

## Persistence and Area Effects in a Stochastic Tritrophic Model

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Ever since the seminal experiments of Huffaker (Huffaker 1958; Huffaker et al. 1963), ecologists have believed that patchiness, dispersal, and spatial heterogeneity are central to the persistence of strong natural enemy-victim interactions (e.g., Taylor 1990; Gilpin and Hanski 1991; Ricklefs and Schluter 1993; Kareiva 1994). Recent work has shown that local, diffusive dispersal can permit the persistence of host-parasitoid interactions played out in an arena of coupled patches, comprising a lattice of cells (e.g., Hassell et al. 1991; Sole and Valls 1992). Even in landscapes with identical patches and inherently unstable within-patch (i.e., local) dynamics, interacting species may persist in the landscape as a whole. This persistence is often accompanied by, and indeed may require the existence of, strong spatial patterning in host and parasitoid densities, including spatial waves, relatively fixed areas of high or low density, and spatial chaos.

Lattice size, or number of suitable habitat patches, has been identified as having a significant effect on persistence (empirically demonstrated by the species-area relation; e.g., Holt 1993; Rosenzweig 1995). For instance, one study (Hassell et al. 1991) reported that simulations of host-parasitoid interactions in coupled lattices were likely

to suffer extinctions if the number of patches in the lattice was too small. Essentially, for fixed dispersal rates, the spatial asynchrony needed for regional persistence tends to disappear in small lattices, and the inherent instability of the Nicholson-Bailey model, used to describe the local dynamics in each patch, reemerges to destabilize the overall system. Extinction occurs when the parasitoid overexploits its host and then goes extinct itself. This is more likely at higher host and parasitoid dispersal rates, for any given lattice size. These theoretical results qualitatively match the outcome of Huffaker's classic experiments, in which the length of time that predatory mites coexisted with their prey mites increased with the number of "cells" (in this case, oranges) in the experimental arenas. Metapopulation models of tritrophic interactions also suggest that food chain length may be constrained by colonization-extinction dynamics (Holt 1997a, 1997b).

In this note, we consider in some detail how metapopulation size might influence the persistence of multispecies communities, focusing in particular on the length of food chains—two trophic layers (host-parasitoid) versus three trophic layers (host-parasitoid-hyperparasitoid)—that can be sustained. Our approach highlights the importance of considering the effects of demographic stochasticity, particularly when dealing with the persistence of interactions in which local population densities are occasionally expected to reach low levels. To address how demographic stochasticity and area influence food chain persistence, a standard deterministic host-parasitoid model is reformulated as a model based on discrete individuals in which encounters between hosts and parasitoids and the fecundity of each host are modeled by simple stochastic processes. There are a number of benefits to this approach. First, deterministic models used in previous work were formulated as a mean approximation to the random process of parasitoids finding hosts, and all had local population size as a continuous variable (but see, e.g., Ruxton 1996; Wilson 1996). However, models that at times have very small numbers of individuals within patches may not be at all well represented by following this mean approximation, due to the effects of demographic stochasticity (Pimm et al. 1988; Rand and Wilson 1991; Stephan and Wissel 1994; Lande 1996).

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Second, it is possible that some of the properties of the deterministic metapopulation models rest heavily on the existence and dispersal of "nano-individuals," an artifact of the assumption of continuity that may introduce pathologies not seen if the models only dealt with discrete individuals. And third, extinctions naturally enter the model through a biologically motivated mechanism, which is simply that the number of hosts be zero. Previous work using models with a continuous state space were forced to introduce extinction in a rather ad hoc manner, for instance, by setting a minimum size below which the local population is deemed to be extinct.

### A Stochastic Formulation

The basic host-parasitoid model is that used in a previous study (Hassell et al. 1991). This assumes a two-dimensional grid, size  $l \times l$ , of patches in which the local dynamics occur. A further trophic layer in this system can be obtained by the addition of a hyperparasitoid species (e.g., see May and Hassell 1981; Hassell et al. 1994). The local dynamics are then given by:

$$\begin{aligned} H'_i &= \lambda(H_i f(P_i))H_i f(P_i); \\ P'_i &= b_1 H_i (1 - f(P_i))g(Q_i); \end{aligned} \quad (1)$$

and

$$Q'_i = b_2 H_i (1 - f(P_i))(1 - g(Q_i)).$$

Here  $H_i$ ,  $P_i$ , and  $Q_i$  are, respectively, the population size of hosts, parasitoids, and hyperparasitoids in patch  $i$ , and the primes denote the respective numbers in the next generation. The quantity  $f(P_i)$  is the fraction of hosts unparasitized,  $g(Q_i)$  is the fraction of parasitoids not hyperparasitized, and  $b_1$  and  $b_2$  are the number of female parasitoids and hyperparasitoids emerging from each parasitized host or parasitoid (henceforth  $b_1$  and  $b_2$  are both assumed to equal 1). The quantity  $\lambda$  is the host net rate of increase and is dependent on the density of hosts after parasitism has occurred. This term could alternatively depend on the density of hosts before parasitism (see May and Hassell 1981 for details). However, our later results are not dependent on the exact way host density dependence has been included and the particular methodology used here has a sound biological interpretation.

Following the stages of reproduction and parasitism within each patch there is a dispersal phase, in which a fraction  $c_H$  of hosts,  $c_P$  of parasitoids, and  $c_Q$  of hyperparasitoids disperse equally to the eight nearest neighboring patches, leaving a fraction  $(1 - c_H)$ ,  $(1 - c_P)$ , and  $(1 - c_Q)$  in each patch. This model is deterministic with continuous population variables and represents an obligate

Table 1: Parameters used in the model

Parameter	Meaning
$\lambda$	Host fecundity
$b_1$	Average number of female parasitoids emerging from one parasitized host (= 1)
$b_2$	Average number of female hyperparasitoids emerging from one hyperparasitized host (= 1)
$a_P$	Attack rate of the parasitoid
$a_Q$	Attack rate of the hyperparasitoid
$K$	Carrying capacity of each patch
$c_H$	Probability of a host dispersing to a neighboring patch
$c_P$	Probability of a parasitoid dispersing to a neighboring patch
$c_Q$	Probability of a hyperparasitoid dispersing to a neighboring patch
Lattice size	Total number of patches in the model
$\delta_t$	Small, within-generation time step in the stochastic model
$T_1$	Length of time hosts are exposed to parasitism (= $1/\delta t$ )
$T_2$	Length of time parasitized hosts are exposed to hyperparasitism (= $1/\delta t$ )

hyperparasitoid, which parasitizes at a later stage than the primary parasitoid.

The function  $f(P_i)$  for survival from parasitism within a patch has normally been given by the standard Nicholson-Bailey model (although the negative binomial model has also been used; see, e.g., Reeve 1990; Comins et al. 1992):

$$f(P_i) = \exp(-a_P P_i), \quad (2)$$

where  $a_P$  is the attack rate of the parasitoid. This assumes that parasitism is random in each patch and that the numbers of hosts and parasitoids is sufficiently large so that the average number of hosts escaping parasitism is given by the zero term of a Poisson distribution with mean  $a_P P_i$ . Similarly,  $g(Q_i)$  is the fraction of parasitoids that escape hyperparasitism and is given by the function  $g(Q_i) = \exp(-a_Q Q_i)$ . The host density dependent function is given by

$$\lambda(H_i f(P_i)) = \lambda \exp\left(\frac{-H_i \exp(-a_P P_i)}{K}\right), \quad (3)$$

where  $K$  is the carrying capacity of a patch (and is the same in all patches). Table 1 has a full list of the parameters used.

We now wish to develop a stochastic model, based on integers, which only differs from the above well-known model in having demographic stochastic effects (i.e., the deterministic limit of the stochastic model should be the Nicholson-Bailey model above, with density dependence included). We first need to model encounters between hosts and parasitoids as a simple stochastic process. Consider first only the host and parasitoid. The probability of a parasitoid encountering a host within a small period of time  $\delta t$  is  $a_p \delta t$ . The probability that a host in patch  $i$  is encountered by at least one parasitoid during this period is then

$$1 - (1 - a_p \delta t)^{P_i} \approx a_p \delta t P_i, \quad (4)$$

where terms that are  $O(\delta t^2)$  are ignored. Therefore the probability that  $j$  hosts are infected during a time  $\delta t$  is

$$\binom{H_i}{j} (1 - a_p \delta t P_i)^{H_i - j} (a_p \delta t P_i)^j, \quad (5)$$

which, as  $P_i \delta t \rightarrow C$ , is approximated by a Poisson distribution with mean  $a_p P_i \delta t$ . Formally, this approximation also requires that  $H_i \rightarrow \infty$ , which will not always be the case here, as  $H_i$  is sometimes as low as one or two individuals. However, as long as  $\delta t$  is very small, such that terms of order  $O(\delta t^2)$  or higher are negligible, then even when host numbers are small this approximation will hold.

In order to facilitate comparison with model (1), discrete generations with synchronized reproduction and dispersal are kept. In addition, model (1) is based on sequential parasitism, with hosts first parasitized by the primary parasitoids that, as they develop within the host, are then in turn parasitized by the hyperparasitoids. Our model thus consists of two parts: a within-season component that describes sequential parasitism of hosts and parasitoids and a between-season component describing reproduction and then dispersal, which relates the distribution of hosts, parasitoids, and hyperparasitoids at the end of one season to the distribution at the start of the next. The within-season component is, for stage 1 ( $t < T_1$ ),

$$H_{i,t+\delta t} = H_{i,t} - \alpha_{i,t},$$

$$p_{i,t+\delta t} = p_{i,t} + \alpha_{i,t},$$

$$P_{i,t+\delta t} = P_{i,t},$$

$$q_{i,t+\delta t} = q_{i,t},$$

and

$$Q_{i,t+\delta t} = Q_{i,t},$$

and, for stage 2 ( $t > T_1$ ),

$$H_{i,t+\delta t} = H_{i,t}, \quad (6)$$

$$p_{i,t+\delta t} = p_{i,t} - \beta_{i,t},$$

$$P_{i,t+\delta t} = P_{i,t},$$

$$q_{i,t+\delta t} = q_{i,t} + \beta_{i,t},$$

and

$$Q_{i,t+\delta t} = Q_{i,t},$$

where  $p_{i,t}$  and  $q_{i,t}$  are the number of parasitoid and hyperparasitoid larvae;  $H_{i,t}$ ,  $P_{i,t}$ , and  $Q_{i,t}$  are the numbers of adults;  $\alpha_{i,t}$  is a random number taken from a Poisson distribution, with mean  $a_p P_{i,t} H_{i,t} \delta t$ ; and  $\beta_{i,t}$  is a random number taken from a Poisson distribution, with mean  $a_q p_{i,t} Q_{i,t} \delta t$  (derived by a similar line of reasoning to the host and parasitoid). In theory,  $\delta t$  should be chosen so small that there would almost always be only a single event in any period  $\delta t$  (which also means that the numbers of adult hosts or parasitoid larvae could never be negative). In practice, its value is chosen as a balance between this theoretical limit and speed of simulation (in which case we need to impose maximum values for  $\alpha_{i,t}$  and  $\beta_{i,t}$  of  $H_{i,t}$  and  $p_{i,t}$ ). All the simulations have been checked with values of  $\delta t$  an order of magnitude smaller and qualitatively similar results were obtained. Stage 1 lasts a time  $T_1$ , and stage 2 occurs directly after stage 1 and lasts a time  $T_2$ . In our simulations, we set these two time intervals equal. After both stages are complete, the between-generation phase occurs:

$$H'_i = Z \left( \lambda \exp \left( -\frac{H_{i,T_1+T_2}}{K} \right) H_{i,T_1+T_2} \right);$$

$$p'_i = 0;$$

$$P'_i = p_{i,T_1+T_2}; \quad (7)$$

$$q'_i = 0;$$

and

$$Q'_i = q_{i,T_1+T_2},$$

where  $Z \sim \text{Poi}(\lambda \exp(-H_{i,T_1+T_2}/K) H_{i,T_1+T_2})$ , so that the fecundity of each individual in a patch is distributed as a Poisson distribution with mean  $\lambda \exp(-H_{i,T_1+T_2}/K)$ . (The distribution of the sum of  $H_i$  independent Poisson random variables each with mean  $\lambda \exp(-H_{i,T_1+T_2}/K)$  is the same as a Poisson distribution with mean  $\lambda \exp(-H_{i,T_1+T_2}/K) H_i$ .) If this model had no stochastic element, then we would return exactly to model (1).

Each individual host, parasitoid, and hyperparasitoid now disperses to a site randomly chosen from one of the

neighboring patches with probability  $c_H$ ,  $c_P$ , and  $c_Q$ , respectively. In the simulations reported here, individuals that disperse beyond the boundaries of the lattice are lost. We have repeated our analyses, using reflecting and wrap-around boundary conditions, and find that the precise boundary conditions do not qualitatively affect the results.

The population densities of species in the model above can follow different paths depending on initial conditions (see Sole and Valls 1992; Adler 1993). All the simulations in this note are started with random initial conditions and have a small amount of immigration at random points within the lattice for the first 300 generations in order to prevent extinctions. This masks the effect of particular initial conditions and allows us to study the long-term behavior of the system. All the results presented are averages over many simulations or are very typical behaviors of a large number of simulations observed. Thus, they catch the robust properties of the system rather than focus on properties that depend on very particular initial conditions.

## Persistence Results

### *Host-Parasitoid*

As a prelude to examining the tritrophic community, and for comparison, we first consider the one host-one parasitoid community with no host density dependence included (by setting the carrying capacity  $K$  to be very large so that it has no effect—set here at  $K = 1.0E+8$ ). Because the model is stochastic with an absorbing state of zero density, in the long run, extinction is inevitable. The parameters and lattice size in effect define the distribution of times to reach extinction. Table 2 investigates persistence over a long time period ( $T_{MAX} = 20,000$  generations) as a function of lattice size and the parasitoid dispersal rate,  $c_P$ .

Three effects are apparent from this table. First, as the lattice size increases then the persistence time also increases. This is particularly marked at small lattice sizes. Second, the persistence time tends to be larger at smaller values of  $a_P$ . When  $a_P$  is small, then the mean population size is large and stochastic effects are averaged out (the unstable parasitoid equilibrium point in the Nicholson-Bailey equation is  $\ln(\lambda)/a_P$ , so that the mean parasitoid abundance per patch is a function of  $1/a_P$  and the logarithm of  $\lambda$ ). Decreasing the host reproductive rate will therefore have a similar effect to increasing  $a_P$ , but it will also have an effect on the stability of the host-parasitoid interaction). Small population sizes at larger values of  $a_P$ , however, mean that stochastic effects become important and that extinctions of both the host and parasitoid local

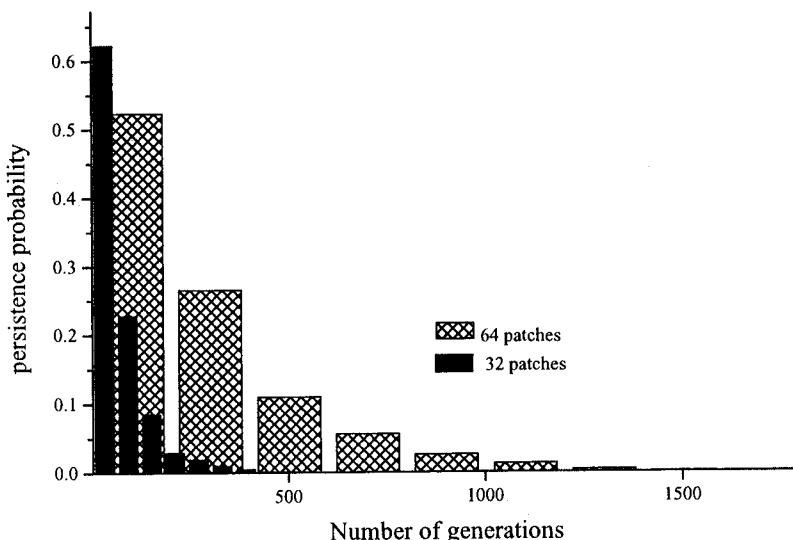
Table 2: Persistence times for the host-parasitoid model with no density dependence

	Lattice size: number of patches				
	25	49	100	196	400
$c_H = .1, c_P = .1:$					
$a_P = .01$	104	7,056	19,502	20,000	20,000
$a_P = .1$	40	121	1,443	19,126	20,000
$c_H = .1, c_P = .4:$					
$a_P = .01$	250	1,406	18,767	20,000	20,000
$a_P = .1$	71	367	9,150	20,000	20,000
$c_H = .1, c_P = .8:$					
$a_P = .01$	119	392	10,176	20,000	20,000
$a_P = .1$	27	31	98	185	906

Note: The maximum number of generations each simulation was allowed to run was 20,000, the host fecundity,  $\lambda$ , was 2, and the carrying capacity,  $K$ , was  $1.0E+8$ . The persistence time in the table is the average of 25 independent simulations started with random initial conditions.

populations become more frequent. The persistence time is therefore that much smaller. Third, at large values of  $a_P$ , both small and large values of the parasitoid dispersal rate need, on average, a larger number of patches for persistence. When extinction at a site is inevitable (due to the locally unstable dynamics), the parasitoid can only persist if it always colonizes a new suitable site (i.e., one with a significant number of hosts). When the parasitoid population is small (high  $a_P$ ), then the fraction of neighboring sites colonized is also small. A greater fraction of parasitoids must therefore disperse to ensure that at least one suitable site is colonized; in other words, a higher dispersal rate is needed. The persistence time, therefore, increases as  $c_P$  increases from small to intermediate values ( $0.1 \rightarrow 0.4$ , table 2). When the parasitoid dispersal rate is large compared to the host ( $c_P = 0.8$ , table 2), then the parasitoids are relatively mobile and hosts relatively sedentary. When the parasitoids also have a high searching efficiency (high  $a_P$ ), then the parasitoid overexploits the host and the two populations will tend to go extinct unless there is a very large number of patches so that rescue effects can always occur (the reverse case, when the host dispersal rate is large and the parasitoid dispersal rate small, not presented here, also tends to be far less persistent than when the dispersal rates are more similar). It should be emphasized that these results are robust to changing other parameter values (e.g.,  $c_H$  and  $\lambda$ ).

The above results all used a maximum persistence time ( $T_{MAX} = 20,000$ ). If either species has not gone extinct by this time, the community is considered persistent. If the results are robust, they should not be sensitive to the particular threshold value chosen. To investigate effects of changing this threshold, the distribution of persistence



**Figure 1:** Persistence time–frequency diagram for the host-parasitoid community with no host density dependence. Parameter values are  $a_p = 0.1$ ,  $c_H = c_P = 0.1$ ,  $K = 1.0E+8$  and  $\lambda = 2$ . Persistence time is the number of generations before either the host or parasitoid went extinct, and the persistence probability is the number of simulations that went extinct in a specified time interval divided by the total number of simulations (100). Simulations were run for a maximum of 20,000 generations.

times is studied. The persistence time–frequency distributions for 1,000 independent simulations are plotted for two different lattice sizes in figure 1. One can note three points from this figure. First, the probability of persistence depends on the choice of time  $T_{MAX}$ . Second, there is an order of magnitude difference between the persistence times of the host-parasitoid community in the two lattices. Choosing a particular threshold time,  $T_{MAX}$ , therefore, affects the absolute value of the persistence probability obtained, but one is still able to make valuable relative comparisons between lattice sizes and parameter configurations. Third, the number of simulations that persist for a certain time exponentially decreases with time. This exponential decay in the number of communities persisting for a fixed time indicates a roughly constant probability of extinction each generation. The value of this extinction rate depends on both particular parameter values and system size.

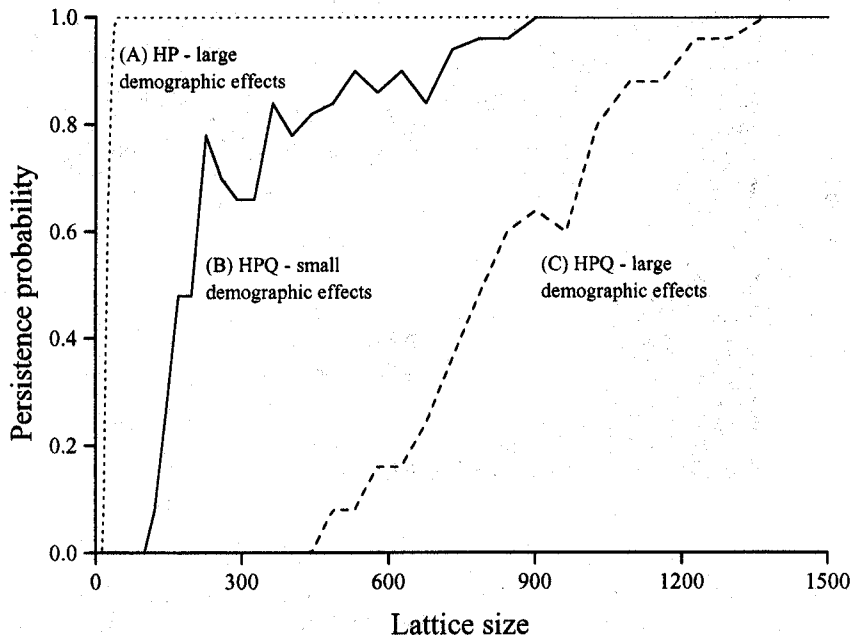
#### *Host-Parasitoid-Hyperparasitoid*

The degree to which the hyperparasitoid can exploit the parasitoid population is determined by attributes of the parasitoid (and host). Deterministic models predict that it is the hyperparasitoid attack and dispersal rates relative to those of the parasitoid that determine persistence (see Beddington and Hammand 1977; May and Hassell 1981; Hassell et al. 1994; Wilson et al. 1996). However, the results in the previous section showed that the degree of demographic stochasticity (the absolute values of the at-

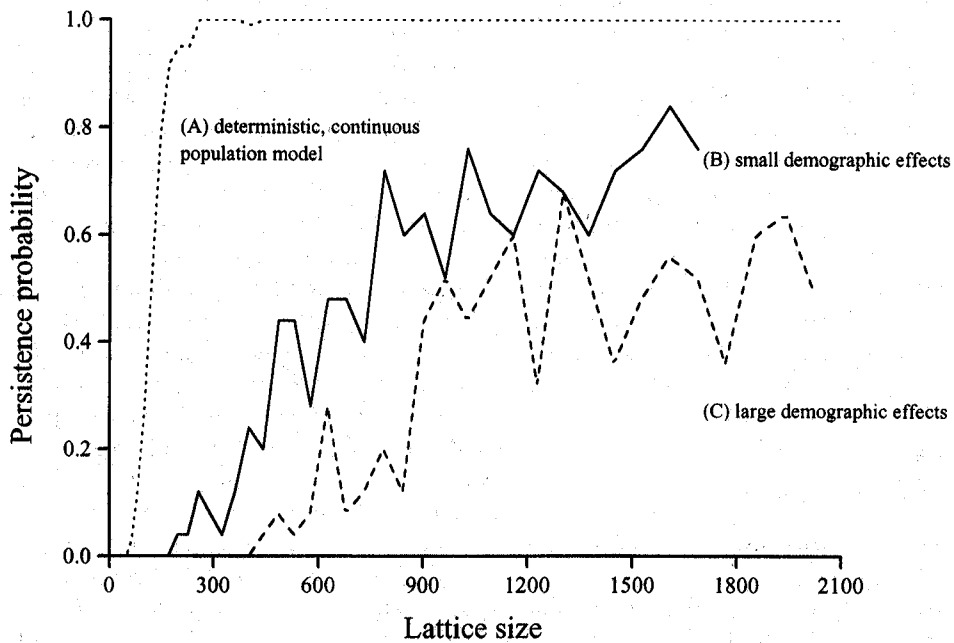
tack rate) strongly influences the persistence of the community. In the tritrophic community, this effect is enhanced further.

In figure 2 the probability of persistence of a host-parasitoid-hyperparasitoid community (no host density dependence) with respect to the lattice size is plotted. The probability of persistence is calculated as the number of simulations where all three species were still present after 2,000 generations divided by the total number of runs (25). If the tritrophic system is compared with the simple host-parasitoid community (*dotted line*, fig. 2), we see that the tritrophic community needs a far greater number of patches for persistence. Furthermore, when the parasitoid and hyperparasitoid have high attack rates (large demographic effects) then the lattice size needed for persistence is much larger again (*dashed line*, fig. 2). Thus the tritrophic system needs a far greater number of patches to persist than the simple host-parasitoid system, and this effect is further enhanced when demographic stochastic effects are large.

The inclusion of host density dependence means that the host population is limited in size according to the carrying capacity, whereas earlier the attack rates of the parasitoids were setting approximate population sizes. This means that the attack rates should not be as important in determining persistence. Figure 3 shows the probability of persistence when the carrying capacity is set at  $K = 10,000$ . The differences between small and large attack rates are now blurred, but the number of patches needed for persistence is still an order of magnitude



**Figure 2:** Persistence of the host-parasitoid-hyperparasitoid community with no density dependence. Parameter values are  $\lambda = 2$ ,  $c_H = c_P = c_Q = 0.1$ ,  $a_P = 0.01$ ,  $a_Q = 0.02$ , and  $K = 1.0E+8$  for the community with the low demographic effects (solid line, B), and  $\lambda = 2$ ,  $c_H = c_P = 0.1$ ,  $a_P = 0.1$ ,  $a_Q = 0.12$ ,  $c_Q = 0.3$ ,  $K = 1.0E+8$  for the community with large demographic effects (dashed line, C). The dotted line (A) is for the host-parasitoid community on its own ( $\lambda = 2$ ,  $c_H = c_P = 0.1$ ,  $a_P = 0.1$ ,  $K = 1.0E+8$ ). The parameter values for the hyperparasitoid were chosen as a typical example from figure 4. The probability of persistence is calculated as the number of simulations where all three species were still present after 2,000 generations divided by the total number of runs (25). As in figure 1, other sets of parameter values show qualitatively similar results.



**Figure 3:** Persistence of the host-parasitoid-hyperparasitoid community with host density dependence included. Parameter values are exactly as in figure 2, except that  $K = 1.0E+4$ . The dotted line (A) is for the deterministic, continuous population variable host-parasitoid-hyperparasitoid community with the same parameter values (including host density dependence) as for the community with large demographic effects (dashed line, C). The solid line (B) is the three-species community with small demographic effects (same as the solid line in fig. 2, except with  $K = 1.0E+4$ ).

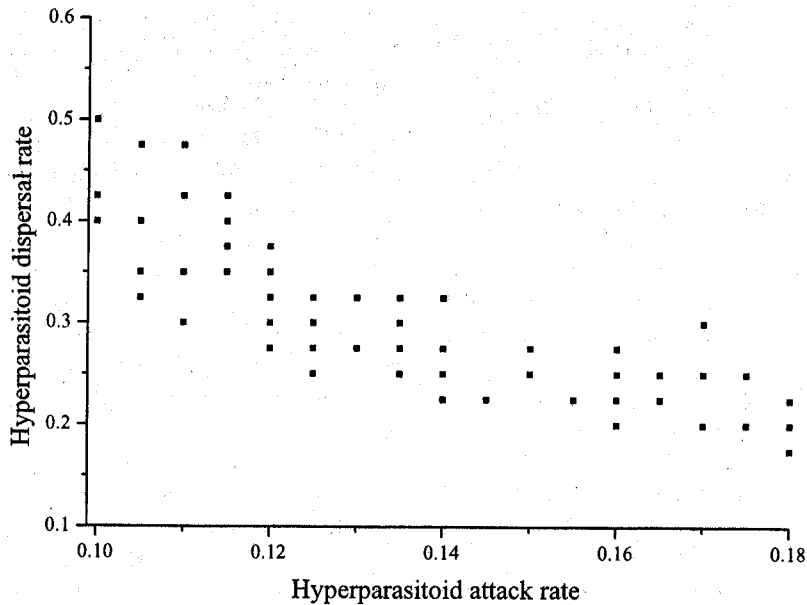


Figure 4: Persistence of the tritrophic system with large demographic effects and no host density dependence. Parameter values are  $\lambda = 2$ ,  $c_H = c_P = 0.1$ ,  $a_P = 0.1$ ,  $K = 1.0E+8$ , and  $0.1 < a_Q < 0.18$ . Five simulations, with random initial conditions, were run for each parameter combination of hyperparasitoid attack and dispersal rate (step size was 0.005 for the attack rate and 0.025 for the dispersal rate). If all three species survived for 2,000 generations in at least half the simulations (i.e., three or more), then that point was plotted. Clearly there is some random scatter due to the random nature of the initial conditions and the model, but the general trend is clear. If many more than five simulations at each point were run (five was chosen as the simulations are quite slow), then the observed pattern would be much smoother. Above the plotted region, the hyperparasitoid is over exploitative and causes the local extinction of the parasitoid and then goes extinct itself. Below the plotted region, the hyperparasitoid is too inefficient at finding the parasitoid and also goes extinct. In between is the region of coexistence.

larger in the stochastic system as compared with the deterministic, continuous population size model (model [1]). Thus, the degree of demographic stochasticity in the system is a major factor influencing persistence.

Figure 4 shows that the most persistent tritrophic systems are those with intermediate hyperparasitoid dispersal rates. Hyperparasitoids that are both good dispersers between patches and good competitors within a patch are too efficient and will quickly deplete both the parasitoids in their patch and also, via local dispersal, parasitoids in neighboring patches. The hyperparasitoid would locally overexploit the parasitoid and, as a direct result, go extinct itself. Hence, long-term persistence requires a trade-off between searching ability within a patch and dispersal rates between patches. If the dispersal rate between patches is large, then the searching efficiency within a patch must be small, and vice versa; otherwise, persistence is impossible. In addition, the region of parameter space where the hyperparasitoid species can coexist with the host and parasitoid (fig. 4) is relatively small. The temporal and spatial variability in the parasitoid population that results from high attack rates and demographic stochasticity makes it extremely difficult for the hyperparasitoid to always be able to locate its prey

and so persist. (When the parasitoid and hyperparasitoid have small attack rates, then the effects of demographic stochasticity are small and the hyperparasitoid has a much expanded region of persistence.)

### Discussion

In this note, the influence of metapopulation area on persistence in communities with two and three trophic layers has been examined in some detail, for a model incorporating demographic stochasticity. We found strong effects of lattice size or patch number on the persistence of host-parasitoid-hyperparasitoid interactions. The effect of lattice size on persistence is particularly dramatic when considering small to medium lattices, with diminishing additional effects on persistence at increasingly large lattice sizes (see table 1 or fig. 2). Some parameter combinations may require very large lattices to persist (e.g., *dashed line*, fig. 2). This area effect is considerably stronger for tritrophic communities than for communities with only two trophic layers (see fig. 2). Lattice size is thus a factor determining dynamic constraints on food chain length (Pimm and Lawton 1977), as opposed to energetic constraints (Hutchinson 1959) or feeding hier-

archy constraints (Cohen et al. 1990). However, we should note that the criticisms of Sterner et al. (1997) about the dynamic constraints hypothesis also apply here, in that no self-regulation of the parasitoids and hyperparasitoids has been included.

The stochastic nature of the interactions has also highlighted three additional effects. First, extinctions caused by demographic stochasticity substantially increase the minimum lattice size needed for persistence. This highlights the importance of including these effects in models that imply strong spatial variability and temporal fluctuations, situations in which even though average population abundance is high, some patches can have small population sizes. Second, communities of hosts and parasitoids with highly asymmetric dispersal rates are disproportionately affected by demographic, stochastic effects. In the continuous population variable model (model [1]), the eight neighboring sites are always colonized, even if only by fractional numbers, so that there is no comparable disadvantage of small dispersal rates at small population sizes. By contrast, in the stochastic model, colonization of sites is a random process. Thus, when the host and parasitoid are dispersing at highly different rates, it is much more likely that, due to chance effects, the host and parasitoid populations will become uncorrelated with respect to one another. The parasitoid cannot then locate hosts and goes extinct.

Third, a high degree of specialization by primary parasitoids (i.e., high  $a_p$ ) results in massively increased spatial and temporal variability due to demographic stochastic effects. This large degree of variability in parasitoid populations that are highly specialized results in it being very difficult for hyperparasitoids to coexist with the host and parasitoid, particularly in small lattices. This is a much stronger result regarding constraints on coexistence than from earlier, deterministic models (e.g., May and Hassell 1981), which predict that hyperparasitoids are able to persist when they have higher attack rates than the parasitoids they exploit. Data from empirical studies of host-parasitoid assemblages suggest that hyperparasitoids (at least ecto-hyperparasitoids) tend to be polyphagous (e.g., C. Mueller and H. C. J. Godfray, unpublished data). This is entirely consistent with our results, which predict that it is difficult for hyperparasitoids of specialized parasitoids to persist when they only attack one parasitoid species.

It should be noted that different biological assumptions in these models might lead to somewhat differing outcomes. For instance, the susceptible stage of the host and the time when the developing parasitoid is susceptible to the hyperparasitoid might be of different lengths. However, at least to some extent, this can be mimicked in the current model by varying the relative magnitudes

of the attack parameters of the parasitoid and hyperparasitoid (as the probability of parasitizing a host-parasitoid is a combination of the time available for search and the searching efficiency, or attack rate, of the parasitoid-hyperparasitoid). Also, by assuming the structure of model (6), we have assumed that the hyperparasitoid begins to attack only after attacks by the primary parasite on unparasitized hosts have ceased. This is consistent with field observations for some host-parasitoid systems. However, an alternative scenario would be that the phases of parasitism and hyperparasitism completely or partially overlap. Although it would be interesting to explore the ramifications of these alternative life-cycle assumptions, we have concentrated here solely on the model defined by (6) as we wanted the stochastic model to be comparable to the deterministic model that already includes the assumption of sequential parasitism. Other scenarios will be addressed thoroughly at a later date.

Our theoretical results are broadly consistent with tri-trophic metapopulation models (see Holt 1997a, 1997b), which suggest that local extinction and recolonization dynamics can constrain the length of specialist food chains. There is a large theoretical literature on the structure of food webs (e.g., see reviews by Lawton 1989; Polis and Winemiller 1996). Nearly all this work to date has ignored the implications of spatial dynamics and constraints of available habitat area for determining food web attributes. We suggest that because localized interactions among individuals are the ultimate processes defining connections in food webs, the consequences of limited area and demographic stochasticity may have important effects on the structure of food webs.

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