



Linking risk and efficacy in biological control host–parasitoid models



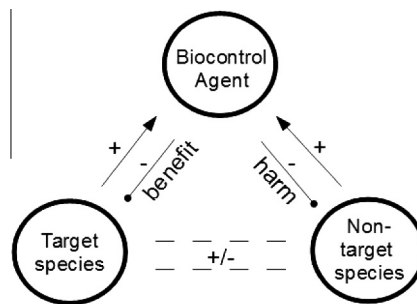
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HIGHLIGHTS

- Classical biological control entails risks as well as potential benefits.
- We use a two-host one-parasitoid model to see how risk and efficacy may interact.
- We focus on model determinants of host range and egg vs. time limitation.
- Apparent competition can have important benefits for biological control.
- However, under egg limitation, attack on low quality hosts can reduce control.

GRAPHICAL ABSTRACT



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ABSTRACT

Exotic invasive arthropods present an increasing threat to native species, ecosystem function, crop production, forests, and other natural resources. Importation ('classical') biological control can be a cost-effective tactic for long-term pest management that reduces insecticide use. However, while importation of biological control agents has great potential benefits, it also entails risks to non-target native species. Therefore, candidate biological control agents are studied prior to release to predict safety. Little is known, however, about how traits affecting the safety of biological control agents may impact their efficacy in terms of reducing pest populations. We use a difference equation model to simulate a one-parasitoid two-host system and evaluate conditions under which biological control safety and efficacy interact. We vary the search efficiency and resistance to parasitism of both host species and interpret the results from the standpoint that one host is a target pest and the other a non-target species. We find that apparent competition can have important benefits for increasing biological control efficacy, even at low levels of non-target impact. However, under conditions of parasitoid egg limitation, high attack rates on resistant non-target hosts can dramatically decrease biological control efficacy while concurrently increasing non-target risk. These findings are discussed in the context of biological control agent pre-release risk–benefit assessment.

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1. Introduction

Classical biological control is an important strategy for controlling the effects of invasive species over broad spatial scales while

potentially minimizing risk of adverse consequences (Messing and Wright, 2006; Thomas and Willis, 1998). There are examples where classical biological control agents have caused harm to native biota (Louda et al., 2003), but there are also many cases of biological control agents safely and effectively controlling pest populations (De Clercq et al., 2011; Hoddle, 2004; Van Driesche et al., 2010). Debate over how best to identify and value harms versus benefits in ecological risk assessment is an ongoing

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conversation in society (Nelson et al., 2009). One role of scientists is to provide stakeholders with the most precise and accurate predictions possible about potential ecological effects of management decisions (e.g. likelihood and magnitude of pest control, and likelihood and magnitude of impact to non-target populations) (Bigler and Köelliker-Ott, 2006). Improved decision-making tools that allow managers to better predict both safety and efficacy of candidate biological control agents are needed (Thomas and Reid, 2007).

No biological control agent release is without risk, and agents should be selected by simultaneously considering both risks and potential benefits (McEvoy and Coombs, 1999; Heimpel et al., 2004; Kriticos et al., 2009). Minimizing harms while maximizing benefits is not straightforward, however, if organismal traits that increase biological control efficacy are the same traits that increase the risk of harm to non-target species (Ehler, 2000). For example, predators and parasitoids with generalist feeding habits may pose higher risk to non-target organisms than do specialists (Simberloff and Stiling, 1996); however, a broader host range might also facilitate establishment of biological control agents, influence stability of the agent–target interaction, or increase suppression of target pests (Murdoch et al., 1985; Symondson et al., 2002). As an illustration of this, a number of studies have shown that the presence of alternative prey or host species can enhance biological control through apparent competition (Chailleux et al., 2014; Langer and Hance, 2004; Murdoch et al., 1985). Apparent competition can also be detrimental to native species, however (Borer et al., 2007; Noonburg and Byers, 2005). For example, rapid population decline of the native green leafhopper, *Erythroneura elegantula*, following the introduction of the variegated leafhopper, *Erythroneura variabilis*, in central California, U.S.A. was likely the result of apparent competition mediated by the shared parasitoid *Anagrus epos*, rather than due to direct competition for resources between hosts (Settle and Wilson, 1990).

There is not necessarily a trade-off between risk and efficacy, however, and many highly effective biological control agents may be low-risk to non-target organisms. For example, specialists may have a faster numerical response to pest outbreaks and they have a lower likelihood of engaging in intraguild predation than do generalists (Snyder and Ives, 2001). A specialist biological control agent may be both safe to non-target species and highly effective at controlling the target pest (Kimberling, 2004; Symondson et al., 2002). The renowned *Rodolia cardinalis*, a specialist predator of cottony cushion scale, *Icerya purchasi*, has been a classical biological control success in many parts of the world where it has been introduced (Caltagirone and Doutt, 1989). In the Galapagos Islands, where *R. cardinalis* is unable to complete its life cycle on any of the local fauna besides the invasive *I. purchasi* (Causton et al., 2004), it has successfully established and is reducing *I. purchasi* by 60–98% (Hoddle et al., 2013).

Laboratory host specificity testing, which estimates the physiological host range of a biological control agent (i.e. the number of species that the agent could complete development on if attacked), provides perhaps the most important evidence used to predict post-release host range (i.e. the ecological host range within the region of importation) (Gilbert and Webb, 2007; Pemberton, 2000; Van Driesche and Reardon, 2004; van Lenteren et al., 2006). The physiological host range can include species that are not preferred by the biological control agent but that, when attacked, are suitable for the agent to complete development. The ecological host range is the suite of suitable hosts that are actually attacked in the field; thus, the ecological host range may often be narrower than the physiological host range (e.g. Hays et al., 2005; Morehead and Feener, 2000). However, insects that are completely unsuitable for agent development are consistently attacked in some cases (Desneux et al., 2009; Heimpel et al., 2003). Laboratory and field studies can supplement host range

information and improve predictions about the ecological host range upon introduction (e.g. Desneux et al., 2009; Wyckhuys et al., 2008, 2009); however, without an appropriate model for host–parasitoid interaction, these studies tell us little about the likely magnitude of impact on non-target field populations. Moreover, host range testing tells us little about how non-target species may influence target pest suppression.

Cases where a biological control agent attacks both a target and a non-target species may result in apparent competition (Holt, 1994), but indirect interactions between host populations may also be +/- (apparent parasitism) (Hoogendoorn and Heimpel, 2002), +/+ (apparent mutualism) (Abrams and Matsuda, 1996), or any other combination of positive, negative, or neutral (Fig. 1). To understand the complexity of outcomes of these potential indirect interactions, and to develop hypotheses for empirical testing, we examined a mathematical model describing two hosts and a shared parasitoid. Previous studies have utilized simple mathematical models to make qualitative predictions about transient risk (Lynch et al., 2002), and risk at equilibrium (Holt and Hochberg, 2001) of biological control agents. Building on this work, we suggest that a model for interpreting pre-release data should evaluate both direct and indirect interactions between the biological control agent and resource populations so that the potential interplay between both harm and benefit can be assessed.

The objective of this paper is to model and evaluate conditions under which the population of a non-target host would affect a target host population indirectly via a shared parasitoid, and also to examine what conditions are associated with impacts to non-target hosts upon release of a parasitoid. We pay particular attention to model representations of physiological host range versus ecological host range and the different effects these components may have on biological control efficacy and non-target impact. We evaluate these parameters within the context of pre-release risk–benefit screening.

2. The model

We ran simulations using a discrete-time Nicholson–Bailey form consumer–resource model described by Heimpel et al. (2003) (Equation set (1)):

$$\begin{aligned} H_{1,t+1} &= e^{r_1} \left(1 - \frac{H_{1,t}}{K_1}\right) H_{1,t} (1 - s_1 (1 - f[E_{1,t}])) \\ H_{2,t+1} &= e^{r_2} \left(1 - \frac{H_{2,t}}{K_2}\right) H_{2,t} (1 - s_2 (1 - f[E_{2,t}])) \\ P_{t+1} &= H_{1,t} s_1 (1 - f[E_{1,t}]) + H_{2,t} s_2 (1 - f[E_{2,t}]) \end{aligned} \quad (1)$$

where $f[E_{i,t}]$ is the escape function for the host species, H_1 and H_2 , which are attacked by a parasitoid, P . Host species i reproduces at

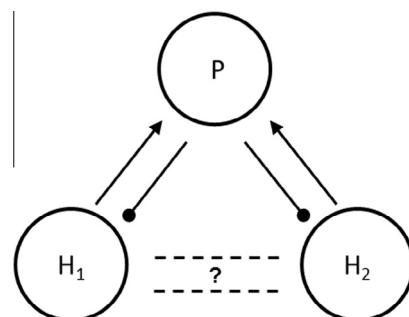


Fig. 1. Levins' diagram (Levins, 1974) depicting two hosts (H_1 and H_2) and potential indirect interactions mediated by a shared parasitoid (P). Arrows represent positive interactions, and clubs represent negative interactions; solid lines represent direct interactions, and dashed lines represent indirect interactions.

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