



Persistence of Multispecies Host-Parasitoid Interactions in Spatially Distributed Models with Local Dispersal

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Recent theoretical studies have shown that dispersal between neighbouring local populations can promote the persistence of interacting metapopulations, even when the local dynamics are unstable and the environment is uniform. This persistence is associated with striking and self-organized spatial patterns in the densities of the local populations. Here we extend previous work on spatially distributed host-parasitoid interactions to wider questions of community structure, by considering various three-species systems: two parasitoid species attacking a common host species; two host species attacked by a single parasitoid species; or a host-parasitoid-hyperparasitoid interaction. In each of these cases, multispecies coexistence of the total populations can occur, even though the local population dynamics are unstable. Furthermore, co-existence tends to be accompanied by some degree of persistent spatial segregation of the competing species, despite the completely uniform environment. At its most extreme, this results in one species being confined to small, relatively static, “islands” within the habitat, giving the appearance of isolated pockets of favourable habitat. That dynamics can impose and maintain such “self-organizing” spatial segregation of competing species, has interesting implications for understanding the local abundance of natural populations.

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Introduction

A number of papers have recently demonstrated that some kind of diffusive dispersal within patchy environments (rather than global dispersal throughout the habitat) promotes the persistence of interacting model populations. This has been demonstrated for competing species (Solé *et al.*, 1992), for plant-pathogen interactions (Swinton & Anderson, 1994), for communities of fungi (Halley *et al.*, 1994) and for host-parasitoid interactions (Hassell *et al.*, 1991; Comins *et al.*, 1992). In all these cases, the populations can persist in situations where this could not occur in corresponding non-patchy environments. The same phenomenon is also observed where individuals diffuse in an environment in which space is a continuous variable (Godfray *et al.*, unpublished results). This paper will deal only with a

range of multispecies host-parasitoid interactions, examining in particular how restricted movement between patches influences coexistence of competing parasitoid or host species.

Most discrete-generation models of host-parasitoid systems in patchy environments have assumed that the entire population of adult hosts and parasitoids disperse each generation by thoroughly mixing and redistributing over the habitat according to a particular foraging rule (e.g., Hassell & May, 1973, 1974; Hassell *et al.*, 1991; Reeve, 1988). In these cases sufficient heterogeneity in the risk of parasitism between host individuals is required if parasitism is to stabilise the system (Chesson & Murdoch, 1986; Pacala *et al.*, 1990; Ives, 1992). However, once dispersing parasitoids move to neighbouring patches rather than mixing globally, the conditions for persistence are markedly changed. Now, even in an environment of identical patches and unstable

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within-patch (=local) dynamics, the total (=regional) populations readily persist as a metapopulation (Hassell *et al.*, 1991; Comins *et al.*, 1992; Hassell *et al.*, 1992; Solé & Valls, 1992). At the same time, striking spatial patterns in the densities of host and parasitoid subpopulations are observed, which may form spiral waves, spatial chaos, or a so-called “crystal lattice” involving the regular spacing of relatively high population densities.

In this paper, we extend this work to consider the dynamics of a range of more complicated, three-species host-parasitoid systems, as initially outlined in Hassell *et al.* (1994). Our principal objective is to determine how the simple process of “diffusive” dispersal in a patchy environment may promote the persistence of more complex, multispecies systems, and then to unravel the underlying mechanisms of any coexistence that occurs. Two of our conclusions are not unexpected: (1) that three-species persistence would occur in a restricted range of conditions compared with the two-species host-parasitoid systems and (2) that three-species persistence would be enhanced by a “balancing” of key parameters between the competing species (e.g., a high searching efficiency in one of the competitors associated with a lower dispersal rate). Much more surprising, however, was the finding that coexistence in all these systems tends to be accompanied by some degree of persistent spatial segregation of the competing species, despite the completely uniform environment. At its most extreme, this resulted in one species being confined to small “islands” within the habitat, giving the appearance of isolated pockets of favourable habitat. In short, the population dynamics is imposing and maintaining a degree of “self-organizing” spatial segregation of the competing species.

The Models

Insect parasitoids are characterised by the adult females being the only “searching” stage and laying their eggs in the hosts that they encounter (normally, the hosts are subsequently killed by the feeding larvae). This feature of having reproduction defined directly by parasitism makes host-parasitoid associations a particularly convenient type of predator-prey system to study. In this paper, we assume that the overall habitat is divided into a large number of discrete patches (e.g., clumps of food plants for an herbivorous insect) in which local populations of adult hosts oviposit, their larvae feed and adult parasitoids search for immature hosts to parasitise. The patches are arranged in a regular, square grid,

taken to be 50-by-50 patches in size unless otherwise specified. Both hosts and parasitoids are assumed to have discrete generations and the parasitoid life cycle is synchronous with that of the host. We have analysed the following three-species, spatially-distributed models: (1) two host species with a shared parasitoid species (H-P-H), (2) a single host species attacked by two parasitoid species (P-H-P) and (3) a host-parasitoid-hyperparasitoid interaction (H-P-Q). These are modelled in much the same way as done for the two-species host-parasitoid systems by Hassell *et al.* (1991) and Comins *et al.* (1992).

In each model generation there are two phases: (1) the interactions of hosts and parasitoids within individual patches and (2) the dispersal of a fraction of the subsequently emerging adult hosts and parasitoids. In the first phase, the interaction within each patch is described by the basic Nicholson & Bailey (1935) host-parasitoid equations, without any of the usual additional features that, for example, complicate the parasitoid functional response or make the host growth rate density dependent (Hassell, 1978). This is done to ensure that the within-patch dynamics will always be locally unstable and that any metapopulation persistence results from the spatially distributed nature of the interaction. Let us assume that the host population density in the i th patch and in the t th generation be represented by $N_{i,t}$ or, if there are two host species, let the densities be $N_{1,i,t}$ and $N_{2,i,t}$. Similarly, let the local parasitoid densities be $P_{i,t}$ or, if there are two competing parasitoid species, let their densities be $P_{1,i,t}$ and $P_{2,i,t}$. The corresponding hyperparasitoid densities, if present, are represented by $Q_{i,t}$. Finally, we let the corresponding population densities after dispersal be distinguished by a prime (e.g., $N'_{i,t}$ instead of $N_{i,t}$). The within-patch dynamics of the three models are given as follows.

PARASITOID-HOST-PARASITOID (P-H-P):

$$\begin{aligned}
 N_{i,t+1} &= \lambda N'_{i,t} \exp(-a_1 P'_{1,i,t} - a_2 P'_{2,i,t}) \\
 P_{1,i,t+1} &= c_1 N'_{i,t} [1 - \exp(-a_1 P'_{1,i,t} - a_2 P'_{2,i,t})] \\
 &\quad \times \left[\frac{a_1 P'_{1,i,t}}{(a_1 P'_{1,i,t} + a_2 P'_{2,i,t})} \right] \\
 P_{2,i,t+1} &= c_2 N'_{i,t} [1 - \exp(-a_1 P'_{1,i,t} - a_2 P'_{2,i,t})] \\
 &\quad \times \left[\frac{a_2 P'_{2,i,t}}{(a_1 P'_{1,i,t} + a_2 P'_{2,i,t})} \right] \quad (1)
 \end{aligned}$$

where λ is the host rate of increase, c_1 and c_2 are the conversion efficiencies for each parasitoid species (i.e., the numbers of female parasitoids emerging

from each host parasitised) and a_1 and a_2 are the per capita attack rates for each parasitoid species. Formulated in this way, we are assuming that the two parasitoids search simultaneously for hosts within a patch. The model treats the two parasitoid species equally, assuming that superparasitism by either species is always unsuccessful. This may be contrasted with the three-species model of May & Hassell (1981) in which the first parasitoid species always excludes the second, either because it attacks first or because it always wins in cases of multiple parasitism (as interpreted by Hogarth & Diamond (1984)). Our model is equivalent after scaling to the “mutant parasitoid” model of Boerlijst *et al.* (1993), in which the two kinds of parasitoids are genotypes of the same species, differing only in attack rate.

HOST-PARASITOID-HOST (H-P-H):

$$\begin{aligned} N_{1,i,t+1} &= \lambda_1 N'_{1,i,t} \exp(-a_1 P'_{i,t}) \\ N_{2,i,t+1} &= \lambda_2 N'_{2,i,t} \exp(-a_2 P'_{i,t}) \\ P_{i,t+1} &= c_1 N'_{1,i,t} [1 - \exp(-a_1 P'_{i,t})] \\ &\quad + c_2 N'_{2,i,t} [1 - \exp(-a_2 P'_{i,t})] \end{aligned} \quad (2)$$

where λ_1 and λ_2 are the rates of increase for each host species, c_1 and c_2 are the conversion efficiencies of each host species into adult female parasitoids, and a_1 and a_2 are the parasitoid attack rates to which each host species is subject. This model is equivalent after scaling to the “mutant host” model of Boerlijst *et al.* (1993).

HOST-PARASITOID-HYPERPARASITOID (H-P-Q):

$$\begin{aligned} N_{i,t+1} &= \lambda N'_{i,t} \exp(-a_1 P'_{i,t}) \\ P_{i,t+1} &= c_1 N'_{i,t} [1 - \exp(-a_1 P'_{i,t})] \exp(-a_2 Q'_{i,t}) \\ Q_{i,t+1} &= c_1 c_2 N'_{i,t} [1 - \exp(-a_1 P'_{i,t})] \\ &\quad \times [1 - \exp(-a_2 Q'_{i,t})] \end{aligned} \quad (3)$$

where λ_1 is the host rate of increase, c_1 and c_2 are the conversion efficiencies for hosts to parasitoids and parasitoids to hyperparasitoids, respectively, and a_1 and a_2 are the attack rates of parasitoids and hyperparasitoids, respectively.

In the dispersal phase of each of these three models, a certain fraction of the new adults in each patch redistribute themselves to the eight immediate neighbouring patches, while the remainder stay behind to reproduce in their native patch. The dispersal is spatially symmetrical for all species, but the fraction of dispersers is species-dependent. The

equations for the dispersal phase in each patch are similar for each species, and have the form:

$$X'_{i,t} = (1 - \mu_X) X_{i,t} + \mu_X X^*_{i,t} \quad (4)$$

where $X'_{i,t}$ represents one of $N'_{i,t}$, $N'_{1,i,t}$, $N'_{2,i,t}$, $P'_{i,t}$, $P'_{1,i,t}$, $P'_{2,i,t}$ or $Q'_{i,t}$ (the post-dispersal population density), $X_{i,t}$ represents the corresponding pre-dispersal population density $N_{i,t}$, $N_{1,i,t}$, $N_{2,i,t}$, $P_{i,t}$, $P_{1,i,t}$, $P_{2,i,t}$ or $Q_{i,t}$, and μ_X (i.e. μ_N , μ_{N1} , μ_{N2} , μ_P , μ_{P1} , μ_{P2} or μ_Q) is the dispersal fraction for the species. Finally, $X^*_{i,t}$ is the average of the pre-dispersal population density over the eight nearest neighbouring patches, given by:

$$X^*_{i,t} = \sum_j X_{j,t} / 8 \quad (5)$$

where j runs over the eight nearest neighbours of patch i . The definition of the average is modified for the boundary patches, giving a reflective boundary, as described by Comins *et al.* (1992).

The conversion efficiencies c , c_1 and c_2 can be scaled out of all three models, using different strategems for each. In addition, one attack rate can also always be scaled out. Thus, for the P-H-P model, we define:

$$n_{i,t} = a_1 c_1 N_{i,t}, \quad n'_{i,t} = a_1 c_1 N'_{i,t}, \quad \alpha = a_2 c_2 / a_1 c_1 \quad (6)$$

and

$$p_{k,i,t} = a_1 c_1 P_{k,i,t} / c_k, \quad p'_{k,i,t} = a_1 c_1 P'_{k,i,t} / c_k \quad (7)$$

for $k = 1$ and 2 . After rewriting the equations in terms of $n_{i,t}$, $n'_{i,t}$, $p_{k,i,t}$, $p'_{k,i,t}$ and α , we replace n by N and p by P to recover the original equations with a_1 , c_1 and c_2 eliminated (i.e. scaled to one) and a_2 replaced by the composite ratio α . For the H-P-H model, we define:

$$p_{i,t} = a_1 P_{i,t}, \quad p'_{i,t} = a_1 P'_{i,t}, \quad \alpha = a_2 / a_1 \quad (8)$$

and

$$n_{k,i,t} = a_1 c_k N_{k,i,t}, \quad n'_{k,i,t} = a_1 c_k N'_{k,i,t} \quad (9)$$

for $k = 1$ and 2 . In the same vein as previously, we replace p by P and n by N after rewriting the equations in terms of $n_{k,i,t}$ and $n'_{k,i,t}$, to recover the original equations with a_1 , c_1 and c_2 eliminated, and a_2 replaced by the ratio α . Note that the dynamics are not affected by the values of c_1 and c_2 since these parameters do not appear in the definition of the scaled parameter α . Finally, for the H-P-Q model, we define:

$$\begin{aligned} n_{i,t} &= a_1 c_1 N_{i,t}, \quad n'_{i,t} = a_1 c_1 N'_{i,t} \\ p_{i,t} &= a_1 P_{i,t}, \quad p'_{i,t} = a_1 P'_{i,t} \\ q_{i,t} &= a_1 Q_{i,t} / c_2, \quad q'_{i,t} = a_1 Q'_{i,t} / c_2, \quad \alpha = a_2 c_2 / a. \end{aligned} \quad (10)$$

As before, after rewriting the equations in terms of $n_{i,t}$, $n'_{i,t}$, $p_{i,t}$, $p'_{i,t}$, $q_{i,t}$, $q'_{i,t}$ and α , we replace n by N , p by P and q by Q , to recover the original equations with a_1 , c_1 and c_2 eliminated, and a_2 replaced by the ratio α . Note again that the dynamics are not affected by the value of c_1 . After this parameter scaling, the local dynamics of the P-H-P and H-P-Q models are characterised by two parameters (λ and α), while the local dynamics of the H-P-H model are characterised by three parameters (λ_1 , λ_2 and α).

Both the P-H-P and H-P-H models have limiting cases in which they become effectively identical to a two-species host-parasitoid model (that is, $\alpha = 1$, and $\lambda_1 = \lambda_2$ for the H-P-H model). In these cases the duplicated species (parasitoids in P-H-P and hosts in H-P-H) are indistinguishable, so they coexist with neutral stability. As with simple two-species competition models without intraspecific competition, the neutrally stable case is an isolated mathematical curiosity surrounded by parameter combinations for which one or other of the duplicate species competitively excludes the other.

The dynamics of each of the three models above are always unstable in the absence of spatial structure. In addition to the oscillatory instability arising from the Nicholson–Bailey description of parasitism by the parasitoids and hyperparasitoids, the single-patch P-H-P and H-P-H models do not have equilibria (even unstable equilibria), except for singular values of α . The single-patch H-P-Q model has an (unstable) equilibrium if and only if $a_2/a_1 > \ln \lambda$ (May & Hassell, 1981).

Results

TWO PARASITIDS AND ONE HOST (P-H-P)

In the P-H-P model the relative competitive advantages of the two parasitoid species can be quantified using the ratios α (defined to be a_2c_2/a_1c_1) and $\mu = \mu_{P2}/\mu_{P1}$. We expect a higher dispersal rate to be a competitive advantage; however, this can be balanced by the less dispersive parasitoid species having a higher attack rate or conversion efficiency (giving $\alpha > 1$ in the scaled model). In order to explore the competitive balance, we performed simulations for a two-dimensional grid of μ and α -values symmetrically arranged around the two-equivalent-species case ($\mu = \alpha = 1$), while keeping μ_N and μ_{P1} constant. The starting points, for the simulations were standard population density maps, with fully developed spatial structures which had been generated with the two-species host-parasitoid model. The single parasitoid population in each cell was replaced by two populations in a specific ratio, either 10:1 in favour of species 1, or 10:1 in favour of species 2. Thus, we only consider cases where all populations are initially well mixed. Boerlijst *et al.* (1993) have shown that a relatively non-competitive parasitoid species may resist invasion by a superior species in reaction-diffusion models with spiral spatial dynamics. This is because an invading parasitoid population cannot reach a new spiral focus unless it disperses across the surrounding “barricade” of expanding spatial waves. However, this effect can be abolished if non-negligible long-distance dispersal is permitted, as illustrated in Fig. 1.

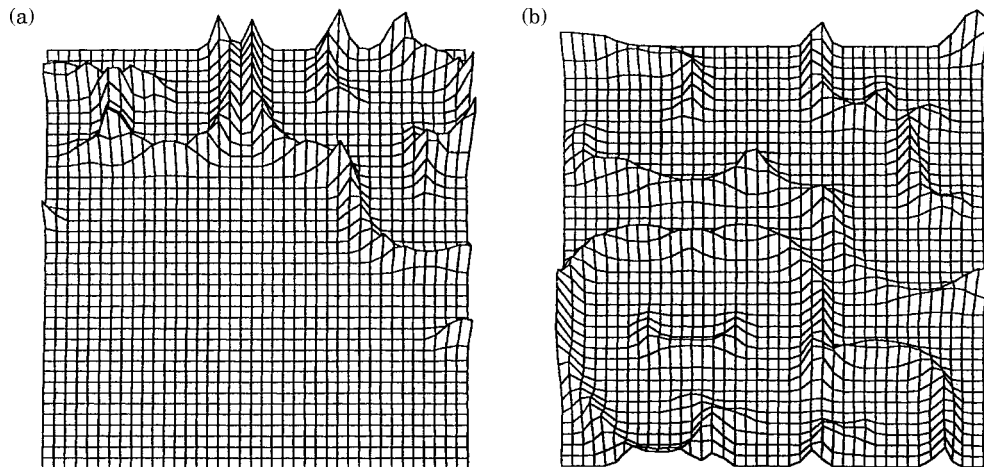


FIG. 1. Maps of the density of parasitoid species 2, 100 generations after its inoculation into the top 10% of the arena previously occupied only by hosts and parasitoid species 1, from the P-H-P model with $\mu_{P1} = \mu_{P2} = 0.2$, $\mu_N = 0.5$, $\alpha = 1.2$. The “mountain ranges” in the maps are the peaks of spiral waves in local population density, and are in continuous motion in a time-evolving simulation. (See Fig. 5 for similar maps for the host and parasitoid species 1.) (a) *Standard model*. Although parasitoid 2 has a superior attack rate, it can only invade the spiral structures very slowly. (b) *Modified model* with 1% of parasitoids performing long-distance dispersal, with equal probability of arriving at any patch (this is in addition to the 20% undergoing short-range dispersal).

Following initialisation, each simulation was run with the required μ and α , and the results examined to determine whether the initially more numerous parasitoid species increased or decreased its advantage over time. Total population densities were calculated using a cosine-windowed average over 30 successive generations; that is, using the weights:

$$w_i = 0.5[1 + \cos(2\pi(t - T)/30)] \quad (11)$$

where T is the centre generation, and t varies from $T - 15$ to $T + 15$. The averaging process is intended to filter out variations due to cycles in population density, while the cosine weighting is used to avoid errors associated with the start and end of the averaging period.

If the initially more numerous species decreases in relative frequency for both the initial density ratios, then this indicates that the particular parameter combination leads to indefinite coexistence of the two parasitoid species. The relative frequency of the two species is observed to fluctuate around some central value, although one cannot speak of an equilibrium ratio in the conventional sense. On the other hand, if a particular species increases in frequency in both cases, then this indicates either competitive exclusion, or indefinite coexistence with the central value of the relative frequency fluctuations being outside the range of the two initial relative frequencies (0.1 and 10).

This process was performed for a set of different starting maps, and for various μ_N and μ_{P1} combinations which cover the range of spiral and chaotic dynamics for the case $\lambda = 2$, as shown by Comins *et al.* (1991) (their fig. 3). Very similar results were obtained in all cases (see Fig. 2), irrespective of the type of spatial pattern present. In general, the pattern implies that competitive exclusion occurs, and that a certain linear combination of $\ln(\mu)$ and $\ln(\alpha)$ [approximately $\ln(\mu) + 0.12 \ln(\alpha)$] can be used as a composite predictor of which is the winning species, where species 1 wins if and only if this value is negative. For parameter combinations very close to the exclusion “watershed”, we observed some cases of two-parasitoid coexistence (other than the two-identical-parasitoid case), as indicated by the dots in Fig. 2. This is a fragile coexistence, since a very close match of attack rates is required.

The fact that coexistence with very similar competitors is possible at all is interesting, and suggests the possibility of separate “disperser” and “exploiter” niches. Consequently, we examined cases which are very far from the two-identical-parasitoids case. These have parasitoid dispersal fractions which differ by up to a factor 10 (which would be plotted about 1.2 scale widths outside the horizontal scale of

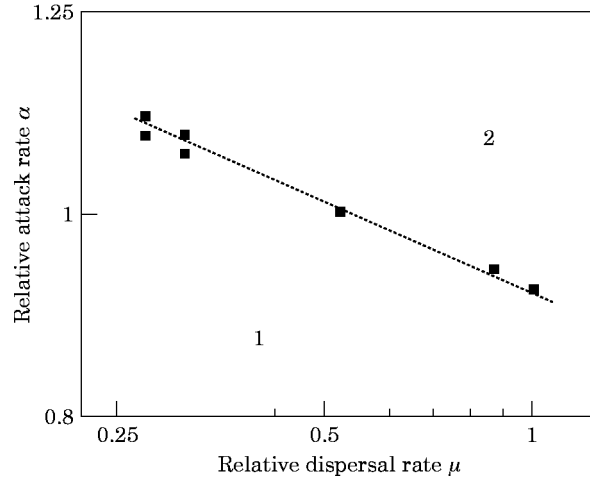


FIG. 2. Simulation outcomes of the P-H-P model with $\lambda = 2$, $\mu_{P1} = 0.5$, $\mu_N = 0.5$. Parasitoid species 2 excludes species 1 in the area above the dashed line, while species 1 excludes species 2 below it. The results near the line vary slightly with starting conditions, and include some cases of apparently persistent 3-species coexistence. In a particular series of runs for a parameter grid ($\mu = 0.25$ to 1 stepping by a factor 1.1487; $\alpha = 0.8$ to 1.25 stepping by a factor 1.0226) the combinations marked by squares resulted in coexistence according to the criterion described in the text.

Fig. 2). Figure 3 shows the much broader range of relative attack rates for which coexistence occurs when the parasitoid dispersal rates are massively different. The occurrence of coexistence for a broad range of relative attack rates also implies that coexistence can be robust (i.e., resistant to perturbations). That is, the coexistence limits are not so restrictive that minor environmental changes can push the system into the non-coexistence region. The figure shows the range of relative attack rate which leads to coexistence for a range of host dispersal rates and $\mu_{P1} = 0.5$, $\mu_{P2} = 0.05$. The vertical slice at $\mu_N = 0.5$ corresponds to a slice of Fig. 2 at $\ln(\mu) = -2.3$ (off scale to the left).

Currently, we distinguish between the different diffusion-induced spatial patterns in our models subjectively, but there is the prospect that proper diagnostic methods can be developed (Cross & Hohenberg 1993; Rand 1994). Our observations of the evolving patterns during simulations suggest that the patterns of host and total parasitoid density in the P-H-P model are no different from those in the 2-species host-parasitoid model (i.e. spirals, spatial chaos, and crystalline structures). The spatial pattern of hosts and total parasitoid densities in a persistent three-species system generally seems to be the same as that of the two-species system consisting of the host and the more numerous parasitoid (see however the results for the individual parasitoid species discussed below).

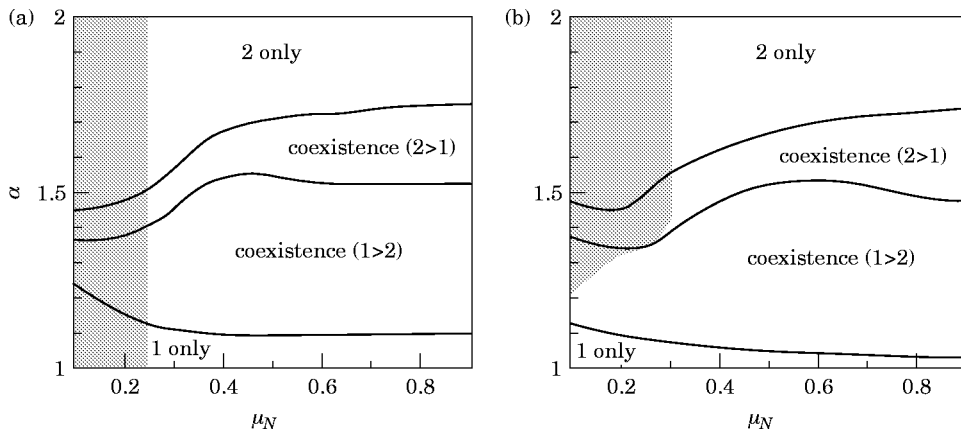


FIG. 3. Simulation outcomes of the P-H-P model with $\lambda = 2$, for a linear grid of host dispersal rates μ_N and relative attack rate α (steps of 0.1 and 0.05, respectively). Parasitoid species 2 is the less dispersive parasitoid. (a) $\mu_{P1} = 0.5$, $\mu_{P2} = 0.05$. (b) $\mu_{P1} = 0.2$, $\mu_{P2} = 0.02$. The regions separated by solid lines are, from top to bottom: species 2 (low disperser) excludes species 1, coexistence with species 2 more numerous, coexistence with species 1 more numerous, species 1 (high disperser) excludes species 2. The shaded areas denote chaotic spatial patterns, while the remaining parameter combinations give spirals.

The results in Fig. 3 were produced by running simulations for a grid of values of relative attack rate α and host dispersal rate μ_N . In each case the simulation was started from a standard spiral pattern and was run for 500 generations. The results are highly reproducible, and the inferred stability boundaries differ only minutely for entirely different starting distributions, provided that they display an established spiral pattern (spiral patterns are found to establish readily from the simultaneous invasion of the grid by hosts and parasitoids, but not from initially uniform distributions). The ratio of total parasitoid populations was calculated, using cosine-weighting over 30 generations (as described above). Then another 200 generations were simulated, and the population ratio was calculated again. Coexistence was inferred if the two population ratios differed by less than a factor of two. In most cases of coexistence the ratio of population densities varies much less than this, whereas competitive exclusion leads to factors of 10 to 1000; the specific factor 2 is used arbitrarily in drawing the coexistence boundary. Figure 3 also categorises the observed spatial patterns as “chaos” or “spiral”. This classification is somewhat fuzzy, being based on a visual comparison of the spatial patterns with the types of pattern generated by the two-species host-parasitoid model, as illustrated by Comins *et al.* (1991) (their fig. 2).

Coexistence occurs over a wide range of relative frequencies of the two parasitoid species, as illustrated in Fig. 4 (Fig. 3 merely shows which species is the more numerous). This unexpected observation motivates the use of the “stable ratio” criterion for coexistence in Fig. 3, as opposed to the “bracketing” criterion which was used in Fig. 2. The bracketing

criterion misinterprets coexistence at low frequency as competitive exclusion (this is found not to be a problem for the parameter combinations in Fig. 2). The large differences in relative frequency can be understood when we examine the spatial distribution of the two parasitoid species at the end of a 760 generation simulation, as is done in Fig. 5. It is clear from this figure that the slowly dispersing parasitoids are concentrated in an unusual niche; namely, the central foci of the spirals which are maintained in an homogeneous environment by the interaction of diffusion and population dynamics (i.e. by reaction-diffusion). The slowly dispersing parasitoid is actually

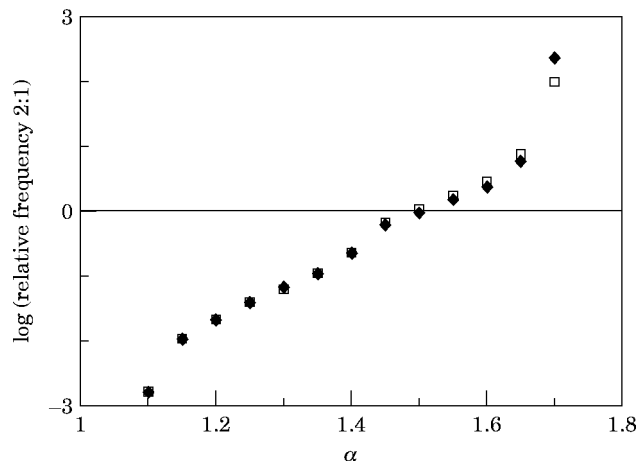


FIG. 4. Illustration of the coexistence criterion using population density ratios after 500 and 730 generations. The squares show the ratios of the spatially and temporally averaged population densities for the two parasitoid species in generations 500–530, while the diamonds show the ratios of the averages for generations 730–759 (using cosine weighting for the time averages). Coexistence is inferred for the range of α values from 1.1 to 1.7. The parameters for this figure correspond to a vertical slice of Fig. 3(a) at $\mu_N = 0.5$.

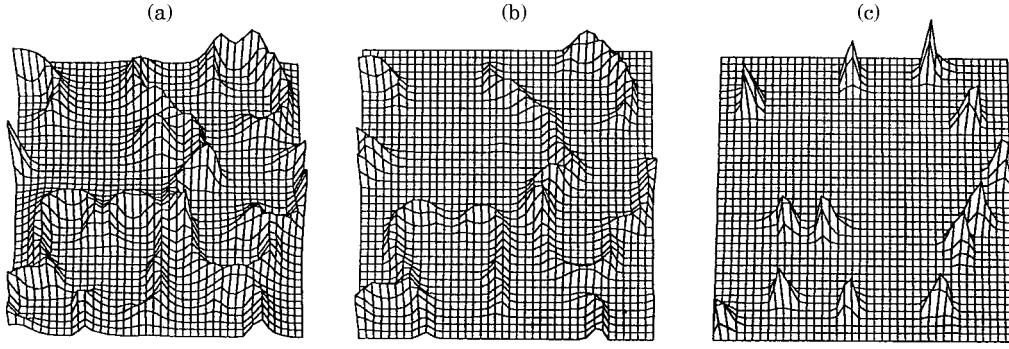


FIG. 5. Maps of the spatial density distribution (with linear scales) of hosts (a), highly dispersive parasitoids (b) and sedentary parasitoids (c), in a snapshot from the dynamics of a persistent P-H-P system with $\lambda = 2$, $\mu_N = 0.5$, $\mu_{P1} = 0.5$, $\mu_{P2} = 0.05$, $\alpha = 1.3$. The grids must be mentally superimposed in order to perceive the relationships between the densities of the various species. Spiral foci exist at the ends of the “mountain ranges” in the left-hand figure (excluding ends at the edges of the grid). In the time-evolution of the system the “mountain ranges” are the peaks of population density waves, and are thus in continuous motion. The foci, by contrast, remain in almost exactly the same place, for indefinitely long times.

the more common in the vicinity of the foci, but these areas represent only a small fraction of the spatial range.

As the relative attack rate of the slowly dispersing parasitoids is increased, they come to dominate larger and larger areas around the foci, and coexistence is still possible when they are the more common type. As may be seen from Fig. 3, the coexistence range is biased towards the slow dispersers being less common. Presumably the mechanism of coexistence is the same in all cases: slow dispersers have an attack rate advantage in the areas where host density fluctuates the least (i.e., near the foci), and fast dispersers have a colonisation advantage in the areas which are swept by the spiral arms. The waves of population density represented by the spiral arms leave relatively depopulated areas in their wake, requiring colonisation.

Coexistence is also possible in cases with spatially chaotic dynamics. However, the range of density ratios of the coexisting parasitoids is less in these cases, and we do not observe coexistence with very low frequencies of slow dispersers. This is consistent with the idea that a stable low frequency of slow dispersers requires them to be locally common at spiral foci. This is only possible if there are clearly defined spiral foci which move around little and do not continually appear and disappear.

H-P-H AND H-P-Q INTERACTIONS

Results for the two-host (H-P-H) and hyperparasitoid (H-P-Q) models were obtained in a similar way to those for P-H-P. The following conclusions emerge:

(1) Competitive exclusion occurs in the H-P-H model for parameter combinations close to the two-identi-

cal-hosts model ($\alpha = 1$, $\lambda_2/\lambda_1 = 1$, $\mu = \mu_{N2}/\mu_{N1} = 1$). Quite similar results are obtained for widely varying parameterisations. As in the P-H-P model, the winning species can be approximately predicted by a linear combination of the logarithms of the parameter ratios. For example, with $\lambda_1 = 2$, $\mu_{N1} = 0.5$, $\mu_{N2} = 0.5$, the winning species is approximately predicted by the sign of the parameter combination:

$$\ln(\mu) + 0.10 \ln\left(\frac{\lambda_2}{\lambda_1}\right) - 0.16 \ln(\alpha) \quad (12)$$

where host species 1 wins if and only if the expression is negative. (Note that this only holds well with identical hosts as above and assumes linearity of the competitive exclusion criterion; the relationship was established from simulation grids similar to Fig. 2.) (2) Two host species with massively different dispersal rates can readily coexist, as illustrated by the stability diagrams in Fig. 6. The spatial pattern of parasitoids and total hosts is similar to that which would occur in a two-species model containing the parasitoid and the more numerous host. In this case the less dispersive host has either a larger intrinsic rate of increase or a smaller parasitoid attack rate. With certain parameter combinations the less dispersive host is restricted to spiral foci, in exactly the same way as the less dispersive parasitoids in Fig. 5.

(3) A parasitoid and hyperparasitoid can coexist if the latter has a higher attack rate and a massively lower dispersal rate (see Fig. 7). The hyperparasitoid may be restricted to spiral foci, just as are the less dispersive competitors in the other two models. Coexistence also occurs in this model with the parasitoid being less dispersive. However, this situation leads to extreme variability of the host population, so that host resource limitation is

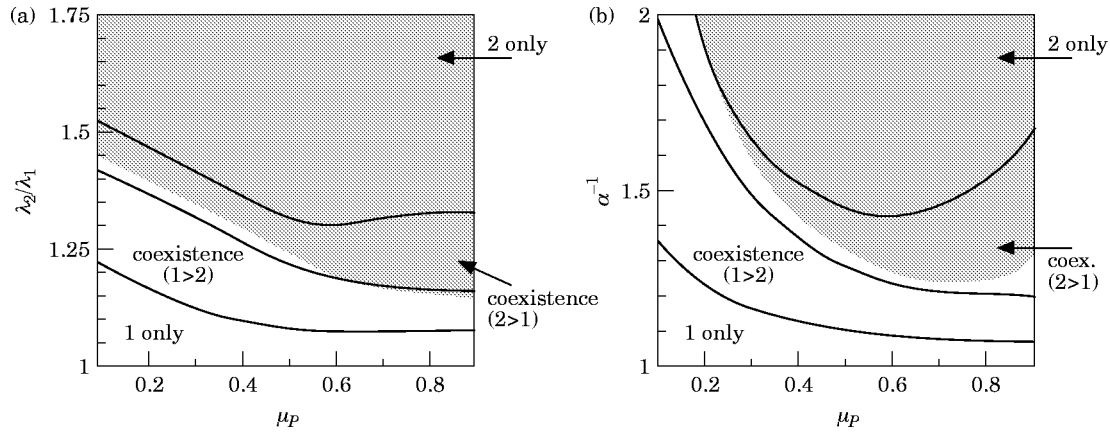


FIG. 6. Simulation outcomes of the H-P-H model with $\lambda_1 = 2$, $\mu_{N1} = 0.5$, $\mu_{N2} = 0.05$, for a linear grid of parasitoid dispersal rates μ_P and of relative attack rate α or relative growth factor λ_2/λ_1 (steps of 0.1 for μ_P and of 0.05 for λ_2/λ_1 and α). Species 2 is the less dispersive host. (a) $\alpha = 1$, λ_2/λ_1 varies. (b) $\lambda_2 = \lambda_1 = 2$, α varies, with larger α (i.e. advantage to host species 1) at the top of the graph. The regions separated by solid lines are, from top to bottom: species 1 (high disperser) excludes species 2, coexistence with species 1 more numerous, coexistence with species 2 more numerous, species 2 (low disperser) excludes species 1. The shaded areas denote chaotic spatial patterns, while the remaining parameter combinations give spirals.

required to make the model realistic. It is also necessary to give the parasitoids a higher attack rate than the hyperparasitoids, which runs counter to some empirical evidence (Hassell, 1979). We therefore do not present results for this case.

Discussion

The three-species cellular models described in this paper are extensions of the host-parasitoid models

described by Hassell *et al.* (1991) and Comins *et al.* (1992). Our aim in adding an additional species has been to examine general conditions for coexistence in multispecies host-parasitoid systems that stem simply from having local populations linked by diffusive dispersal. All three models give remarkably similar results: a third species (be it another host, another parasitoid or a hyperparasitoid) can coexist stably within the spatial dynamics (spiral waves or chaos) generated by an existing two-species, host-parasitoid

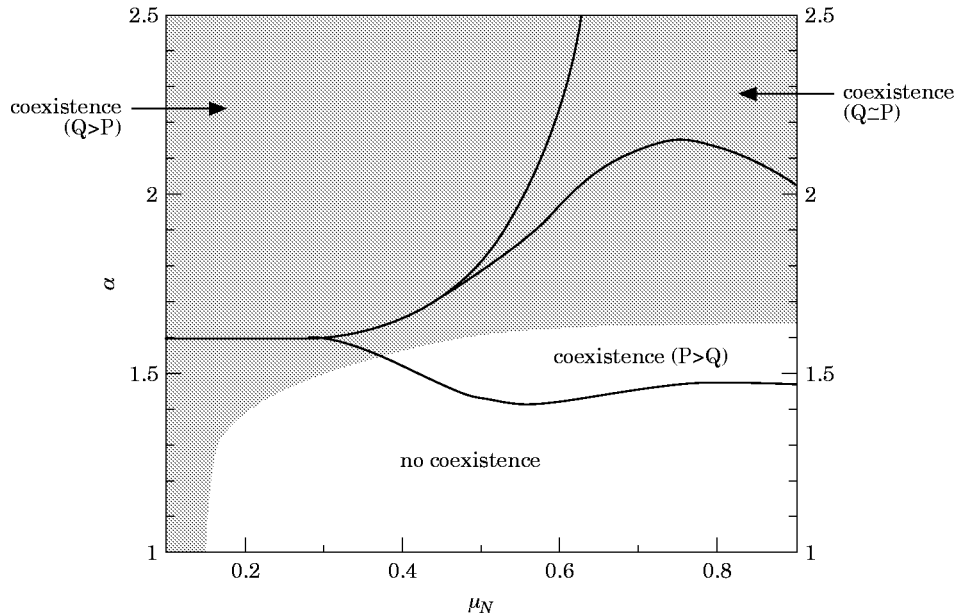


FIG. 7. Simulation outcomes of the H-P-Q model with $\lambda = 2$, $\mu_P = 0.5$, $\mu_Q = 0.05$, for a linear grid of host dispersal rate μ_N and of relative attack rate α (steps of 0.1 and 0.05, respectively). The regions separated by solid lines are, clockwise from top left: coexistence with hyperparasitoids more numerous, coexistence with hyperparasitoids and parasitoids about equally numerous, coexistence with hyperparasitoids less numerous, no coexistence. The shaded areas denote chaotic spatial patterns, while the remaining parameter combinations give spirals.

interaction, provided that it is relatively sessile compared to its competitor. Coexistence thus depends upon a kind of fugitive coexistence (Hutchinson, 1951; Levins & Culver, 1971; Horn & MacArthur, 1971; Hanski & Ranta, 1983; Nee & May, 1991; Hanski & Zhang, 1993). For, example, in the two parasitoid-one host system, coexistence occurs most easily when the two parasitoids species have very different dispersal rates provided that low dispersal is matched by high within-patch searching efficiency, and vice versa. Similarly, in the case of two host-one parasitoid interactions, coexistence occurs readily when the two host species have very different dispersal rates and the relatively immobile species has either the larger rate of increase or is less susceptible to parasitism. Finally, in the host-parasitoid-hyperparasitoid system, coexistence demands that the hyperparasitoid has a higher searching efficiency than the parasitoid and a much lower dispersal rate. That the hyperparasitoid should have the higher searching efficiency is also in accord with the conclusions from non-spatial models of host-parasitoid-hyperparasitoid interactions (Beddington & Hammond, 1977; Hassell, 1979; May & Hassell, 1981).

A striking and less expected result has been the finding that coexistence in these systems tends to be associated with some degree of self-organising niche separation between the competing species. This is best seen when the spatial dynamics show clear spirals. Thus, in the case of two competing parasitoids with very different dispersal rates, the relatively immobile species tends to be confined to the central foci of the spirals where it is the most abundant species, and the highly dispersive species occupies the remainder of the "trailing arm" of the spirals, as shown in Fig. 5. Since the foci of spirals are relatively static in these models, the less mobile species appears to occur only in isolated, small "islands" within the habitat, much as if these were pockets of favourable habitat. As the dispersal rates become less divergent between the species, the niche of the less dispersive species spreads further into the arm of the spirals. Such spatial segregation of the competing species, purely as a consequence of the dynamics, is an intriguing property of these spatial models.

Although these three-species systems persist over very long periods of time (no extinctions observed in 20 simulations of 30000 generations each), they are sensitive to imposed minimum population sizes and to changes in the range of dispersal. An approximate means of simulating the effect of finite population sizes is to introduce a lower bound on each local population, with the population being set to zero if it falls below this threshold. With lower bounds of less

than about 0.0001 in scaled units there is little effect on the dynamics in the cases so far examined. But with higher thresholds, there is an increasing tendency for the "focus-living" species to be eliminated from some of the foci, and then being unable to reinvade the vacant foci. This, however, is counteracted by the introduction of a small fraction of long-range dispersal, which permits reinvansion of the vacant spiral foci (see Fig. 1). A proper treatment of this effect requires consideration of individual dispersers, which is outside the scope of this paper.

Theoretical studies of spatially distributed populations with local dispersal between patches have revealed a fundamental tendency for populations to become spatially organised into spiral or chaotic patterns of local abundance; spirals are associated with cycles in average population size over time, while chaotic patterns lead to time series that are also chaotic. A necessary condition for these appear to be local patch dynamics that are unstable, but the results persist with very low host rates of increase ($\lambda = 1.01$), with very low dispersal rates and even if a small minority of adults disperse much more widely. Several interesting features follow on from these patterns, such as (1) the spatial segregation of competing species observed in this study and (2) the relative non-invasibility of populations showing spiral waves observed by Boerlijst *et al.* (1993) (see Fig. 1). Theory is far ahead of experiment or observation in this instance. Direct observation of these kinds of spatial patterns of dynamics in the field presents enormous logistical problems. It may be possible, however, to determine properties of the population density distributions which are diagnostic of spirals or spatial chaos (for example, particular patterns of delayed covariance). This could then lead to indirect tests of the existence of these patterns in nature.

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