

Persistence of multiple identical parasitoid species in a single-host, spatial simulation

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We explore the problem of persistence of multiple obligate parasitoids on a single host in a discrete time, spatially explicit system. In general, the parasitoids experienced extinction until one species remained well before the 50 000-generation time limit, but the rate varied according to the parameters of the system. Smaller arenas had a greater chance of extinction. Artificially increasing interspecific competition produced rapid extinction, while decreasing competition increased persistence to the maximum time limit of the simulation. Increasing the parasitoid search efficiency or decreasing dispersal of the parasitoids relative to the host produced less longevity as did increasing host reproduction, while increasing the rate of “patch extinction” reduced the variation among the times to extinction, but did not change the time to the first extinction. Finally, increasing noise in the search parameter first reduced longevity, but then it rapidly increased near the point where the noise reached an amplitude similar to the parameter itself, where coexistence of the four parasitoids was achieved.

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Multiple parasitoids, including multiple obligate specialists, often coexist on a single host (for example Hawkins 1993b, Memmott et al. 1994). Explanations of parasitoid coexistence generally stipulate some difference between the competitors that allows them to exploit different resources, or a mechanism that allows for spatial or temporal differences in their attacks. In the case of specialist parasitoids with the same host, the differences are often subtle.

There have been a number of articles discussing mechanisms or models developed to explain the continued coexistence of such parasitoids, or similarly, of competitors for a

single resource. A prevalent theme is that of a behavioral mechanism or physiological difference between competing species, such as a trade-off between dispersal and searching abilities, or a variation on this theme (Hassell et al. 1994, Comins and Hassell 1996, Ruxton and Rohani 1996). Similarly, in a source-sink resource flow, Loreau and DeAngelis (1997) showed that a tradeoff between exploitative and interference ability led to a partitioning of resources, and continued coexistence of competitors. Amarasekare (2000) demonstrated a similar tradeoff between local searching ability and competitive (intraguild predation) power, but on a local level.

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Another theme is that of dominance, where the first competitor to arrive at a host or resource patch is able to exclude the other, by a priority effect (Levin 1974). Of this theme are models that postulate a superior competitor for local patches, possibly through intraguild predation or hyperparasitism, but another species is able to exploit unused patches through aggregation and dispersal mechanisms (May and Hassell 1981, Klopfer and Ives 1997).

There are also models that demonstrate that female aggregation to the host species or patchy resource allows for persistence of multiple competitors (Shorrocks et al. 1979, Ives 1988). (May 1978), and Hogarth and Diamond (1984) showed that two identical parasitoids can survive attacking the same host, if they are both sufficiently aggregated. This was shown in a non spatially-explicit model, with negative binomial attack patterns.

Finally, Hawkins (1993a) and Hochberg and Hawkins (1993) showed a relationship between the effectiveness of a physical host refuge and the diversity of the associated parasitoid community: refuges of moderate effectiveness allow for more parasitoid diversity than those of either less or more effectiveness.

With the exception of studies exploring the trade-off between dispersal and searching abilities (Hassell et al. 1994, Comins and Hassell 1996, Ruxton and Rohani 1996), the models described above are not explicitly spatial. To further explore the persistence of multiple parasitoids in a spatially-explicit system, we combine ideas from several of these studies and introduce a model with four parasitoids, each obligate on the same host species, and each having identical parameters and search conditions. Our model is based on a spatially explicit map-based discrete system with random dispersal of all parasitoids and the host. We explore the parameters of this system to discover which have the greatest impact on the persistence of the multiple-parasitoid system, and which values will allow for long-term coexistence.

The model

General arena conditions

The parasitoids and host were modeled in a square, homogeneous discrete arena with a default size of 30×30 cells. Following the method of Comins et al. (1992), we started the parasitoids together with the host in a single cell, third from the left in the top row. All species were introduced with a density of 1. This starting condition facilitates the development of spirals and the coexistence of the five species in the crucial early development of the system. We used reflecting boundaries in our spatial arena, but found that in arenas of this size, the edge condition (reflecting, absorbing, or periodic) has only a small effect on the final outcome or the spatial patterns found (unpubl.; also see Rohani and Ruxton 1999, Kean and Barlow 2000)

Parasitoid-host growth and interaction

We use a host-parasitoid model where the host has a Ricker (1954) reproductive function, and the parasitoids feed proportionately on the hosts similar to the Beddington et al. (1975) model. A two-parasitoid model of this type was used by Comins and Hassell (1996) and Ruxton and Rohani (1996): we expand it here to include a host H and four parasitoids P , Q , R and S . The densities of the host and parasitoids at each time step are:

$$\begin{aligned} H_{t+0.5} &= H_t \exp(r(1 - H_t/k) - aP_t - aQ_t - aR_t - aS_t) \\ P_{t+0.5} &= \frac{aP_t}{aP_t + acQ_t + acR_t + acS_t} \cdot H_t (1 - \exp(-aP_t - aQ_t - aR_t - aS_t)) \\ Q_{t+0.5} &= \dots \\ R_{t+0.5} &= \dots \\ S_{t+0.5} &= \frac{aS_t}{aP_t + acQ_t + acR_t + aS_t} \cdot H_t (1 - \exp(-aP_t - aQ_t - aR_t - aS_t)) \end{aligned} \quad (1)$$

where all population densities H , P , Q , R and S are functions of spatial positions x and y . For our purposes, all four parasitoids, P , Q , R and S have identical parameters for every model run. This model proportionately allocates host resources to the parasitoids at each cell location, and simulates scramble competition, where the parasitoid that reaches the host first will parasitize it, denying that opportunity to the other parasitoids. We also add a new parameter “ c ”, which represents an interspecific competition coefficient and is explained in detail below. The host has no refuge from the parasitoids, save any dynamic spatial refuge created by the heterogeneity of the parasitoid population distributions. Reproduction and parasitoid attack take place in the first half of a time step, and dispersal occurs in the second half.

The maximum number of parasitoids emerging from one host is set here to 1. Consistent with the Beddington type of model, there is no limitation on the numbers of hosts that can be parasitized per generation by each parasitoid, except for the constraint imposed by the parasitoid search parameter, a .

The carrying capacity, k , is arbitrarily set to 1000 for the simulations presented here. This value was large enough that the isolated cells acted much like Nicholson-Bailey (Nicholson and Bailey 1935) systems that would undergo divergent oscillations to extinction, so any longevity in the spatial system must be the result of spatial processes: e.g. a “rescue effect” (Allen et al. 2001). The use of a carrying capacity here is simply to prevent absurdly large breakouts of host densities in local areas.

Competition parameter

We have introduced a competition parameter, c , to the parasitoid growth equations. Increasing this parameter above 1 increases the interspecific competition among the parasitoids relative to intraspecific competition. That is, each species reproduces less in the presence of

heterospecifics than conspecifics, though the host is still consumed at the same rate regardless of parasitoid species composition. Values of $c < 1$ reduce interspecific competition, and at a value of 1, interspecific and intraspecific competition are equal.

Extinction threshold

Computer models can continue with population numbers that are small enough to introduce division errors, so a positive determination of local extinction was required. Any host or parasitoids whose densities in a cell fell below 10^{-3} were set to zero (cell extinction). The exact threshold used was not critical for our purpose, and Wilson and Hassell (1997) showed that this modification to similar models did little to change the spatial dynamics of the system, but understandably caused more local extinction, and a greater probability of global extinction.

Perturbations

Noise

The a parameter was held constant for 300 generations after the start of each model run to allow for the host and all parasitoids to spread equally across the arena and form a “steady state” system (after Comins et al. 1992). After the 300th generation, uniformly distributed noise was added independently to each parasitoids’ a parameter at each spatial location (simulating spatial variance in the difficulty in locating hosts due to foliage thickness, for example):

$$a[x, y] \sim U[a - ap, a + ap] \quad (2)$$

where p is a noise amplitude factor. For small levels of perturbation, the use of the a parameter was not critical, since perturbing other parameters gave similar results: the net result was simply to allow for divergence of the species while preserving the characteristic dynamics resulting from the parameter space. Noise was not added early in the simulation because of the sensitivity of the very small populations.

Extinctions

Periodically, a 7×7 cell square in a random location was made to undergo an extinction event, where all the organisms in those cells were removed. This perturbation has the effect of breaking up stable or forming spiral patterns, and generally unsettling the whole arena (see Hastings and Higgins 1994). Leaving the spirals intact would decrease the probability of extinction for those parasitoid species fortunate enough to occupy a spiral focus (Boerlijst et al. 1993).

Dispersal kernel method

Description

To disperse hosts and parasitoids, we used a discrete spatial convolution method (Gonzalez and Woods 1992). This is similar to a “blur filter” used by many image-processing computer programs, and is a process that takes the contents of a cell and redistributes it according to a discrete dispersal kernel at each time step. This dispersal method is based on those used and described by (Allen et al. 1995, Brewster and Allen 1997) for modeling whitefly populations, and by Hastings and Higgins (1994) for modeling the Dungeness crab.

We used a discrete normal dispersal kernel, where the height of the kernel, $k_{[x,y]}$ at each location (x, y) relative to the cell where it is applied is:

$$k_{[x,y]} = \int_{x-0.5}^{x+0.5} \int_{y-0.5}^{y+0.5} \frac{1}{2\sigma^2} \exp\left(-\frac{x^2 + y^2}{2s^2}\right) \quad (3)$$

and the hosts and parasitoids are dispersed according to:

$$\begin{aligned} H_{t+1} &= k_H * H_{t+0.5} \\ P_{t+1} &= k_P * P_{t+0.5} \\ Q_{t+1} &= \dots \\ R_{t+1} &= \dots \\ S_{t+1} &= k_S * S_{t+0.5} \end{aligned} \quad (4)$$

where $*$ is the discrete convolution operation, s is the standard deviation of the normal dispersal function, and k_P , k_Q , k_R and k_S are the dispersal kernels for each species. Here, all parasitoids disperse equally so that $k_P = k_Q = k_R = k_S$, and the kernel was calculated at each location (x, y) out to 6 standard deviations.

The dispersal kernel size was generally quite small, so that only a small proportion of parasitoids actually leave the cell. This “decouples” the cells from each other, making them more independent. While dispersal is destabilizing where it effectively couples all the cells of a system, a low rate of diffusion stabilizes asynchronous coupled host-parasitoid systems (Adler 1993, Hastings 1993, Allen et al. 2001 among others).

Running the model

We varied most of the parameters in the model singly to explore their effect on the longevity of multiple-parasitoid existence. Holding all other parameters at their default values (Table 1), the model was run for 50 000 generations. Between each run, the parameter of interest was stepped through a range of values. The time to extinction was recorded for each parasitoid species during each run.

Hassell et al. (1991) showed that the probability of extinction of a single parasitoid in a spatially explicit H-P

Table 1. Parameters used in the 4-parasitoid model, including their default values, and the range over which they were tested.

Parameter	Meaning	Default	Range
n	Arena side length	30	20–100
s	Standard deviation of dispersal	0.5	0.2–0.9
c	Competition coefficient	1.01	0.99–1.01
a	Parasitoid search efficiency	0.3	0.05–1
r	Host growth rate	2	1–4
r	Amplitude of a parameter noise	0.1	0.0001–1
r	“Patch extinction” frequency	10	1–3000

model increases in smaller spatial arenas. To explore the effect of arena size on multiple-parasitoid longevity, we used several different sizes of square arenas for our studies, from 20×20 to 100×100 .

Hassell et al. (1991) also found that increasing the rate of dispersal also contributed to a higher probability of extinction, for a given arena size. We ran the model with host and parasitoid dispersal kernel standard deviations of 0.2 to 0.9 cells.

The competition coefficient, c , is interesting, because it has the ability to change the amount of host resources available to the parasitoids. In effect, it increases the search capacity of the competing parasitoids, but this happens for each parasitoid in turn. By default, c is set to 1.01, which decreases the number of parasitoids that emerge from a given number of hosts when heterospecific parasitoids are present. This can be explained as inefficiency due to the increased interspecific competition. We did look at a range of c values, including those < 1 . While probably not biologically realistic, simulating low values of c allows us to see what effect synergy among the parasitoids would have on coexistence.

As the parasitoid search efficiency, a , increases, the equilibrium levels of the host and parasitoid tend to decrease. We were interested to see if this makes the parasitoids more likely to go extinct more quickly.

We varied the host reproductive rate from 1 to 4. With a Ricker reproductive map, these values of r span the range from stable interactions, through bifurcation, into the chaotic region. (Allen et al. 1993) found that the chaotic zone of the Ricker map was associated with a markedly lower global extinction rate in a single species model. Similar, though less dramatic results have been found for a host-parasitoid spatial model (Allen and Slone unpubl.), so an interesting question is whether we will see a reduction in the rate of species loss in the chaotic parameter region of this model.

Finally, the two stochastic parameters, noise in the a parameter (p) and periodic patch extinctions, were varied over several orders of magnitude. p was varied from 10^{-3} to 1, and the frequency of patch extinction was varied from one event in 3000 generations to one event each generation.

If any values of parameters lead to long-term coexistence close to the maximum number of generations, then a test for invasibility will show whether the observed coexistence would be likely to continue indefinitely (Chesson 1991). If a species introduced at a low density relative to the other competitors tends to increase to higher population levels, then the invasibility criterion is satisfied. This test was performed by introducing one parasitoid species at a density 10 times less than the other species, then running the model as usual. The individual species' time to extinction were then recorded and plotted by species. We would expect that if there were not mechanism to promote coexistence, the species introduced at a lower density would on average go extinct before the other species. In this simulation, the presence of the c parameter would hasten the extinction of the introduced species even more because it would be outnumbered by heterospecifics, around which it would reproduce less. If all four species coexisted for the full 50000 generations, this would be taken as evidence that there is a positive mechanism promoting long-term persistence.

Results and discussion

Results from the model runs are reported in a graphical format, with each chart having similar features. The vertical axis will show the number of generations to extinction of the first three species to go extinct in each simulation run. The open circle will represent the time to the first species extinction. Similarly, the open square will represent the second extinction, and the open triangle, the third. Each point on a chart represents 6 replications of the simulation from the 6 different computers, with standard error bars calculated after log transformation of time to extinction. For the tests presented here, only three parasitoid extinctions are shown: the last surviving parasitoid invariably entered a stable coexistence with the host to the full limit of 50000 generations. Using the parameters specified here, the density level of the host was generally regulated at a density of approximately 50 individuals per cell.

There were two possible effects from parameter changes. First, the number of generations until the first extinc-

tion varied. Second, the variability among extinction times also varied.

Similar to Hassell et al. (1991), we found that smaller arenas had a greater chance of extinction. Here, the host and at least one parasitoid species remained alive for the duration of the 50 000-generation model run, but smaller arenas contributed to the other parasitoid species experiencing extinction earlier in the simulation. Increasing the n parameter caused an increase not only in longevity with increasing arena size, but also an increase in variability (Fig. 1a). The increase in longevity can be attributed to more cells for the interactions to take place in. The increased spread between the first and subsequent extinctions may be attributed to increased numbers of spiral foci allowed by the larger arenas, each possibly dominated by a different parasitoid species. The periodic "patch extinction" events prevented stable spirals from existing indefinitely, but because the size of the extinction patch did not grow with arena size, it had progressively less effect on the spirals. As

mentioned previously, stable spirals are relatively uninvadable, so a parasitoid species established within remains alive as long as the spiral exists (Boerlijst et al. 1993).

There was a small change in longevity associated with different parasitoid or host dispersal distances (s). Again, similar to results of (Hassell et al. 1991), we found that increased host dispersal led to more rapid extinction, though the effect here was very slight (Fig. 1b). An increase in parasitoid dispersal produced greater longevity (Fig. 1c), and also a reduction in variability. A characteristic of host outbreaks where there is parasitoid overdispersal is that the edge area has a low parasitism rate, as found by (Hastings et al. 1997) and (Brodmann et al. 1997) in tussock moth outbreaks. With a high host/parasitoid density ratio, it is possible that these areas had lower intensities of predator competition, and so led to greater persistence. Finally, increasing both host and parasitoid dispersal simultaneously resulted in slightly less time to extinction (Fig. 1d), a result commonly seen in other models when overall dispersal in-

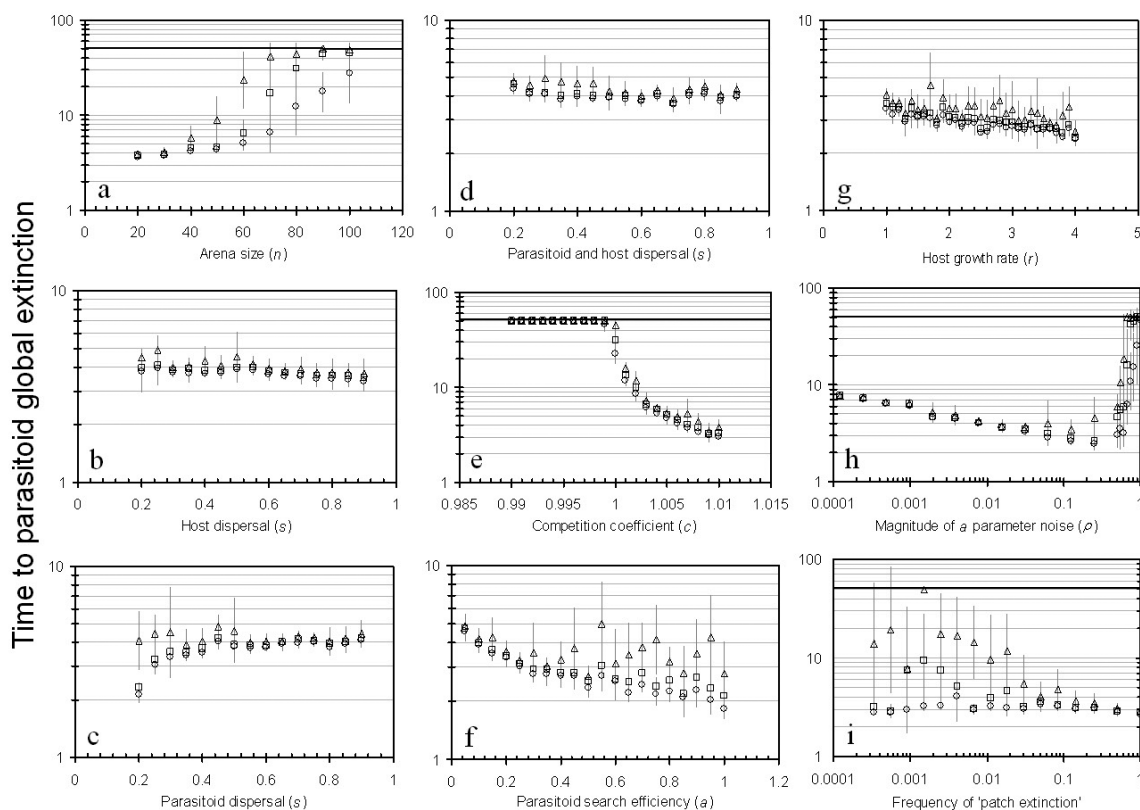


Fig. 1. Results of 4-parasitoid model. The vertical axis on all sub-graphs is the number of generations to extinction for the first three species to go extinct in each simulation run. The open circle on each sub-graph represents the first species extinction, the open square represents the second extinction, and the open triangle, the third. Points are the average of 6 replications, with standard error bars calculated after log transformation of time to extinction. The graphs show the effects of changing (a) arena size, (b) host dispersal rate, (c) parasitoid dispersal rate, (d) both parasitoid and host dispersal rate, (e) rate of interspecific competition, (f) parasitoid search efficiency, (g) host reproduction, (h) random noise magnitude, and (i) rate of local extinction events on the rate of parasitoid extinction.

creases, reducing the isolation of the individual cells (for example Comins et al. 1992).

Increasing the competition coefficient (c) above its neutral value of 1 produced a rapid increase in parasitoid extinction rate (Fig. 1e). Below the neutral value, the longevity of the four parasitoid species rapidly reached the maximum value of 50 000 generations, and stayed at that level. The default level of the competition coefficient we used (1.01) was enough to dramatically hasten the extinction rate of the competing species, but at the same time was not strong enough to cause the inexorable extinction of the first species with a depressed population. A cursory glance at time plots of the simulation runs showed many cases of parasitoid populations recovering from low densities and going on to be the surviving species.

Increasing the parasitoid search efficiency (a) produced a gradual decline in parasitoid persistence, but also an increase in variability (Fig. 1f). By increasing the rate at which parasitoids find their host, it would appear that the scramble competition for hosts increased, leaving less to support multiple species. As with any other parameter that increased the rate of contact among the species, this increased the extinction rate of the parasitoids.

The r parameter was varied through the period-doubling ($r > 2$) and chaotic ($r > 2.7$) regions of the Ricker map, but these points show no special change in parasitoid coexistence. Instead, a gradual decrease in persistence is seen as the reproductive rate increases (Fig. 1g). This may have been due to the noise in the model masking the effects of chaos, or perhaps the protection of chaos in the single species model simply does not apply in a simple way to multi-species systems.

The two variables associated with noise input (the only forms of stochasticity in the model) showed different effects on the system. The amplitude of the a parameter noise (ρ) produced interesting results. Increasing this parameter has the effect of increasing "spatial asynchrony" (Hassell and May 1973), so we might expect an increase in the longevity of the parasitoids. For most of the range we tested, the opposite held true: increasing this variable from 0.001 to 0.3 produced a slow monotonic reduction in longevity (Fig. 1h). Abruptly thereafter, the longevity of the parasitoids increased rapidly, until noise at an amplitude of 1 times the a parameter produced coexistence to the limit of the test. In this model, it appears that only extreme levels of asynchrony are able to prevent rapid extinction of the competitors.

The second noise variable, the frequency of patch extinction, caused different behavior. With increasing frequency, the variation in times to the three first parasitoid extinctions became smaller, but the time to the first extinction remained similar throughout (Fig. 1i). With a low rate of patch extinction events, some parasitoids coexisted longer than when the system experienced a high rate of extinction events by existing in separate, long-lived spiral waves. This result is consistent with the findings of Boerlijst et al. (1993) who noted that established spirals are uninvadable by local dispersal, because the dispersing competitors cannot cross the expanding zones of extinction that travel between the host+parasitoid waves to get to the center, which is the source of the waves. When the four parasitoids were introduced into the center of their own spiral waves and left undisturbed, we found that persistence to the full length of the simulation was the norm (Slone and Allen unpubl.).

The parameter space explored here contained only one area (besides the c parameter < 1) where the four species coexisted for the full 50 000 generations of the model. This occurs where the ρ parameter (amplitude of the a parameter noise) is close to one (Fig. 2). With this stochastic parameter set this high, the competitors cannot be viewed as identical anymore, but rather equivalent, though their dis-

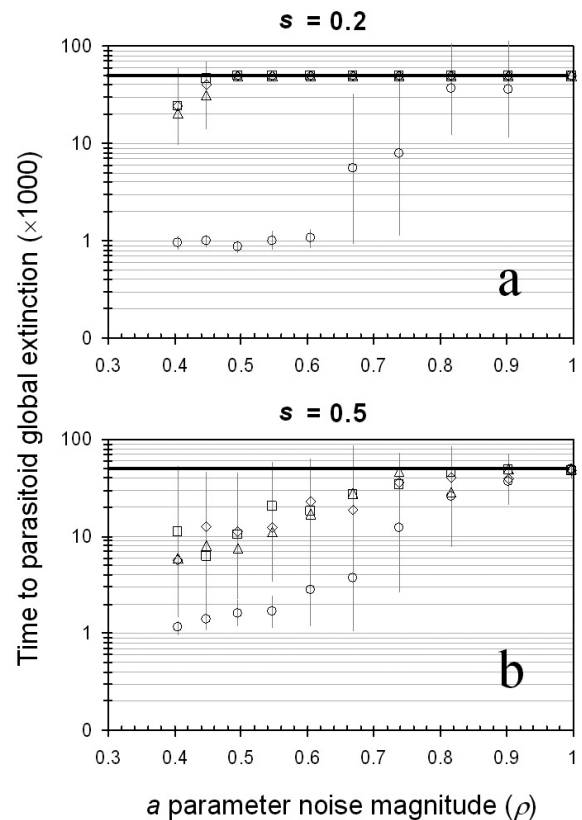


Fig. 2. Results of invasion test at dispersal kernel sizes of (a) $s = 0.2$ and (b) $s = 0.5$. The vertical axis on the sub-graphs is the number of generations to extinction for all four species of parasitoid. This plot differs from Fig. 1 in that the parasitoid species are kept separate, instead of ranked by time-to-extinction. The open circle on each sub-graph represents parasitoid "P", which was introduced at a density 0.1 times the others. The open square, triangle and diamond represent parasitoids "Q", "R", and "S" respectively. Points are the average of 6 replications, with standard error bars calculated after log transformation of time to extinction.

persal behaviors are still identical. With this in mind, we found that for values of ρ very close to 1, the invasive criteria of a low-density species having an advantage was satisfied, demonstrated by having the low-density competitor quickly recover to similar densities as the other competitors (Fig. 3), and coexisting for the full run of the model. There was some support for the lower-density parasitoid at lower values of ρ as well, but not generally enough for it to survive for the full run.

We see here that if noise totally dominates the dynamics of the system, survival of the parasitoids is greatly increased. Compare this result to those obtained by Allen et al. (2001), who found that spatially mixing 2 extreme habitats, where survival was not possible in either, produced a stable model population in a single parasitoid system. An implication of these results is that a highly variable habitat (in time or space) has the potential to foster very long-term persistence in general, and coexistence of competitors. For example, one species might survive a very cold winter bet-

ter, while another could have more success at reproduction during a mild winter (a temporal version of a "fugitive" strategy; see Amarasekare and Nisbet (2001) for a recent example). The results found here predict that a series of years that include variable winter temperatures would be more conducive to the survival of both competitors than a series of years where the winters were always moderate. Some investigation revealed that the reason for the variable system being more conducive to the survival of low-density competitors is that, although the higher density species generally have a higher local growth rate (a result of the c parameter set higher than 1), the low density species has more resources per capita, and so has the capacity for more explosive growth when conditions are favorable. These favorable areas are more available when the system is more variable.

Conclusions

In general, the four parasitoid species were reduced to one species well before the 50 000-generation time limit, which reinforces the idea that different species need distinct ecologies to coexist indefinitely. It is worth noting, however, that even with a force working against coexistence (c parameter > 1), the minimum time that all four species coexisted considering all model runs was almost 2000 generations. In evolutionary time, how long is coexistence necessary before external forces change the community regardless of its internal dynamics? It seems quite possible that any species involved in such an unlikely assemblage of identical competitors would see climatic, ecological or genetic changes before being driven to extinction by its competitors (or conversely driving its competitors out). Hubbell (2001) made this point with his Neutral Theory, postulating that species differences can be ignored when estimating the biodiversity of a system and the longevity of its constituent species. Here, we demonstrate through simulation that mathematically equivalent species are persistent for an ecologically meaningful amount of time in a spatial environment. Even discounting the possibility of a "noisy" environment prolonging the assemblage, competitive exclusion in a spatial world would seem to not have a powerful influence on community structure in the short to medium term.

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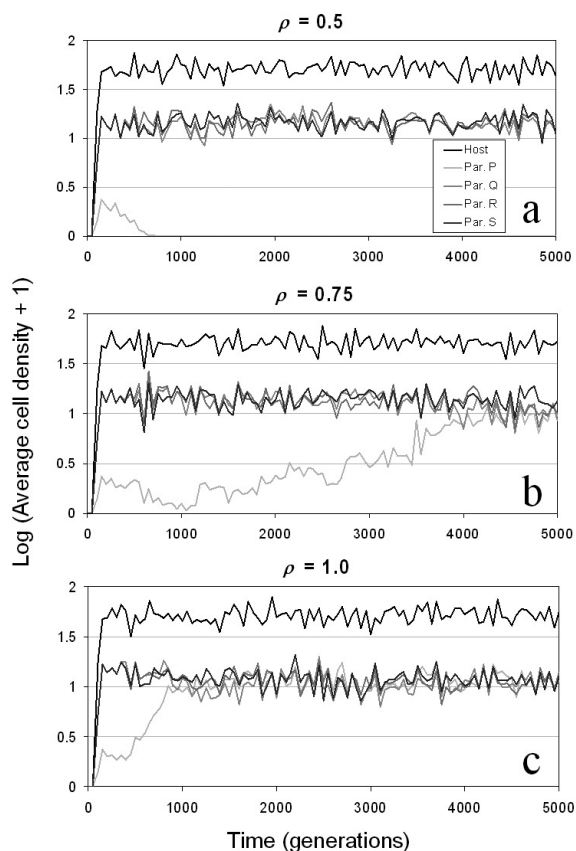


Fig. 3. Example time plots of the model for the first 5000 generations, with the output sampled every 50 generations. Three levels of perturbation are shown in (a) $\rho = 0.5$, (b) $\rho = 0.75$, and (c) $\rho = 1.0$, with a greater advantage for low-density species seen as ρ increases.

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