

1 Coevolution of dispersal in a
2 parasitoid-host system

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4 July 10, 2009

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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 (η_k) and parasitoid eggs (π_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.

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

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

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

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 λ , and active patches similarly
 132 becoming inactive with probability μ . 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 ρ_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 ρ_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 ρ_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 ρ
 151 chosen from a normal distribution with mean zero and standard deviation σ , 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 ρ 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 ρ 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 ρ 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 ρ_H and
182 ρ_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 ρ_H and intermediate ρ_P , population
188 sizes are less sensitive to the values of ρ .

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 λ and μ , 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 ρ 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 λ/μ
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 λ (Fig. 4). Higher λ 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 λ . However, parasitoid dispersal rate is additionally affected by patch removal
225 rate μ . Higher μ 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 ρ_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.

322 **Acknowledgements**

323 With thanks to Charles Godfray and Istvan Kiss for helpful comments on the
 324 manuscript.

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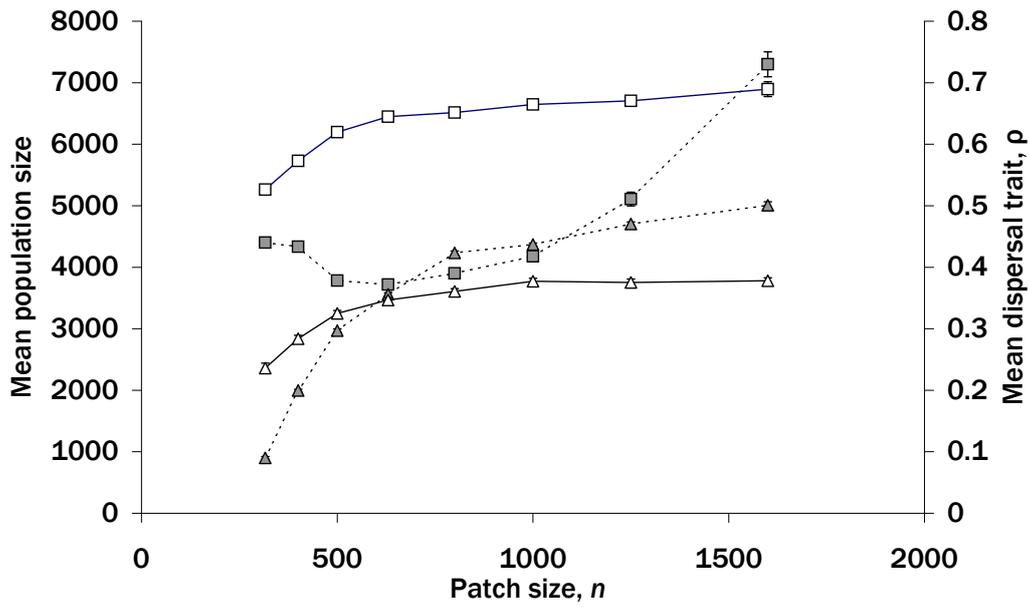
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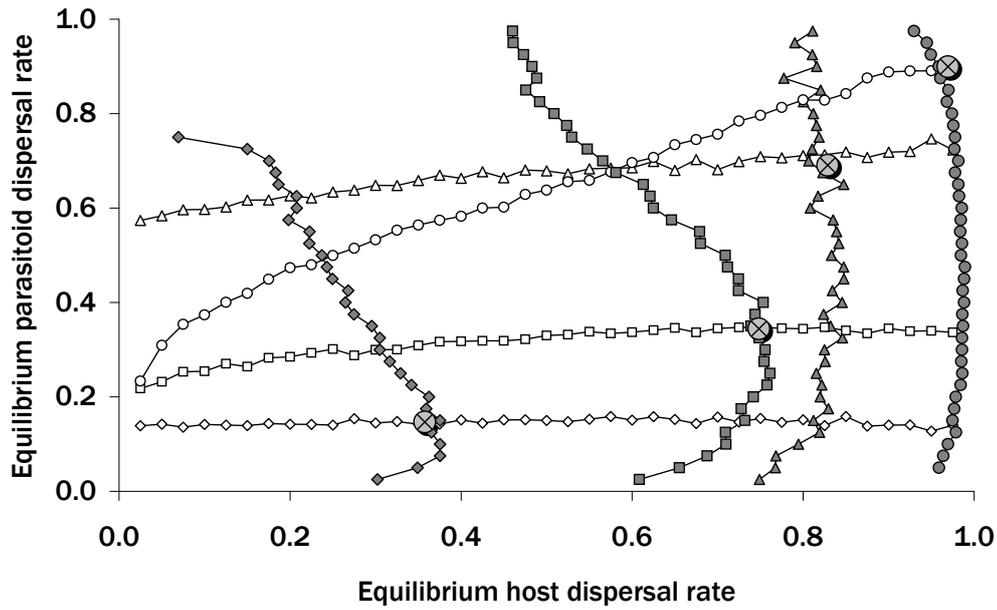
429 **Table 1.** Ranges of parameter values used (favoured values given in
 430 parentheses).

	N	Number of patches	100
	n	Patch area (carrying capacity)	250 – 1600 (500)
	λ	Rate of patch activation	0.0367 – 0.333 ($1/4$)
431	μ	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



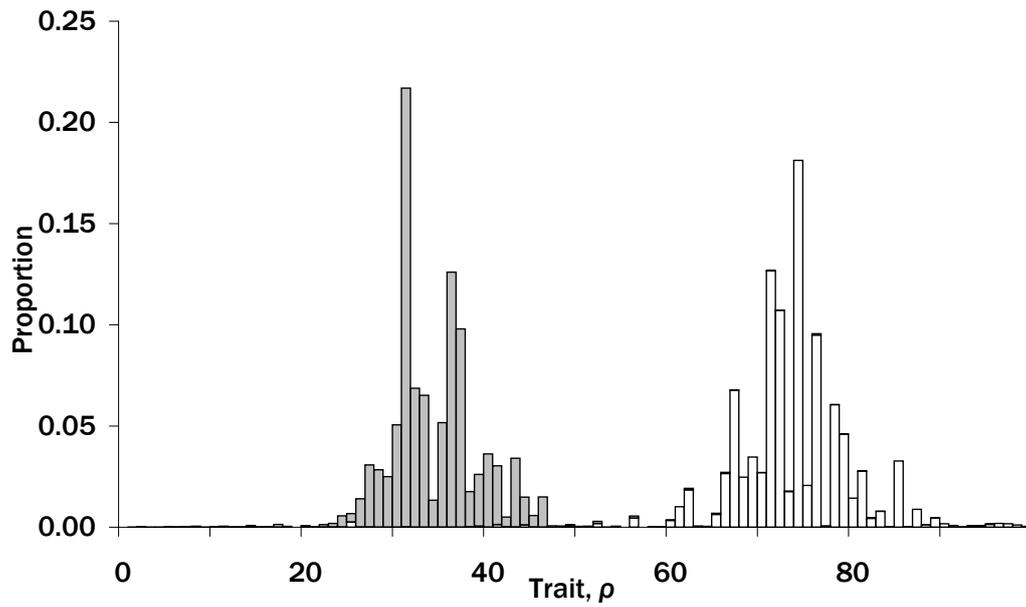
432

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.



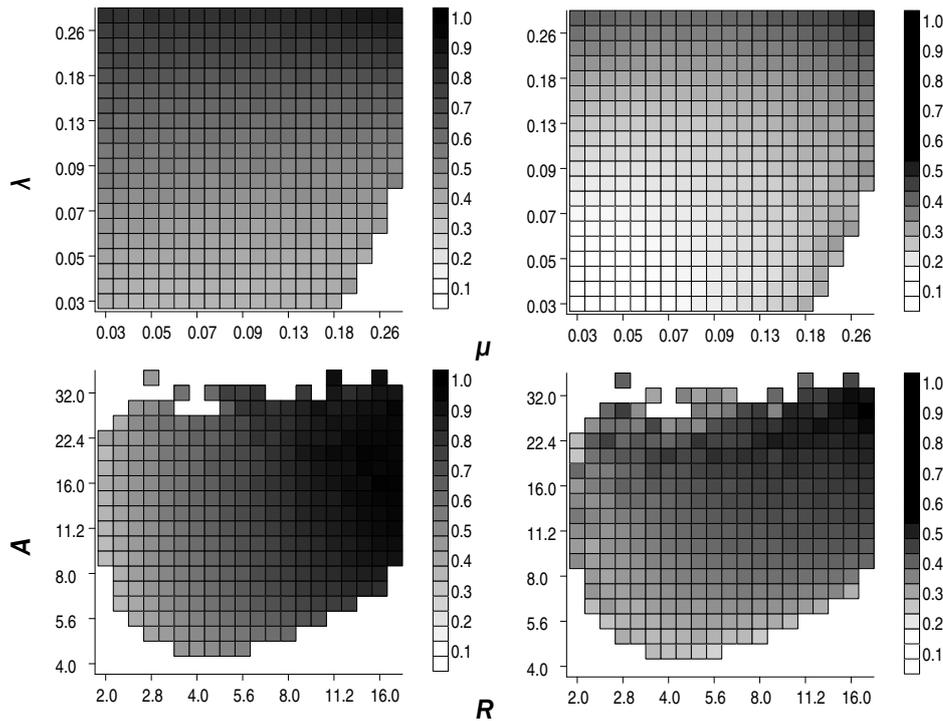
438

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 ρ_H (x -axis).
 441 Filled symbols: equilibrium host $\bar{\rho}_H$ (x -axis) for fixed parasitoid ρ_P (y -axis). Mean
 442 durations of patch activity (μ^{-1}) and inactivity (λ^{-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.



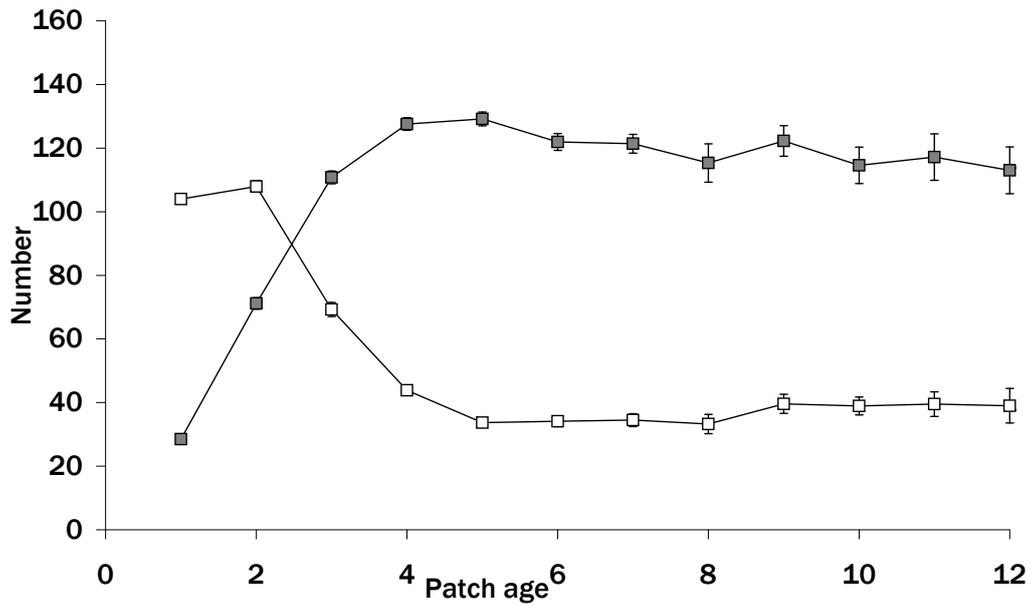
447

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



450

451 **Figure 4.** Long-term means for ρ_H (left) and ρ_P (right) versus varied patch dynamic
 452 parameters (top) and host and parasitoid parameters (bottom). Top: μ (x -axis) versus λ
 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.