour* (New Series), **17**(2), 78–83.
- Murray, J., Murray, E., Johnson, M. S. & Clarke, B. (1988). The extinction of *Partula* on Moorea. *Pacif. Sci.*, **42**, 150–53.
- Nafus, D. M. (1992). Impact of intentionally and accidentally introduced biological control agents on unintended hosts, *Hypolimnas anomala* and *H. bolina* (Lepidoptera: Nymphalidae) on Guam. *Pacif. Sci.*, **46**, 394–5.
- National Academy of Sciences (1987). *Research briefings 1987: report of the research briefing panel on biological control in managed ecosystems*. National Academy Press, Washington, DC.
- Nechols, J. R. & Kauffman, W. C. (1992). Introduction and overview. In *Selection criteria and ecological consequences of importing natural enemies*, ed. W. C. Kauffman & J. E. Nechols. Entomological Society of America, Lanham, Maryland, pp. 1–5.
- Norton, B. G. (1987). *Why preserve natural variety?* Princeton University Press, Princeton, New Jersey.
- Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.*, **4**, 355–64.
- Paine, R. T. (1966). Food web complexity and species diversity. *Amer. Nat.*, **100**, 65–75.
- Paine, R. T. (1969). A note on trophic complexity and community stability. *Amer. Nat.*, **103**, 91–3.
- Prokopy, R. J., Diehl, S. R. & Cooley, S. S. (1988). Behavioral evidence for host races in *Rhagoletis pomonella* flies. *Oecologia, Berl.*, **76**, 138–47.
- Roderick, G. K. (1992). Postcolonization evolution of natural enemies. In *Selection criteria and ecological consequences of importing natural enemies*, ed. W. C. Kauffman & J. E. Nechols. Entomological Society of America, Lanham, Maryland, pp. 71–86.
- Rolston, H., III (1991). Environmental ethics: values in and duties to the natural world. In *Ecology, economics, ethics: the broken circle*, ed. F. H. Bormann & S. R. Kellert. Yale University Press, New Haven, Connecticut, pp. 73–96.

- Schroder, D. (1980). The biological control of thistles. *Biocontrol News and Information*, **1**, 9–26.
- Simberloff, D. (1991). Keystone species and community effects of biological introductions. In *Assessing ecological risks of biotechnology*, ed. L. R. Ginzburg. Butterworth-Heinemann, Boston, pp. 1–19.
- Simberloff, D. (1992). Conservation of pristine habitats and unintended effects of biological control. In *Selection criteria and ecological consequences of importing natural enemies*, ed. W. C. Kauffman & J. E. Nechols. Entomological Society of America, Lanham, Maryland, pp. 103–117.
- Simberloff, D. (1994). The ecology of extinction. *Acta Palaeontol. Pol.*, **38**, 159–74.
- Taylor, T. H. C. (1937). *The biological control of an insect in Fiji. An account of the coconut leaf-mining beetle and its parasite complex*. Imperial Institute of Entomology, London.
- Tomich, P. Q. (1986). *Mammals in Hawai'i*, 2nd edn. Bishop Museum Press, Honolulu.
- Turner, C. E., Pemberton, R. W. & Rosenthal, S. S. (1987). Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) in California. *Environ. Entomol.*, **16**, 111–15.
- United States Congress, Office of Technology Assessment (1993). *Harmful non-indigenous species in the United States*. Washington, DC.
- Waage, J. K. & Greathead, D. J. (1988). Biological control: Challenge and opportunities. *Phil. Trans. R. Soc. Lond.*, **B 318**, 111–28.
- Warren, G. L. (1994). Ecologically disruptive non-indigenous freshwater invertebrates in Florida. In *An assessment of invasive non-indigenous species in Florida's public lands*, ed. D. C. Schmitz & T. C. Brown. Florida Department of Environmental Protection, Tallahassee, pp. 104–9.
- Williamson, M. (1992). Environmental risks from the release of genetically modified organisms (GMOs)—the need for molecular ecology. *Molec. Ecol.*, **1**, 3–8.