

# Indirect Interactions, Community Modules and Biological Control: a Theoretical Perspective

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## Abstract

Indirect interactions are almost inevitable in any multi-species community. Understanding the implications of such interactions is a challenging task, in light of the very large number of ways species can be tied together in complex food webs. One approach to this complexity is to focus on strong interactions among a relatively small number (e.g. 3–6) of species interacting in defined configurations: community modules. In recent years, the discipline of community ecology has developed a substantial body of theory focused on such modules. Modules often clearly describe the basic features of empirical systems, particularly in simplified anthropogenic landscapes, and also help to isolate and characterize key processes driving the dynamics of more complex communities. In this chapter, we draw out a number of insights from ecological studies of modules which we believe are relevant to biological control. We emphasize in particular the module of 'shared predation', where a natural enemy attacks two or more species of prey. Theoretical studies suggest a number of 'rules of thumb', including: (i) the greatest risk to non-targets may occur from control agents that are only moderately effective on the target; (ii) targets with a high reproductive capacity can indirectly endanger non-targets; (iii) there can be transient phases of extinction risk for non-targets during the establishment phase of control agents, particularly for species with high attack rates; (iv) at a landscape scale, mobile agents can endanger the fate of non-targets at sites

other than the area of control; (v) using specialist natural enemies can pose risks to non-targets, if there are generalist resident predators/parasitoids which can exploit these introduced agents. The theoretical models help to highlight circumstances when these effects should be particularly strong.

## Introduction

Recent years have seen a growing chorus of concerns about classical biological control because of the potential harm posed by non-indigenous control species, introduced to control exotic pests but also influencing the lives of other, non-pest species (Simberloff and Stiling, 1996; Williamson, 1996; Hawkins and Marino, 1997; Frank, 1998; Hopper, 1998; Philogène, 1998; Thomas and Willis, 1998; Walter *et al.*, 1998). Our purpose in this chapter is to stand back from the details of particular systems and cost/benefit analyses, so as to provide a perspective from more general theoretical studies in community ecology. We will not dwell on the details of equations, but rather on broad conceptual insights in community ecology which we believe are pertinent to indirect effects of biological control.

Generalizations in ecology are often necessarily cast at a broad scale, but are hardly ever universally true (Lawton, 1999). The laws or rules that we do have are often contingent in form, tailored to particular sets of organisms and given structures of interactions and environments. A broad message emerging from community ecology in recent decades is that indirect interactions among species are pervasive in natural communities (Bender *et al.*, 1984; Polis and Holt, 1992; Menge, 1995, 1997). Such interactions are often quantitatively as important as direct trophic or interference interactions, and can occur even over short time-scales (Menge, 1997). Indirect interactions arise because most species live in a complex web of interactions, and in principle this makes it difficult to predict the response of even well-understood systems to environmental change (Yodzis, 1988). Some ecologists even despair of identifying general patterns (Polis and Strong, 1996). Despite these complexities and difficulties, however, we would argue that the development of management tools to address specific biological control problems can draw useful messages from the basic insights of theoretical studies of indirect interactions. Such studies identify major, repeatable themes which biological control practitioners can incorporate into their conceptual repertoire.

## Classical biological control is deliberate 'community assembly'

The use of non-indigenous species in pest control, and the potential impact of such species on native non-target species, represents an applied

analogue of a basic theme in ecology, *assembly dynamics*. Over time, local communities necessarily arise from a historical process of assembly (Holt, 1993; Ricklefs and Schluter, 1993), involving both colonization from larger biogeographical regions and local extinctions. A central theme of community ecology (in some ways, its most basic paradigm (Law and Morton, 1996)) is that local communities (defined at spatio-temporal scales where individuals can potentially interact) are restricted subsets of larger regional pools (Roughgarden and Diamond, 1986). This restriction may arise due to chance, or because species' basic autecological requirements are not met at a particular site, or because of interactions between invaders and residents. In the last case, community structure (i.e. non-randomness in species composition) arises because of patterns in the success or failure of repeated invasion attempts (e.g. exclusion of invaders by competition with or predation from resident species).

Understanding community assembly in general requires one to consider three distinct processes. First, one focuses on the ability of an invading species to increase when rare – *establishment*. If a given species always declines rapidly to extinction whenever it attempts to colonize, it will not become a member of the local community. Second, following establishment, one examines the effects (direct and indirect) of the successfully invading species upon the local community – its *impact*. In some cases, invasions may have little impact. For instance, a commensal specialized to a single species may invade and have very little impact on the resident community, so there is a simple additive increase in local species richness. If, by contrast, a highly effective predator or competitor for local resources invades, a single invasion can unleash a wave of local extinctions, so local species richness declines. Third, in many circumstances one must explicitly consider flows of individuals and resources among spatially distinct communities – *landscape context* (Holt, 1996; Polis *et al.*, 1997). Some species may be present in a local community because of sufficient rates of recurrent immigration (the 'mass effect' of Shmida and Wilson, 1985). This can quantitatively influence local dynamics in a wide variety of ways, for instance by providing alternative prey for resident predators (Huxel and McCann, 1998). Other species may only persist precisely because they can utilize a variety of habitat types (Holt, 1997a). The importance of these effects depends on many different aspects of landscapes (e.g. patch areas and shapes, connectivity) and is an active area of research (Polis *et al.*, 1997).

These three fundamental aspects of community assembly processes – establishment, impact and landscape context – are also basic considerations in evaluating potential indirect effects of introduced biological control agents. We will focus on impact and landscape context, rather than establishment.

## One approach to complexity: community modules

In the past few decades, there has been substantial growth in our understanding of the dynamics of single populations (e.g. in the conditions that promote chaos or stability, or in dealing with the intricacies of stage-structured dynamics). The discipline of community ecology is not so well developed. The basic reason for this is that ecological communities are incredibly complex entities. We are all familiar with depictions of food webs articulated at the species level, which resemble a tangled plate of spaghetti (e.g. Winemiller, 1990; Closs *et al.*, 1999); merely compiling the information to construct such webs involves a gargantuan effort, and at the end one is still far from a clear understanding of the dynamics governing the system. We have argued that a useful conceptual way-station between the relative simplicity of single-species dynamics and the almost overwhelming richness of entire communities is the analysis of *community modules* (Holt, 1997b). The basic idea is that there are recurrent structures, involving a small number (e.g. 3–6) of species interacting in a specified pattern, often (although not necessarily) strongly. These modules involve multi-species extensions of basic pairwise interactions (e.g. host–parasitoid dynamics).

Figure 2.1 depicts a smorgasbord of some of the most familiar of these modules, cast so as to be relevant to biological control. There are a number of rationales for focusing on community modules. First, empirical systems may closely match the structure of a module. Subwebs of natural communities with strong interactors and well-defined functional groups often quite naturally fit a particular module (e.g. Evans and England, 1996). Given that biological control agents are deliberately chosen to have a strong interaction with at least one other species – the target species one would like to control – then a modular structure may readily be discerned in many control situations. Second, modules can be viewed as building blocks of full, complex communities. Close analyses of modules permit one to isolate certain key processes which may be general drivers of the dynamics of entire communities. The discipline of community ecology is replete with theoretical and empirical studies of community modules (e.g. May and Hassell, 1988; Holt and Lawton, 1993, 1994; Holt, 1997b). The broad aim of the remainder of this chapter is to relate insights from this body of work in basic ecology to the applied problem of indirect impacts of biological control. We will focus in particular on risks posed by shared predation, which may be the most general situation in biological control where a consideration of indirect interactions is important. Murdoch and Briggs (1996) note that although ecological theory has not historically been all that useful in the practice of biological control, recent theoretical advances in population dynamics do have important messages for practitioners. We suggest that the same is true for theoretical studies of multi-species interactions.

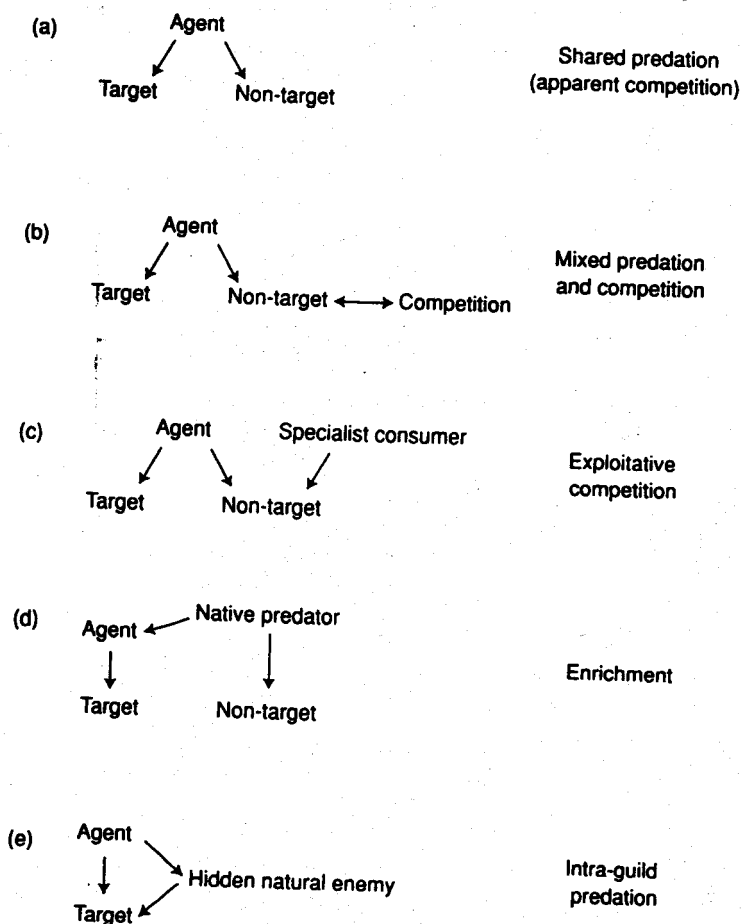


Fig. 2.1. Community modules. The word 'module' refers to a specified structure of interactions among a small number of species. A number of modules are likely to describe indirect impacts of biological control. For simplicity, the lines indicate that two species interact (a more detailed food web diagram would have pairs of arrows and signs, describing reciprocal impacts of each species). (a) Shared predation: impacts upon non-targets reflect interactions between agent and target (as in apparent competition). (b) Mixed predation and competition: impacts upon non-targets are aggravated by the presence of competing species. (c) Exploitative competition: the agent exploits a non-target species which is required by another non-target consumer. (d) Enrichment: introduction of the agent enriches the diet of a native predator, with impacts upon non-target prey (a more elaborate version of the shared predation module). (e) Intra-guild predation: the agent both competes with and attacks a non-target natural enemy.

## Shared predation: identifying extinction risks for non-target prey

The 'shared predation' module focuses on situations where a natural enemy can attack two or more species of prey (Fig. 2.1a). A recognition of the potential importance of shared natural enemies has a long pedigree in entomology (e.g. Banks, 1955; van Emden and Williams, 1974). There is a large theoretical and empirical literature on the consequences of shared predation and parasitism for species coexistence (e.g. Holt, 1977, 1984, 1997a; Holt and Lawton, 1994; Begon and Bowers, 1995; Bonsall and Hassell, 1999; Courchamp *et al.*, 1999; Namba *et al.*, 1999). This module pertains very broadly, for instance, to: (i) a herbivore attacking two or more plant species (e.g. Louda *et al.*, 1997; Louda, 1998); (ii) a parasitoid attacking two or more host species (e.g. Müller and Godfray, 1999a); (iii) a hyperparasitoid sustained by two primary parasitoid species (e.g. van Nouhuys and Hanski, 2000); (iv) an internal pathogen capable of infecting multiple hosts (e.g. Thompkins *et al.*, 1999); (v) predatory arthropods attacking several prey arthropods (e.g. Karban *et al.*, 1994); (vi) vertebrate predators attacking vertebrate prey (e.g. Hoi and Winkler, 1994; Lawler *et al.*, 1998).

Structurally, there are three basic situations where risks due to shared natural enemies naturally arise in biological control:

1. Within a community, an introduced specialist agent may itself be consumed by resident generalist natural enemies. This does not directly match the labels of Fig. 2.1a, which refers to one agent attacking multiple target species, but is structurally similar in that there can be indirect interactions between species at one trophic level mediated through responses by a higher trophic level. If the introduced agent can be sustained at high abundance upon the target species, this could indirectly enrich the diet of resident natural enemies, which in turn then attack more effectively other resident prey or host species. An example of this effect has recently been reported by van Nouhuys and Hanski (2000). Experimental introductions of *Cotesia glomerata*, a parasitoid on pierid butterflies, were made into populations of the wasp *Cotesia melitaeorum*, which parasitizes a nymphalid butterfly, *Melitaea cinxia*. This increased greatly levels of attack by a hyperparasitoid, *Gelis agilis*, even to the point of local extinction for *Cotesia*. Studies of natural host-parasitoid assemblages reveal that hyperparasitism is common (Müller *et al.*, 1999), providing a route for impacts of introduced specialist agents upon other species. Schönrogge *et al.* (1996) suggest that an additional risk of invasion by an alien herbivore is that it can enhance the abundance of native inquilines and parasitoids, thus placing at risk an array of native hosts. We are unaware of any screening programmes that assess the potential of this kind of risk factor in biological control.

2. Within a community, an agent may attack one or more species other than its putative target (see Fig. 2.1a). The danger of this effect is of course widely recognized (Howarth, 1990). What is not so widely recognized is that the magnitude of the danger posed to non-targets can be strongly influenced by the population dynamics of the target-agent interactions, and so will often involve indirect interactions among targets and non-targets. Below, we will use simple models to illustrate this basic point.

3. Risks due to shared predation can reach across habitat boundaries. Dispersal by introduced agents can couple dynamics of spatially segregated species. A habitat in which an agent interacts persistently with a target species can provide a source for immigration into nearby habitats with non-target but vulnerable species, or colonization into distant locales. The magnitude of these effects, once again, will depend upon the details of local population dynamics, as well as upon rates of spatial flows of individuals in heterogeneous landscapes. These effects can also be demonstrated with relatively simple models.

## Disparate impacts of shared predation

Theoretical studies of the shared predation module suggest the following general, qualitative insight: the rate of attack by a generalist natural enemy upon a focal victim species depends upon: (i) the entire suite of victims sustaining that enemy, and more precisely their abundances, productivities and organismal traits relevant to attack rates; (ii) other aspects of population regulation; and (iii) the details of enemy behaviour. Because our concern is basically with the risk of species extinction, it is useful to concentrate on the conditions for a focal non-target species to increase when it is rare.

For simplicity, we will focus on situations where there is a single target species, and a single non-target species at risk. For a species with continuous generations, the per capita growth rate when rare can be described qualitatively (Holt and Lawton, 1994) by  $r - a(N)P(N)$ , where  $r$  is the intrinsic growth rate of the non-target species,  $a(N)$  is the attack rate per enemy on the non-target species, expressed as a function of abundance of the target species,  $N$ , and  $P(N)$  is the abundance of the control agent, which also depends upon the target species. [A technical aside: in actual models, predator abundance may not be expressed mathematically as a direct function of prey abundance, but it usually will indirectly depend upon consumption of prey and thus prey abundance, cumulated across predator generations.] For a species to be maintained in the community, one must have  $r > a(N)P(N)$ . All else being equal, one expects non-target species to be most at risk when: (i) the non-target has a low intrinsic growth rate (which makes it difficult for it to replenish losses); (ii) the natural enemy has high attack rates upon the non-target, even when the non-target is rare (this is most likely if the natural enemy is not easily satiated, or does not

show switching behaviour; Murdoch and Oaten, 1975); and (iii) a high abundance of the natural enemy is sustained by the target species. The last effect is the key ingredient in *apparent competition*, the reduction in one prey or host species because of heightened attacks permitted by the presence of an alternative prey or host (Holt and Lawton, 1994).

Empirical studies of shared predation in biological control reveal a wide range of potential outcomes for shared predation. Sometimes, shared predation implies relaxed predation on each species. An example of this was described by Bergeson and Messina (1997) for lacewing (*Chrysoperla plorabunda*) predation upon two aphid species. Adding bird-cherry aphids (*Rhopalosiphum padi*) to treatments with predators increased the per capita growth rate of the Russian wheat aphid (*Diuraphis noxia*). Two crucial facts about this experiment are that the experimental treatment involved changes over short time periods, relative to predator generation length, and that the experiments were in a greenhouse, precluding predator aggregation from external sources. Predator numbers were thus fixed, and the only indirect interaction between the two prey was via behavioural responses by predators to the two prey types (e.g. saturating functional responses, switching, shifts in microhabitat use). In a follow-up study, Bergeson and Messina (1998) showed that non-target prey in the field also hampered the short-term effectiveness of biological control. In circumstances where predators have weak or negligible numerical responses, or where a study is conducted over short time-scales, one should often expect to observe indirect mutualism between alternative prey or hosts (Holt and Lawton, 1994).

In contrast, in a manipulative field experiment, Hanna *et al.* (1997) showed that a focal species, the Pacific spider mite (*Tetranychus pacificus*) was substantially depressed in local abundance by the introduction of a second species, the Willamette spider mite (*Eotetranychus willamettei*), because of a strong numerical response by the predatory Western orchard mite (*Metaseiulus occidentalis*). This study exemplifies a growing body of experimental work in field situations demonstrating the capacity of strong, indirect negative interactions between prey species sharing predators. For instance, a considerable number of recent studies have shown that the dynamics of aphid species utilizing different host species (thus precluding direct or exploitative competition) can be linked by shared natural enemies (Evans and England, 1996; Müller and Godfray, 1997, 1999a,b; Rott *et al.*, 1998). For instance, Müller and Godfray (1999b) showed that two species of aphids (*Aphis jacobaeae* and *Brachycaudus cardui*) were quite rare or absent during a long-term survey of a study site, despite their abundance in nearby habitats and availability of suitable host species. Using predator exclusion cages, they demonstrated that this local rarity was due to resident predation. Other experiments using direct manipulations of prey (Müller and Godfray, 1997; Rott *et al.*, 1998) suggest that this exclusion reflects numerical responses by predators to prey. The review by Howarth (1990)



includes numerous examples in which it is reasonable to suspect that alternative prey, by sustaining predator populations, permit the suppression of focal prey species; hence, the indirect interaction between prey of apparent competition (Holt, 1977; Holt and Lawton, 1994). For instance, the coconut moth *Levuana iridescens*, endemic to Fiji, was driven extinct by the introduced tachnid fly *Bessa remota*: the fly is still common, presumably because alternative hosts are sufficiently available, though the taxonomic identity of the major surviving hosts on Fiji is unknown.

It should be noted that in some circumstances, the indirect interaction of apparent competition is essential for effective biological control in the first place. Settle *et al.* (1996) experimentally demonstrate that alternative prey, available throughout the year, help facilitate generalist predators in maintaining control of tropical rice pests, which are more seasonally pulsed. When a control agent is first established, its persistence may crucially depend upon its ability to utilize alternative species in addition to the target species (Obrycki and Kring, 1998). Moreover, a consideration of indirect interactions may contribute to the value of biological control in the first place. For instance, if the target species is a superior competitor, a natural enemy which selectively attacks that species can promote persistence of native inferior competitors (Mogi and Chan, 1997); this effect will be facilitated if the natural enemy can be sustained on these alternative prey. Indeed, indirect interactions between resident prey mediated through resident natural enemies may be a key factor in the ability of alien species to spread in the first place (Yela and Lawton, 1997). However, in this chapter our focus is on worrisome negative consequences of indirect effects of control.

## Simple messages from theory

### Message 1

Even simple models illuminate different aspects of the potential negative impacts of shared predation. The first message we illustrate is: 'intermediate levels of control may pose the greatest risk for non-targets'. In selecting control agents, one can readily assess attacks in controlled laboratory settings, without being able to predict effectiveness of control in the field. Consider a group of potential control agents consisting of relatively specialized predators. When introduced, each of these predators will attack a target pest species, but they vary in their effectiveness. Only one will be selected for introduction. Although relatively specialized, these predators can also incidentally attack a second non-target prey species, with negligible reciprocal effects of such attacks on the predator's own dynamics. Given the large number of potential non-target prey species present in many settings, it is impractical to screen them all for vulnerability.

The impact of any of these predators upon non-targets should scale with the abundance of the predator, as sustained by interaction with the target prey. Assume that all these predators have a fixed per capita attack rate upon the non-target. Then, the total mortality imposed by the predator upon the non-target prey will be directly proportional to predator density. For a broad range of models, the maximal predator density sustained by a target prey density is realized at intermediate levels of control. A specific example of this effect is shown in Fig. 2.2, where we plot both  $q$  (an inverse measure of control) and  $P^*$  (predator abundance) as a function of per capita attack rate upon the target species for a prey-dependent Lotka–Volterra model. In general terms, when individual predators are highly effective at capturing the target prey, the predator population as a whole can more readily overexploit that prey; at equilibrium, fewer predators are then sustained by the target population. A predator that is very ineffective, of course, is unlikely to persist at all. The maximal predator population arises when individual predators have intermediate efficiency at capturing prey.

The basic reason for this effect is that equilibril predator abundance tends to increase with total prey production, which in turn is maximized when prey numbers are at intermediate levels – neither near their intrinsic

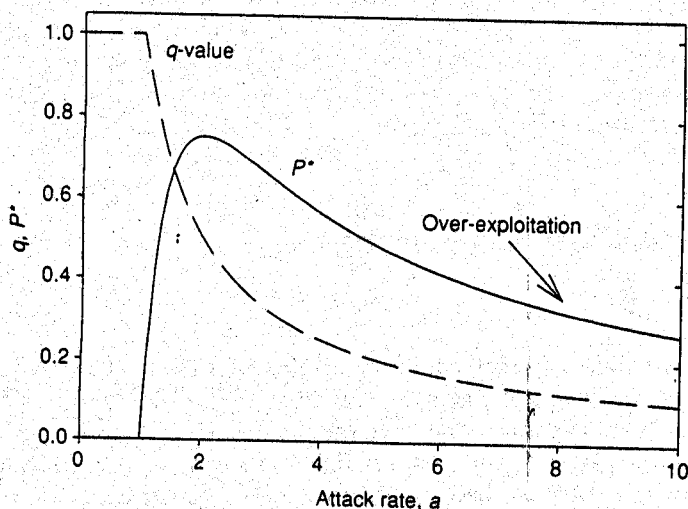


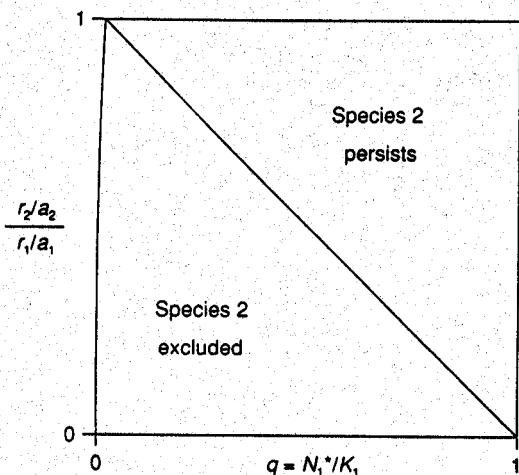
Fig. 2.2. A little control can be dangerous. The quantity  $q = N^*/K$ , where  $K$  is target carrying capacity (target abundance in the absence of control), and  $N^*$  is target abundance after control is established. The quantity  $a$  is the attack rate, per agent, per target.  $P^*$  is the abundance of the control agent (e.g. a predator). The example depicted assumes a Lotka–Volterra predator model, with logistic target prey growth and linear functional responses. At low attack rates, the predator cannot persist. At high attack rates, the predator overexploits its prey. Maximal predator abundance is observed at intermediate levels of attack, corresponding to intermediate levels of  $q$ .

carrying capacity, nor too near zero. In other words, predator abundance is maximized at intermediate control (e.g.  $q \approx 0.5$ ) of the target prey. Hence, among our array of potential control agents, the greatest risk of incidental predation comes from those agents which are only moderately effective in control, because these are the ones that will not overexploit their prey. Murdoch and Briggs (1996), in reviewing models of specialist parasitoid-host interactions, suggest the following criterion for identifying an effective biological control agent: 'pest equilibrium density is suppressed most by the parasitoid species that needs the fewest host individuals to allow a female parasitoid to replace herself in the next generation'. A comparable rule-of-thumb for systems with multiple prey or host species is that the greatest indirect damage should be observed, for a given enemy-victim interaction, by that host species which can sustain the highest density of natural enemies (Holt *et al.*, 1994).

It is intriguing that reported cases of indirect agent impacts often do involve agents of intermediate effectiveness upon target species (see Lynch *et al.*, Chapter 6, this volume). We suggest that this tentative empirical generalization is consistent with existing predator-prey theory. And we caution that the above result has to do with predators with a fixed per capita attack rate on a non-target; agents with a high attack rate across all prey species will tend to overexploit all their prey, and so obviously should not be introduced in biological control.

## Message II

The second simple message is that: 'measuring predator preferences does not suffice to estimate potential indirect impacts on alternative hosts/prey'. Assume that the predator can potentially persist on either the target or non-target species, taken alone, and that the two prey species have separate resource bases, and so do not directly compete. Let species 1 be the target species, and species 2 the non-target. Figure 2.3 shows results for a simple model. The model assumes continuous generations, spatially well-mixed prey populations, logistic prey growth, and linear functional responses to each prey taken separately or together (with no refuges from predation). The figure depicts how the conditions for coexistence of the two prey species vary as a function of the level of control of the target species (assuming the other species is absent). What determines persistence of the non-target is the value of a compound parameter, the ratio  $r/a$ , for the non-target, as compared with the target. If the non-target has the higher value for  $r/a$ , it will not be excluded. If the non-target has a lower value for  $r/a$ , then given effective control of the target species, the non-target is in danger of exclusion. If the predator can effectively limit the numbers of either prey species, considered one at a time, prey species coexistence is unlikely. Non-target species are vulnerable if: (i) one prey has a much

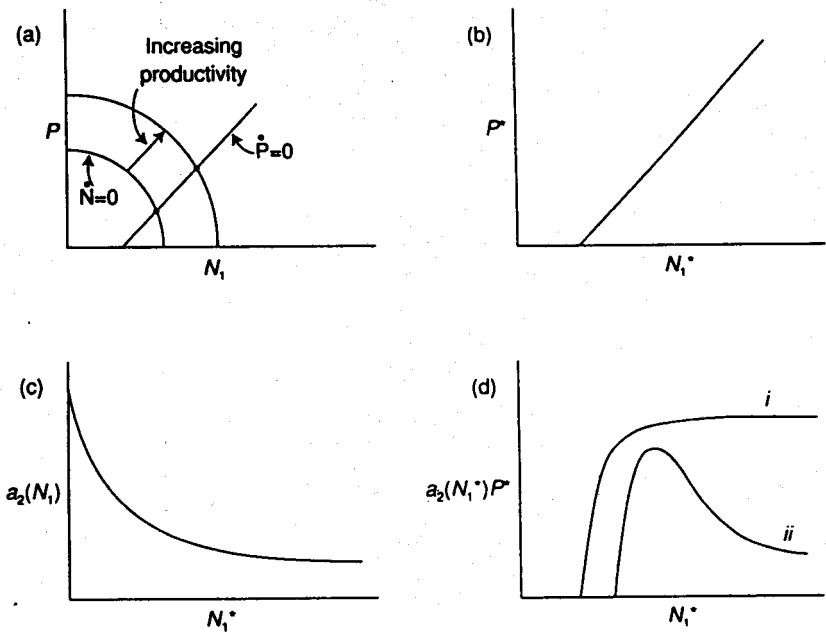


**Fig. 2.3.** Conditions for two prey species to coexist in apparent competition. The model (analysed in Holt, 1977) assumes logistic prey growth and linear predator functional responses. The quantity  $r$  is the intrinsic growth rate, and  $a$  is the attack rate. The quantity  $r/a$  can be interpreted as a measure of resistance by a prey population to predation, taking into account its ability to replenish its numbers via recruitment. We assume that prey species 1 has the higher value for  $r/a$ . Prey species 2 persists only if it has a sufficiently high value of  $r/a$ .

higher value for  $r/a$ ; (ii) one prey type is particularly vulnerable to predation  $a$ ; (iii) the prey species with higher  $r/a$  also has a high carrying capacity; and (iv) the predator is very effective on both prey species. Similar results arise in a variety of circumstances (e.g. alternative hosts for parasitoids (Holt and Lawton, 1994) or alternative hosts for pathogens (Holt and Pickering, 1985)). The simple take-home message is that knowledge of relative attack rates (preferences) alone is a poor guide to predicting the actual risk of the non-target species.

### Message III

The third message is that 'field assessment of risk to non-targets concentrated in regions of high target abundance may underestimate risk in other conditions'. Apparent competition does not automatically occur whenever there is shared predation or parasitism. If: (i) predators easily saturate (or 'switch'); and (ii) predators experience strong density-dependence, for reasons other than via exploitation of prey, then alternative prey may experience indirect mutualism (because of a 'dilution' effect on predator attacks of alternative prey; Holt and Lawton, 1994). Figure 2.4 uses a graphical model to display this effect (after Holt, 1997b). The basic strategy is first to analyse the interaction between the target species and the control



**Fig. 2.4.** A graphical model depicting complex interactions between prey species (modified from Holt, 1997b). (a) A standard isocline predator-prey model, with direct density-dependence in the predator; higher prey productivity pushes the prey isocline away from the origin. (b) As prey productivity increases, both  $N_1^*$  (equilibrium prey abundance, for resident prey) and  $P^*$  (equilibrium predator abundance) increase. (c) The attack rate upon an invading prey species, per predator, per individual of the invading prey declines with increasing abundance of resident prey. (d) The net attack rate combines predator numbers and per predator attack rates. The former increases with resident prey numbers (see b), whereas the latter declines (see c). Overall predation is greatest at intermediate resident prey numbers. The magnitude of the 'hump' effect depends upon the details of the model (e.g. line *i* arises with small handling times, and line *ii* with large handling times).

agent, and then to evaluate potential impacts upon a second, non-target species, whose numbers are sufficiently rare that it does not influence the predator's own dynamics.

Figure 2.4a shows a standard predator-prey graphical isocline model, for a resident predator (the control agent) interacting with a resident target prey species. The target prey isocline is that combination of predator and prey densities where the prey has a zero growth rate. Because prey can compete for resources or otherwise experience direct density-dependence, there will be a maximal prey population size (its carrying capacity); this is the intersection of this isocline with the prey axis. The intersection of this isocline with the predator axis is the maximal number of predators that this prey could confront, and still persist. In more productive environments,

one expects the prey carrying capacity to be higher, and the prey to be able to withstand higher predator numbers. If the predator can be satiated on this prey, then the prey isocline tends to bow away from the origin (and may even show a hump). From the predator's perspective, there will be some density of prey below which it cannot persist; this is the intersection of the predator isocline with the prey axis. If there are direct interactions among predators (e.g. interference or cannibalism) as predator numbers rise, there must be more prey for the predator population to remain in equilibrium; the predator isocline thus has a positive slope. The system equilibrates where the two isoclines cross. We assume that the presence of direct density-dependence in predator and prey suffices for the system as a whole to tend to remain stable. Given small environmental fluctuations, the equilibrium provides a reasonable approximation of time-averaged abundances. Thus, along a gradient in productivity, one expects to see increases in both predator and target prey numbers (Fig. 2.4b).

We now examine the impact of predation upon the non-target. Assume that the predator can be satiated, or has limited handling time. As target prey numbers rise, each individual predator's attacks will thus be diluted. Figure 2.4c shows how attacks, per predator, per prey, upon the non-target prey species should vary as a function of abundance of the target prey. If predator numbers were fixed, non-targets would enjoy lower predation pressure with higher abundance of the target species. However, given our assumptions, predator numbers should tend to rise with increasing target prey numbers (Fig. 2.4b). The net mortality (per prey) imposed on the target is the attack rate times the number of predators. In effect, we can multiply the relationships of Fig. 2.4b and c to produce Fig. 2.4d, which expresses the net rate of predation upon the non-target species (per individual of the non-target) as a function of the abundance of the target species. In general, one expects this relationship to be humped.

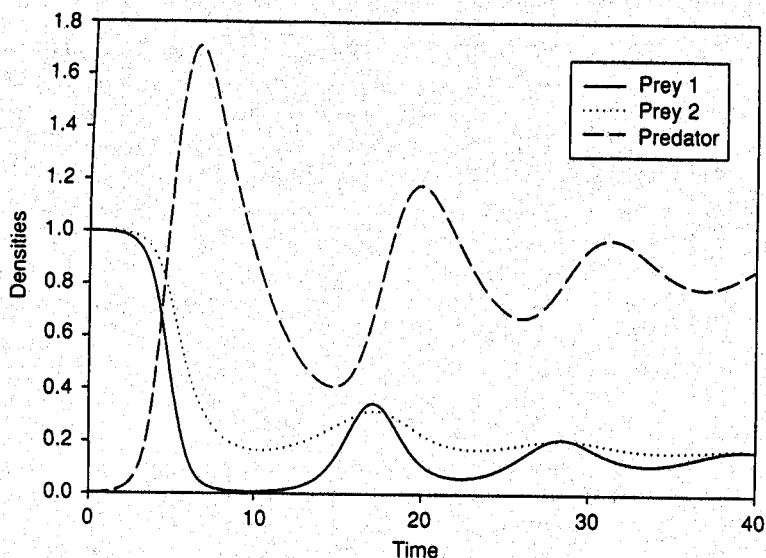
Over a given range of productivities, with little saturation and weak direct density-dependence in the predator population, the risk experienced by a non-target species tends to be greater if the target species has higher productivity (because this sustains the greatest number of natural enemies). However, if natural enemies readily saturate, and experience direct density-dependence (e.g. due to interference), the greatest risk to non-target prey may be associated with intermediate levels of productivity of the target prey. If the target population is sufficiently abundant, the agent may be limited by factors other than food availability (i.e. have a weak numerical response, thereby permitting indirect mutualisms, say because of saturating functional responses, to operate unchecked). Assessments of risk to non-targets, which focus on areas of high abundance of the target species, may underestimate risk to non-targets in areas with low target abundances. These realistic complications in predator-prey and other natural enemy-victim interactions may make it difficult to generalize across sites, even for the same set of species.

## Indirect interactions influence transient risks during agent establishment

The above simple messages were derived from theoretical studies of models for shared predation, evaluated at a long-term stable equilibrium. Predator-prey systems are of course prone to strong oscillations in abundance, which can alter the expected direction of interactions among species in shared predation (Abrams and Roth, 1994; Abrams *et al.*, 1998). Moreover, all biological control systems involve a deliberate introduction, which means there is a transient phase of non-equilibrium dynamics as the agent increases in numbers, driving shifts in target and non-target species. Transient risks of extinction may arise during the initial phases of agent establishment and be aggravated by indirect interactions. A general feature of natural enemy-victim models is that a very effective enemy is expected to increase when rare, and overshoot its long-term equilibrium abundance (R.D. Holt, unpublished results). This implies that there may be a transient phase of intense predation upon non-target species, posing a risk of extinction even for non-target species able to persist with the introduced natural enemy in a long-term equilibrium (see also Lynch *et al.*, Chapter 6, this volume).

An example of this phenomenon is shown in Fig. 2.5. The example shown assumes the same basic model form as used for Fig. 2.3 (logistic prey growth, etc.). In this model, if two prey species have equal values for the compound parameter  $r/a$ , they are expected to have abundances in equilibrium with the predator that are proportional to their carrying capacities without the predator (Holt, 1984). In the example shown, the two prey species have equal carrying capacities and so should have equal abundances when in equilibrium with the predator. However, en route to this equilibrium the trajectories of two prey species can strongly diverge. The example depicted has prey species 1 with a higher attack rate than prey species 2, and a correspondingly higher intrinsic growth rate. Following introduction of the predator, its numbers rise while those of the two prey decline. The prey with higher  $a$  (species 1) experiences a long period of low densities, before gradually increasing with oscillations back to its expected long-term equilibrium. This highlights the importance of absolute attack rates in determining transient risks.

Numerical studies suggest that the pattern shown in Fig. 2.5 is generally observed in transient dynamics: effective predators can impose transient phases of extinction risk for prey as colonization occurs. Because of these transients, extinctions may occur due to demographic stochasticity at low numbers (an effect not captured in the deterministic model used to generate Fig. 2.5). As an introduced control agent moves across a homogeneous landscape with both target and non-target species throughout, there could be local extinctions of some non-target species in some locales, but not others, because of the chance vicissitudes of extinction risk during the



**Fig. 2.5.** A numerical example of transient risks of introduced natural enemies. The model is the same as in Fig. 2.3. The two prey have equal carrying capacities, and equal values for  $r/a$ , but prey 1 experiences a higher attack rate. The predator is introduced at time zero. At equilibrium both prey have the same abundance, but during the transient dynamics the species experiencing higher attacks suffers a disproportionate reduction in numbers.

initial phases of agent colonization. One long-lasting signature of transient dynamics may be great variability among sites in the realized community impacts of generalist control agents.

### **Landscape-scale indirect effects: the importance of community openness**

So far, we have considered principally modules in local communities, for instance where a predator encounters each of several prey types during its daily foraging activities. There is increasing recognition of the importance of placing local community dynamics into broader landscape and even biogeographical scales (Ricklefs and Schluter, 1993). Useful insights come from examining community modules in a spatial context. In general, spatial segregation of species in heterogeneous landscapes promotes coexistence under shared predation (Holt, 1984; Bonsall and Hassell, 1999). However, following introduction, spatial flows of control agents from areas where control is desirable can potentially suppress non-target species in areas spatially removed from the focal control area. Such



spillover, when it occurs regularly, in some ways is analogous to regular augmentation in biological control (May and Hassell, 1988).

Exclusion due to spillover through apparent competition can be illustrated with the following continuous-time Lotka-Volterra model, where it is assumed that the agent is present in a source habitat, and has a constant per capita rate of movement into a 'sink' habitat (with no back-flow, an assumption that greatly simplifies the algebra).

Source habitat dynamics:

$$\text{Predator: } \frac{dP}{dt} = P[abT - (e + d)]$$

$$\text{Target prey: } \frac{dT}{dt} = rT(1 - T/K) - aPT$$

Sink habitat dynamics:

$$\text{Predator in non-target habitat: } \frac{dP'}{dt} = P'[a'b'N - m] + eP$$

$$\text{Non-target prey: } \frac{dN}{dt} = rN(1 - N/K') - a'PN$$

Here,  $P$  is the density of the introduced agent in the source, and  $T$  is the density of the target species. In the sink,  $P'$  is the density of the agent, and  $N$  the density of the non-target. The quantity  $eP$  is the 'spillover' of predators from target to non-target populations. We assume that without such regular immigration, the predator could not persist on the non-target species (i.e.  $K' < m'/a'b'$ ). At equilibrium, the non-target host in the adjacent habitat is excluded (i.e. unable to increase when rare) if:

$$(e/m') (r/a) (1 - q) > r'/a'$$

where  $q = T^*/K$  measures the effectiveness of biological control on the target species. Assume effective control (namely,  $q$  near 0). Exclusion of a non-target species due to predator 'spillover' from a habitat where the predator is sustained with a target species is more likely if: (i) the source habitat is more productive than the sink habitat (i.e.  $r > r'$ ); (ii) the non-target prey is strongly attacked (high  $a'$ ); (iii) predator movement rates are substantial (moderately high  $e$ ; at very high  $e$ , predator numbers are depressed because of emigration); and (iv) predator mortality in the non-target habitat is low (low  $m'$ ). Of these, (ii) and (iv) also make it more likely that the predator can successfully colonize and suppress the non-target prey, even without recurrent immigration. It is interesting that if  $r = r'$ , and  $a = a'$ , one can still see exclusion due to apparent competition 'at a distance' if  $e > m'$ . In analogous fashion, dispersal of the control agent out of the target habitat can lead to competitive exclusion of other natural enemies in other habitat, if the target habitat is sufficiently productive.

## Transient dynamics in shifting landscapes

In heterogeneous landscapes, land-use changes can lead to transient phases of enhanced extinction risks. We will not examine this effect in any detail, but it is useful to consider a scenario where there is biological control established in a landscape with ongoing habitat destruction and fragmentation. If landscape change occurs rapidly, and predators are mobile and respond to a worsening environment by leaving, such movement permits predators to aggregate in the remaining habitat fragments. As with the introduction of predators in the first place, but to a more extreme extent, this leads to a transient spike in predator abundance in the recipient habitat, well above the numbers sustainable on the local prey base. As predators decline from this spike, there can potentially be a large reduction in prey numbers in the recipient habitat. In general, the impact of such transient dynamics on the recipient habitat will be greater if the source has a larger intrinsic growth rate or carrying capacity (R.D. Holt, unpublished results). The main conclusion is that landscape dispersal can lead to transient phases of high extinction risk due to an influx of enemies which attack prey found in the habitat fragments. This greatly increases extinction risks if the habitat fragments are low in the productivity of resident prey, and the predators are moving out of newly disturbed, productive habitats.

Finally, we briefly consider likely effects of shared predation at the scale of regional dynamics. Since the time of Huffaker (1958), it has been recognized that strong predator-prey interactions may persist because of metapopulation dynamics, wherein recurrent colonization balances local extinction (a kind of 'permanent transiency'). Metapopulation dynamics can lead to prey exclusion in some habitats. Formal analysis of a metapopulation model of this effect is described elsewhere (Holt, 1997a). Here we just describe the main results. The basic scenario is that the landscape consists of a mosaic of two kinds of discrete habitat patches, separated by unsuitable habitat. For each habitat, there is a single species present and specialized to that habitat. One of these species is a target in biological control, the other is a non-target. An agent is introduced which effectively limits the target species' local abundances, leading to local extinctions, but the agent can also exploit the non-target. The basic agent-target interaction persists because of metapopulation dynamics, with colonization balancing local extinctions.

A metapopulation by definition involves dispersal. Many organisms make mistakes during dispersal. Colonization by control agents into non-target habitats can increase extinction rates of non-target prey, reducing patch occupancy (the fraction of landscape occupied) of the non-targets. This can even lead to regional extinction. This indirect exclusion of one prey by another can occur even though the two prey species are never found in the same habitats, and even though predators are never found in empty habitats suitable for the excluded prey species.

Regional extinction of the non-target is particularly likely if the habitat it requires is scarce in the landscape, because this reduces the potential for recolonization following extinction. The risk of extinction of non-targets is also enhanced if the level of control by agents of targets is not sufficiently severe to risk local extinction (because this increases the fraction of the landscape which can harbour the predator), and if there is an intermediate level of exploitation in each target species patch (because this increases the local population size of predators, which increases the number of colonizing predators emanating from patches occupied by the target, ending up in patches occupied by the non-target).

The landscape of the modern world is becoming increasingly dominated by human activities, in particular by habitat destruction and fragmentation. Many species will in the future be restricted to scattered habitat remnants, surrounded by agricultural and other anthropogenic landscapes. Such species will be particularly vulnerable to indirect effects of biological control efforts, mediated by the spatial 'spillover' of agents into non-target habitats.

## **Indirect interactions and evolution**

We have focused on the indirect ecological consequences of biological control. It should be stressed that comparable multi-species models are required to evaluate the potential risk of evolutionary host shifts, which could endanger non-target species which are currently safe. The direction of natural selection in the control agent will be channelled by the basic ecology of its interactions with other species, and in particular by the relative and absolute abundances of alternative hosts (M.E. Hochberg and R.D. Holt, unpublished results). Moreover, a control agent which has a large population size because it is only moderately effective at control will be able to harbour more genetic variation upon which selection can act to promote a host shift.

## **Conclusions**

Theoretical studies of the 'shared predation' community module suggest a number of 'rules-of-thumb' which need to be considered when evaluating risks posed by introduced biological control agents:

1. A control agent which is only moderately effective at limiting target species numbers may be much more abundant than an effective agent, and thus pose a greater risk of incidental attacks on non-targets.
2. Given shared predation within a given habitat, the risk of extinction is enhanced for the non-target if it has either a higher attack rate or a lower intrinsic growth rate than the target species. The important message here is

that measuring the magnitude of attack alone does not fully characterize risk to non-targets; species that have little capacity to replace additional losses (e.g. due to low  $r$ ) are differentially at risk.

3. The risk to non-targets is greater if the natural enemy experiences little density-dependence due to factors other than its own resource availability (e.g. due to higher-order predators, or direct interference). The absence of such factors increases the number of predators, parasitoids, etc., sustained by a target victim species, thus increasing the exposure of non-targets to attacks.
4. The risk to non-targets is greater if predators have high maximal attack rates at high prey abundances (e.g. little satiation). This inflates the indirect effect of target species on non-targets, mediated through a shared natural enemy. By contrast, if predators readily satiate, alternative prey can experience indirect mutualisms.
5. If (3) and (4) both hold, the greatest risk to non-targets arises if target prey species can sustain high production in the face of predation (e.g. with weak predator density-dependence, increases in prey production can greatly increase both prey and predator numbers).
6. If, instead, (3) and (4) do not hold, the risk to non-targets may actually be greater at intermediate abundances of alternative prey. Considering realistic features of natural enemy-victim interactions (e.g. predator satiation, direct density-dependence) suggests that the same species pair could exhibit either positive or negative interactions, depending upon quantitative details of the entire suite of interactions in which that pair is embedded. This is a general feature of indirect interactions in complex food webs (Yodzis, 1988), and highlights the difficulty of devising simple theoretical predictions that will work in almost all circumstances.
7. Non-target species which can coexist with a control agent at equilibrium may none the less risk extinction during transient phases of agent establishment. During these phases, absolute attack rates may matter more than relative attack rates or reproductive rates.
8. Exclusion due to shared natural enemies can occur, even if target and non-target species never co-occur in the same habitats. This threat is particularly acute for non-target species which exist in habitat fragments commingled with the habitats occupied by target species, and when the agent is only moderately effective at limiting target numbers (i.e. no overexploitation) and the target species is highly productive.
9. Utilizing specialist natural enemies does not preclude all negative effects of shared predation, because such specialists can at times themselves be prey for resident generalist enemies. This is more likely to be of concern for some natural enemies (e.g. primary parasitoids, which can sustain hyperparasitoids) than for others (e.g. many internal pathogens).

We have focused on the shared predation community module, because this pattern of interspecific interactions is at the heart of recent debates

about the dangers of biological control. We close by emphasizing that several other community modules exist (see Fig. 2.1) which isolate major avenues for indirect effects of biological control. All of these could be important in evaluating risks of biological control in some systems. Relating theoretical studies of modules to real-world control situations requires a thorough understanding of the natural history of one's system. Comparing theoretical studies of the different modules in Fig. 2.1 shows that the dynamics of a system can be qualitatively changed by adding or deleting a single strong interaction, or by altering the functional forms of relationships. It is difficult to evaluate the likelihood of this happening in general, but an awareness of how different module structures map on to different expectations of system dynamics is essential to understanding potential indirect effects of biological control. An understanding of the implications of indirect interactions in community modules should, we suggest, become part of the conceptual repertoire of biological control workers. Taking a 'modular' approach can help to crystallize one's understanding of core dynamical processes, which can then be discerned (if at times opaquely) in the working of complex communities (Hairston and Hairston, 1997; Belyea and Lancaster, 1999; Courchamp *et al.*, 1999; Persson, 1999).

Analyses of modules also suggest fresh hypotheses for empirical studies. When faced with the concrete details of real-world examples, failures in the match between theory and data provide pointers towards the development of a richer body of 'contingent theory' (Lawton, 1999), tailored to the specific details of particular communities. However, often one can discern the action of the broad forces identified in theoretical studies of modules in more detailed, realistic models. To mention one specific example, Schreiber and Gutierrez (1998) develop a realistic, physiologically based model of multi-species interactions in biological control and apply it to several biological control systems; the overall conclusions of their model (regarding competitive displacement) nicely match empirical outcomes observed in these systems, as well as the qualitative features of more abstract theoretical models. Finally, an explicit consideration of the population dynamic consequences of multi-species interactions is a necessary preamble to predicting the risk of evolutionary shifts from target to non-target species in biological control.

In closing, despite the risks of indirect interactions in biological control, aspects of which are explored in the above models, we wish to emphasize that biological control may often be the only reasonable approach to dealing with devastating pest problems (McFadyen, 1998). We hope that continued study, both theoretical and empirical, of community modules will help refine the long-term environmental soundness and sustainability of biological control efforts.

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