

Chapter 2

Demographic Processes in Spatially Structured Host-Parasitoid Systems

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Abstract We explore the demographic control effects that arise from the foraging behaviour and reproductive strategies of host-parasitoid metapopulation systems under the influence of spatio-temporal variations in patch quality. Parasitoid populations are characterised by different levels of density-dependent sex ratio adjustments and interference competition. Using a spatially explicit mathematical model, in which the habitats are described by the frequency and distribution of host resources, we assume that the species are subjected to density-dependent effects in two different periods of their life cycles: pre- and post-dispersal. During the pre-dispersal period, the number of individuals that disperse or remain in each patch depends on the species “optimal decision” to explore or to leave the current patch, which is affected by the local number of individuals. After dispersal, individuals arriving in a new patch are influenced by the local densities, which define the host survival rate and reproductive success of parasitoids. We show that different demographic control levels, which arise from species behaviour and ecological processes in response to changes in patch quality, lead to different spatial distributions and species abundance in the landscape. The results elucidate how host-parasitoid life history affects species establishment and the efficiency of parasitoids as biological control agents.

Keywords Spatial structure • Host-parasitoid dynamics • Demography • Metapopulation • Patch dynamics • Biological control • Foraging behaviour • Landscape structure • Sex ratio • Density-dependence

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2.1 General Introduction

Entomologists' interest in host-parasitoid interactions increased in the beginning of the twentieth century with the possibility of using parasitoids to control insect pests (Godfray and Shimada 1999). The research developed to include several important aspects of species life history, behaviour and communities of host-parasitoid systems. More recently, efforts have also been directed to model and understand these many characteristics theoretically, guided by data obtained from experimental and field studies (Godfray and Shimada 1999; Hassell 1978, 2000).

Parasitoids depend strongly on their hosts to complete their life cycle. This vital dependence paints an extremely complex ecological interaction, and elucidating its intricacies requires understanding ecological and behavioural aspects. The density of hosts in a patch and the way they are exploited by parasitoids are governed by complex chemical, visual and tactile cues in the localisation of hosts and in the parasitoid's adaptive behaviour through learning, aiming at increasing efficiency. This complex behaviour also involves the evolution of searching strategies, clutch size and sex ratios (Godfray 1994; Bernstein and Driessen 1996; Godfray and Shimada 1999; Wajnberg 2006; Amat et al. 2009). Due to the complexity involved in host-parasitoid interactions and the difficulties in acquiring large amounts of data to test many of these processes on species dynamics, numerous mathematical models have been developed to provide insights into several aspects of parasitoid biology.

Nicholson and Bailey (1935) pioneered a simple theoretical model that describes the host-parasitoid dynamics. Although this Nicholson and Bailey (NB) model displays unstable dynamics, where host and parasitoid populations cannot coexist, the NB model is frequently used as a starting point for many theoretical studies to add more realistic aspects to host-parasitoid models (Hassell 2000). The inclusion of biological realism in the NB model involves modifications to several aspects of the problem, such as the specific way parasitism is described, the inclusion of spatial structure and forms of demographic control in host and parasitoid populations (Chesson and Murdoch 1986; Pacala and Hassel 1991; Hassell 2000).

Generally, the high rates of attack observed for many parasitoid species lead to an over-exploitation of hosts and to their local extinction, which causes the subsequent extinction of parasitoid populations. Many theoretical and empirical works have suggested that the existence of an underlying spatial structure can stabilise the host-parasitoid dynamics (Briggs and Hoopes 2004; Cronin and Reeve 2005; Kerr et al. 2006; Rauch and Bar-Yam 2006; Arashiro and Tome 2007). Other stabilising factors include processes of demographic control (e.g., host carrying capacity, parasitoid interference, invulnerable age classes, different types of functional response and non-random parasitoid attack) (Murdoch and Oaten 1975; Hassell 1978, 2000; Briggs and Hoopes 2004) and food web structure (Price 1991; Hawkins 1992). This chapter focuses on the effects of spatial structure for host-parasitoid dynamics and considers the effects of some demographic processes on species dispersal rates.

Numerous spatial models have been developed to consider spatial structure in the host-parasitoid interaction (Murray 1993; Briggs and Hoopes 2004; Hassell and May 1973; Diekmann et al. 1988; Jongejans et al. 2008). These models describe

how dispersal can change the stability and persistence of otherwise unstable host-parasitoid dynamics (Briggs and Hoopes 2004; Cronin and Reeve 2005) and how a spatial structure can lead to different spatial patterns of species distribution (Hassel et al. 1991; Briggs and Hoopes 2004; Stacey et al. 2012). However, the species response to spatial subdivision and habitat connectivity can vary according to the behaviour of the species considered. In this context, few theoretical studies have made biological contributions, such as species foraging and reproductive behaviour, on species movements across a landscape (Hassell et al. 1983; Comins and Wellings 1985; Lozano et al. 1997; Meunier and Bernstein 2002; Reigada et al. 2012).

In this study, we consider foraging behaviour, reproductive strategies and population dynamics. Specifically, we consider an adjustment in the sex ratio of offspring and mutual interference among foragers as effects of demographic control in parasitoid populations and build our model on a spatially structured framework. In Sect. 2.2, we describe our mathematical model by detailing the landscape structure, the interaction functions and the dispersal mechanisms. We started from the NB approach and then go on to show how many biological aspects can be included, such as parasitoid sex ratio control and mutual interference and density-dependent species dispersal for host-parasitoid dynamics. In Sects. 2.3 and 2.4, we review and explore the results of previous works (Reigada and de Aguiar 2012; Reigada et al. 2012) by describing the influences of habitat quality, reproductive and foraging behaviour on species demography and dispersal rates. More specifically, in Sect. 2.3, we explore the effects of landscape patches in terms of frequency and distribution of host resources on species persistence and spatial distribution. In Sect. 2.4, we analyse how sex ratio adjustment and mutual interference in parasitoid populations can result in different patterns of species distribution on the landscape. We end the chapter by discussing possible future directions in this area of research, particularly considering more complex spatial structures with different spatial arrangements of patches and their interconnections. We also comment on the inclusion of co-evolution in reproductive and foraging response dynamics, which would allow researchers to understand how species adapt to different environmental conditions.

2.2 Modelling Host-Parasitoid Dynamics with Spatial Structure

2.2.1 *The Nicholson Bailey Model*

One of the first mathematical models that described host-parasitoid systems was provided by Nicholson and Bailey (1935). To situate our own model within the literature, we present a brief review of this classic model in this subsection. The Nicholson Bailey (NB) model describes the evolution of populations of hosts and parasitoids at discrete generations in the form of a finite differences system of equations:

$$\begin{aligned} N_{t+1} &= F(N_t, P_t) \\ P_{t+1} &= G(N_t, P_t) \end{aligned} \quad (2.1)$$

The subscript is an integer that indicates the generation, and it is assumed that the populations at time $t + 1$ can be completely determined from the populations at time t . The functions F and G control the growth of the populations and how they interact with each other.

The most general aspect of the host-parasitoid interaction is that the adult female parasitoid lays its eggs on or in the bodies of other insects, their hosts. The parasitoid eggs hatch, and the larvae consume its host either immediately or after a delay during which the host continues to feed and grow in size. In either case, the parasitised hosts die. The three basic assumptions of the NB model are:

1. The hosts that are not parasitised give rise to the next generation of hosts;
2. The parasitised hosts die and give rise to the next generation of parasitoids;
3. The proportion of parasitised hosts depends on the encounter rate between individuals of the two populations and might also depend on the density of each population.

These assumptions allow us to write the following dynamical equations:

$$\begin{aligned} N_{t+1} &= \lambda N_t f(N_t, P_t) \\ P_{t+1} &= c P_t (1 - f(N_t, P_t)) \end{aligned} \quad (2.2)$$

where λ is the reproduction rate of hosts, c is the number of parasitoid eggs laid per host and $f = f(N_t, P_t)$ the fraction of hosts that are not attacked. Notably, in the absence of parasitoids, $f(N_t, P_t) = 1$, and the host population increases or decreases exponentially fast if $\lambda > 1$ or $\lambda < 1$, respectively.

To complete the dynamical equations, we still have to make assumptions about the form of the term $f(N_t, P_t)$. The NB model makes the following extra assumptions:

4. The encounters between hosts and parasitoids are random and independent. They are directly proportional to each of the population densities as:

$$N_e = \alpha N_t P_t, \quad (2.3)$$

where α is a parameter related to the efficiency of parasitoid searches. The mean number of effective encounters per host is then

$$\mu = \frac{N_e}{N_t} = \alpha P_t. \quad (2.4)$$

5. The only significant encounter is the first one, and it always results in a successful attack. Subsequent encounters do not affect the host's state.

The probability of n encounters is approximated by a Poisson distribution with characteristic parameter μ , and the probability of no encounters is given by $e^{-\mu}$, which is precisely the proportion of hosts that are not attacked. The model is then given by the following equations:

$$\begin{aligned} N_{t+1} &= \lambda N_t e^{-\alpha P_t} \\ P_{t+1} &= c P_t (1 - e^{-\alpha P_t}) \end{aligned} \quad (2.5)$$

The above equations are known as the NB model, which was developed in 1935 by the biologist AJ Nicholson and the physicist VA Bailey. This system presents a non-trivial equilibrium point (non-zero population densities), which is unstable for $\lambda > 1$ and any values of the parameters α and c . Because a model in which the only equilibrium point is unstable may not be appropriate to describe realistic data, many modifications have been proposed to the NB equations, which add more accurate biological aspects to the population growth and interaction terms. Some of these aspects, such as the carrying capacity for the host's growth, presence of refuges for hosts, demographic processes operating within the interaction patches and the addition of spatial structure, can stabilise the equilibrium point. For a more detailed description of these aspects, see (Briggs and Hoopes 2004; Edelstein-Keshet 2005).

2.2.2 *Extended Spatial Model*

We now turn to the construction of a more detailed model that will allow researchers to study different aspects of the host-parasitoid interaction, including the spatial distribution of populations. The species distribution patterns in a landscape depend strongly on the fraction of emigrants and on the dispersal rates of the species among patches. Therefore, we include two processes of demographic control in our model that are provided by the interference competition and control of the offspring sex ratio. Although a more complex mathematical treatment will be required, our approach will hopefully be more realistic. By describing a larger set of species behaviours and interaction details, the equations of this new model will be constructed following the reasoning of the NB model.

The three main aspects to be explored by the new model are:

1. **Space.** The equations of the NB model are finite difference equations that do not describe any underlying spatial structure. These types of models, also called spatially implicit models, are useful to describe well mixed populations or interactions that are localised in one or a few small patches. In cases where the geographical distance between individuals plays a major role in the way the species interact with each other, it is important to consider the range of action and dispersal of individuals, which might be related both to the physical limitations of the landscape and to intrinsic strategies of each species. These models are typically called spatially explicit models.

2. Sex allocation. In nature, most parasitoid species exhibit a type of haplodiploid reproduction called arrhenotoky, where females are born from fertilised eggs and males from unfertilised eggs, and thus, females control the sex ratio of their offspring (Charnov 1982). In our model, we considered that arrhenotokous parasitoid populations can adjust the progeny sex ratio according to the conditions of the exploited patch. The control of the sex ratio is intrinsically connected to the patch quality, which is related to the number of conspecific foragers and to the host abundance. This is an important concept and plays a crucial role in the dynamics of the interaction, as only female parasitoids attack hosts.
3. Interference competition. Another important aspect in host density fluctuations is the way parasitoids interact with each other. Female parasitoids may detect hosts that are already parasitised and keep searching for healthy hosts. In a population with a high parasitoid density, the ability of a female to detect parasitised hosts affects its probability of laying eggs and thus introduces interference competition.

With these three aspects in mind, we define the overall habitat as a set of connected patches, where host growth is limited by the carrying capacity. The dynamics are divided into two phases: first, hosts and parasitoids interact within every patch, and subsequently, a fraction of the emerging adult hosts and female parasitoid disperse to other patches.

2.2.2.1 The Interaction Phase

$H_{i,t}$, $F_{i,t}$ and $M_{i,t}$ represent populations of hosts, female and male parasitoids in patch i at time t . The following equations represent the in-patch interactions:

$$\begin{aligned}
 h_{i,t+1} &= H_{i,t} \left(\frac{\lambda k}{H_{i,t}(\lambda - 1) + k} \right) [1 - p(H_{i,t}, F_{i,t})] \\
 f_{i,t+1} &= c H_{i,t} p(H_{i,t}, F_{i,t}) s(H_{i,t}, F_{i,t}) \\
 m_{i,t+1} &= c H_{i,t} p(H_{i,t}, F_{i,t}) [1 - s(H_{i,t}, F_{i,t})]
 \end{aligned} \tag{2.6}$$

where the lower case letters for the populations in generation $t + 1$ represent the pre-dispersal populations.

For small populations, the hosts grow exponentially fast, but the growth slows down when it approaches the limit defined by the carrying capacity k . The carrying capacity represents the limited amount of resources (both food and space) available in each patch, and that prevents the populations from growing indefinitely. If resources were unlimited, $k \rightarrow \infty$ and would recover the term $\lambda H_{i,t}$, for host growth. The growth term is multiplied by $(1 - p(H, F))$, where $p(H, F)$ is the fraction of hosts that are attacked by female parasitoids and might depend on the densities of both hosts and female parasitoids.

The population of parasitoids in the next generation depend on the product $H_{i,t}$ $p(H_{i,t}, F_{i,t})$ and is multiplied by c , the mean number of adult parasitoids emerging from each host (the parasitoids are assumed to be gregarious).

Finally, the function $s(H, F)$ defines the proportion of female parasitoids in the progeny and is adjusted according to the patch quality. The proportion of male parasitoids is then represented by $(1-s(H, F))$.

Starting with these general equations, we must make assumptions on the forms of the functions $p(H, F)$ and $s(H, F)$. For the fraction of parasitised hosts $p(H, F)$, we define:

$$p(H_{i,t}, F_{i,t}) = \begin{cases} 1, & \text{if } v(H_{i,t}, F_{i,t}) > 1 \\ v(H_{i,t}, F_{i,t}) & \text{if } v(H_{i,t}, F_{i,t}) \leq 1 \end{cases}, \quad (2.7)$$

where

$$v(H_{i,t}, F_{i,t}) = \frac{32\alpha F_{i,t}}{H_{i,t} + \beta F_{i,t}^2} \quad (2.8)$$

and α is the parasitoid attack rate.

We assume that no host can be parasitised by more than one parasitoid (super-parasitism), as female parasitoids can differentiate between healthy and parasitised pupae. The parameter β controls the efficiency with which they search and recognise healthy pupae. The interference among conspecific parasitoids is classified as low ($\beta = 0.01$), medium ($\beta = 0.03$) or high ($\beta = 0.05$). A low degree of interference characterises parasitoid populations that can detect healthy hosts in a parasitoid-crowded patch efficiently, consequently causing higher host mortality than parasitoid populations with medium and high levels of response to conspecifics. The consequences of different levels of interference competition for the host population are presented in Fig. 2.1. The smaller the β value, the lower the degree of interference among conspecifics. The number 32 represents the maximum number of hosts that can be parasitised by one parasitoid in the absence of parasitoid competition.

The proportion of female parasitoids in the progeny, $s(H, F)$, is defined as

$$s(H_{i,t}, F_{i,t}) = \exp\left(-\frac{\gamma F_{i,t}}{H_{i,t}}\right), \quad (2.9)$$

where γ controls how the ratio of females to hosts affects the sex ratio adjustment. If F/H is high, a female tends to increase the proportion of males in its progeny to increase the probability that her male offspring mate with the other females in the next generation. Thus, the parameter γ is related to the sensitivity of the sex ratio control to the F/H ratio, which is related to the patch quality. In our model, parasitoid populations can exhibit three different responses to fluctuations in patch

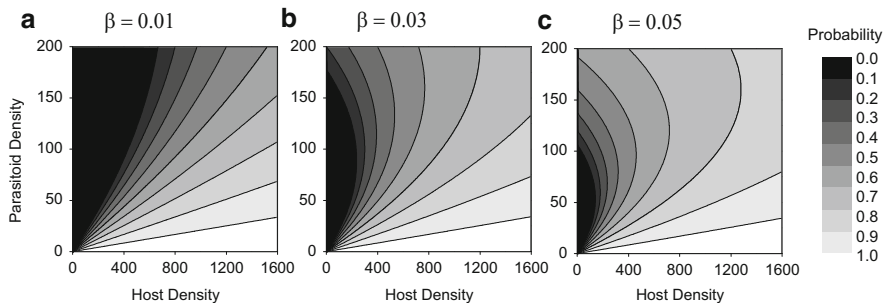


Fig. 2.1 Probability of survival for host populations interacting with a parasitoid population under different levels of interference competition in a patch. The contour plots are drawn for (a) low effect ($\beta = 0.01$), (b) medium effect ($\beta = 0.03$) and (c) high effect ($\beta = 0.05$) of interference competition (Reprinted from Ecological Modelling: Reigada et al. (2012), Copyright (2012), with permission from Elsevier [3136490533560])

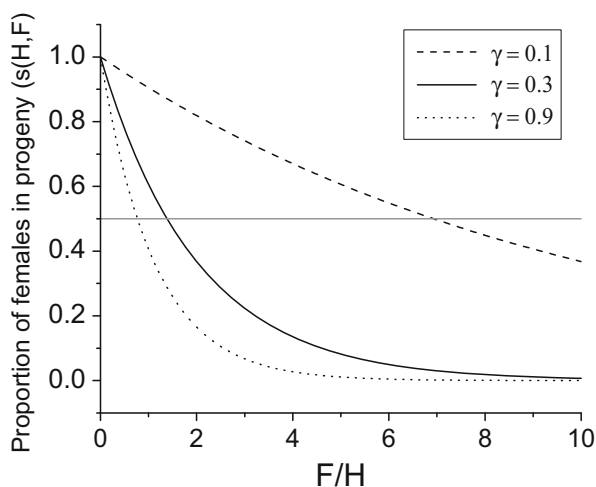


Fig. 2.2 Proportion of female offspring (decrease in the sex ratio) in parasitoid populations with different levels of sex ratio adjustment as a function of change in the quality of local conditions (F/H). An increase in the F/H represents a decrease in the patch quality. A sex ratio adjustment in the parasitoid population can be translated as the F/H proportion necessary to provoke changes in the ratio of a female parasitoid's progeny. The dashed line represents low ($\gamma = 0.1$), the solid line medium ($\gamma = 0.5$) and the dotted line high ($\gamma = 0.9$) degrees of sex ratio adjustment. More than 50 % of the offspring will be female for the following patch qualities: $F/H < 6.93$ for $\gamma = 0.1$, $F/H < 1.39$ for $\gamma = 0.5$ and $F/H < 0.77$ for $\gamma = 0.9$ (Reprinted from Ecological Modelling: Reigada et al. (2012), Copyright (2012), with permission from Elsevier [3136490533560])

quality: low ($\gamma = 0.1$), medium ($\gamma = 0.5$) and high ($\gamma = 0.9$) variations in the sex ratio. Parasitoid populations with larger values of γ respond more effectively to variations in the exploited patch. Patches with low γ values are expected to have a high female density (Fig. 2.2).

2.2.2.2 Dispersal Phase

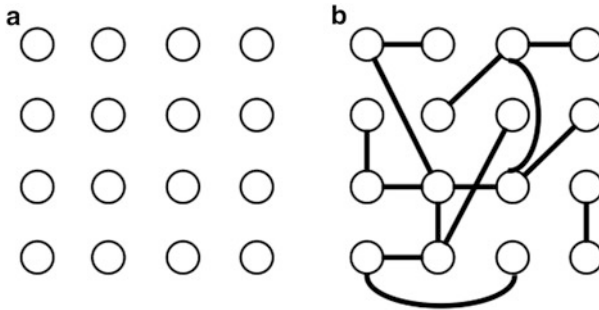
After reproduction and parasitism occur in each patch, the populations may disperse to other patches representing habitats for local subpopulations. The set of patches that constitute the overall environment are placed on a two-dimensional square grid of $L \times L$ sites with reflective boundary conditions. However, not every site on the regular grid is necessarily a patch, as some sites may have no resources and, therefore, may not be useful for colonisation. Additionally, not every patch is connected to each other. Labeling the actual patches from 1 to N , we introduce the adjacency matrix A with elements $A_{ij} = 1$ if patches i and j are connected (and direct migration from one to the other is possible) and $A_{ij} = 0$ if not (Fig. 2.3). The introduction of the adjacency matrix allows us to generalise the form in which the patches are connected and consider landscapes of different topographies.

Adult hosts and female parasitoids can either disperse to other patches or remain on their home patch, depending on the local conditions. The number of hosts that leave the original patch, $h_{i,t+1}^{out}$, is represented by the following equation:

$$h_{i,t+1}^{out} = \frac{\mu_H h_{i,t+1}^2}{h_{i,t+1} + h^0}. \quad (2.10)$$

where, μ_H is the maximum dispersal rate of hosts in highly populated patches, and h^0 is the tolerance to conspecifics. In this manner, the number of hosts that leave the patch depends on the local host density; if the density is low, then a large fraction of hosts stay in the patch. The dispersing hosts $h_{i,t+1}^{out}$ are divided among the neighbouring connected patches j , ($j \neq i$). The number of hosts arriving on patch j coming from patch i is represented by the following equation:

$$\Psi_{j,t+1}^i = \frac{0.05}{r_{i,j}} h_{i,t+1}^{out}, \quad (2.11)$$



where $r_{i,j}$ is the distance between the current patch and the destination patch measured in units of the lattice parameter so that $r = 1$ for patches located on adjacent sites.

After dispersal, the new generation of hosts is updated to

$$H_{i,t+1} = h_{i,t+1} + \sum_{j=1}^{L^2} A_{i,j} \left(\Psi_{i,t+1}^j - \Psi_{j,t+1}^i \right), \quad (2.12)$$

where A is the adjacency matrix as defined above. This accounts for the local population minus the amount that dispersed to neighbouring patches and plus the hosts that arrived from the same patches.

Because the parasitoids experience a longer period of maturation to reach the adult stage, their dispersal occurs after the dispersal of the hosts. The number of dispersing female parasitoids (male parasitoids do not disperse) depends on the number of parasitoids as well as on the number of hosts in the originating patch and is represented by

$$f_{i,t+1}^{out} = \begin{cases} \mu_F \frac{H^0}{H^0 + H_{i,t+1}} \frac{f_{i,t+1}^2}{f_{i,t+1} + f^0}, & \text{if } H_{i,t+1} > 0 \\ f_{i,t+1}, & \text{if } H_{i,t+1} = 0 \end{cases}, \quad (2.13)$$

where μ_F is the maximum parasitoid dispersal if the host density is small and the female density is high (low quality patch). The constant factors H^0 and f^0 represent the number of hosts needed to keep the female parasitoids from dispersing and the tolerance to other female parasitoids, respectively. The number of dispersing females that arrive at patch j coming from patch i is represented by the following equation:

$$\phi_{j,t+1}^i = \begin{cases} \frac{0.25}{r_{i,j}} f_{i,t+1}^{out}, & \text{if } H_{i,t+1} > 0 \\ 0, & \text{if } H_{i,t+1} = 0 \end{cases} \quad (2.14)$$

Comparing this expression with the corresponding equation for the hosts, we note that hosts may disperse to more distant patches than the parasitoids, as has been documented in field observations (Tscharntke et al. 2005). The final population of female parasitoids in each patch at generation $t + 1$ is provided by the following equation:

$$F_{i,t+1} = f_{i,t+1} + \sum_{j=1}^{L^2} A_{i,j} \left(\phi_{i,t+1}^j - \phi_{j,t+1}^i \right). \quad (2.15)$$

2.3 Resources Quality, Frequency and Duration

2.3.1 General Overview

In nature, it is common to find a high aggregation of consumer individuals in landscape areas where resource quality is high. However, the quality and duration of a resource in the landscape can change over time and affect the distribution and abundance of species. In this section, we study this situation by considering changes in location and lifetime of resource patches and explore the consequences of ephemeral resource patches for the persistence of host-parasitoid metapopulations and the spatial distribution of individuals in the landscape.

The main purpose of this section is to compare host-parasitoids dynamics in landscapes where host resources can be either constant or ephemeral. We investigated how the frequency with which ephemeral resources occur in the landscape affects the populations by progressively reducing its likelihood. In communities structured in metapopulations consisting of ephemeral local patches, the extinction of local populations depends on the resource lifetime, their distribution and their frequency in the landscape, as the persistence of species is related to the production of emigrants in a patch and on their inter-patch dispersal. In these landscapes, the recolonisation of a patch is conditioned to the appearance of new resources at the same site in the next time step, which makes it a new ephemeral patch. We also quantified the effects of variation in the quality of the resource patch, which was measured in terms of host carrying capacity (k).

The spatial structure was modelled using a regular square network with 2,500 (50×50) sites (or nodes) that are connected to neighbour sites by potential migration. The dispersion patterns follow the Eqs. 2.10, 2.11, 2.12, 2.13, 2.14 and 2.15 provided in Sect. 2.2, and migration is possible to all neighbours within a radius R_H for hosts and R_F for parasitoids. In this manner, considering sites i and j , we determined the elements of the Adjacency matrix, $A_{ij} = 1$, if $r_{ij} \leq R_H$, for hosts, or $r_{ij} \leq R_F$, for parasitoids. In this study, $R_H = 3.61$ and $R_F = 3$. After accounting for the fraction of migrant hosts and parasitoids in each site (Eqs. 2.10 and 2.13), dispersing populations were allocated in neighbour sites until all of the migrant fraction was distributed, with the closest neighbours receiving first (if two or more neighbour sites are the same distance away from the considered site, they are chosen in a random order) or until the maximum distance is achieved.

To clearly distinguish between locations with and without resources, we use the term patch for the former and site for the latter. Therefore, a patch is a site with resources. We started the simulations with 300 hosts and 4 parasitoids at a single patch located in the centre of the landscape. Resources were randomly distributed with a probability pr for each site at the beginning of each generation and removed at the end of the generation following a new allocation of resources. The distribution of resources at each generation is independent of the previous distributions. Notably, although the presence of resources at a site makes it available to receive hosts, the

actual occupation is only possible through migration of individuals from neighbour patches. For simulating landscapes with a continuous presence of resources, $pr = 1$.

For the dynamical model, we assumed high interference competition ($\beta = 0.06$) and an intermediary sex ratio adjustment ($\gamma = 0.5$). The details of the host-parasitoid dynamical model and the complete set of parameters used are described in Sect. 2.2. To study the effects of resource quality, we used two values for the carrying capacity: (i) a fixed size for the ephemeral basal resources ($k = 1,600$ host individuals per patch) and (ii) variable sizes for ephemeral basal resources (the carrying capacity assigned to a patch was uniformly selected in the interval $1,600 \leq k_{rand} \leq 8,000$ host individuals). For each simulation, we ran the host-parasitoid dynamic for 10,000 time-steps.

2.3.2 Simulation Results

We explored the effects of fixed and random carrying capacities ($k = 1,600$ and $1,600 \leq k_{rand} \leq 8,000$ host individuals). In both cases, the allocation probability (pr) had important implications for species persistence and distribution in the landscape. For $pr < 0.4$, hosts and parasitoids were extinct in both scenarios. For $pr = 0.5$, host populations persisted, and parasitoid populations became extinct. Coexistence was observed only for $pr \geq 0.6$ (Fig. 2.4), where large values of pr increased host-parasitoid abundance and changed the dynamics and the spatial pattern distribution.

Although the frequency of resource allocation (pr) affected the persistence of hosts and parasitoids equally in both fixed and variable resource quality conditions, the resulted fluctuation dynamics were different. In landscapes comprised by low quality patches ($k = 1,600$), host and parasitoid population sizes fluctuated with low abundances (Fig. 2.4a). Conversely, the size and fluctuation of species populations in a landscape composed by patches of different quality ($1,600 \leq k_{rand} \leq 8,000$) was systematically higher (Fig. 2.4b), indicative of the importance of the resource dynamics for species occupancy and global abundance distribution.

For fixed low resource sizes, the parasitoids could not occupy all patches in the landscape, and patches with hosts but no parasitoids were observed at all values of pr (Fig. 2.4a). In these cases, the dynamics converged to a regime of large population fluctuations, where host and parasitoid abundances were largely variable in space and time as shown in Fig. 2.5a for times 9,990, 9,995 and 10,000. For $t = 9,990$, patches with a high density of hosts were clearly observed, whereas for $t = 9,995$, the parasitoid population in these patches increased significantly due to overexploitation. For $t = 10,000$, the parasitoid population decreased again due to a lack of hosts because of the intense parasitism at previous times.

For variable resource sizes, host populations occupied all available patches in the landscape, but the parasitoids did not occupy all patches with hosts when the frequency of resource occurrence was low ($pr = 0.6$), and the population fluctuations resulted in oscillatory host and parasitoid abundances (Fig. 2.5b). For $pr \geq 0.6$, all patches were occupied by hosts and parasitoids, with the parasitoid metapopulation

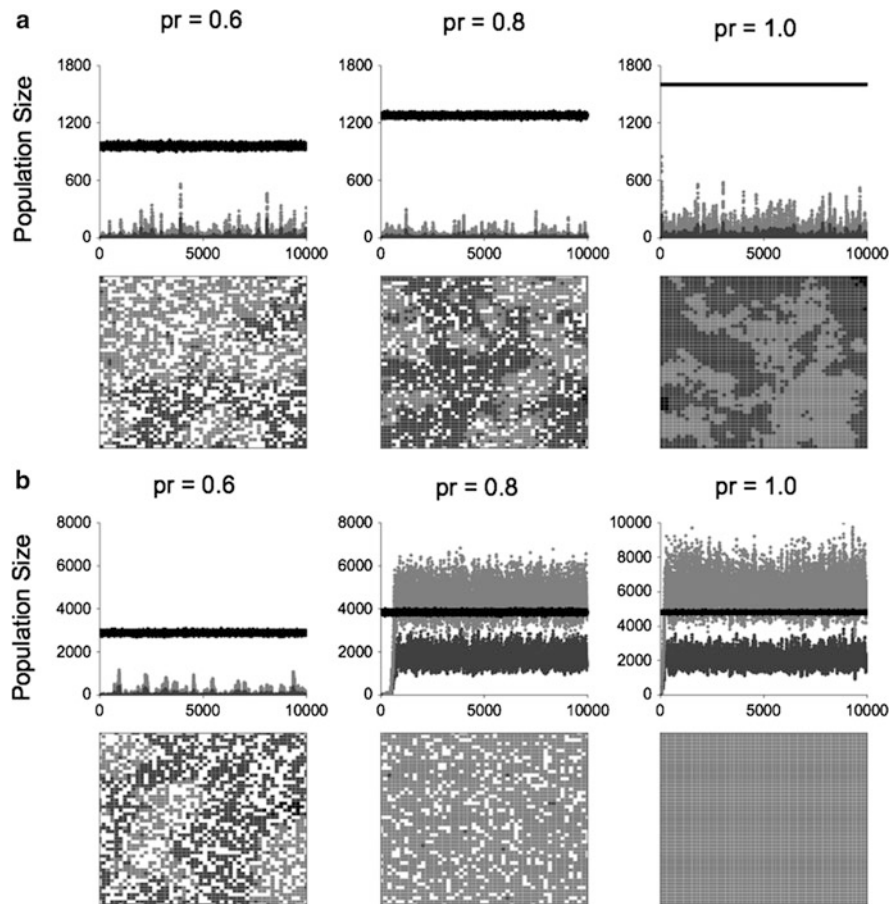


Fig. 2.4 Spatial occurrence and persistence of hosts and parasitoids after 10,000 time-steps as a function of time. The landscape has 50×50 sites with reflective boundary conditions. The results are displayed for different probabilities of ephemeral resource occurrence (pr). **(a)** A fixed size of the ephemeral resource ($k = 1,600$ host individuals) and **(b)** variable ephemeral resource size ($1,600 \leq k_{rand} \leq 8,000$ host individuals). Black, dark gray and light gray symbols represent, respectively, the basal ephemeral resource, host and parasitoid abundances. Parameter values: $\lambda = 1.5$; $\alpha = 0.34$; $\beta = 0.06$; $c = 20$; $\gamma = 0.5$; $\mu_H = 0.85$; $\mu_F = 0.4$ (Reprinted with minor adaptations from Oikos: Reigada and de Aguiar (2012), Copyright (2012), with permission from John Wiley and Sons [3117141225588])

divided into two subgroups, where abundances oscillated synchronously (Fig. 2.5b). We also simulated landscapes with a stable level of high-quality resource patches ($k = 8,000$). The same qualitative patterns displayed in Fig. 2.4b were observed, suggesting that the existence of high-quality patches increases the number of dispersal individuals so that host populations exist in all areas of the landscape where resources are available.

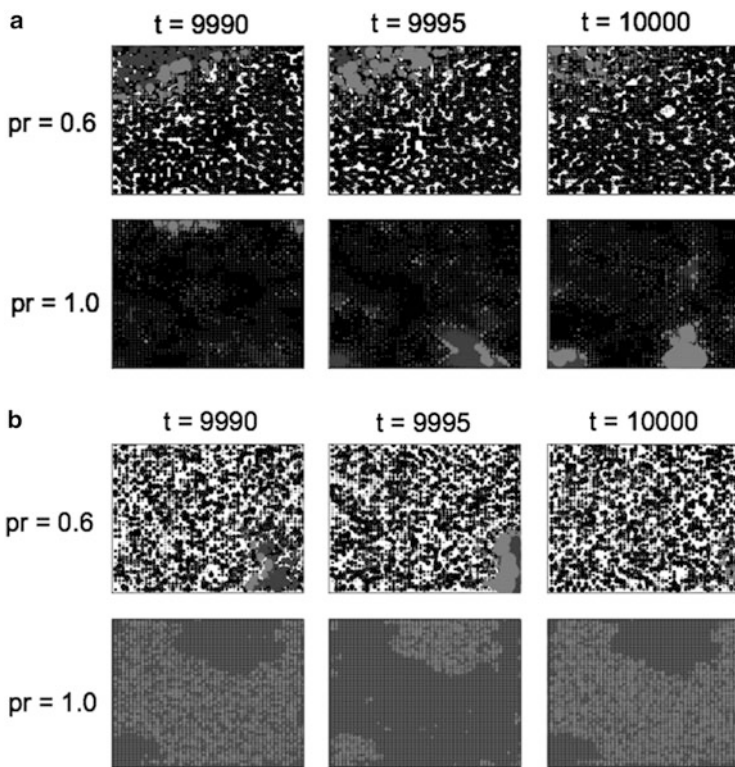


Fig. 2.5 Snapshots of the basal resource, host and parasitoid spatial occupancy for $t = 9,990$, $t = 9,995$ and $t = 10,000$ time-steps. *Black, dark gray and light gray* symbols represent, respectively, the basal ephemeral resource, host and parasitoid abundances within each patch. The sizes of the *dots* are proportional to the population at each site. The results are displayed for two values of the basal resource occurrence ($pr = 0.6$ and $pr = 1.0$). (a) $k = 1,600$ and (b) $1,600 \leq k_{rand} \leq 8,000$. Parameter values $\lambda = 1.5$; $\alpha = 0.34$; $\beta = 0.06$; $c = 20$; $\gamma = 0.5$; $\mu_H = 0.85$; $\mu_F = 0.4$. The number of sites and boundary conditions are the same as in Fig. 2.4 (Reprinted from *Oikos*: Reigada and de Aguiar (2012), Copyright (2012), with permission from John Wiley and Sons [3117141225588])

2.3.3 Discussion

The spatial structure has been postulated as the principal mechanism for increasing the persistence time of host-single parasitoid interactions, as the likelihood that an individual host is parasitised depends on its spatial location and on the overall host distribution (Bailey et al. 1962; Hassell and May 1974; Hassell et al. 1991). However, the persistence of a metapopulation occurs only if the species display limited dispersal and if the subpopulation dynamics is asynchronous (Levins 1969, 1970; Gilpin and Hanski 1991; Hanski and Gilpin 1997). Our results demonstrated that variations in resource frequency and quality affected the number of dispersing

individuals and species colonisation rates with important consequences for species occupancy and distribution over the landscape. Different resource qualities lead to different fluctuation patterns of host and parasitoid populations.

Previous studies have argued that density fluctuations increase the extinction risk of local populations, especially when the populations are small and the patches ephemeral (Lande 1993; Legendre et al. 1999). Several studies have also reported that high carrying capacities can cause instability that may lead to the extinction of the metapopulation (Lande 1993; Saether et al. 1998). Even narrow density fluctuations can disrupt the regulation within local patches and lead to the extinction of the metapopulation (Bonsall et al. 2002).

In our simulations, host-parasitoid interactions occurring in poor-quality environments ($k = 1,600$) produced a low host density that led to an increase in the number of males in the parasitoid progeny and consequently a decrease in the parasitoid dispersers (females). This relatively low number of female parasitoids, combined with the higher dispersal rate of hosts compared to parasitoids, led to the development of large changes in species distribution over time. Landscapes with high-quality resources had smaller fluctuations in the populations and higher number of dispersed parasitoids, which spread to all available patches in the landscape. In simulations with higher carrying capacities, we observed a small probability of local extinctions, and parasitoids were present in all patches with hosts.

Although several studies have considered the influence of the carrying capacity on the persistence of populations, much less effort has been made towards understanding communities that depend on ephemeral basal resources. Our results have demonstrated how species abundance and distribution can change depending on the characteristics of the basal resource for a host-parasitoid trophic interaction. Bottom-up effects are important to the parasitoid community (Price 1991; Hawkins 1992), and the lower trophic level (host resources) can constrain the number and strength of trophic links in host-parasitoid webs (Price 1991). We observed that resource sizes and their spatial distributions are important for determining the number of host and parasitoid migrants. The variability in ephemeral resource sizes (fixed or random) affected the species' spatial distribution pattern, and coexistence was possible only for high probabilities of ephemeral resources in the landscape.

Host-parasitoid persistence was negatively affected by the presence of ephemeral patches because of the isolation of ephemeral subpopulations (due to a low occurrence of resources in these sites) and due to the low total resources. The results demonstrated that host-parasitoid persistence requires a minimum number of patches in the landscape, which in turn depends upon the probability of resource allocation. A low occurrence of resources caused the isolation of patches in the landscape. Conversely, landscapes with a high density of patches yielded a formation of clusters of host-parasitoid populations. The clusters were linked by dispersion and helped to ensure the persistence of both species.

We demonstrated that increasing the carrying capacity leads to a higher number of migrants that spread and colonise new patches in the spatial structure. When

the resources were low, coexistence was not observed. These results highlight the importance of demographic fluctuations, environmental factors and patch connectivity for the density of migrants and host-parasitoid persistence in landscapes with ephemeral resources.

In this section, we demonstrated that landscapes composed by ephemeral patches can lead to the persistence of host and parasitoid species depending on the number of sites with resources. Our results have the potential to provide broad management guidelines for host-parasitoid and other insect interactions with stochastic environmental characteristics (e.g., ephemeral resources, fragmented habitats, crop rotations in agricultural ecosystems or schedules of harvest in managed cultures) and demographic processes (e.g., arising from behaviour, genetic and physiological factors). The results presented here are also relevant to the control of patchily distributed pests, which can be maintained by the occurrence of ephemeral resources in the landscape.

2.4 Foraging and Reproductive Strategies

2.4.1 *General Overview*

Production of dispersers is essential for colonising empty patches and for promoting the global persistence of a metapopulation (Levins 1970; Hanski 1999). The dispersal of parasitoids from their current patch to a new patch occupied by hosts is the fundamental process that determines coexistence in these systems. Dispersion also affects their spatial distribution and metapopulation structure, as parasitoid aggregation is lower in patches with a low host density, which allows hosts in these patches to escape extinction and contributes to the coexistence of hosts and parasitoids (Hassell 2000). We demonstrated in the previous section that within-patch dynamics are essential to promote emigration and directly impact species movement. In this section, we explore how the effects of sex ratio adjustment and interference competition contribute to controlling the demography, species movement and the coexistence probability of host-parasitoid systems.

Parasitoid reproductive success is directly related to host abundance and the way hosts are exploited (Godfray 1994; Outreman et al. 2005). However, successful parasitism depends not only on host density but also on parasitoid density, given that higher numbers of parasitised hosts in an exploited patch can decrease the reproductive success of a female parasitoid. Depending on the density of conspecifics and on the host density in the patch, a female parasitoid can adopt different patch exploitation strategies thereby “optimising” its results. These conditions determine the “quality” of the exploited patch and can be measured by the ratio of non-parasitised host per parasitoid, H/F (Fauvergue et al. 2006; Reigada et al. 2012; Reigada and de Aguiar 2012).

The profitability of host patches changes over space due to competition by hosts and over time due to host depletion (Fauvergue et al. 2006). A decrease

in patch quality reduces the reproductive success of female parasitoids and can stimulate them to leave the patch and search for a better one, which increases the species dispersal rate among patches in the landscape. To maximise its chances for reproduction, a foraging female parasitoid needs to decide whether to leave its natal patch in search of better conditions or to stay. The choice is determined by the patch quality required by the species (Fretwell and Lucas 1970; Charnov 1976) and by their dispersal capability. Once a patch is selected, the female parasitoid must optimise her reproductive potential to ensure that her genes are passed on.

In nature, arrhenotokous parasitoid species usually mate in isolated groups before dispersing to new host patches and frequently show female-biased sex ratios. Hamilton (1967) observed this characteristic and proposed the theory of Local Mate Competition (LMC). This theory has been the basis for numerous studies about adaptive sex ratio adjustment in parasitoid species (Hassell et al. 1983; Godfray 1994; Godfray and Werren 1996; Santolamazza-Carbone and Rivera 2003; Shuker et al. 2006; Reigada et al. 2012) and assumes that females can control the sex ratio of their offspring in an haplodiploid population. Therefore, females can reduce the mating competition between their male offspring in response to foundress numbers (female that lay eggs) and the number of parasitised hosts in the patch (Hamilton 1967; Shuker et al. 2006; Grillenberger et al. 2009).

The adjustment of the progeny sex ratio can be understood as a strategy of female parasitoids to control sib-mating in patches of parasitised hosts. In addition to inbreeding control, arrhenotoky also influences the population growth within patches. In fact, the variation of the parasitoid sex ratio as a function of host and parasitoid densities observably affects the host-parasitoid dynamics, given that only mated females are able to produce female offspring capable of parasitising hosts. This method of population control prevents the overexploitation of hosts and consequently increases the stability of the host-parasitoid interaction (Hassell et al. 1983; Comins and Wellings 1985; Meunier and Bernstein 2002; Reigada et al. 2012; Reigada and de Aguiar 2012).

In this section, we explore how variations in patch quality influence the host-parasitoid coexistence, their dispersal and spatial distribution over the landscape. In addition, we will analyse the effects of different levels of parasitoid responsiveness to patch quality on species persistence and distribution on the landscape.

Throughout this section, the landscape is represented by a regular grid with 1,600 connected patches (40×40), where host resources are permanent, but host populations are limited by a carrying capacity. Only hosts and female parasitoids are allowed to disperse to other patches, and because male parasitoids are unable to disperse, we assume that mating occurs in their native patch. We also define the parasitoid foraging behaviour by their competitive abilities and by their ability to change the sex ratio of the progeny according to variations in patch quality. Competitive ability is a measure of the parasitoid efficiency in recognising parasitised hosts and laying their eggs on healthy hosts (interference competition). We consider parasitoid populations with three different levels of competitive ability, classified as low, medium and high, according to three different values of the parameter β (Fig. 2.1). The three degrees of sex ratio adjustment, which are also classified as low, medium or high, refer to the values of parameter γ (Fig. 2.2).

2.4.2 Simulation Results

2.4.2.1 Effects of Interference Competition and Sex Ratio Adjustments

In this sections, all simulations were initialised with 300 hosts and 4 female parasitoids at a single patch located at the centre of the landscape, where all other patches were empty. The host and parasitoid populations evolved according to the model described in Sect. 2.2, where the response of parasitoids to patch quality is based on three different foraging behaviours: (i) the decision to remain in or leave the current patch; (ii) the control of the progeny's sex ratio and (iii) the competitive abilities of the female parasitoids. Sex ratio control occurs in response to spatio-temporal fluctuations of host density, and competitive abilities are associated with delays in successive ovipositions, which decrease the potential to attack hosts due to interference from conspecifics in the exploited patch.

For simulations where female parasitoids explored patches extremely efficiently, displaying low interference competition with conspecifics ($\beta = 0.01$), we observed a low coexistence probability (Fig. 2.6, circles). Similar results were obtained for females that were less responsive to variations in patch quality (H/F) and produced a high number of female offspring in poor-quality patches ($\gamma = 0.1$). Both cases evolved towards the overexploitation of hosts, which resulted in the extinction

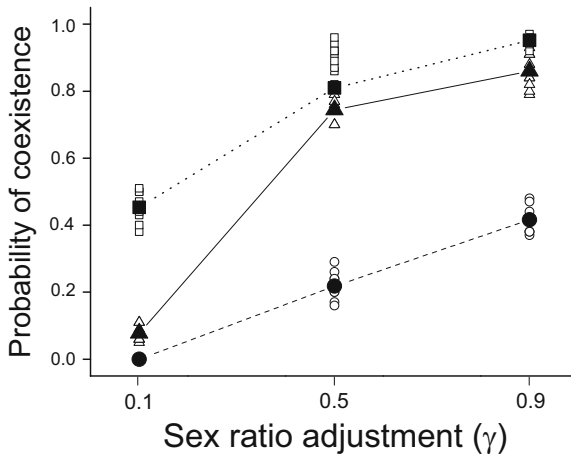


Fig. 2.6 Coexistence probabilities of host-parasitoid metapopulations as a function of the parasitoid sex ratio index (γ) for different values of the competitive interference parameter (β) after 5,000 time-steps ($\lambda = 1.5$; $\alpha = 0.15$). Open symbols represent the coexistence probability obtained from simulations with several combinations of host (μ_H) and parasitoid (μ_P) dispersal rates, with $0.1 \leq \mu_H \leq 1.0$ and $0.1 \leq \mu_P \leq 1.0$. Full symbols represent the average over five replicates of these simulations. The circles and dashed lines, triangles and solid lines, and squares and dotted lines represent the results for low ($\beta = 0.01$), medium ($\beta = 0.03$) and high ($\beta = 0.05$) parasitoid interference competition, respectively (Reprinted from Ecological Modelling: Reigada et al. (2012), Copyright (2012), with permission from Elsevier [3136490533560])

of the parasitoid population. Conversely, for parasitoid populations displaying some degree of demographic control, the probability of host-parasitoid coexistence was significantly higher (Fig. 2.6). In the rest of the section, we detail cases of medium and high levels of conspecific interference, as these are the most interesting situations where coexistence is possible.

Our results demonstrate that parasitoid populations where females are more responsive to patch quality have a higher probability of persistence. In these cases, this observation occurs because the number of female offspring is restricted when hosts are abundant in the patch. The fluctuations in population density also decreased when the sex ratio adjustment was high (Fig. 2.7).

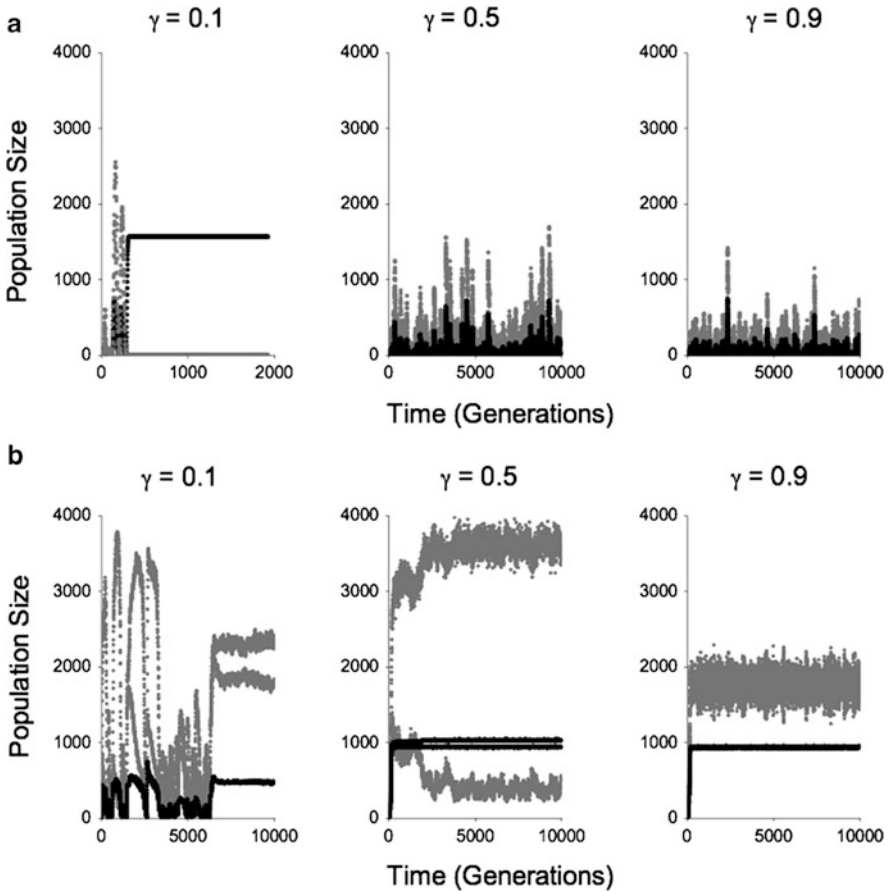


Fig. 2.7 Representative numerical simulations display the mean populations of hosts (*black*) and parasitoids (*gray*) over a grid of 20×20 patches as a function of time. In panel (a), $\beta = 0.03$ and in panel (b), $\beta = 0.05$. For both values, the degree of sex ratio adjustment varies from $\gamma = 0.1$ to $\gamma = 0.9$. The simulations were performed with $\lambda = 1.5$, $\alpha = 0.15$ and $\mu_H = \mu_F = 0.5$ (Reprinted from Ecological Modelling: Reigada et al. (2012), Copyright (2012), with permission from Elsevier [3136490533560])

Considering the effects of the female parasitoid foraging efficiency, we observed that parasitoids with a high degree of interference competition ($\beta = 0.05$, Fig. 2.7b) exhibited reduced oviposition rates in patches with a high density of parasitoids. This drastically decreased the oscillations in the parasitoid population. For medium levels of sex ratio adjustment ($\gamma = 0.5$), the host and parasitoid populations oscillated around two values in the abundance distribution. Conversely, parasitoid populations with intermediate interference competition ($\beta = 0.03$) always exhibited less stable oscillations, which reached extremely low population values (Fig. 2.7a). The combined results from the sex ratio adjustment and degree of interference competition suggest that stability in host-parasitoid populations occurs only when the population growth strongly correlates with patch conditions.

The different strategies of parasitoid foraging and reproductive behaviour have consequences for the spatial distribution of the populations in the landscape. Figure 2.8 presents snapshots of the patch occupancy of hosts and parasitoids for three instants of time separated by five steps of high degree of sex ratio adjustment ($\gamma = 0.9$) and two degrees of competitive interference, $\beta = 0.03$ and $\beta = 0.05$. For intermediate competitive interference ($\beta = 0.03$), the abundance distribution displays fluctuations for host and parasitoid species. This dynamical behaviour causes large peaks of high abundances in a patch that decreases to zero in a few generations and leaves the patch empty or nearly empty (Fig. 2.8a). This behaviour was observed for intermediary and high sex ratio adjustment values. For low values, ($\gamma = 0.1$), the parasitoids went extinct.

For a large degree of interference competition ($\beta = 0.05$) and intermediary and high sex ratio adjustment values, the behaviour changed drastically. The

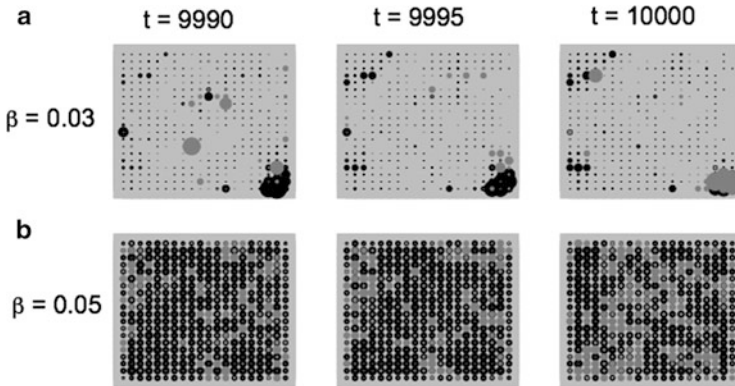


Fig. 2.8 Snapshots of host and parasitoid spatial occupancy for $t = 9,990, 9,995$ and $10,000$. Black and dark gray symbols represent host and parasitoid abundance within each patch ($\lambda = 1.5$, $\alpha = 0.15$), respectively. The size of the dots is proportional to the population at the site. We compared the effects of different levels of competitive interference for $\gamma = 0.9$, $\mu_H = 0.2$ and $\mu_F = 0.8$. $\beta = 0.03$ in panel (a) and $\beta = 0.05$ in (b). (Reprinted with minor adaptations from Ecological Modelling: Reigada et al. (2012), Copyright (2012), with permission from Elsevier [3136490533560])

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