

1                   Coevolution of dispersal in a  
2                   parasitoid-host system

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8

**Abstract**

9 Interspecific interactions and the evolution of dispersal are both of interest when  
10 considering the potential impact of habitat fragmentation on community ecology,  
11 but the interaction between these processes is not well studied. We address this by  
12 considering the coevolution of dispersal strategies in a host-parasitoid system. An  
13 individual-based host-parasitoid metapopulation model was constructed for a  
14 patchy environment, allowing for evolution in dispersal rates of both species. Highly  
15 rarefied environments with few suitable patches selected against dispersal in both  
16 species, as did relatively static environments. Provided that parasitoids persist, all  
17 parameter values studied led to stable equilibria in dispersal rates for both species.  
18 There was a tendency towards higher dispersal rates in parasitoids due to the  
19 asymmetric relationships of the two species to the patches: vacant patches are most  
20 valuable for hosts, but unsuitable for parasitoids, which require an established host  
21 population to reproduce. High host dispersal rate was favoured by high host  
22 population growth rate, and in the parasitoid by high growth rates in both species.

23 *Keywords: Competition • Difference equation • Dispersion • Nicholson-Bailey*  
24 *model*

## 25 **Introduction**

26 In patchy landscapes, dispersal is potentially as important as reproductive life-history  
27 traits in determining overall fitness (Clobert et al. 2001), and the optimal dispersal  
28 strategy for a species will depend upon the nature of this environment (Bowler and  
29 Benton 2005). The hierarchical nature of population dynamics in such metapopulations  
30 is well studied (Hanski 1999), as is the evolutionary ecology of the dispersal process  
31 itself (Gandon and Rousset 1999; Heino and Hanski 2001; Murrell et al. 2002).

32 Metapopulations provide a stabilising effect on populations where local population  
33 fluctuations are to a degree independent. Thus, local extinction does not necessarily  
34 imply extinction of the whole population. Too low a dispersal rate, and colonisation  
35 cannot keep pace with the rate of local extinction on small patches. However, at very  
36 high dispersal rates, population dynamics across the whole landscape become  
37 synchronised, and the stabilising effect of the metapopulations is lost (Reeve 1990).

38 Species do not exist in isolation. Various studies have considered dispersal in  
39 interacting species, both in the field (Rauch and Weisser 2007; see Elzinga et al. 2007  
40 for a summary) and theoretically (Reeve 1990; Rohani and Ruxton 1999; Briggs and  
41 Hoopes 2004; Lett et al. 2005). However, the evolutionary ecology of dispersal in  
42 interacting species is not well studied. What are the evolutionary dynamics of  
43 dispersal strategies in interacting species, and how does the strategy adapted by one  
44 species depend upon its competitor, prey, or predator species? Here, we address this  
45 with a theoretical study, using an individual-based model of the evolution and  
46 coevolution of dispersal traits in a host-parasitoid system.

47 Both dispersal and coevolutionary interactions of hosts and parasitoids have  
48 long been the focus of studies of evolutionary biology, both theoretically (Hochberg  
49 1997; Fellowes and Travis 2000; Godfray and Sasaki 2000; Sasaki 2000; Bonsall et al.  
50 2002) and experimentally (Fellowes and Godfray 2000; Green et al. 2000; Weisser  
51 2000; Bonsall et al. 2002). Their interactions are closer than that found in many other  
52 forms of symbiosis, especially the potentially tight coevolutionary interactions of highly  
53 host-specific koinobiont parasitoids (Janzen 1980; Askew and Shaw 1986), which allow  
54 the host – which they develop on or within – to continue development after parasitism.

55 We here consider a model appropriate for a system such as the fruit fly *Drosophila*  
 56 *melanogaster* and its Hymenopteran parasitoids, including *Asobara tabida*,  
 57 *Pachycrepoideus vindemiae* or *Leptopilina boulardi*: short-lived, tightly interacting  
 58 species reliant on ephemeral, patchy, resources.

59 Intraspecific competition is an important driver in the evolution of dispersal  
 60 (Bowler and Benton 2005). The traditional model of host-parasitoid interaction, the  
 61 Nicholson-Bailey (N-B) model (Nicholson and Bailey 1935), implicitly accounts for  
 62 intraspecific competition in the parasitoid. Here, we amend the model to account for  
 63 intraspecific competition in the host in a complementary manner as has been done by  
 64 other authors (e.g., Beddington et al. 1975).

## 65 **Model**

### 66 **Single-patch model**

67 In brief, there are three key features of our two-species metapopulation model: First,  
 68 within-patch dynamics are modelled using the N-B model, formulated to account for  
 69 intraspecific host competition. Second, the landscape consists of multiple patches,  
 70 divided into those suitable and those unsuitable for host reproduction. Patches switch  
 71 between these states according to a simple Markov process. Third, both hosts and  
 72 parasitoids disperse across patches, with the propensity to disperse being an inherited  
 73 trait subject to mutation.

74 The classical Nicholson-Bailey (1935) model of host-parasitoid dynamics is as  
 75 follows:

$$76 \quad H_{t+1} = RH_t F_t$$

$$77 \quad P_{t+1} = H_t (1 - F_t)$$

$$F_t = \exp(-aP_t) \quad (1)$$

78 Here,  $H$  denotes the number of of hosts,  $P$  the number of parasitoids, and  $F$  the  
 79 proportion of hosts that escape parasitism and go on to reproduce. In the absence of  
 80 parasitoids, the host population grows with growth factor  $R$ ; and  $a$  denotes the

81 searching efficiency of the parasitoids.

82 This model can be derived from some simple assumptions concerning the  
 83 behaviour of the hosts and parasitoids, but is unsatisfactory in that the maximum size  
 84 of host and parasitoid populations are unbounded. The model developed in this paper  
 85 steps back to an individual-based approach which constrains the populations of hosts  
 86 and parasitoids to a maximum size dependent on host carrying capacity. It is assumed  
 87 that larval hosts show scramble competition, as has been demonstrated for *Drosophila*  
 88 *melanogaster* and *D. simulans* (Miller 1964). Scramble competition is implemented as  
 89 suggested by Beddington et al. (1975) and by Brännström and Sumpter (2005), which  
 90 follows the Ricker model (Ricker 1954). In contrast, intraspecific competition amongst  
 91 parasitoids is modelled assuming contest competition. The main model concepts are  
 92 illustrated in Fig. S1 in Electronic Supplementary Material.

93 At time  $t$ , the population consists of sets  $H_t$  of adult hosts and  $P_t$  of adult  
 94 parasitoids, which both reproduce asexually. The model ‘patch’ consists of  $n$  sites, each  
 95 of which provides enough resources to produce one host or parasitoid. Each host makes  
 96 a number of visits drawn from a Poisson distribution with mean  $R$ , amongst the  $n$  sites  
 97 (at random, with replacement), depositing one egg per visit. Each parasitoid similarly  
 98 makes a number of visits drawn from a Poisson distribution with mean  $A = an$  (thus  $A$   
 99 and  $R$  have the same units), depositing one egg at each visited sites with host eggs.  
 100 What emerges from each site  $k$  at the end of timestep  $t$  depends upon the form of the  
 101 competition, and the numbers of host eggs ( $\eta_k$ ) and parasitoid eggs ( $\pi_k$ ) laid. Under  
 102 scramble competition, no adult stage of either species is produced if  $\eta_k \neq 1$ . If  $\eta_k = 1$ ,  
 103 then an adult host is produced if  $\pi_k = 0$  or an adult parasitoid otherwise (contest  
 104 competition).

105 As with the classical N-B model, all individuals survive for one time-step only. A  
 106 deterministic representation of this model, equivalent to that given by Beddington et  
 107 al. (1975) is given by the following set of equations, as shown in Fig. S2 in ESM. The  
 108 correspondence between these two modelling approaches is explained in Appendix A.

$$H_{t+1} = F_t R H_t \exp\left(\frac{-R H_t}{n}\right)$$

$$P_{t+1} = (1 - F_t) RH_t \exp\left(\frac{-RH_t}{n}\right)$$

$$F_t = \exp\left(\frac{-AP_t}{n}\right) \quad (2)$$

109

110 The basic N-B model has no stable states for  $H > 0$  and  $P > 0$ . In particular, it  
 111 shows oscillations of ever-increasing magnitude in both  $H$  and  $P$  for many  
 112 combinations of  $a$  and  $R$ . The presence of a carrying capacity for the host population in  
 113 the model presented here is a fundamental difference, substantially altering the  
 114 population dynamics. The dynamics of the single-species Ricker model (Eq(s). 2;  
 115 obtained where  $A = 0$ ) are complex, showing a range of behaviour from a single stable  
 116 state, with period doubling through limit cycles to chaos as  $R$  is varied, as shown in  
 117 Fig. S3 in ESM for a single patch. Including a second species increases the complexity  
 118 of the model (Fig. S3). The concern of this paper lies, however, in examining the model  
 119 at the much longer-term level of the evolutionary and coevolutionary dynamics.

## 120 Multiple-patch model

121 The single-patch model described above is extended to multiple patches with migration  
 122 between them. The model ‘world’ consists of  $N$  patches, each of which is divided into  
 123 the  $n$  sites,  $Nn$  sites in total. It is assumed that inter-patch distance is small compared  
 124 with possible lifetime travel distance, as may be the case for various parasitoid species  
 125 (Elzinga et al. 2007), and thus local spatial dynamics are less important. Accordingly, a  
 126 spatially implicit metapopulation model is developed where all patches are modelled as  
 127 effectively equidistant from each other. The state of each patch  $i$  ( $1 \leq i \leq N$ ) at time  $t$  is  
 128 denoted by  $S_{i,t}$ . Each patch can be ‘active’ ( $S_{i,t} = 1$ ), in which case it provides resources  
 129 to support host larval development, or ‘inactive’ ( $S_{i,t} = 0$ ), in which it does not. Patches  
 130 switch between states according to a first-order Markov process, with inactive patches  
 131 at time  $t$  becoming active at time  $t + 1$  with probability  $\lambda$ , and active patches similarly  
 132 becoming inactive with probability  $\mu$ . Patches thus persist according to a form of  
 133 geometric distribution, remain for mean duration  $\frac{1}{\mu}$  time steps, and the proportion of  
 134 patches active is given by  $\frac{\lambda}{\lambda + \mu}$ .

135 At the beginning of each time step  $t$ , the population consists of a set of newly

136 emerged adult hosts and parasitoids each identified by an index  $j$ , located at patch  $s_j$   
 137 each with an inherited dispersal trait  $\rho_j$ . The population of hosts and parasitoids on  
 138 patch  $i$  are denoted by sets  $H_{i,t}$  and  $P_{i,t}$ . Individual  $j$  disperses with probability  $\rho_j$ , in  
 139 which case it is relocated to a patch  $s'_j$  at time  $t'$  (indicating the time after dispersal for  
 140 time-step  $t$ ), drawn at random from the whole population of patches, whether active or  
 141 inactive:  $s'_j = \text{Uniform}(1, N)$ ; otherwise,  $s'_j = s_j$ .  $H'_{i,t}$  and  $P'_{i,t}$  then represent the sets of  
 142 hosts and parasitoids at this new time  $t'$  in patch  $i$  for which  $s'_j = i$ .

143 For all active patches  $S_{i,t} = 1$ , local reproduction and parasitism proceeds  
 144 according to the individual-based simulation above. For inactive patches,  $H_{i,t+1}$  and  
 145  $P_{i,t+1} = \emptyset$ . The trait value of an individual emerging from a site is derived from that of  
 146 its parent, subject to mutation. Mutation was modelled in two ways. First, it occurs  
 147 with probability  $m$ , in which case  $\rho_j$  is assigned a random number in the range  $[0, 1]$ ,  
 148 regardless of the parent trait. This allows long-distance changes in trait value, as  
 149 might be appropriate where a trait is encoded by few loci. Alternatively, for a more  
 150 polygenic trait, mutation was modelled using cross-generational increments in  $\rho$   
 151 chosen from a normal distribution with mean zero and standard deviation  $\sigma$ , subject to  
 152 the bounds  $0 \leq \rho_j \leq 1$ . Where  $\sigma = \frac{1}{3}\sqrt{\frac{\pi}{2}}m$  the mean difference in  $\rho$  between generations  
 153 is equal in the two methods (Appendix B). Preliminary results showed no qualitative  
 154 differences in equilibrium behaviour between the two models and so the simpler  
 155  $m$ -based one is used throughout below.

## 156 **Simulation**

157 The model has seven parameters, listed in Table 1. Throughout, we use a mutation  
 158 rate  $m = 0.001$ , sufficient to allow evolution without qualitatively affecting any  
 159 equilibria, and a fixed number of patches  $N = 100$ . A model run was initialised with  
 160 10000 hosts and 1000 parasitoids, distributed randomly across the  $N$  patches, each  
 161 with a value of  $\rho$  chosen independently from the uniform distribution  $(0, 1)$ . The  
 162 starting population did not affect the long-term evolutionary dynamics. Each  
 163 simulation was run for 500 time units, which preliminary analysis showed to be  
 164 sufficient to allow coevolutionary dynamics to reach a quasi-equilibrium, subject to

165 stochastic fluctuation (below, simply “equilibrium”). Means of total host population size  
166  $\bar{H}$ , parasitoid population size,  $\bar{P}$ , host dispersal rate  $\bar{\rho}_H$  and parasitoid dispersal rate  $\bar{\rho}_P$   
167 were recorded and averaged across the last 100 time units of the simulation.  
168 Population dynamics in the absence of dispersal were studied with single-patch  
169 simulations of size  $n = 10000$ . The evolutionary dynamics with only a single species  
170 evolving were studied with simulations in which the other species had a fixed, constant  
171 dispersal trait for all individuals.

## 172 **Results**

### 173 **Population dynamics**

174 At small patch sizes, stochastic extinction of the parasitoids occurred on average at the  
175 39th time-step for  $n = 250$ , and at the 15th for  $n = 200$  under the parameters used in  
176 Fig. 1. For higher patch sizes, the evolutionary responses  $\rho$  varied little with patch size  
177 as shown in Fig. 1, though this is not the case for the population dynamics. Therefore  
178 to simplify the analysis of dispersal rate,  $n$  is fixed at 500 throughout below – a level  
179 sufficiently high that stochastic extinction is a relatively unimportant factor for most  
180 parameter combinations examined.

181 Mean size of host and parasitoid populations are shown as a function of  $\rho_H$  and  
182  $\rho_P$  (fixed dispersal strategies) in Fig. S5 in ESM. At the highest and lowest parasitoid  
183 dispersal rates, host population size is negatively correlated with parasitoid population  
184 size, as these parasitoid dispersal strategies are less successful, resulting in lower  
185 parasitism pressure reducing the size of the host population. For the lowest host  
186 dispersal rates, host population size is in turn low, with a concomitant reduction in  
187 parasitoid population size. Otherwise, for higher  $\rho_H$  and intermediate  $\rho_P$ , population  
188 sizes are less sensitive to the values of  $\rho$ .

### 189 **Evolutionary dynamics**

190 The evolutionary response of dispersal strategy of each species to different fixed  
191 strategies in the opposing species is shown in Fig. 2 for three different combinations of

192 patch-dynamic parameters  $\lambda$  and  $\mu$ , plus permanently active patches. Where the lines  
193 are not parallel to the axes, the optimum dispersal trait for one species depends upon  
194 the dispersal strategy adopted by the opposing species. This suggests possibilities for  
195 coevolutionary dynamics. That the pairs of lines for the two species intersect suggests  
196 an equilibrium is possible for both dispersal traits in a full coevolutionary model, but  
197 does not in itself dictate whether such an equilibrium would be stable or unstable.  
198 Therefore, simulations allowing for coevolution of both species were performed.

199         Simulations allowing both species to coevolve confirmed the presence of a single  
200 stable equilibrium in dispersal rate for both species, located at the point in trait space  
201 predicted by the single-species evolution models (Fig. 2). Where these equilibria for  $\bar{\rho}$   
202 are intermediate between 0 and 1, the populations of both parasitoids and hosts show  
203 peaked distributions of  $\rho$  around these means (Fig. 3). No branching of populations into  
204 low- and high-dispersal-strategy sub-populations was observed for either species using  
205 either model of mutation. Parasitoid dispersal rate  $\bar{\rho}_P$  was found to be consistently  
206 lower than that for the host population (Fig. 4). This is reflected in the mean  
207 within-patch host-parasitoid dynamics, demonstrated in Fig. 5 as a function of patch  
208 age.

## 209     **Dispersal with varied patch dynamics**

210 Equilibrium dispersal rates for both species depend upon both patch-dynamic and  
211 life-history parameters, as shown in Fig. 2 and more fully explored in Fig. 4. Lower  $\lambda/\mu$   
212 decreases the density of active patches, and at a sufficiently low patch density,  
213 populations do not persist. Where patches are permanently active, equilibrium  
214 dispersal rate for both species is high, especially so for hosts, and the optimal value of  
215 dispersal in one species depends only weakly on the dispersal trait adapted by the  
216 other (Fig. 2). However, even in the absence of inactive patches, dispersal traits do not  
217 reach fixation with every individual dispersing. Without patch dynamics, patches are  
218 more homogeneous, removing a selection pressure for increased dispersal. Higher  
219 dispersal traits are found where the majority of patches are active, though with a fast  
220 turnover of active patches. For hosts, the main determiner of dispersal rate is the patch

221 activation rate  $\lambda$  (Fig. 4). Higher  $\lambda$  increases active patch density with no effect on  
222 active patch lifetime, benefitting dispersal.

223         The same effect applies to parasitoid dispersal with higher dispersal rate at  
224 higher  $\lambda$ . However, parasitoid dispersal rate is additionally affected by patch removal  
225 rate  $\mu$ . Higher  $\mu$  results in a shorter patch lifetime, giving a greater benefit to  
226 dispersal. This effect may be pronounced only for parasitoids, since whereas host  
227 density is highest in new active patches, density of parasitoids is highest for older  
228 patches (Fig. 5).

### 229         **Dispersal with varied life-history parameters**

230 For the lowest levels of the parasitoid searching parameter  $A$ , parasitoid populations  
231 do not persist; however, too high a value for  $A$  and in a stochastic model, the host  
232 population is driven to extinction. Similarly,  $R$  is constrained by being high enough to  
233 support a host population with extreme values of  $R$  causing frequent stochastic  
234 extinction through the Ricker process. Where either the parasitoid or both species do  
235 not persist, blank areas are seen in the lower panels of Fig. 4 (the host population in  
236 the absence of parasitoids not being modelled here).

237         Host dispersal is selected for under conditions of high  $R$  (Fig. 4). Here, intense  
238 competition between hosts and high host fitness in empty, active patches benefits  
239 increased dispersal. Host dispersal rate is largely independent of  $A$ , with some  
240 reduction in  $\bar{\rho}_H$  for low  $A$ . However, parasitoid dispersal rate is highly dependent upon  
241  $R$ . Parasitoid dispersal is selected for where both  $R$  and  $A$  are high. Four selection  
242 pressures contribute to this result: First, host dispersal and reproduction rates are also  
243 high, and newly active patches will establish host populations quickly. Second,  
244 parasitoid population density is high and intra-patch competition amongst parasitoids  
245 strong. Third, high  $A$  increases the relative benefit of dispersing to newly established  
246 host populations to avoid intraspecific competition. Fourth, with very high  $R$ , local host  
247 extinction becomes more likely.

248 **Discussion**

249 Dispersal is a double-edged sword: it promises benefits of locating unoccupied habitat  
250 and reduced competition, but carries risk of lower fitness or mortality if such habitat is  
251 not found. The model formulation above implicitly assumes that parasitoid and host  
252 competitive ability is unaffected by  $\rho_j$ , and that neither hosts nor parasitoids can  
253 determine the value of a new patch before settling upon it. The implicit cost of  
254 dispersing is therefore the risk that the patch travelled to is of poorer quality than that  
255 left behind, with the potential benefit that a new, unoccupied (for hosts) or  
256 unparasitised (for parasitoids) patch may be discovered. Other authors have included  
257 terms for explicit costs of dispersal (e.g., Murrell et al. 2002). Here, no such energy cost  
258 is included, but dispersal is automatically costly in a naturalistic manner under our  
259 model framework, where individuals disperse to an inactive patch, with higher cost in  
260 more rarefied environments. Other potential costs could include Allee effects where  
261 reproduction is more difficult in sparsely populated patches.

262         These benefits and costs are asymmetrical, due to the different relationships of  
263 hosts and parasitoids to the patches. Host reproduction is quickest in newly active,  
264 vacant patches free from intraspecific competition. Parasitoids, however, require an  
265 established host population before they can reproduce. Therefore, there is a greater  
266 probability of dispersing to an unsuitable patch for a parasitoid than for a host. With a  
267 lower dispersal rate in the parasitoid and a need for an established host population  
268 before parasitoid reproduction, there is a lag between host colonisation of a newly  
269 active patch and the establishment of a resident parasitoid population (Fig. 5). Once  
270 established, the parasitoid population reduces host density in subsequent generations.  
271 This lower dispersal in the parasitoid is in agreement with field studies, with several  
272 showing relatively restricted levels or distances of dispersal in parasitoids (Elzinga et  
273 al. 2007). Mostly short-distance dispersal, with sufficient long-distance dispersal to  
274 account for long-distance colonisation (Elzinga et al. 2007) could result from a  
275 dispersal kernel with a heavy tail, as might be generated through power-law Lévy  
276 flights (Viswanathan et al. 1999). The fruit fly *D. melanogaster* shows fractal periods of  
277 activity which might generate such flight patterns (Cole 1995).

278 Our model assumes that larval competitive ability is unaffected by parasitism,  
279 which would be most appropriate where parasitism occurs after larval competition, as  
280 is the case for *Drosophila* pupal parasitoids such as *Pachycrepoideus vindemiae* rather  
281 than larval parasitoids such as *Leptopilina* spp. Also, both host and parasitoid  
282 dispersal occur before reproduction and after intraspecific competition, which is also  
283 reasonable for *Drosophila* and its parasitoids. However, this will not be the same for all  
284 species interactions. Dispersal is selectively advantageous where kin competition is  
285 avoided by dispersing individuals (Hamilton and May 1977; Bach et al. 2006; Poethke  
286 et al. 2007), as is the case where dispersal occurs earlier than larval intraspecific  
287 competition. For systems where the dispersing host stage is itself parasitised, selection  
288 on parasitoid dispersal rate may still operate via the potential of parasites to  
289 manipulate the dispersal behaviour of their hosts (Thomas et al. 2005; Lion et al.  
290 2006), potentially leading to direct coevolutionary arms-races. For example, the  
291 optimal parasitoid dispersal rate may depend upon the number of other species it can  
292 parasitise, and the rate at which its subpopulations are subject to stochastic extinction  
293 even where hosts persist.

294 Dispersal as modelled above is not plastic. Whether dispersal is advantageous  
295 over a whole lifetime, and at a specific instant can be treated as separate questions. For  
296 example the presence of a parasitoid can be a proximal trigger for dispersal, as seen in  
297 the production of winged aphid morphs (Slogett and Weisser 2002). More plastic  
298 dispersal strategies, for example where dispersal rates are density dependent (Travis  
299 et al. 1999), could be a future addition to our model. Models show that plastic dispersal  
300 strategies are selectively advantageous and will evolve where there is the potential to  
301 do so (Travis et al. 1999).

302 The model predicts that change in the dispersal trait of one population can drive  
303 reciprocal change in the dispersal trait of the other species. This is not a direct  
304 selection pressure, but operates via the population dynamics – the ‘ecological loop’ of  
305 Bowler and Benton (2005): Changing dispersal rates in one species alters the  
306 population dynamics of both, leading to changes in fitness, driving the evolution of  
307 dispersal in the second species.

308 As habitats become further fragmented through habitat destruction, species are  
309 increasingly reliant on dispersal between patches to maintain viable populations.  
310 However, dispersal is not necessarily in the interest of the individual where dispersal is  
311 costly (Travis et al. 1999). Habitat fragmentation causes greater susceptibility of  
312 species to extinction and lower species diversity, especially at higher trophic levels  
313 (Bascompte and Solé 1998; Gilbert et al. 1998; Bonsall et al. 2002; Elzinga et al. 2007),  
314 with extinction of one species leading to further extinction of other, linked, species  
315 (Memmott et al. 2006). Given that the optimal dispersal strategy for a species will  
316 depend on the nature of its environment (Bowler and Benton 2005), habitat change and  
317 destruction may lead to selection pressures acting on dispersal strategies. Use of pest  
318 management strategies such as introduction of parasitoids of pest species may  
319 similarly shift the optimum for pest dispersal traits. Where polymorphism in dispersal  
320 trait exists (e.g., Appleby and Credland 2001), selection may favour different morphs,  
321 potentially compromising the efficiency of pest control.

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## 325 **Appendix A**

326 Assume a single patch of size  $n$  sites with populations  $H_t$  of hosts and  $P_t$  of adult  
327 parasitoids. Each host makes a Poisson distributed number of independent egg-laying  
328 ‘visits’ to sites at random with mean  $R$ . Similarly, each parasitoid makes a  
329 Poisson-distributed number of visits with mean  $A$ . Therefore, the number of visits  
330 made to individual sites are in turn Poisson distributed as  $\eta \sim \text{Poisson}(RH_t/n)$  for hosts  
331 and  $\pi \sim \text{Poisson}(AP_t/n)$  for parasitoids. Given this distribution, the probabilities of a  
332 site being visited once by hosts, and zero times by parasitoids are given by:

$$p(\eta = 1) = \frac{RH_t}{n} \exp\left(-\frac{RH_t}{n}\right)$$

$$p(\pi = 0) = \exp\left(-\frac{AP_t}{n}\right). \quad (3)$$

333 Visits are independent for hosts and parasitoids, therefore multiplying gives the  
 334 probabilities of a site having one host visit and no parasitoid visits  $p(\pi = 0)p(\eta = 1)$ ,  
 335 which sites give rise to a host; and the probability of one host visit and  $> 0$  parasitoid  
 336 visits  $(1 - p(\pi = 0))p(\eta = 1)$ , which sites give rise to a parasitoid. Multiplying by the  
 337 number of sites  $n$  and rearranging gives Eqns. (2) above. Alternatively, where  $n = 1$ ,  
 338  $p(\pi = 0)$  is equivalent to the original equation for  $F$  in Eqns. (1).

## 339 **Appendix B**

340 The mean absolute difference between two random numbers chosen independently and  
 341 uniformly in the range  $[0, 1]$  is given by  $\frac{1}{3}$ . The mean absolute value of numbers chosen  
 342 from the standard normal distribution is given by  $\sqrt{\frac{2}{\pi}}$ . As a first-order rule to allow  
 343 comparison between the two mutation models (assuming random drift of  $\rho$ ), we  
 344 therefore apply  $\frac{1}{3}m = \sqrt{\frac{2}{\pi}}\sigma$ , and thus  $\sigma = \frac{1}{3}\sqrt{\frac{\pi}{2}}m$ .

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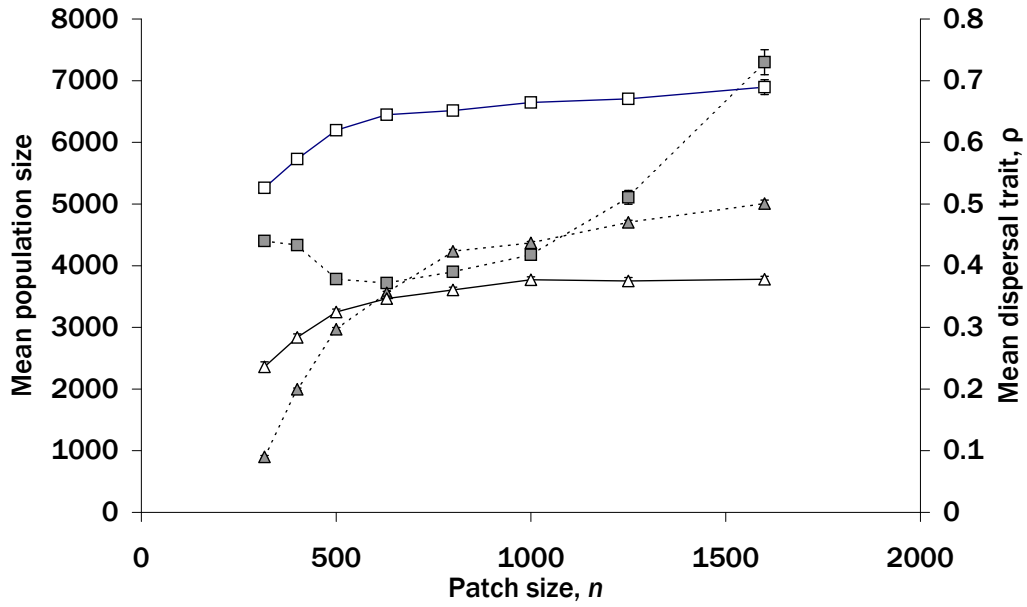
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429 **Table 1.** Ranges of parameter values used (favoured values given in  
 430 parentheses).

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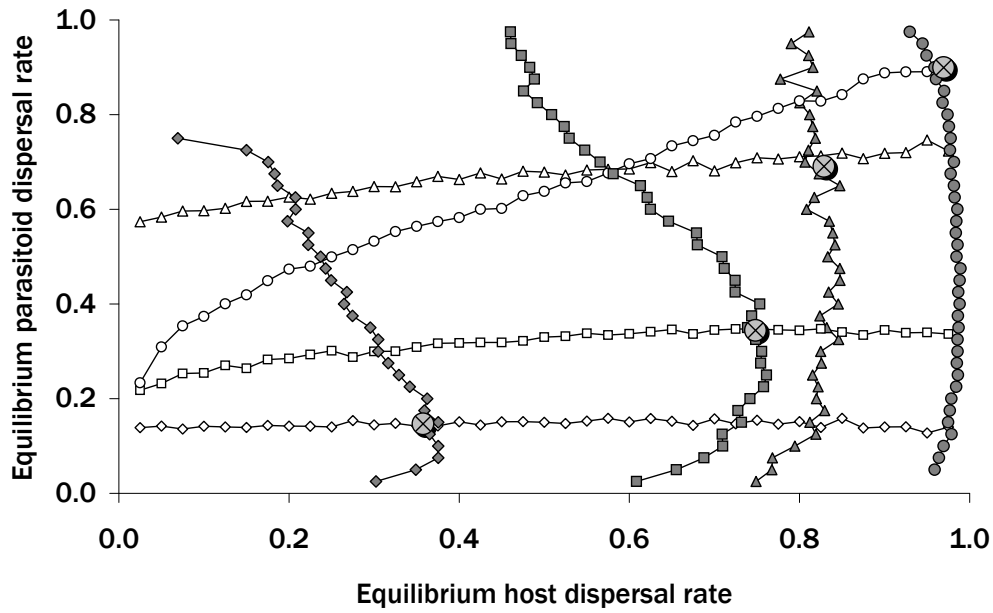
	$N$	Number of patches	100
	$n$	Patch area (carrying capacity)	250 – 1600 (500)
	$\lambda$	Rate of patch activation	0.0367 – 0.333 ( $1/4$ )
431	$\mu$	Rate of patch inactivation	0.0367 – 0.333 ( $1/4$ )
	$R$	Growth factor of hosts without parasitoids	2 – 18 (8)
	$a$	Patch area searched by a single parasitoid	0.008 – 0.072 $\times n$ (0.016)
	$A$		4 – 36 (8)
	$m$	Mutation rate	0.001

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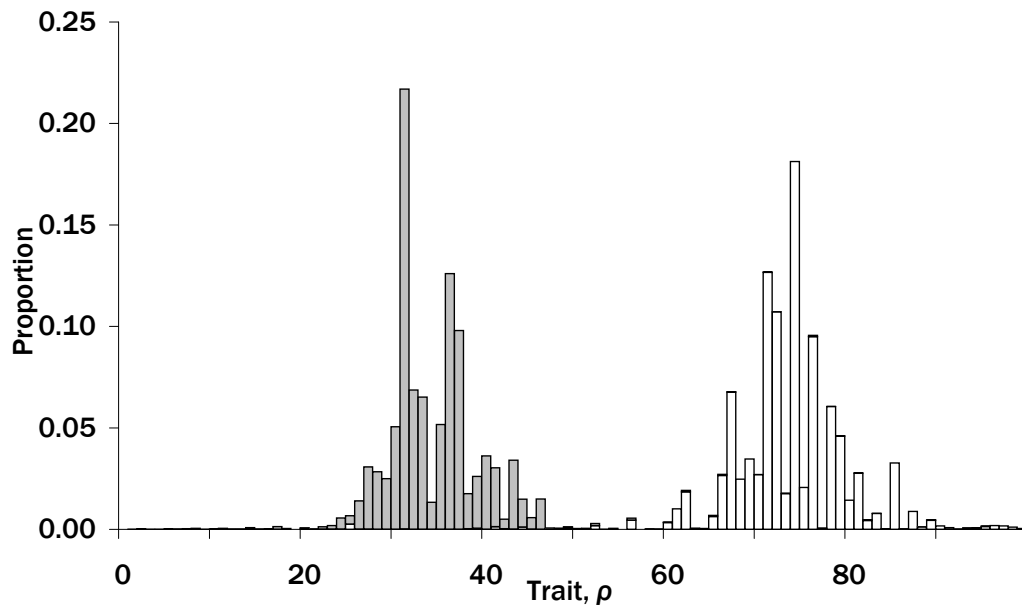
432

433 **Figure 1.** Equilibrium conditions versus patch size  $n$ . Numbers of hosts ( $\bar{H}$ , ■) and  
 434 parasitoids ( $\bar{P}$ , ▲) are shown by dotted lines and the left-hand axis; mean dispersal rate  
 435 for hosts ( $\bar{\rho}_H$ , □) and parasitoids ( $\bar{\rho}_P$ , △) are shown by solid lines and the right-hand  
 436 axis. Default parameters (Table 1). Standard errors are included for both variables  
 437 (each of 16 replicates), but generally too small to be shown.



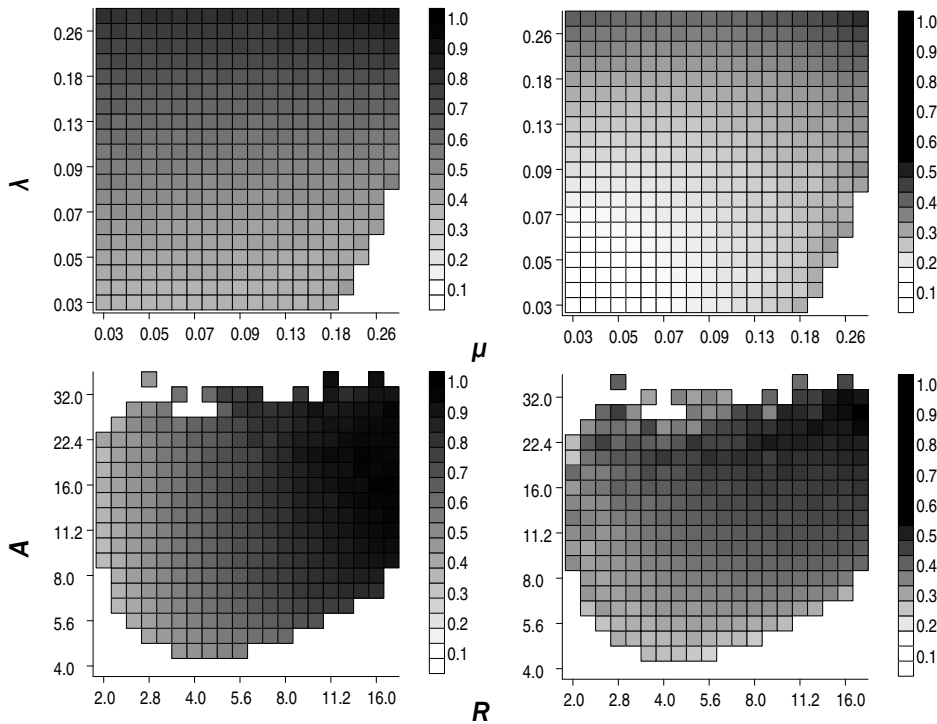
438

439 **Figure 2.** Equilibrium conditions with evolution of one or two of the interacting  
 440 species. Open symbols: equilibrium parasitoid  $\bar{\rho}_P$  ( $y$ -axis) with fixed host  $\rho_H$  ( $x$ -axis).  
 441 Filled symbols: equilibrium host  $\bar{\rho}_H$  ( $x$ -axis) for fixed parasitoid  $\rho_P$  ( $y$ -axis). Mean  
 442 durations of patch activity ( $\mu^{-1}$ ) and inactivity ( $\lambda^{-1}$ ) were  $\triangle$ : always active;  $\square$ : 4  
 443 4 inactive;  $\circ$ : 3 active, 1.5 inactive;  $\diamond$ : 10 active, 20 inactive. Default life-history  
 444 parameters (Table 1). Means of ten simulations are shown for each point. Larger  
 445 crossed circles at the intersections indicate where both species were allowed to evolve  
 446 (means of 30 simulations). Some extreme dispersal values led to extinction.



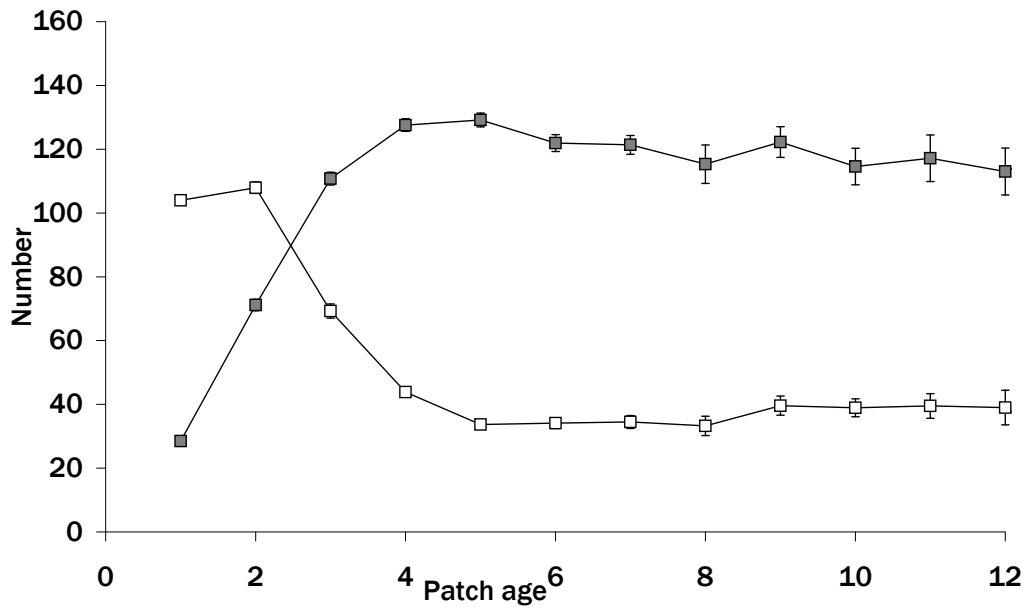
447

448 **Figure 3.** Distribution of final host  $\rho_H$  (open symbols) and parasitoid  $\rho_P$  (filled  
449 symbols), aggregated over 10 model runs. Default parameters (Table 1).



450

451 **Figure 4.** Long-term means for  $\rho_H$  (left) and  $\rho_P$  (right) versus varied patch dynamic  
 452 parameters (top) and host and parasitoid parameters (bottom). Top:  $\mu$  ( $x$ -axis) versus  $\lambda$   
 453 ( $y$ -axis); bottom:  $R_0$  ( $x$ -axis) versus  $A$  ( $y$ -axis). Means of 15 simulations are plotted (or  
 454 fewer with stochastic extinction). Regions where one or both species do not persist are  
 455 shown empty. A colour version is provided in ESM (Figure S4).



456

457 **Figure 5.** Mean numbers of hosts (open symbols) and parasitoids (filled symbols) in a  
458 given patch versus patch age (time steps), accumulated over 10 model runs. Default  
459 parameters (Table 1). Standard errors are included, but generally too small to be  
460 shown.