

Indirect effects of host-specific biological control agents

Dean E. Pearson^{1,2} and Ragan M. Callaway¹

¹Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

²Current address: USDA Forest Service, Rocky Mountain Research Station, Box 8089, Missoula, MT 59807, USA

Biological control is a crucial tool in the battle against biological invasions, but biocontrol agents can have a deleterious impact on native species. Recognition of risks associated with host shifting has increased the emphasis on host specificity of biocontrol agents for invasive weeds. However, recent studies indicate host-specific biocontrol agents can also exhibit substantial nontarget effects through indirect interactions and food-web subsidies. Based on an evaluation of these studies, we conclude that the interaction strength between biocontrol agents and their hosts is at least as important as host specificity for determining the outcome of biocontrol introductions. Host-specific biocontrol agents that establish, but fail to reduce the densities of their hosts can facilitate bottom-up effects that link the target weed to other native organisms through food webs, thereby expanding the impacts of the invasive weed. We believe that indirect nontarget effects of host-specific biocontrol agents arising from food-web subsidies could prove more deleterious to native species than are the direct nontarget effects currently recognized from host shifting.

Biological invasions increasingly threaten the biological diversity and ecological integrity of natural ecosystems [1]. Classic biological control (referred to henceforth as biocontrol), the importation of natural enemies for the control of exotic, invasive species, is a powerful management tool that has proven effective at controlling numerous invasive species [2,3]. However, biocontrol also poses significant risks to nontarget, native taxa [4–8]. The most notable examples of nontarget effects occur when biocontrol agents expand their host range to attack native organisms (host shifting) [3,5,6,9–12]. Recognition of the risks associated with host shifting has spawned an intense debate over the importance of the host specificity of biocontrol agents [2,3,5–7,13–17]. We believe that this debate has improved the field of biocontrol of exotic plants by establishing host specificity-requirements for biocontrol agents that reduce risks for nontarget species [2,3,14]. However, recent studies examining insect biocontrol of invasive plants indicate that even host-specific biocontrol agents can incur significant nontarget effects on native species [18–20]. Yet, indirect threats have not been considered in biocontrol theory or practice. Here, we

discuss the indirect effects of biocontrol agents in the context of the current theory and practice of biocontrol and recent advances in community ecology to illustrate that host-specific biocontrol agents can exhibit nontarget effects on native species and ecosystems. We focus our discussion on insect biocontrol of invasive plants, but the general concepts also apply to biocontrol of invertebrate pests [21].

Biocontrol in theory and practice

The conceptual model underlying biocontrol was derived from predator–prey theory (Fig. 1) [22,23] and is based on the notion that exotic species become invasive by escaping the controlling influence of their natural enemies [24–26]. We refer to this model as the ‘natural enemies model’. In this model, control of the invasive species is achieved when the introduction of its natural enemies reduces its mean equilibrium density below some economically or ecologically defined threshold [22,23]. The model predicts a direct negative effect of the biocontrol agent on its intended host that translates into an indirect positive effect on native species and a negative feedback that reduces and regulates its own populations (Fig. 2).

When biocontrol is successful, it is truly elegant. Cases of successful biocontrol demonstrate that top-down control

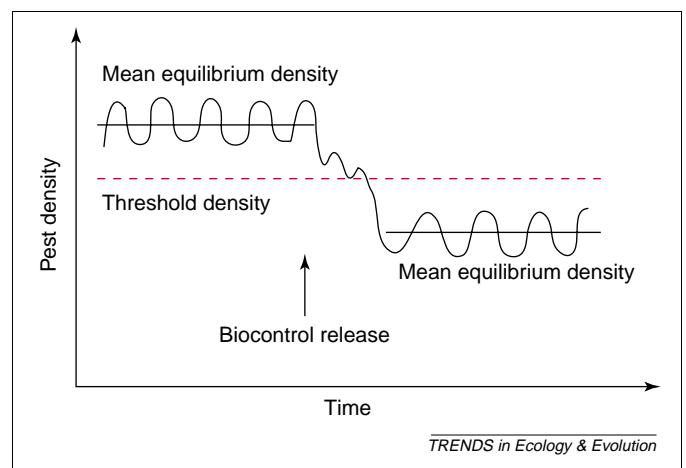


Fig. 1. Theoretical control of pest species using biocontrol agents, illustrating how pest densities might fluctuate over time before and after the introduction of a successful biocontrol agent. Before the introduction of the biocontrol agent, the pest density fluctuates around a mean equilibrium density that is above a threshold of economic or ecological impact. Following the introduction of the biocontrol agent, the pest densities stabilize at a new equilibrium level that is below the threshold of impact. Adapted, with permission, from [23].

Corresponding author: Dean E. Pearson (dpearson@fs.fed.us).

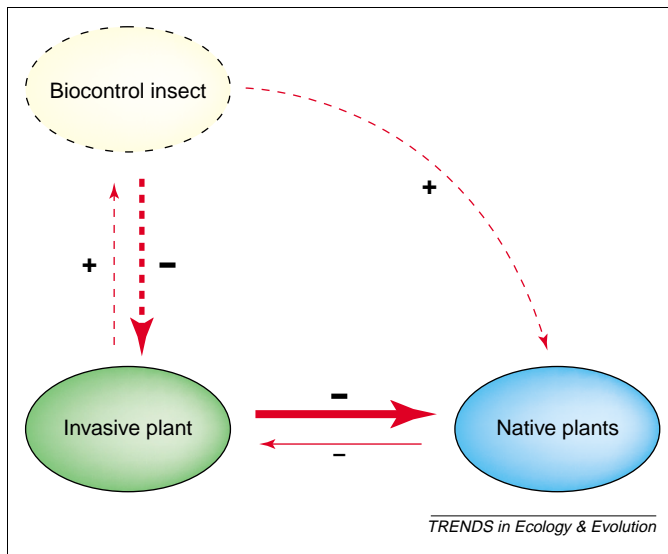


Fig. 2. Theoretical control of pest species using biocontrol agents presented in the context of the natural enemies model, illustrating direct (straight lines) and indirect effects (curved lines) predicted by the model. Line weight indicates interaction strength. Dotted lines indicate empty niche of primary consumer and postulated effects of introducing a biocontrol agent. This illustrates how the natural enemies model focuses on the direct negative effect of the biocontrol on the target pest and the resulting indirect positive effect on the native species, but ignores other community interactions that might arise within the system (i.e., they are not addressed by the model).

can be achieved over invasive species using natural enemies when the biocontrol behaves as a keystone species (an organism with community effects that are disproportionately large relative to its abundance) [27]. This point is well illustrated by the control of klamath weed *Hypericum perforatum* by the chrysomelid beetle *Chrysolina quadrigemina* [28]. Klamath weed is an exotic forb that had invaded nearly 1 million ha of rangeland in northern California by the mid 1900s, causing dramatic reductions in the biomass and diversity of native species. The introduction of *C. quadrigemina* reduced Klamath weed to <1% of its peak invasion densities and facilitated recovery of the native system within 12 years of the initial release. These two species currently persist at densities well below the threshold of ecological impact. Presumably, experimental removal of *C. quadrigemina* would result in klamath weed recovering its former range at great expense to the native community. This keystone phenomenon is also demonstrated by other successful biocontrol agents in natural systems [2,3] and illustrates the importance of interaction strength (the population-level impact of one species on another [29]) for achieving successful control. Although the host specificity of *C. quadrigemina* might have contributed to its success, host specificity alone was not sufficient to attain this success. Most plant biocontrol agents remain host specific, yet fail to control their target pest [26,30]. The key to the success of *C. quadrigemina* was its interaction strength, that is, its strong negative effect on klamath weed populations.

Although the natural enemies model predicts that biocontrol agents will successfully control their target species, most biocontrol agents fail to do so [30,31] and, therefore, the outcomes of most introductions are unknown. Introduced biocontrol agents can host shift and attack nontarget species [4–15], resulting, in some

cases, in biologically significant negative impacts on those species [5,6,9–12]. Recognition of the risks associated with host shifting has led to an increased emphasis on host specificity in screening prospective biocontrol agents [14]. However, most biocontrol introductions result in the establishment of host-specific biocontrol agents that exhibit weak negative effects on their host [30]. Such agents are presumed safe because host specificity is believed to ensure their neutrality toward nontarget species [2,3,22]. This assumption has contributed to the ‘multiple release’ strategy in biocontrol [4,31,32] that advocates introducing multiple agents for each target species with little regard for interaction strength. The ironic result of this approach is that exotic biocontrol insects now far outnumber the exotic plants that they were introduced to control [30,31], and new research [18–20] suggests that host-specific biocontrol agents can incur strong nontarget effects through indirect interactions associated with ecological replacement, compensatory responses and food-web subsidies.

Nontarget effects of host-specific biocontrol agents

Ecological replacement

Indirect nontarget effects can occur through ecological replacement when a biocontrol is used against a pest that has become integrated into the native community by physically or functionally replacing native species. Although biocontrol in cases involving ecological replacement can result in indirect nontarget effects on native species, this is not a failure of the biocontrol or the natural enemies model. The natural enemies model predicts that those organisms directly interacting with the pest species will be affected by its control (Fig. 2), and well established exotic species can be expected to develop interactions with native organisms. For example, biocontrol of exotic European rabbits *Oryctolagus cuniculus* in the UK is believed to have resulted in the extirpation of the large blue butterfly *Maculina arion* through a series of indirect effects that fatally linked this species to the rabbits [33]. The large blue required nests of the ant *Myrmica sabuleti* for the development of their larvae. These ants in turn were dependent upon rabbit grazing to maintain open habitat for their nests, so biocontrol of the rabbits with the *Myxoma* virus initiated a cascade of interactions believed to have led to the extinction of the large blue. Recognition of the risks associated with indirect nontarget effects from ecological replacement has helped to avoid repeating the story of the large blue. For instance, proposed biocontrol of saltcedars *Tamarix* spp. in southwestern USA was rejected because of risks to the endangered subspecies of the southwestern willow flycatcher *Empidonax traillii eximius* [34], which currently relies on saltcedars for nesting sites in areas where these exotics have replaced its native nesting habitat [35]. The concern was that biocontrol of saltcedars would remove nesting habitat before the native vegetation could be restored. The problem of ecological replacement is likely to increase as biological invasions proliferate and exotics become increasingly entrenched within native communities [36]. Therefore, it will become increasingly important to assess effectively the extent of ecological replacement by invasive species to determine

the potential for unintended indirect nontarget effects arising from the biocontrol of well established invaders.

Compensatory responses

Herbivory does not always result in direct negative effects on plants. Plants can alter the outcome of biocontrol herbivory through compensatory growth or increased production of secondary compounds. For example, field and greenhouse experiments indicate that herbivory by the root-boring biocontrol moth *Agapeta zoegana* on the invasive forb *Centaurea maculosa* might deleteriously affect native grasses, such as *Festuca idahoensis*, through an indirect effect [18,37]. Application of *A. zoegana* did not significantly decrease *C. maculosa* biomass and actually stimulated small but significant decreases in *F. idahoensis* reproduction and trends towards lower *F. idahoensis* biomass. The mechanism for this unusual indirect effect is not clear, but there are three non-mutually exclusive hypotheses. First, *C. maculosa* exhibits a very strong compensatory growth response to herbivory [37–39], and resource competition might intensify with increased resource uptake. Second, herbivory can stimulate increased production of harmful root exudates [18,40]. Finally, the negative effect of biocontrol herbivory on *C. maculosa* could be mediated by mycorrhizal fungi [41,42]. These studies illustrate the potential for unpredictable indirect effects of host-specific biocontrol agents to impact negatively the native species that they were intended to help.

Food-web interactions

Introduced biocontrol agents that become established have the potential to become superabundant within the host environment because they encounter plentiful food, little competition and few natural enemies of their own. If biocontrol agents are strong enough to control their host populations, their superabundance will be ephemeral because the biocontrol will decline as it depletes its food resource. However, if an established biocontrol is ineffective at reducing its host densities, populations of the biocontrol are likely to remain abnormally high. High resource concentrations present a lucrative opportunity for native consumers, and native consumers are commonly observed preying upon biocontrol agents [43–47]. However, predation on biocontrol agents has simply been viewed as a source of interference with the biocontrol, and there has been little regard for the potential for deleterious indirect nontarget effects within the native system. In fact, biocontrol subsidies to native consumers have been interpreted as a ‘means by which previously little-used resources benefit various food chains in the environment’ [48]. This view is dangerously over simplistic.

Recent studies of food subsidies to communities provide convincing evidence that many organisms are food limited and that food subsidies to key organisms at various trophic levels can serve to restructure community interactions, whether inputs come from native or exotic sources [49–54]. For example, the introduction of exotic kokanee salmon *Oncorhynchus nerka* to Flathead Lake in western Montana [50] resulted in annual fall salmon runs up the Flathead River system into Glacier National Park. This

spawning activity created a concentrated food resource that was exploited by a variety of native consumers, including bald eagles *Haliaeetus leucocephalus*, gulls *Larus* spp., grizzly bears *Ursus arctos*, and coyotes *Canis latrans*. Although the indirect effects associated with exotic subsidies to native predators were not quantified in this system, they have been quantified elsewhere. On the northern Channel Islands off the coast of California, exotic feral pigs *Sus scrofa* are facilitating the extirpation of the endemic island fox *Urocyon littoralis* by subsidizing recently established golden eagle *Aquila chrysaetos* populations [54]. Energy budgets demonstrate that the exotic pigs are key to this interaction because the eagles cannot sustain their populations on native prey alone [54]. Negative impacts on native species have also been documented from exotic crop subsidies to snow geese *Chen caerulescens* and exotic insect subsidies to parasitoids [53,55]. These studies indicate that exotic food resources can subsidize important native consumers with unpredictable and potentially significant indirect effects for native species through food webs. Thus, it is reasonable to expect that exotic biocontrol agents could subsidize native consumers with similar outcomes.

Although native consumers commonly exploit biocontrol agents [27,43–47], studies examining the outcomes of such interactions usually focus on the consumer’s effects on the biocontrol, whilst ignoring the potential effects of the biocontrol on the native consumer [43–47]. However, recent studies [19,20] of gall fly *Urophora* spp. biocontrol agents introduced to control spotted knapweed *Centaurea maculosa* indicate that biocontrol agents can have significant direct and indirect nontarget effects on native species through food-web interactions when biocontrol agents provide food subsidies to generalist consumers, such as native deer mice *Peromyscus maniculatus* (Box 1).

The knapweed–*Urophora*–deer mouse case study serves to illustrate the importance of interaction strength and the direction of energy flow between the biocontrol and the invasive plant. If the *Urophora* biocontrol had a strong negative effect on the target plant as intended, it would have initiated top-down control over the invader that would have resulted in an indirect positive effect on the native plants and a negative feedback on its own populations. This outcome would have restricted the set of interactions to those recognized by the natural enemies model and effectively prevented both exotics from significant interactions with the native community. However, because the biocontrol produced only weak negative effects on its highly prolific host, biocontrol populations increased and, instead of restricting interactions to those associated with the natural enemies model, served to facilitate the bottom-up flow of energy from primary producers into the larger community through food-web interactions (Box 1). How far these effects reach into the system will depend on the interaction strength, particularly that of the interaction between the pest and the biocontrol. If *Urophora* had a very weak positive effect on deer mice, the potential for indirect effects would be limited. However, it is difficult to imagine that doubling or tripling populations of a native consumer, such as the deer mouse, which so effectively infiltrates native food webs as an aggressive generalist

Box 1. The *Urophora* case study

In the early 1970s, two species of gall flies, *Urophora affinis* and *U. quadrifasciata*, were introduced to western North America for the biocontrol of spotted and diffuse knapweeds *Centaurea maculosa* and *C. diffusa* [30]. The *Urophora* spp. successfully established and have remained host specific, but have failed to control populations of their host plants [56]. As a result, these biocontrol agents have become superabundant, occurring in North America at densities of 3000 larvae m^{-2} [57].

Not surprisingly, this abundant resource has drawn the attention of many native consumers [46], and recent studies show that the gall flies subsidize populations of at least one very important generalist predator, the deer mouse *Peromyscus maniculatus* [19,20]. Gall fly larvae, which overwinter within knapweed seedheads, are readily exploited by deer mice, and these larvae now comprise 85% of the deer mouse winter diet in grasslands invaded by knapweed [19]. The result of this subsidy has been an increase in overwinter survival that has elevated deer mouse

populations two- to threefold in knapweed-invaded grasslands [20]. Subsidizing this generalist predator has potentially significant ramifications. Deer mice are aggressive predators of seeds and insects, compete with other small mammals, and are important prey for larger predators [19,58,59]. They are also the primary vector for the deadly Sin Nombre hantavirus [60]. Thus, gall fly subsidies to deer mouse populations could disrupt established food webs and elevate the prevalence of a deadly zoonotic disease (Fig. 1). Moreover, these subsidies might exacerbate the impacts of knapweed on the native community through indirect effects. For example, seed predation by deer mice can significantly reduce recruitment in native plant populations [59]. Therefore, gall fly subsidies that elevate deer mouse populations in knapweed-invaded habitats could cause reduced recruitment of native plants already impacted by knapweed invasion. A similar case can be made for deer mouse predation on ecologically important invertebrate prey.

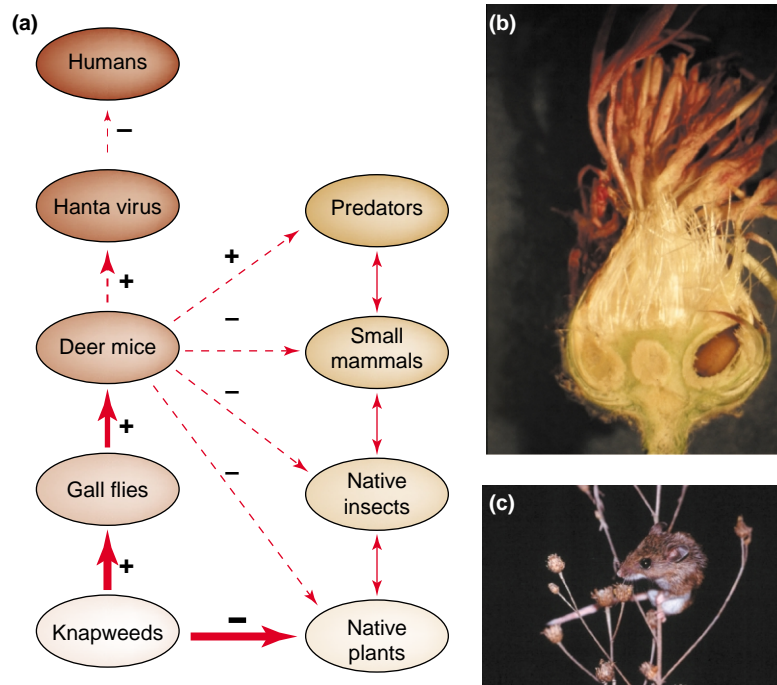


Fig. 1. Currently documented (solid lines) and postulated (dotted lines) direct and indirect effects (a) associated with gall fly *Urophora affinis* and *U. quadrifasciata* biocontrol agents introduced for the control of spotted knapweed *Centaurea maculosa* (b). The *Urophora* biocontrol agents exhibit very weak negative top-down effects on *C. maculosa*. Because of their lack of control over the weed, *C. maculosa* exhibits very strong bottom-up effects on the biocontrol agents. The resulting superabundance of the biocontrol has facilitated the bottom-up flow of energy further out into the native system by subsidizing native predators such as deer mice *Peromyscus maniculatus* (c) [19] that are integrated into native food webs. The extent to which this unintended outcome is likely to carry out into the system is a function of the strength of the various interactions. The most important interaction is that between the biocontrol and the native consumer. In the case of the deer mouse, this interaction has proven to be very strong [20], increasing the likelihood that other postulated nontarget indirect effects will follow. Line thickness indicates interaction strength. (c) reproduced with permission from Milo Burcham.

predator, a prominent prey item, and a vector for zoonotic disease, will not translate into significant impacts on native species and, potentially, humans. When a biocontrol fails to serve as a keystone predator that maintains top-down control over the system, it has the potential to serve as an 'ecological bridge' for bottom-up effects that links the invasive species to other native organisms, thereby expanding the impacts of the invasive species further into the native community through indirect effects. Such a biocontrol could qualify as a keystone species if its impact on the system is large relative to its biomass [27].

Conclusions

Biocontrol theory focuses on simple predator-prey relationships, but ignores more complex community interactions. As a result, biocontrol programs encourage the release of multiple host-specific biocontrol agents for each target pest [30–32] with little regard for indirect nontarget effects. This strategy has been criticized because successful biocontrol agents are being sought through a lottery rather than through ecological understandings of natural enemy-host relationships [32]. The best way to minimize the potential for nontarget effects is to minimize

the number of biocontrol agents introduced whilst maximizing the potential for control. McEvoy and Coombs [31,32] have discussed applying rules of parsimony to biocontrol programs to introduce the minimum number of agents necessary for control. This approach involves selecting biocontrol agents that represent different functional groups proven to disrupt transitions in the life cycle of the plant [31]. This strategy holds ecological merit because it focuses on emphasizing interaction strength and avoiding redundancy when attempting to construct effective 'natural enemy complexes' or 'biocontrol guilds'. However, deploying biocontrol guilds implicitly assumes that multiple biocontrol agents will be more effective than would be individual control agents. For this to occur, biocontrol agents must either have additive effects or achieve synergistic effects through interactions that increase their collective impact on pest populations [61]. Although constructing biocontrol guilds comprised of distinct functional groups of biocontrol agents will favor parsimony in multiple release programs, it does not ensure additive or synergistic effects that increase control. For example, synergistic effects that increase the overall effectiveness of biocontrol might arise from behaviors of biocontrol agents [61] or pest responses that are independent of biocontrol functional group. If we are to deploy multiple biocontrol agents effectively, more research on community aspects of multispecies predator-prey interactions [61–63] is needed to understand how predator complexes function as natural enemies. Additionally, comparative studies examining invasive pests in their native and introduced ranges would help us to understand when escape from natural enemies is the mechanism for invasiveness versus other mechanisms [24,64–66], to determine which invaders are most susceptible to control by natural enemies and which natural enemies are most likely to be effective biocontrol agents. Host specificity is an important attribute for safe, effective biocontrol [14,15,67]. However, host-specific biocontrol agents can impact nontarget species through indirect effects arising from ecological replacement, compensatory responses, and food-web subsidies, and nontarget effects arising from such subsidies can profoundly impact native systems. Strong, host-specific biocontrol agents should be the paradigm for future biocontrol.

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