Host–parasitoid spatial models: the interplay of demographic stochasticity and dynamics

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SUMMARY

Host–parasitoid metapopulation models have typically been deterministic models formulated with population numbers as a continuous variable. Spatial heterogeneity in local population abundance is a typical (and often essential) feature of these models and means that, even when average population density is high, some patches have small population sizes. In addition, large temporal population fluctuations are characteristic of many of these models, and this also results in periodically small local population sizes. Whenever population abundances are small, demographic stochasticity can become important in several ways. To investigate this problem, we have reformulated a deterministic, host–parasitoid metapopulation as an integer-based model in which encounters between hosts and parasitoids, and the fecundity of individuals are modelled as stochastic processes. This has several important consequences: (1) stochastic fluctuations at small population sizes tend to be amplified by the dynamics to cause massive population variability, i.e. the demographic stochasticity has a destabilizing effect; (2) the spatial patterns of local abundance observed in the deterministic counterpart are largely maintained (although the area of ‘spatial chaos’ is extended); (3) at small population sizes, dispersal by discrete individuals leads to a smaller fraction of new patches being colonized, so that parasitoids with small dispersal rates have a greater tendency for extinction and higher dispersal rates have a larger competitive advantage; and (4) competing parasitoids that could coexist in the deterministic model due to spatial segregation cannot now coexist for any combination of parameters.

1. INTRODUCTION

In recent years, there has been a growing recognition of the importance of dispersal within spatially distributed populations in influencing the persistence of species interactions (Kareiva 1994). Central to this growth in understanding, has been the use of metapopulation models. Metapopulation models have developed along quite different paths (Taylor 1990; Gilpin & Hanski 1991). Some stem from the original single-species formulation of Levins (Levins 1969; Levins & Culver 1971) in which all individual patches (= local populations) are equally in contact with each other and can only have the states of being empty or occupied. Others are spatially explicit so that each habitat containing a local population has specific neighbours. Both spatially implicit and explicit models may only record different states of habitat occupancy (e.g. Wolfram 1984; McCauley *et al.* 1993; Durrett & Levin 1994; Rand & Wilson 1995; Rand *et al.* 1995) or may deal explicitly with the dynamics of the local populations (e.g. Reeve 1990; Taylor 1990; Comins *et al.* 1992; Solé & Valls 1992; Rohani *et al.* 1994; Swinton & Anderson 1994).

This paper concentrates on spatially explicit models which deal explicitly with the dynamics of the local populations and on one particular type of interaction—between insect hosts and their parasitoids. A number of conclusions have come from the body of work on this topic. This includes results on host–parasitoid persistence (Hassell *et al.* 1991); the effect of initial conditions (Sole & Valls 1992; Adler 1993); evolutionary aspects (Boerlijst *et al.* 1993); coexistence of competing parasitoids (Hassell *et al.* 1994); and on parasitoid aggregation and parasitoid searching efficiencies (Rohani & Miramontes 1995). Rohani *et al.* (1997) gave a review of some of this work.

The majority of this work is based on deterministic models of the host–parasitoid interaction. This raises the interesting question of how robust the models are to various forms of stochasticity. Some work on environmental stochasticity already exists. Comins *et al.* (1992) and Hassell *et al.* (1994) have shown that the characteristic spatial patterns of abundance are only appreciably affected by random variability in the environment when the spatial units of variability are on roughly the same scale as the spatial patterns themselves. More recently, Ruxton & Rohani (1996) have attempted to show that environmental stochas-

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tivity has little effect on the coexistence of competing parasitoids.

A quite different, and possibly more important, form of random variation is demographic stochasticity. The models used in the work described above were formulated as a mean approximation to the random process of parasitoids finding hosts, and all had local population size as a continuous variable. However, models which 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 & Wilson 1991). Additionally, it is possible that some of the properties of these deterministic metapopulation models rest heavily on the existence and dispersal of ‘nano-individuals’, which would not be seen if the models only dealt with discrete individuals.

Demographic stochasticity has received a great deal of attention in the literature recently as it is important in estimating the probability of population extinctions (see, for example, Burgman *et al.* 1993; Stephan & Wissel 1994; Lande 1996). Less attention has been focused on the effects of demographic stochasticity on population dynamics more broadly (but see, for example, Ruxton 1996; Wilson 1996). This paper utilizes an individual-level approach to examine the effects of demographic stochasticity on host–parasitoid metapopulations. In particular, we examine: (i) persistence of the host–parasitoid interaction (long-term coexistence is associated with the formation of self-maintaining spatial patterns of local abundance that promote asynchrony between the local patches); (ii) the coexistence of competing parasitoid species (due to spatial segregation of the competitors); and (iii) the relationship of host–parasitoid persistence with the size of the metapopulation (i.e. the number of patches). In other words, we ask the question: ‘are these properties of persistence, spatial patterning of abundance and multi-species coexistence also a feature of metapopulation models that include demographic stochasticity?’ To answer this we use an integer-based model, analogous to the deterministic population models used previously, in which encounters between hosts and parasitoids and the fecundity of each host are modelled by simple stochastic processes. There are a number of benefits to this approach. First, it is now impossible for fractions of individuals to disperse. Second, the problem of small numbers of individuals and the mean approximation is addressed. Third, demographic stochasticity and extinctions naturally enter the model through a biologically motivated mechanism (rather than simply setting a minimum size below which the local population becomes extinct).

2. A STOCHASTIC FORMULATION

The host–parasitoid metapopulation models previously explored (see, for example, Hassell *et al.* 1991, 1994; Comins *et al.* 1992; Comins & Hassell 1997) assume a two-dimensional grid, size $l \times l$, of patches

in which the local dynamics occur. These are given by

$$H'_i = \lambda H_i f(P_i), \quad P'_i = bH_i[1 - f(P_i)]. \quad (1)$$

Here H_i and P_i are, respectively, the population size of hosts and parasitoids in patch i and the primes denote numbers in the next generation. The quantity λ is the host net rate of increase (discounted to take into account mortalities other than parasitism), $f(P_i)$ is the fraction of hosts unparasitized and b is the number of female parasitoids emerging from each parasitized host (henceforth assumed to be one). Following the stages of reproduction and parasitism within each patch there is a dispersal phase, in which a fraction c_h of hosts and c_p of parasitoids disperse equally to the eight nearest neighbouring patches, leaving a fraction $(1 - c_h)$ and $(1 - c_p)$ in each patch.

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 (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 $a_p P_i$.

Our model differs in that encounters between hosts and parasitoids are modelled by a simple stochastic process which is mimicked by the Nicholson–Bailey model above. Consider a small period of time δt . The probability of a parasitoid encountering a host is then $a_p \delta t$. The probability that a host in patch i is encountered by at least one parasitoid during this period is then:

$$1 - (1 - a_p \delta t)^{P_i} \approx a_p \delta t P_i, \quad (3)$$

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

$$p(j) = \binom{H_i}{j} (1 - a_p \delta t P_i)^{H_i - j} (a_p \delta t P_i)^j, \quad (4)$$

which, as $P_i \delta t \rightarrow 0$, is approximated by a Poisson distribution with mean $a_p P_i H_i \delta t$. Formally, this approximation also requires that $H_i \rightarrow \infty$, which will not always be the case in our simulations. However, as long as δt is very small such that terms of order $O(\delta t^2)$ or higher are negligible, then even when host numbers are small (e.g. less than five) this approximation will be good. To check our results in the following sections, therefore, values of δt ten times smaller than the stated value were also used (so that $\delta t^2 = 0.000\,025$), and in all cases qualitatively similar results were obtained.

In order to facilitate comparison to model (1), we keep discrete generations with synchronized reproduction and dispersal. Our model thus consists of two parts: (i) a within-season component that describes parasitism of hosts; and (ii) a between-season

component describing reproduction and then dispersal and which relates the distribution of hosts and parasitoids at the end of one season to the distribution at the start of the next. The within season component is given by

$$H_i(t + \delta t) = H_i(t) - s_i(t), \quad P_i(t + \delta t) = P_i(t), \quad (5)$$

where $s_i(t)$ is a random number taken from a Poisson distribution with mean $a_p P_i(t) H_i(t) \delta t$, and $P_i(t)$ and $H_i(t)$ are now integers. At the end of each season ($t = T$) there is a reproduction phase:

$$H'_i = Z(\lambda H_i(T)), \quad P'_i = H_i(0) - H_i(T), \quad (6)$$

where $Z \sim \text{Poi}(\lambda H_i(T))$, so that the fecundity of each individual in a patch is distributed as a Poisson distribution with mean λ (the distribution of the sum of H_i independent Poisson random variables each with mean λ is the same as a Poisson distribution with mean λH_i). If this model had no stochastic element, (i.e. if $s_i(t) = a_p P_i(t) H_i(t) \delta t$ and the fecundity of each individual was a fixed number) then we would return exactly to model (1).

Each individual host and parasitoid now disperses to a site randomly chosen from one of the neighbouring patches with probability c_h and c_p , respectively. Individuals that disperse beyond the boundaries of the lattice are lost (the boundary conditions do not affect any of the results). When the number of individuals within a patch is small, the dispersal process is not even, and there may be no dispersal to some neighbouring patches. This has important effects which we will return to later. We refer to this stochastic, integer-based model as the SIB model, and its deterministic counterpart with continuous population variables as the DET model.

To initialize the lattice, each patch is ‘seeded’ with a small number of each species, and there is a small immigration term for each species into a randomly chosen patch every generation. After 200 generations the immigration term is set to zero; prior to this point all species are guaranteed to be present. Starting simulations in this manner has two benefits: it tends to mask effects of the specific initial conditions chosen and allows us to study the long-term behaviour of the system, and it separates effects of long-term persistence from the dynamics of invasion.

3. POPULATION DYNAMICS

The first important difference between the stochastic integer-based (SIB) model and the corresponding deterministic (DET) model concerns the population abundances as a function of the parasitoid attack rate, a_p . In figure 1, we plot the mean parasitoid abundance with respect to this attack rate. At small values of a_p , the SIB and DET models behave similarly. This is not surprising as the mean parasitoid abundance per patch is a function of $1/a_p$ (the unstable parasitoid equilibrium point in the Nicholson–Bailey equation is $\ln(\lambda)/a_p$). At small values of a_p , therefore, the mean population size is large, stochastic effects are averaged out and the two models behave very similarly.

Figure 1. The parasitoid mean abundance as a function of the attack rate a_p . Each simulation is started with 10 hosts and one parasitoid in each cell. For the first 200 generations there is a small immigration term: four hosts and four parasitoids in a randomly chosen patch each generation. The simulation is then run for a further 1000 generations to remove any transient effects. The abundance is calculated as an average over all cells over a period of 2000 generations and averaged over 200 different simulations. The lattice size is 20×20 , $\lambda = 2.0$, $c_h = c_p = 0.1$ and δt for the stochastic model was 0.05. One should note here that the value of a_p at which extinctions occur increases with the size of the lattice. So that for a lattice size 20×20 , $a_p > 0.2$ causes extinctions; 40×40 , $a_p > 0.25$; and for 60×60 , $a_p > 0.29$.

Figure 2. A particular time series from the stochastic and the deterministic model. The parameters are as in figure 1 except that $a_p = 0.1$. The parasitoid mean abundance at one time is an average over all the cells.

At larger values of a_p , however, the behaviour of the two models diverge. In the DET model, as a_p increases the mean parasitoid abundance continues to decrease at a rate proportional to $1/a_p$. In the SIB model, however, the small population sizes at larger values of a_p mean that stochastic effects become important and extinctions of both the host and parasitoid local populations become more frequent. This results in the parasitoid population going extinct in some patches in which the host is present. This then frees the host from control by the parasitoid and the numbers of hosts in those patches

increases exponentially. When parasitoids eventually disperse into that patch their numbers also increase rapidly. This results in host and parasitoid populations that are more variable in space and time. The population ‘explosions’ in individual patches causes an actual increase in the average abundance, as illustrated in figure 2. The same effect is observed if host self-regulation is included, either as a proportionate decrease in the host fecundity with host population size, or if there is a maximum host population size within a patch. The only effect is to cause a ceiling in the host population ‘explosions’. As a_p increases further, demographic stochasticity eventually causes the extinction of the parasitoid population in all the patches. No such extinctions occur in the DET model and the mean abundance continues to decrease at a rate proportional to $1/a_p$.

There are thus three different regions in the SIB model (although there is a smooth transition between them), defined by low values of a_p where stochastic effects are small, by intermediate values of a_p where we might expect to see qualitative differences between the DET and SIB models and large values of a_p which cause extinctions.

Searching efficiency has rarely been estimated in natural populations of hosts and their parasitoids, but reported values include 0.35 per generation (Ives 1976) and between 0.04 and 0.7 per generation (Hassell 1980). These values fall well within the range explored in this paper.

4. SPATIAL PATTERN

Hassell *et al.* (1991) reported that their DET model displayed some remarkable spatial patterns; including spatial chaos, spirals and a crystal lattice structure. Does the SIB model also display these patterns? Figures 3*a, b* show the corresponding diagram to that in Hassell *et al.* (1991) for both the region of relatively small ($a_p = 0.01$) and large ($a_p = 0.1$) stochastic effects. The region of spatial chaos and spirals is largely maintained even when the stochastic effects are large (figure 3*b*). However, the region of spatial chaos is greatly increased in figure 3*b* (large stochastic effects) and slightly increased in figure 3*a* (small stochastic effects). This is intuitive as stochastic effects would be expected to tend to disrupt the large-scale patterns. The spirals, however, remain a fairly robust feature of the model (at least, as here, with no long-range dispersal of individuals).

The much smaller region of parameter space where a crystal lattice structure is observed in the DET model is not seen in the SIB model. In this region, in the SIB model, either both the host and parasitoid populations tend to extinction (figure 3*b*), or there is a tiny region where parts of the lattice tend to a fixed structure similar to the crystal lattice but the lattice as a whole never settles to an equilibrium (figure 3*a*). Hassell *et al.* (1991) also identified a region of ‘hard-to-start spirals’, where simulations started from single cells tended to go extinct before spiral structures were formed. The initial conditions used

Figure 3. Spatial patterns in the stochastic model. The lattice size is 30×30 , $\lambda = 2.0$ and δt for the stochastic model was 0.05. (a) The approximate boundaries of the various spatial patterns observed in the stochastic model when $a_p = 0.01$. (b) The approximate boundaries of the various spatial patterns observed in the stochastic model when $a_p = 0.1$. In both figures, the dotted line is the boundary between spatial chaos and spirals for the deterministic model (from figure 3 in Hassell *et al.* 1991). The boundaries for the SIB models have been obtained by observation of simulations and are thus only approximate and entirely subjective. Differences between figure (a) and that obtained by Hassell *et al.* (1991) could be entirely due to observational differences. However, the relative differences between (a) and (b) are still clear.

here enabled all the simulations in this region to persist and form spiral structures (in the DET model). In the SIB model, however, there is still a region where simulations tended to go extinct, as shown in figures 3*a, b* (although it was possible to form spiral structures for some parameter values in this region by slowly increasing the host dispersal rate from the region of persistence).

5. PERSISTENCE AND LATTICE SIZE

The probability of host and parasitoid persistence is plotted in figure 4*a* as a function of lattice size for the DET model, and in figure 4*b* for the SIB

Figure 4. The probability of persistence as a function of the lattice width (total number of cells is therefore the lattice size squared). The parameter values are $\lambda = 2.0$, $c_h = 0.1$ and δt for the stochastic model was 0.05. The persistence probability is calculated as the number of simulations where both the host and parasitoid still persist after 3000 generations (after immigration for the first 100 generations). (a) The deterministic model with $a_p = 0.1$ (different values of a_p give the same figure). (b) The stochastic model with $a_p = 0.01$. (c) The stochastic model with $a_p = 0.1$.

model in the region where stochastic effects are small ($a_p = 0.01$). Note that there is little difference in the persistence properties between the two types of model; small stochastic effects clearly have very little influence on the mechanism for persistence (i.e. on the asynchrony between patches so that those becoming extinct can be recolonized from occupied neighbouring patches).

The picture, however, is very different if a_p is large ($a_p = 0.1$) in the SIB model, as shown in figure 4c. In this case low dispersal rates have a much smaller probability of persistence in small lattices. 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 large number of hosts). When the parasitoid population is small (high a_p), then the fraction of neighbouring 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. In the DET model, in contrast, the eight neighbouring sites are always colonized, even if only by fractional numbers, so that even if only one of the neighbouring sites is suitable, the parasitoid will always persist. There is thus no comparable disadvantage of small dispersal rates at small population sizes in the DET model.

6. COEXISTENCE OF COMPETING PARASITIDS

Hassell *et al.* (1994) and Comins & Hassell (1997) reported that in a system with a single host and two competing parasitoid species competitive exclusion of one of the parasitoids generally occurred. In extreme examples, however, where the dispersal rates of the two species differed by an order of magnitude, they were able to coexist. In these cases, coexistence of the two parasitoids is facilitated because the slowly dispersing parasitoids (which have a higher a_p) are concentrated in an unusual niche; namely, the central foci of spirals where host density fluctuates the least and the population density of the host is high. The fast dispersers have a colonization advantage in the areas where host density is fluctuating strongly (the areas swept by the spiral arms). Persistent spatial separation of the two competing parasitoid species is maintained by this mechanism.

In corresponding simulations with the SIB model, stochastic effects prevent the slow-dispersing parasitoid from maintaining itself at the focus of the spirals; when it cannot stay here it is outcompeted by the other parasitoid with the higher dispersal rate and becomes extinct. In the absence of long-distance dispersal, the spiral focus cannot then be re-invaded and the slow-dispersing parasitoid goes extinct at each of the spiral foci until it is extinct in every patch (a fact briefly mentioned in the context of thresholds, by Comins & Hassell (1997)). This is illustrated in figure 5. This is true for the whole parameter range of coexistence reported in Comins & Hassell (1997). At small values of a_p , the stochastic effects are not great but still enough to prevent coexistence of the two competing parasitoid species; at higher values of a_p , extinction of the slower disperser is much quicker. The balance of coexistence between the two species has been shifted in favour of the parasitoid with a higher dispersal rate.

Figure 5. A particular time series for two competing parasitoids from both the deterministic and stochastic models. The simulations were started as in figure 1 with just a single host and a single (the fast dispersing) parasitoid. After 500 generations (to remove transient effects) half the parasitoids in each patch are split between the fast-dispersing and slow-dispersing parasitoids. The time series plotted follows on from this point. The lattice size is 50×50 , $\lambda = 2.0$, $c_h = 0.5$, $c_{pf} = 0.5$, $a_{pf} = 0.01$, $c_{ps} = 0.05$, $a_{ps} = 0.014$ and δt for the stochastic model was 0.05. Note that the parasitoid density is on a log scale and the x -axis is every fifth generation.

7. DISCUSSION

Recent analyses of host-parasitoid metapopulation dynamics have largely used deterministic models with populations as continuous variables. The main problems with this approach are that tiny fractions of the number of individuals are allowed to survive and disperse, and that the mean of the assumed stochastic process of parasitoids finding hosts may not be a good approximation. Some of the results of these models are therefore not robust to realistic levels of stochasticity. Clearly, in real populations there are thresholds in both the population density within a patch and in the numbers dispersing. We have addressed these problems by using an integer-based model, and by directly modelling the stochastic process of parasitoids encountering hosts. The introduction of demographic stochasticity and extinctions has enabled us to investigate the interesting question of whether demographic stochasticity is a stabilizing or destabilizing influence on the host and parasitoid population dynamics.

First, large levels of demographic stochasticity destabilize the population dynamics and cause the parasitoid population to go extinct. Second, intermediate levels of demographic stochasticity cause population explosions by freeing the host in some patches from regulation by the parasitoid. Thus the small fluctuations at small population abundances within a patch are amplified by the dynamics to cause massive population fluctuations. Clearly, demographic stochasticity in excitable populations is of great importance to the population dynamics (see also Rand & Wilson 1991) and raises interesting questions about whether observed population fluctuations

are due to intrinsic population dynamics or noise (e.g. Ellner 1991). In this case, noise is amplified by the intrinsic dynamics so that the two processes cannot be separated. Finally, small levels of stochasticity brings the SIB model much closer to its deterministic counterpart.

In general, therefore, it seems that demographic stochasticity has a destabilizing influence on the population dynamics. Contrary to the expectation that the increase in spatial heterogeneity in hosts and parasitoids caused by the stochasticity would help to stabilize the dynamics, stochasticity tends to disrupt the parasitoids' ability to regulate the host, which then increases unchecked (or at least to carrying capacity).

Within our integer-based model, stochasticity enters in three different ways: (i) random dispersal by individuals; (ii) the stochastic process of parasitoids encountering hosts within a patch; and (iii) a random number of individuals are born to each host. Logically, the first two processes are joined, so that it makes little sense to have an integer-based dispersal process but continuous population variables within a patch and vice versa. However, further simulations with different models have indicated that, whilst all three processes have important effects, it is the individual nature of the dispersal process that causes the greatest difference between the SIB and DET models. At small population sizes, this random process means that host and parasitoid dispersers tend to colonize different patches. Thus, freed from control from the parasitoid, the host increases exponentially fast and the inherent instabilities of the local dynamics return.

Dispersal by discrete individuals means that competing parasitoid species that could coexist in the deterministic model cannot now coexist. Coexistence, in the deterministic case, is facilitated by spatial segregation of the two species in which the slow dispersing parasitoid is able to maintain itself in the region of dense hosts (near the centres of spirals). However, demographic stochasticity means that the slower dispersing parasitoid is not able to fix itself at one precise location (relative to the host population) forever. The slow-dispersing parasitoid then goes extinct at each of the spiral centres and recolonization is unlikely as the centres are spatially separated 'islands'. It remains to be seen whether occasional long-distance dispersal is able to overcome this effect, and allow the coexistence of the two competing parasitoids.

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