



# Hidden risks and benefits of natural enemy-mediated indirect effects

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Polyphagous natural enemies can mediate a variety of indirect interactions between resource populations. Such indirect interactions are often reciprocally negative (i.e. apparent competition), but the sign of effects between resource populations can be any combination of positive (+), negative (–), or neutral (0). In this article we focus on parasitoids to illustrate the importance of natural enemy-mediated indirect interactions in predicting risk and efficacy in biological control. We review recent findings to illustrate how an improved understanding of parasitoid behavioral ecology may increase model accuracy.

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Current Opinion in Insect Science 2016, 14:105–111

This review comes from a themed issue on **Parasites/Parasitoids/Biological control**

Edited by **Paul Ode** and **George Heimpel**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 15th February 2016

<http://dx.doi.org/10.1016/j.cois.2016.02.004>

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## Introduction

In the 1925 publication ‘Elements of Physical Biology’, Alfred J. Lotka noted “a singularly interesting conclusion” [1]: when a second resource population was added to a consumer-resource model, the first resource population could be driven to extinction [1]. Such an interaction could occur if, for example, the second resource increases the carrying capacity of the consumer such that it completely consumes the first resource, the preferred prey. This result was due to what is now referred to as ‘apparent competition’ — that is a reciprocally negative indirect interaction between resource populations mediated by a shared consumer (Figure 1) [2]. Since Lotka’s early theoretical work, it has become clear that apparent competition is important in structuring many ecological communities [3–7]. However, natural enemy-mediated indirect interactions between resource populations (hereafter referred to as ‘enemy-mediated interactions’) are not

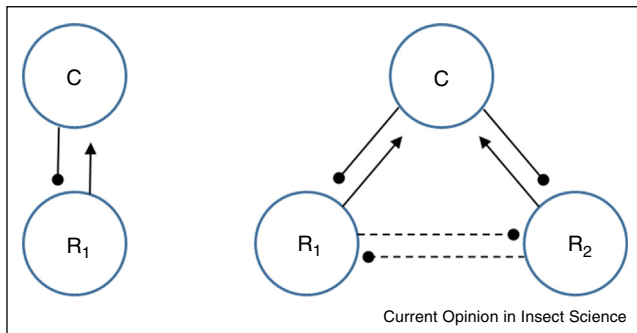
always reciprocally negative (–,–) [8\*]; they may result in apparent parasitism (–,+ [9], amensalism (0,–) [10], commensalism (0,+ [11], or mutualism (+,+ [12]. In this article we focus on parasitoids to review some of the latest research on enemy-mediated interactions. We argue that a community framework incorporating enemy-mediated interactions would aid ecological management [13], and these interactions have particular importance for both safety and efficacy in biological control [14,15].

## Background

Some important characteristics and complexities of enemy-mediated interactions are illustrated by the now classic study of Settle and Wilson [16]. The invasive variegated leafhopper *Erythroneura variabilis* (Hemiptera: Cicadellidae) was found to displace regionally populations of the native *E. elegantula* in California. This displacement was not caused by resource competition between leafhoppers, which was roughly symmetrical both intra-specifically and interspecifically. Rather, displacement occurred as a result of asymmetrical apparent competition mediated by the shared egg parasitoid *Anagrus epos* (Hymenoptera: Mymaridae) (but see Triapitsyn [17] and Triapitsyn et al. [18] regarding potential confusion of parasitoid taxonomic status) [16]. The *A. epos*-mediated invasion of *E. variabilis* occurred in two different phases: First, *A. epos* reduced *E. elegantula* densities, thereby alleviating resource competition between leafhoppers and allowing initial establishment of *E. variabilis*. Second, after local establishment of *E. variabilis*, the density of *A. epos* increased, causing increased parasitism of leafhoppers. Because *A. epos* attacked *E. elegantula* at a higher rate than *E. variabilis*, *E. elegantula* was displaced [16].

The leafhopper–*Anagrus* study demonstrates the importance of enemy-mediated effects for determining community structure. Additionally, by linking these experimental observations with theory, we can highlight three points important to the study of enemy-mediated interactions. First, it should be noted that the negative enemy-mediated effect of *E. variabilis* on *E. elegantula* is an effect on population density; that is, an increase in the population density of *E. variabilis* indirectly causes a decrease in the density of *E. elegantula*. However, the sign of interaction between populations [positive (+), negative (–), or neutral (0)] need not necessarily be measured in terms of population density. Interaction effects are also commonly measured in terms of population growth rate, individual fitness, and theoretically can be measured for any population level phenomenon [19].

Figure 1



Levins' diagrams [70] showing a single consumer–single resource model (left), and a single consumer–two resource model with apparent competition occurring between resource populations. Solid lines represent direct interactions, and dashed lines represent indirect interactions; arrows represent positive effects on density, and circles represent negative effects on density.

When interpreting and synthesizing experimental findings and theoretical developments on indirect effects, it is important to be clear about how the sign of interaction is measured [20]. The same point can be made for how the indirect effect is mediated by the natural enemy — that is the effect due to an increase in density of the natural enemy, or due to some other factor? Furthermore, it is important to differentiate between density-mediated and trait-mediated indirect effects [21]. Density-mediated indirect effects are exemplified in the apparent competition model introduced by Lotka [1] and refined by Holt [2], where the population density of the natural enemy is increased by one resource population thereby allowing for increased consumption of a different resource population. Apparent competition in the *E. variabilis* invasion is density mediated. Trait-mediated indirect effects, on the other hand, involve behavioral changes in one or more of the interacting populations. An example of this is in the avoidance behavior of the polyphagous parasitoid *Aphidius ervi* (Hymenoptera: Braconidae) in the presence of the intraguild predator *Coccinella septempunctata* (Coleoptera: Coccinellidae). This behavioral change results in an indirect mutualism between prey/host aphids *Acyrtosiphon pisum* and *Sitobion avenae* [12] when both natural enemies are present.

A second feature of enemy-mediated interactions illustrated by the *A. epos*–leafhopper system [16] is that the signs and strengths of the interaction may vary in space and time. The first phase of the *E. variabilis* invasion is perhaps better described as apparent amensalism (–,0) rather than apparent competition. There is an indirect negative effect of *E. elegantula* on *E. variabilis*, but little or no effect of *E. variabilis* on *E. elegantula*. Until *E. variabilis* reaches greater than 50% of the total leafhopper population, its contribution to the parasitoid population is

very small. Thus, the density of *A. epos* is largely determined by the resident *E. elegantula* population during the first phase. It is only later, in the second phase of invasion, when *E. variabilis* has increased the parasitoid's equilibrium population size that a reciprocally negative interaction (i.e. apparent competition) is observed.

The asymmetry of the apparent competition in the *E. elegantula*–*E. variabilis* system leads to a third point worth illustrating. Theory suggests that coexistence of resource populations experiencing apparent competition requires that  $r_i > a_i P$  (i.e. the intrinsic rate of increase,  $r$ , of resource population  $i$  must be greater than the attack rate,  $a$ , by the shared consumer on resource  $i$ , multiplied by the average density of the shared consumer,  $P$ ) [2,6]. Therefore, changes to intrinsic growth rates (e.g. via reduced resource competition between leafhopper species), changes in the density of the shared consumer (e.g. via arrival of a new resource population), or changes in attack rate (via functional response or other factors influencing host preference) could tip the balance between coexistence and exclusion. By increasing the density of *A. epos*, the ensuing *E. elegantula* mortality overwhelmed its intrinsic rate of increase. However, because the attack rate of *A. epos* on the invasive *E. variabilis* was sufficiently small, *E. variabilis* could persist.

The attack rate,  $a$ , represents many aspects of parasitoid searching behavior and host use. Host use is multifaceted [21] with search efficiency, host suitability, and the relative contribution of egg and time limitation all known to influence attack rate [22,23,24\*,25,26]. Moreover, host preference factors may be dynamic and host suitability can be mediated by the abiotic environment [27] as well the internal microbiome of the host [28\*]. In most interspecific interactions, the effect of density of one species on the growth rate of a second species is likely to be a nonlinear process [20]. A key to developing better predictive models is to identify the form of functions describing these interactions [20]. Recent breakthroughs in our understanding of the factors that shape enemy-mediated interactions promise to make predictions more accurate. In the remainder of this article we review recent research on enemy-mediated interactions in classical biological control. We focus on parasitoids, which represent about 75% of the classical biological control introductions against arthropod pests [29], and we highlight the advantages of a community framework incorporating enemy-mediated interactions for evaluating biological control outcomes.

## Case studies in biological control

### Natural enemy-mediated effects and risk

Classical biological control involves the intentional importation and establishment of non-native natural enemy populations to control target non-native pests. Proponents of classical biological control point to its low cost-benefit

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