

The prevalence of asymmetrical indirect effects in two-host–one-parasitoid systems

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Abstract

Empirical studies of indirect effects mediated by shared enemies have been characterized by several puzzling features: (a) there exist far fewer documented cases than for interactions via shared resources; (b) the majority of empirical studies have measured indirect effects where one of the two reciprocal effects could not be distinguished from zero; (c) there is a lack of documented positive effects mediated by a shared enemy, in spite of several mechanisms that could produce such effects. One potential explanation is that these are statistical expectations over the range of potential species characteristics. We systematically examine the indirect interactions between two hosts with a shared parasitoid across all potential parameter values, using a family of simple models. By including a detection limit for nonzero interspecific effects, we demonstrate that $(-,0)$ indirect interactions between hosts are the most common type for many variants of the model. However, the absence of positive indirect effects in empirical studies constitutes a puzzling inconsistency between the empirical and theoretical literatures.

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1. Introduction

Shared enemies appear to be as ubiquitous in food webs as shared resources (Cohen et al., 1990; Muller et al., 1999), but the number of documented indirect interactions via shared enemies is far smaller than the number of documented interactions via shared resources. This can be seen by comparing the reviews of field studies of exploitative and interference competition (Connell, 1983; Schoener, 1983; Gurevitch et al., 1992; Denno et al., 1995) with those of apparent competition (Holt and Lawton, 1994; Chanton and Bonsall, 2000). While Schoener (1983) found 31 of 174 studies that demonstrated mixed results, i.e., traditional competition present in some species and absent in other species, Chanton and Bonsall (2000) found 26 of 34 studies in which shared enemies lead to effects in which one of the

two indirect effects between the prey was indistinguishable from zero. Quantitatively asymmetric effects have been demonstrated in interactions via shared resources in which species differ in the strength of the competition effect (Denno et al., 1995), but interactions via shared enemies exhibit qualitatively asymmetric effects in which one effect is zero (Lawton and Hassell, 1981; Connell, 1983; Schoener, 1983). Neither a lack of significant effects nor a high frequency of highly asymmetric effects has been predicted by previous theory. Another puzzling feature of experimental studies of shared predation is the lack of positive effects of one prey species on the long-term population density of another. The review of experimental studies of shared predation or parasitism by Chanton and Bonsall (2000) includes a number of very short-term studies among its 34 measurements of indirect effects. Long-term positive effects can in theory arise via several mechanisms: (1) saturating functional or numerical responses combined with direct predator density dependence (Holt, 1984; Abrams and Matsuda, 1996); (2) adaptive adjustment of anti-predator behavior

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by the prey in response to greater predation, leading to more prudent exploitation of its own resource (Abrams, 1987); (3) increased amplitude of cycling counteracting the impact of additional prey on predator density (Abrams et al., 1998; Abrams and Kawecki, 1999). Observed positive effects via shared enemies have been confined to short-term effects that reflect changes in predator behavior rather than numbers (reviewed in Holt and Kotler, 1987).

The preceding paragraph has argued that we lack theoretical explanations for the comparative scarcity of effects via shared enemies, the frequent large asymmetry in effect magnitudes, and the lack of observed positive effects. However, all of these features could be consistent with existing models. This possibility cannot currently be assessed because the expected magnitude of effect signs and sizes has not been calculated over all possible parameters for any model of shared predators or parasitoids. Thus, it could be that the general lack of demonstrations of apparent competition is because very small indirect effects between prey or hosts occur for most potential characteristics of those species and their shared enemy. Similarly, the lack of demonstrations of positive effects may simply be a consequence of most positive effects being small in magnitude, and therefore likely to go undetected. Alternatively, positive effects could occur over only a narrow range of parameter combinations. Asymmetry of effects may also be a simple statistical expectation over parameter space. Previous theoretical studies of apparent competition (i.e., $(-, -)$ effects) have not explored the expected size or asymmetry of these effects. Theoretical predictions of significant positive effects have mainly come from studies in which prey species are assumed to be equivalent in the growth and predator vulnerability parameters (for example Abrams et al., 1998). However, differences in growth and vulnerability parameters characterize most of parameter space. Both tradeoffs between resource exploitation and predator vulnerability (Lima, 1998), and character displacement of these traits (Abrams, 2000; Abrams and Chen, 2002) are likely to magnify the asymmetry expected under random parameter selection. These parameter differences may lead to asymmetric indirect effects between prey, as well as possibly reducing the occurrence of large positive effects. However, none of the suggestions in this paragraph can be evaluated without a complete analysis of the frequencies of different types and sizes of indirect effects for a basic model of shared natural enemies.

This article will determine the distribution of types and sizes of indirect effects between hosts for a model of two hosts with a shared parasitoid. This analysis will reveal whether simple statistical expectation of effect sign and/or magnitude is a potential explanation for any of the empirical features discussed above. Of course, a single model cannot represent all natural systems, and

parameters in nature are unlikely to represent random samples from across parameter space. Nevertheless, if a range of plausibly defined subsets of parameter space produce consistent predictions, then the ‘statistical expectation’ hypothesis gains considerable support.

A complete compilation of indirect effects in a model of shared predation has additional justifications. First, it will identify those conditions under which different types of indirect effects are most likely to be observed. This is clearly important for directing experimental studies that attempt to find particular types of effects. In addition, the analysis can be used to compare the types and sizes of indirect effects that occur in models exhibiting different types of dynamics. Recent work (Abrams et al., 1998; Holt and Barfield, 2003) has suggested that models characterized by cyclic dynamics may be more likely to exhibit positive indirect effects between prey than are analogous models having parameters that produce stable equilibria, and are similarly less likely to exhibit negative effects. There is no doubt that this is true for some families of models (cf. Holt, 1977 to Abrams et al., 1998). However, the lack of a complete assessment of potential indirect effects leaves open the possibility that differences in effect sign between stable and unstable systems characterize a relatively small region of parameter space, or a region where all effects are generally small.

2. Models

We chose to examine a discrete host-parasitoid model in this study, both because many empirical studies have been carried out using organisms with discrete generations, and because discrete models have received less attention in analyses of indirect effects than have continuous models. We show later that discrete predator–prey models yield similar conclusions. We begin by reviewing some properties of the one-host–one-parasitoid model that forms the basis of our study of two-host systems. We then extend the system to include a second host species, summarizing the general effect of differences in various host parameters, as well as determining the relative areas of parameter space that result in qualitatively different indirect interactions between host species. For the initial analysis we restrict parameters to values that allow coexistence of the two hosts, which is appropriate for indirect effects measured by species removal. The theory in this paper focuses on long-term indirect effects across multiple generations; therefore, we quantify the indirect effects based on arithmetic averages of densities over time. Arithmetic mean population sizes are widely used in empirical studies to detect interactions, as they are implicit in the use of ANOVA’s to detect effects (for example Bonsall and Hassell, 1998). Arithmetic means have been used in

all empirical measurements of effect magnitude and to measure interactions in theoretical studies (Abrams et al., 1998; Abrams and Kawecki, 1999; Abrams, 1999, 2003; Holt and Barfield, 2003). We adopt a detection threshold below in which small indirect effects are classified as a zero effect. In order to test the robustness of results, we vary the range of parameters examined. We investigate subsets of parameter space characterized by qualitatively different types of dynamics and by biologically reasonable correlations between different parameters. We also investigate an expanded parameter set that includes cases in which the two hosts are unable to coexist.

2.1. One-host–one-parasitoid model

An analysis of a one-host–one-parasitoid model demonstrates the impact of variation in population densities on the long-term population means. Because many of the systems we examine undergo cycles, it is important to review the one-host model in order to understand the effect of cycling on mean densities without the confounding issue of multiple hosts. The model used here is the classical Nicholson–Bailey model (Nicholson and Bailey, 1935) modified to include host density-dependence (Beddington et al., 1975, 1976):

$$\begin{aligned} N_{t+1} &= N_t \exp \left[r \left(1 - \frac{N_t}{k} \right) - aP_t \right], \\ P_{t+1} &= bN_t(1 - \exp[-aP_t]), \end{aligned} \quad (1a, b)$$

where N_t is the host density at time t , P_t the parasitoid density at time t , r the host growth rate, k the host carrying capacity, a the parasitoid attack rate, and b the number of parasitoids produced per attacked host. Kaitala et al. (1999) investigated the dynamics of a very similar system. The equilibrium of Eq. (1) with positive densities of both species is often unstable, leading to cycles, because of the time delay inherent in difference equation models. In the absence of the parasitoid, the host cycles when its maximum per capita growth rate is high because it overshoots its carrying capacity (May, 1973). At moderate attack rates, the addition of the parasitoid stabilizes many cycling host systems because the parasitoid population prevents the host from overexploiting its resources (Kaitala et al., 1999). Above a threshold attack rate, sustained fluctuations, from periodic to chaotic, are generated because the parasitoid overexploits the host (Kaitala et al., 1999). Prey cycles result in a decrease in mean predator density relative to its equilibrium, due to the greater effect on the predator growth rate of a reduction versus an equal increase in prey density (Chesson, 1991; Abrams et al., 1998).

2.2. Two-host–one-parasitoid model

Eqs. (1) were extended to include a second host as follows:

$$\begin{aligned} N_{1,t+1} &= N_{1,t} \exp \left[r_1 \left(1 - \frac{N_{1,t}}{k_1} \right) - a_1 P_t \right], \\ N_{2,t+1} &= N_{2,t} \exp \left[r_2 \left(1 - \frac{N_{2,t}}{k_2} \right) - a_2 P_t \right], \\ P_{t+1} &= b_1 N_{1,t}(1 - \exp[-a_1 P_t]) + b_2 N_{2,t}(1 - \exp[-a_2 P_t]). \end{aligned} \quad (2a-c)$$

Dimensional analysis was used to reduce the number of parameters in Eqs. (2). Host densities were scaled by their carrying capacity while parasitoid density was scaled to be proportional to the attack rate on host 1. The reproductive value of host i to the parasitoid, denoted α_i , combines both b_i , the average number of parasitoids produced per attacked host, and k_i , the host carrying capacity with the attack rate parameter a_i ($\alpha_i = a_i b_i k_i$). Since k_i also scales N_i it is easiest to think of differences between α_1 and α_2 as differences between b_1 and b_2 . The third scaled parameter, β , is the ratio of the attack rates ($\beta = a_2/a_1$). If a_1 is defined as the smaller attack rate, then $\beta > 1$. This results in a new set of dimensionless equations:

$$\begin{aligned} N_{1,t+1} &= N_{1,t} \exp[r_1(1 - N_{1,t}) - P_t], \\ N_{2,t+1} &= N_{2,t} \exp[r_2(1 - N_{2,t}) - \beta P_t], \\ P_{t+1} &= \alpha_1 N_{1,t}(1 - \exp[-P_t]) + \alpha_2 N_{2,t}(1 - \exp[-\beta P_t]). \end{aligned} \quad (3a-c)$$

The long-term mean (i.e., the expected mean density over a period of time T , as T approaches infinity) of any one of the three species in this model determines the mean of the other two, assuming coexistence of all three species. Taking the long-term mean of Eq. (3), leads to Eq. (4):

$$\begin{aligned} \langle N_1 \rangle &= 1 - \frac{1}{r_1} \langle P \rangle, \\ \langle N_2 \rangle &= 1 - \frac{\beta}{r_2} \langle P \rangle. \end{aligned} \quad (4a, b)$$

Increases in the long-term mean of the parasitoid, $\langle P \rangle$, must decrease the long-term mean of each host. An explanation of the response of one species to a change in one or more parameters of the system is enough to explain the responses of all three species. As in the one-host–one-parasitoid model, host cycles decrease the mean parasitoid density compared to its density at the unstable equilibrium. The changes in mean density with a given parameter can be complicated, nonmonotonic relationships, because the dynamics of the system may shift repeatedly between various types of cycles and chaos as a parameter is changed (Kaitala et al., 1999).

2.3. Simulations

Initial densities for both hosts and the parasitoid were chosen as random numbers between 0 and 1 for each parameter set. The same initial densities were used to compare sympatric and allopatric systems as described below. The simulations consisted of 2500 iterations, with long-term means calculated over the last 2000 iterations. Repeated simulations with the same parameters but randomly selected initial conditions typically result in a standard deviation of the effect size (described below) less than 1% when there was a single attractor (for example see Fig. 2). For the purposes of this study, simulations of this length adequately approximate the asymptotic long-term mean. Only those parameters for which all three species coexisted were included in this analysis. Populations whose scaled densities dropped below 10^{-6} were considered to have gone extinct. All simulations were conducted using a procedure coded in C++. The simulation code was checked by re-computing solutions using Mathematica 4.0 (Wolfram Research, 1999) in order to confirm that the limits of numerical analysis in the C++ code was not having a significant effect on the results.

To determine the sign of the effect of one species on another, we iterated Eqs. (3) to determine the long-term arithmetic mean of each host in a sympatric system, where both hosts and the parasitoid were present. This was then compared to the mean density of the focal host in an allopatric system (i.e., in the presence of the parasitoid but without the second host). The effect magnitude of host i on host j was measured by the difference between the mean density of host j in sympatry and allopatry divided by the mean density of host j in sympatry. For example, a greater density of host i in the three-species system compared to the two-species system, lacking host j , implies that host j has a positive effect on host i . (See below for a discussion of alternative measures of effect size.) The reciprocal interaction was determined by reversing the roles of the focal and manipulated species.

One issue that needs to be considered in measuring indirect effects is the possibility of alternative attractors. By using randomly chosen initial conditions, we are likely to observe different attractors approximately in proportion to the size of their basins of attraction. Because we are interested in the distribution of different types of interaction over parameter space rather than obtaining a complete description of a limited range of parameters, we did not attempt to classify interactions for each alternative that might exist for a particular set of parameter values. We used simulations with different initial densities for each parameter combination to determine the approximate frequency of alternative attractors in parameter space (see below).

When the host parameters are identical ($r_1 = r_2$; $\alpha_1 = \alpha_2$; $\beta = 1$), the entire parameter space is represented by the two axes r and α . The two hosts have identical traits, but still represent separate populations that only interact indirectly. At sufficiently large values of α the variance in the density of either host increases sufficiently after adding the other host to decrease the mean parasitoid density, resulting in (+,+) interactions between the hosts. Synchronous cycles of the two hosts allow for the greatest (+,+) interaction because synchrony produces the greatest change in cycle amplitude when one host is removed. However, when the hosts cycle asynchronously, the presence of each host can help to maintain the parasitoid density through periods of low density in the other host (Abrams and Kawecki, 1999). Across the full range of parameter space where host parameters are identical, nearly all interactions are symmetrical, either (+,+) or (-,-). The few cases where this was not true represent cases with alternative attractors.

When hosts differ, either in their growth parameters or their interaction with the parasitoid, a systematic analysis of parameter space is needed to fully understand the indirect effects in this model. Presumably most pairs of host species in real-world systems do not have identical values of ecologically important traits.

2.4. Effects of nonequivalent parameters on the nature of indirect effects

Differences between host parameters in Eqs. (3) can exist along three axes. The hosts can have different growth rates, r_1 and r_2 . The hosts can have different reproductive values to the parasitoid, α_1 and α_2 , which translate to differences in the carrying capacity (k) of the host or differences in the number of eggs that can produce adult parasitoids per host (b). Finally, the parasitoid can have different attack rates on the hosts, measured by its relative rate of attacking prey 2, β ($\beta > 1$). The effect of differences between hosts in each of these cases is discussed below.

First consider differences in host growth rate, r . When both hosts have the same growth rate, r , and there is a sufficient increase in cycle amplitude in the two-prey system, then each host experiences an indirect benefit from the presence of the other (+,+). Such interactions occur for parameter values close to the diagonal line $r_1 = r_2$ in Fig. 1a, which assumes a value of α that is high enough so that cycles or chaos characterize the entire range of growth rates shown. The more host growth rates differ, the more likely it is that the two-way interaction is qualitatively asymmetric, (+,-). The species with the higher r can increase faster from low densities, and therefore usually has an advantage over the slower-growing host; this results in the predominance of red below and blue above the $r_1 = r_2$ line in

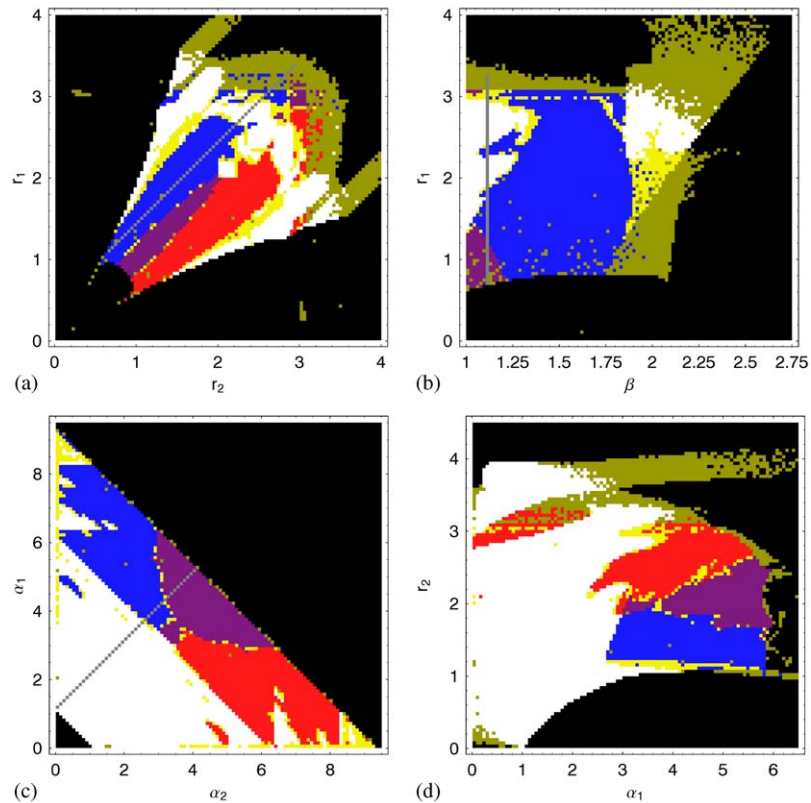


Fig. 1. Reciprocal interactions for the two-host model. Interactions are measured based on complete removal of other host (see text). Black = at least one species extinct; White = $(-, -)$; Blue = $(+, -)$ host 1 benefits; Red = $(-, +)$ host 2 benefits; Purple = $(+, +)$; Dark yellow (ochre) = extinction-based alternative attractors; Light yellow = nonextinction-based alternative attractors (see text). Light gray lines are referenced in Fig. 2. (a) The diagonal represents the symmetrical parameter set. Fixed parameters are: $\alpha_1 = \alpha_2 = 3.5$, $\beta = 1$. (b) The vertical axis represents symmetrical cases. $\alpha_1 = \alpha_2 = 3$, $r_1 = r_2$. (c) The diagonal represents the symmetrical parameter set. Fixed parameters are $r_1 = r_2 = 2$, $\beta = 1$. (d) Indirect effects as a function of r_2 and α_1 when $r_1 = 2.0$; $\alpha_2 = 3.5$; $\beta = 1.0$.

Fig. 1a. In cycling systems, the host with the higher r experiences a positive indirect effect from the slower-growing host when the benefit from increased cycle variance outweighs the cost from increased parasitoid abundance.

There is a small region of parameter space in which a host can experience an indirect benefit by having the smaller r (in the upper-right region of Fig. 1a). When the r of the faster-growing host is large enough to generate cycles in the absence of the parasitoid, the host with the smaller r experiences the indirect benefit from the presence of the faster-growing host species. The presence of the latter leads to large-amplitude cycles in the parasitoid and, thus, a reduction or extinction of the parasitoid. The presence of the slower-growing host has a negative effect on the faster-growing host by preventing the parasitoid from going extinct.

Differences in the ratio of the two attack rates, represented by a β value larger than unity, often shift the interaction to $(+, -)$ (Fig. 1b). Recall that larger values of β mean higher ratios of the attack rate on host 2 relative to the attack rate on host 1. Generally, $(+, -)$ interactions occur at intermediate values of β , involving

an increase in the less vulnerable host 1 and a decrease in the more vulnerable host 2 when the two come into sympatry. Intermediate β values are large enough to shift the burden of attacks to host 2, but not so large that they shift the system out of cycling dynamics. Host 2 always experiences an indirect negative effect when it is much more vulnerable than host 1 (very large values of β) although host 1 may also be harmed indirectly by host 2.

At low parasitoid reproductive values, α_1 and α_2 , the system either does not cycle or the variance remains low, resulting in apparent competition $(-, -)$. When α_1 and α_2 are high enough, the system abruptly shifts to greater amplitude cycles, resulting in a large $(+, +)$ parameter space surrounding the diagonal line $\alpha_1 = \alpha_2$ in Fig. 1c. Differing parameters can lead to $(+, -)$ interactions, for example, when α_1 is large enough to sustain cycles in the absence of host 2 and α_2 is small enough to be stable in the absence of host 1. In this case, the presence of host 2 increases the variance in densities to the benefit of host 1, while the presence of host 1 increases the mean parasitoid density to the detriment of host 2.

Figs. 1a–c provide a picture of the consequences of between-host differences in a single type of parameter for the nature of indirect effects between hosts. The figures show that such differences often produce $(+,-)$ or $(-,+)$ interactions rather than simply producing $(-,-)$ or $(+,+)$ effects in which the effect sizes differ in magnitude. However, $(+,-)$ effects are confined to regions of parameter space in which the system does not have a stable equilibrium. Stable regions are characterized by $(-,-)$ effects, such as the lower left-hand corner of Fig. 1c. We investigated several combinations of unequal parameters in two or more types, and Fig. 1d is one example in which the combined effects of differences in r and α are illustrated. Such combined differences did not result in qualitatively different generalizations than those evident from different values of a single type of parameter. When the interaction is $(+,-)$, the host experiencing the positive effect is likely to have the larger per capita growth rate, the larger carrying capacity, or the smaller attack rate. Because the number of parasitoids produced per attacked host, b , scales with the host carrying capacity in the parameter α , the host that produces the greater number of parasitoids is also likely to experience the positive effect in an asymmetrical interaction. These results are consistent with the characterization of the dominant host in apparent competition models having a stable equilibrium (Holt and Lawton, 1993).

Alternative attractors appear to be common in many subsets of this parameter space based on our numerical simulations. Two different types of alternative attractors occur. In ‘extinction-based’ alternative attractors, repeated simulations result in varying numbers of remaining populations, dependent on the initial starting conditions. In many cases, this is due to one population dropping below the extinction threshold during transient dynamics leading to what would be an attractor on which all densities remain above the extinction threshold. A small proportion of extinction-based alternative attractors may be cases in which an alternative attractor itself drops below the threshold. In the first case, the addition of a threshold density effectively creates an additional attractor that is not present in the original system of equations. Areas of parameter space for which 10 randomly selected initial conditions led to extinction-based alternative attractors are labeled as dark yellow (ochre) in Fig. 1. It is important to note that the boundaries of these dark yellow areas in parameter space are dependent on the extinction threshold chosen for the simulation and on the range of initial conditions. By selecting only 10 initial conditions we are identifying cases where such extinction is reasonably common. Presumably, these extinction-based alternative attractors exist across a broader range of parameters than those identified here but with very small basins of attraction. The second type of alternative attractors,

shown in Fig. 1 by light yellow, represent cases with two or more alternative attractors that exist for the original equations (2) and that do not involve densities that drop below 10^{-6} in either sympatry or allopatry. If any of 10 randomly selected initial conditions resulted in a different qualitative characterization of parameter space and no populations went extinct in sympatry or allopatry, that parameter set was labeled as light yellow in Fig. 1. Because it does not include alternative attractors for which both attractors result in the same qualitative indirect interactions, the light yellow area underestimates the parameter space for which alternative attractors exist. Due to the finite time interval used to estimate the long-term means, a small number of the cases classified as alternative attractors were the result of different round-off errors in different simulation runs when one of the actual effects was very close to zero. The isolated light yellow squares between the purple and red regions in Figs. 1a and c are examples of such approximation effects. Such points represent a very small fraction of parameter space. Because our goal was to characterize the fractions of qualitatively different indirect interactions over the whole parameter space, by randomly selecting starting densities in the simulations described below, we sampled across alternative attractors (including cases of extinction due to low density) in proportion to the size of their basins of attraction. This is presumably closely related to their probability of being observed in a natural system that is accurately described by Eqs. (2).

Thus far, we have not discussed the size of the indirect effects between hosts. Fig. 2 shows the actual changes in density that occur along the gray transect lines shown in Figs. 1a–c. The pattern of change in population density with a parameter shown in Fig. 2 is highly irregular over some parameter ranges. Many of the qualitative changes in dynamics with changes in parameter values are the result of shifts between chaotic and periodic attractors, or between alternative attractors, and an ecological explanation for the shifts cannot be given. However, some generalizations are possible about the average magnitudes of different types of effects. When measured as the change in density upon removal of the other host, divided by the focal host density in the three species system, positive indirect effects were usually less than 0.2. However, negative indirect effects often represented 100% or more of the host density in sympatry (i.e., an effect size greater than 1). This difference in magnitudes is partially due to the method by which an indirect effect was calculated; the theoretical maximum indirect benefit is 100%, while the theoretical maximum negative effect is infinite. To compensate for this bias, the larger of the allopatric density or the sympatric density can be used in the denominator. As a result, positive effects have the sympatric density in the denominator and negative effects have the allopatric density in the denominator

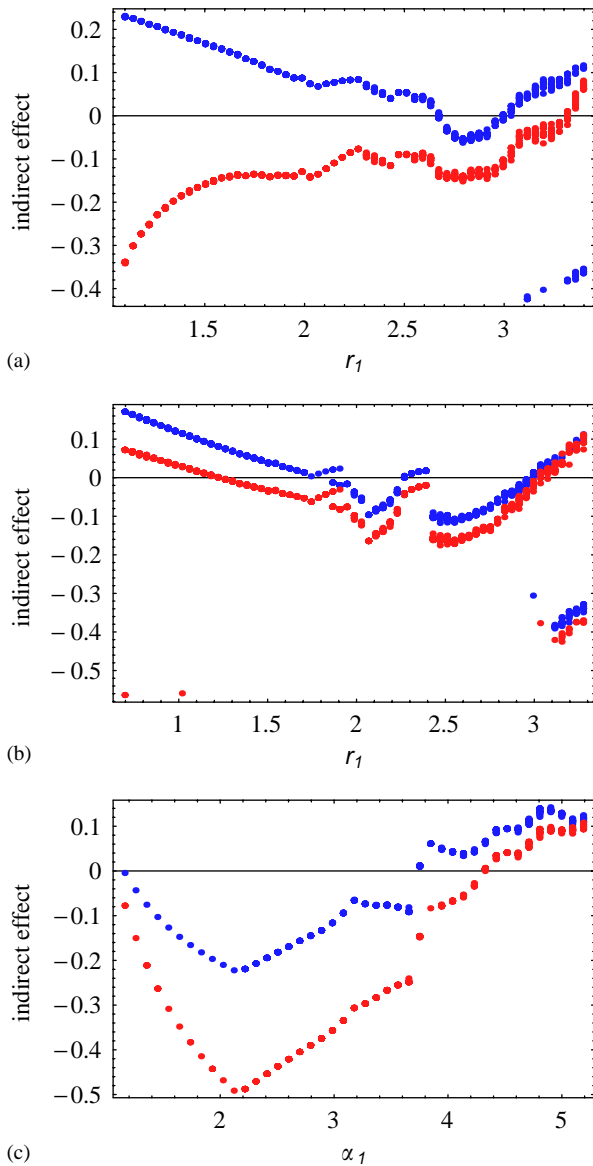


Fig. 2. The magnitude of the indirect effect, measured as a fraction of the sympatric population density upon complete removal of the other host, along the light gray line on 1a,b and c, respectively. The effect calculated for each parameter combination is plotted ten times at randomly selected initial conditions. The blue points are host 1; the red points are host 2. Small-scale scatter of the points is due to error associated with random initial conditions and a finite time period over which the mean was calculated. Large discrete differences among points within a color represent alternative attractors.

each with a theoretical maximum of 100%. Restricting analysis to cases in which all three species remain extant in both sympatry and allopatry, we examined the entire parameter space of the model. Using the larger density in the denominator, the mean effects are 7% for positive effects and 37% for negative effects.

The above analysis is based on long-term means calculated over 2000 generations. This results in a repeatable classification of parameter space and is appropriate for characterizing the asymptotic long-term

behavior. However, all field and lab studies we know of have been conducted over much shorter time spans, and often encompass only a few generations. To assess the applicability of our findings to such studies, we recalculated indirect effects over a time span of five generations. Examining indirect effects over the first five generations following a host removal experiment results in all indirect effects being $(-, -)$. In this case, eliminating a host always leads to an initial increase in the remaining host. Depending on the mechanics of how particular experiments are conducted, this initial dominance of $(-, -)$ effects may help explain the lack of positive indirect effects being observed in natural systems. After a few more generations the initial $(-, -)$ effect dissipates and the indirect effects more closely resemble the long-term characterization. Averaging over generations 5–10 following a host removal experiment, only 2% of parameter space is characterized as $(+, +)$, while is 20% characterized as $(+, -)$, and 78% as $(-, -)$. Averaging over generations 10–15 following removal, 11% is $(+, +)$, 28% is $(+, -)$, and 61% is $(-, -)$ (Fig. 3). This is approaching the proportions calculated over 2000 generations as in Fig. 1c, 12% $(+, +)$, 40% $(+, -)$, and 47% $(-, -)$. For any particular set of parameters, using only 5 generations often results in an incorrect estimate of the long-term mean. However, the proportions of parameter space giving each qualitative type of outcome, and the locations in parameter space where

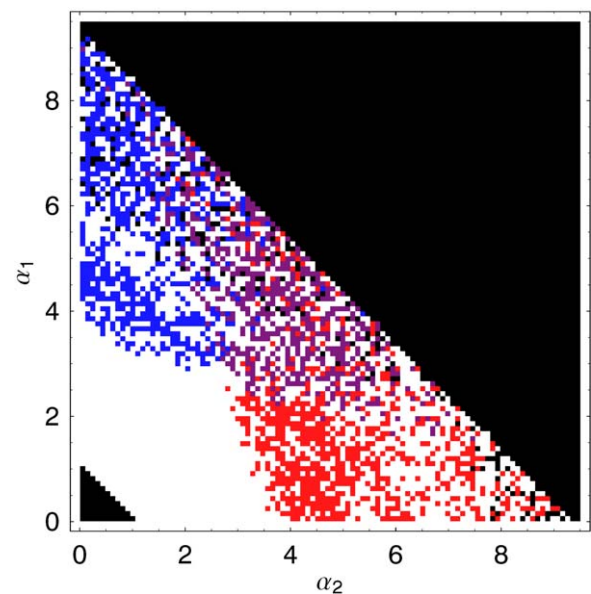


Fig. 3. The same parameters as shown in Fig. 1c, however instead of classifying interactions by averaging over 2000 generations, interactions are classified by averaging over 5 generations. In addition, alternative attractors are ignored and the result of a single initial condition at each parameter combination is plotted. Interactions are reclassified using the average density from generations 10–15 following host removal. While a more realistic number of generations results in more noise, the general regions can still be seen. The figure uses the same parameters and color coding as Fig. 1c.

each type of interaction is most common are changed relatively little by calculating means over five generations provided that the measurement is initiated approximately 10 generations or more following the experimental manipulation (Fig. 3).

2.5. Complete characterization of parameter space

In order to avoid the limited scope of the parameter set “slices” in which only a pair of parameters differ (Fig. 1), an analysis of the entire parameter space was conducted by randomly selecting (Press et al., 1992) parameter values from within a range that encompassed the space where all three species remain extant. The resulting interactions observed are classified in Table 1. In order to sample parameter space without the bias that might be produced by limited systematic sampling, parameters were randomly selected until 40,000 cases were found in which all three species remain extant in sympatry. Repeated re-sampling showed that this number was sufficient to accurately estimate the proportions of qualitatively different pair-wise indirect interactions (see note below Table 1). It is highly improbable that each point in parameter space is equally likely in nature, but in the absence of further information, random selection of parameters represents a first step in systematically understanding the relative size of parameter ranges leading to different indirect effects. Percentages of parameter space that lead to qualitatively different forms of indirect effects are presented in Table 1. Initially, we ignore cases where each single host system could exist but coexistence of both hosts with the parasitoid does not occur; see below for the effects of including these cases.

Parameter space is dominated by $(-, -)$ interactions, representing 78% of parameter space, while 21% of the parameter space is $(+, -)$ and only 1% is $(+, +)$. However, this classification ignores the size of the effect.

Empirical studies operate under the real constraints of detection limits; all empirical studies will have some finite statistical power to distinguish small effects from no effect. The detection limit in any single empirical study will depend on the variability of the populations under study and the study design. However, past studies provide an indication of the kind of statistical power that is commonly achieved in studies of predator-mediated indirect effects. Chaneton and Bonsall’s (2000) review includes 13 studies that examined reciprocal effects; for 6 of these we were able to determine effect

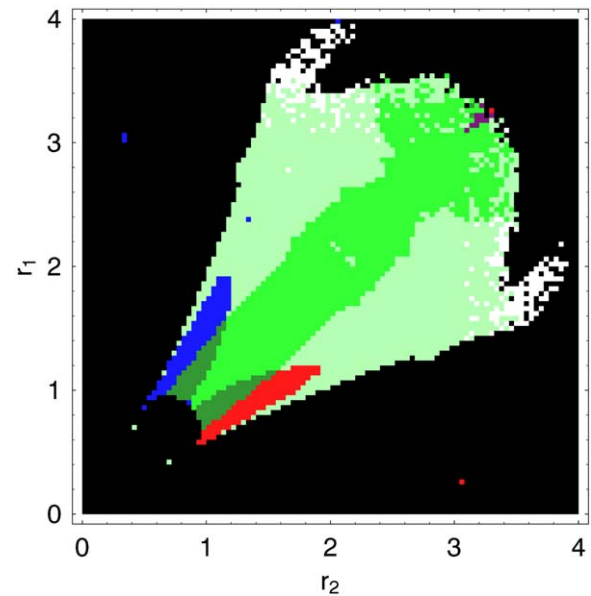


Fig. 4. The results from Fig. 1a with interactions reclassified using a 15% threshold for detection. In addition, alternative attractors are ignored and only the outcome of a single set of initial densities is plotted for each parameter combination. The detection threshold results in large regions of parameter space in which one of the interactions is characterized as a 0 interaction. The colors have the same meaning as in Fig. 1, with the addition of; dark green = $(+, 0)$; medium green = $(0, 0)$; light green = $(-, 0)$.

Table 1
Percent of parameter space characterized by indirect interactions between hosts

Model	Indirect effect					
	$(+, +)$	$(+, -)$	$(-, -)$	$(0, 0)$	$(-, 0)$	$(+, 0)$
Regular model (no detection limit) Eq. (3)	0.8	20.8	78.4	0.0	0.0	0.0
Regular model (15% limit) Eq. (3)	0.0	5.7	35.5	3.9	47.7	7.2
10% detection limit	0.1	8.0	46.5	1.9	37.2	6.4
5% detection limit	0.1	12.5	60.7	0.6	21.5	4.6
Trade-off in host	0.0	3.0	45.1	3.5	46.3	2.1
Hosts stable in absence of parasitoid $r_1, r_2 (0, 2)$	0.0	2.6	35.3	3.5	56.5	2.1
Higher extinction threshold (10^{-4})	0.2	8.9	34.9	3.2	44.5	8.3
Only need one host extant in allopatry	0.0	1.1	10.0	1.9	86.6	0.3

Note: If the change in the population density due to host removal resulted in less than a 15% change in the population density, the interaction is labeled as a 0 indirect effect in all except the 1st, 3rd, and 4th rows of the table. In all models, parameters were randomly chosen from the following ranges: $\alpha_1, \alpha_2 (0, 15)$; $\beta (1, 10)$; $r_1, r_2 (0, 7)$. Additional parameter ranges are listed with each model heading. Based on repeated simulations of the regular model, typical 95% confidence intervals are between ± 0.2 and ± 0.4 .

size (Kotler et al., 1994; Balciunas and Lawler, 1995; Brown and Morgan, 1995; Marvier, 1998; Bonsall and Hassell, 1998; Schmidt and Whelan, 1998). The smallest indirect effect classified as nonzero was a 12% change in density of one host following addition or removal of the other host. The largest effect classified as zero was a 16% change. This suggests that a 15% detection limit is a realistic detection limit for the types of studies of predator-mediated indirect effects that are likely to be carried out under current funding and time constraints. We reclassified indirect effects using this detection limit, which greatly altered the overall classification of outcomes. For example, Fig. 1a, which assumed that an effect of any size could be detected, classified most of parameter space as (+,–) or (–,–). With a 15% detection threshold, most of the parameter space for Fig. 1a becomes (–,0) or (0,0) (Fig. 4). Parameter space is now dominated by (–,0) interactions, representing 48% of the space, while 36% of the space is (–,–). Large magnitude (+,–) interactions represent only 6% of parameter space. The shift in proportions is not as large with a 10% or 5% detection threshold, but zero interactions still represent a large fraction of parameter space under these thresholds (Table 1). Introducing the detection threshold decreases the relative area of parameter space with at least one positive effect, because positive effects are, on average, smaller than negative effects. In the next few sections, we utilize a 15% detection limit and demonstrate that the relative sizes of areas of parameter space characterized by different types of interactions are fairly robust to model variations. The result of the full parameter space analysis for Eq. (3) is presented in Table 1 along with results from variant models discussed later. The percentages should be interpreted loosely, focusing on rank order and patterns across the models. The exact percentages will depend on a variety of factors, including additional constraints delineating biologically probable areas of parameter space, and scaling of the parameters.

2.6. Restrictions and extensions of parameter space

Our analysis implicitly assumes that all parameters that result in coexistence of the three species are equally likely to occur. Although there are no rigorous grounds for excluding any particular parameter range, this assumption of equally probable parameters is unlikely to be true. To investigate the potential effects of restrictions on parameter values, we investigated several biologically based restrictions. These are: (1) the presence of a tradeoff between host growth rate and vulnerability to the parasitoid; (2) the restriction to hosts that have a stable equilibrium in the absence of the parasitoid; (3) the restriction to systems in which minimum host densities do not drop below 10^{-4} .

The observation that there is often a tradeoff between intrinsic growth and predator avoidance (e.g. Lima, 1998), suggests that it might be reasonable to assume that a host with a large growth rate, will also have a large attack rate. The attack rate was modeled as a linear function of the growth rate, $a_i(r_i) = A r_i$. The resulting dimensionless equation is (3) with each instance of P_i multiplied by r_i . The results when parameter space is sampled randomly with this restriction are very similar to those obtained without the restriction. There is a slight decrease in positive effects, but parameter space is still dominated by (–,0) and (–,–) interactions, given the 15% detection limit (Table 1).

There is still considerable debate about the prevalence of cyclic dynamics resulting from density dependence (Turchin, 1999). If host growth rates are generally small enough that host dynamics reaches a stable equilibrium in the absence of parasitoids, then we should restrict our analysis to cases with $r_i < 2$. In these cases, cycles are generated as a result of species interactions. Limiting host growth rate resulted in an overall decrease in positive interactions, although they are still a non-negligible fraction of parameter space (Table 1).

In our analysis, populations were presumed to have gone extinct when their densities drop below 10^{-6} . There do not appear to be well-documented cases of organisms with cycles greater than 6 orders of magnitude. Murdoch (2003) suggest that the largest documented cycles have amplitudes of 4 orders of magnitude. In addition, even populations of 10^6 individuals or greater may be at risk of stochastic extinction under density fluctuations considerably less than 6 orders of magnitude. Thus, it might be more appropriate to restrict our analysis to systems with higher minimum population sizes. Raising the extinction threshold to 10^{-4} , and consequently reducing the allowable size of fluctuations, results in a categorization of parameter space very similar to that based on an extinction threshold of 10^{-6} (Table 1).

The above method has ignored cases in which either host could exist with the parasitoid, but the two hosts cannot coexist. These cases might be especially relevant to examples in which the invasion of an exotic host may be leading to the extinction of the native host (Settle and Wilson, 1990), or laboratory systems in which exclusion is documented (Bonsall and Hassell, 1998). Once extinction of a host has occurred, these cases would be characterized as (–,0) interactions, so we have redone analysis of the basic model to determine how much parameter space yielding (–,0) effects would increase with these cases included. The result is a dramatic increase in (–,0) interactions; nearly 87% of interactions are categorized as (–,0) interactions given the 15% detection limit. The absolute magnitude of the increase in (–,0) interactions produced by this redefinition of effect size is very sensitive to the detection limit.

3. Discussion

A variety of previous models have suggested that interactions via a shared enemy can be characterized by several different combinations of + and – effects (Holt, 1977; Holt, 1984; Abrams, 1987; Holt and Kotler, 1987; Abrams and Matsuda, 1996; Abrams et al., 1998). In spite of this, there has never been a systematic examination of parameters to determine the relative frequencies of different types of interactions. We have carried out this analysis for a parasitoid–host model and found that asymmetrical interactions consisting of one negative effect and one near-zero effect are the most common category of indirect interactions between host species. The next most common interaction types are the (–,–) interactions normally associated with the term ‘apparent competition’. In nearly all models, positive interactions represent a non-negligible fraction of parameter space. While additional models and additional model variations should be analyzed in concert with empirical systems, we feel that the detailed analysis of the host–parasitoid model presented here provides a possible explanation for the relative scarcity of (–,–) interactions, as well as broad conditions under which positive interactions might be observed in long-term studies of indirect effects with a shared enemy. This discussion is largely devoted to a comparison of these predictions with the results of previous empirical studies.

Comparison of our results with published studies is difficult in part because of the limited number of studies that have clearly tested the reciprocal effects and the limited number of studies that examined long-term apparent competition (Chaneton and Bonsall, 2000). Many studies which demonstrate apparent competition have only examined one of the two indirect effects that characterize the interaction between the two prey/host species (for example Settle and Wilson, 1990; Grosholz, 1992). Chaneton and Bonsall (2000) reviewed studies of indirect effects with a shared enemy and found 26 out of 34 studies either documented or suggested a non-reciprocal interaction (–,0). Their literature review found (–,–) interactions to be the second most common indirect effect, another finding consistent with our results. Of course, their review included a broader diversity of systems and mechanisms than those modeled here. In addition biologically likely parameter space may have more limits than those modeled here. Several of the studies that Chaneton and Bonsall review found (–,0) interactions because one of the two hosts went extinct when the two were sympatric, a case which was not included in our main analysis. Chaneton and Bonsall (2000) found only 5 studies that explicitly tested the reciprocal effect and examined the long-term indirect effect (i.e., an effect that was mediated by changes in predator density rather than simply by changes in

distribution or behavior). The empirical study that appears to be most closely related to the models presented here is a multi-generation host–parasitoid system consisting of *Venturia canescens*, *Plodia interpunctella*, and *Ephestia kuehniella* in which an asymmetrical indirect effect was shown to exist (Bonsall and Hassell, 1997, 1998). Using a repeated-measures analysis of variance, they demonstrated a (–,0) interaction between hosts, although the 0 effect may have been a nonzero effect of small magnitude. It is possible that this general correspondence between theory and empirical work is due to biases in systems studied. The set of previous empirical studies of apparent competition is certainly not a random sample of all natural systems in which dynamics are heavily influenced by shared predation or parasitism, and very few of the studies have spanned enough generations to calculate meaningful average densities. However, it seems plausible that these empirical studies reflect a predominance of (–,0) or (–,small) effects in natural systems.

A number of mechanisms may explain the preponderance of zero effects in shared enemies systems. As previously discussed (Chaneton and Bonsall, 2000), very different host growth parameters or attack rates could themselves produce effects that are very unequal in magnitude. The analyses of full parameter space presented here include both stable and cycling situations, but limiting analysis to stable parameter combinations and including a detection limit will still lead to a large proportion of asymmetric effects. Limiting the analysis to stable parameter combinations in Eq. (3) will produce apparent competition across that parameter space, but at least one of the negative effects will often be of small magnitude. Using a 15% detection limit, 59% of stable interactions are reclassified as (–,0) interactions, 39% remain (–,–) interactions, and 2% are classified as (0,0) interactions. Thus even in stable models a preponderance of asymmetrical (–,0) effects can be expected due to basic life history differences among hosts. The other mechanism for zero effects in the models described here involves a weakening of the indirect effect due to cycling. Decreases in the amplitude of cycles following removal of one host counteract the decrease in predator density that would occur in the absence of any change in cycles. Our analysis shows that this cancellation affects a wide range of parameter space. In addition, dynamically stable systems may experience stochastic variation due to environmental noise, in some cases mimicking the effects of deterministic cycles (Brassil, unpublished). A third mechanism not modeled here is the counteracting effects of predator satiation or switching versus increases in predator density following the addition of a new prey or host species when there is direct predator density dependence (Abrams and Matsuda, 1996). Satiation is closer to the rule than the exception (Hassell, 2000) and direct density

dependence in the predator/parasitoid allows the effect of a second host (prey) on the parasitoid's (predator's) numerical response to be stronger than the effect on the predator's numerical response. Unpublished results (Brassil and Abrams) show positive indirect effects to be more common than negative ones in models with both satiation and direct density dependence in the parasitoid. Excluding (0,0) interactions, 78% of parameter space consists of (+,0) interactions, and 87% consists of interactions with at least one positive effect.

The focus of this paper has been on host–parasitoid models, but shared enemy literature includes both host–parasitoid models and predator–prey models. The model presented here can be modified to model a predator–prey system with little difference in the general results. Whereas parasitized hosts can continue to consume resources after being attacked, prey are immediately consumed, reducing the number of prey that are consuming resources. In order to model this difference, Eq. (3) was modified so that density dependence was proportional to the average number of surviving prey over the season as opposed to the number of hosts at the beginning of the season. While the timing of density dependence can alter some interactions (May et al., 1981), in this case, the majority (62%) of interactions that fell above the 15% detection threshold were still (–,0).

Whether or not switching, satiation, and/or direct density dependence are common in predators or parasitoids, the lack of empirical studies documenting positive long-term indirect effects is puzzling. Most of our model variants suggest that (+,0) interactions should be observed in a significant fraction of studies of shared predation/parasitism. However, examples of positive effects remain undocumented (Abrams and Matsuda, 1996; Chanton and Bonsall, 2000). Positive indirect effects may have gone undocumented because (1) they are generally smaller in magnitude than negative effects and consequently are harder to demonstrate; (2) researchers are not looking for them; or (3) they often require measures over multiple generations in a cycling system, a situation likely avoided by many researchers.

Schoener (1993) and Wootton (1994) discuss some potential mechanisms that could prevent indirect effects or diminish their importance. These include: weak direct interaction, environmental noise, and opposing interactions that cancel out indirect effects. One should add to this list the possibilities that: (1) long-term indirect interactions may be diminished when changes in population cycling counteract otherwise strong interactions; (2) the indirect effect of one species on another may consist of a mixture of positive and negative pathways. The latter is true when saturation of the functional response counteracts an increase in parasitoid abundance.

There are a variety of ways that the theory presented here could be extended. Generalizations about the three-species web may be modified when the system is only a portion of a larger food web (Yodzis, 2000). Minimally, the robustness of these results should be examined in systems that have additional prey or host species, systems that have multiple predators, and systems with predators on higher trophic levels. Shared predation modules imbedded within more complex food webs may exhibit a variety of indirect interactions depending on the form of the web (Holt, 1977). Additional insight could come from studies that extended these results to include adaptive behavior of the parasitoid, the hosts or both. The presence of a host refuge is also likely to affect the magnitude of indirect interactions. Both continuous models of shared predation and various models of shared prey or resources could be investigated to determine how well the observed outcomes of experiments correspond to the statistical expectation of effects when parameters are chosen randomly for simple models.

In summary, we found that a large fraction of parameter space, across many models, resulted in (–,0) interactions, a finding consistent with some empirical studies of shared predation. At the same time, we found that a significant fraction of parameter space was characterized by pair-wise interactions consisting of at least one non-negligible positive effect, a result that has yet to be supported by empirical studies.

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