Evolution of host life-history traits in a spatially structured host-parasite system

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B.1 Persistence of the hosts

In the non-spatial model, and in the absence of parasites, the condition for host persistence is

$$b_{\text{S}} > d \tag{B.1}$$

and the equilibrium density of hosts is

$$\hat{p}_{\text{S}}^{\text{NS}} = 1 - \frac{d}{b_{\text{S}}} \tag{B.2}$$

In the spatial model, when there is no parasite in the population, the model reduces to:

$$\frac{\mathrm{d}p_{\text{S}}}{\mathrm{d}t} = B_{\text{S}}\, p_{\text{S}} = \left(b_{\text{S}}\, q_{\circ|\text{S}} - d\right) p_{\text{S}} \tag{B.3}$$

Consequently, the host population persists in the absence of parasites only if B_{S} is positive; but we have not been able to derive an explicit general condition for persistence. This is however possible using the pair approximation (Matsuda et al., 1992). The pair approximation consists in following pair correlations, neglecting triplet correlations (Sato et al., 1994); we find that the hosts persist when

$$\frac{b}{d} > \frac{n}{n-1} \tag{B.4}$$

where n is the number of neighbors in the lattice (see table 1 in the main text). The equilibrium density of the hosts in the spatial model under the pair approximation is:

$$\hat{p}_{\text{S}} = \frac{b\,(1-n) + d\,n}{b\,(1-n) + d} \tag{B.5}$$

Note that equations (B.1) and (B.2) are the equivalents of equations (B.4) and (B.5) when the number of neighbors, n, tends to infinity. The condition for persistence in the spatial model (B.4) is actually a lower bound – this is due to the use of the pair approximation. Note also that the condition for persistence is harder to fulfill in the spatial model, due to local competition.

B.2 Persistence of the parasites

Let us now derive the conditions for the persistence of the parasites.
In the non spatial model, there is a stable endemic equilibrium when $R_0^{\text{NS}} > 1$, with

$$R_0^{\text{NS}} = \frac{\hat{p}_{\text{S}}^{\text{NS}}\, \alpha\, \beta}{d + \gamma + \nu} \tag{B.6}$$

where $\hat{p}_{\mathrm{S}}^{\mathrm{NS}}$ is the equilibrium density of the host in the absence of parasites, in the non spatial model (equation (B.2)).

Again, we have not been able to derive an explicit general condition for the persistence of the infection in the spatial model. We can however derive a condition for the persistence of the infection if we consider a saturated host population and use the pair approximation. A saturated host population corresponds to a case where host fecundity is much greater than host mortality, such that all sites are occupied, and that a dead host is immediately replaced by a new host. In this case, we have $\hat{p}_{\mathrm{S}} = 1$. Using the pair approximation, we find that the parasite can invade provided that

$$\frac{\alpha\,\beta}{d + \gamma + \nu} > \frac{n}{n - 1} \tag{B.7}$$

This is the equivalent of condition (B.6) in a saturated population ($\hat{p}_{\mathrm{S}}^{\mathrm{NS}} = 1$), when n tends to infinity. Again, the condition for persistence is harder to fulfill in the spatial model.

As there is no point investigating the evolution of host defense strategies if there are no parasites in the population, we will focus on cases where $R_0^{\mathrm{NS}} > 1$ and where condition (B.7) is fulfilled (but keeping in mind that this does not necessarily mean that the parasite persists in the unsaturated spatial model).

C Next-generation method

C.1 Principle of the next-generation method

We give here a brief description of the next-generation method. For more details, see Hurford et al. (2010).

We first have to linearize the non linear system of equations of our model, near the resident's equilibrium:

$$\dot{X} = \mathbf{A}\,X \tag{C.1}$$

where X is the vector of the model's variables.

The mutant can invade when $s(\mathbf{A})$, the spectral bound of $\mathbf{A}$, is strictly positive.

The next-generation theorem (NGT) (Diekmann et al., 1990; van den Driessche and Watmough, 2002) states that for a decomposition of the matrix $\mathbf{A}$ of the form $\mathbf{A} = \mathbf{F} - \mathbf{V}$, which satisfies $\mathbf{F} \geq 0$, $\mathbf{V}^{-1} \geq 0$, $s(-\mathbf{V}) < 0$, we have:

$$s(\mathbf{A}) > 0 \Leftrightarrow \rho(\mathbf{F}\,\mathbf{V}^{-1}) > 1 \tag{C.2}$$

where $\rho(\mathbf{M})$ is the spectral radius of a matrix $\mathbf{M}$.

Let x be the resident's trait, and y the mutant's trait. Assuming weak selection, $\rho(\mathbf{F}\mathbf{V}^{-1})$ can be approximated as (Hurford et al., 2010):

$$\rho(\mathbf{F}\mathbf{V}^{-1}) \approx 1 + v^T \left(\left.\frac{\partial \mathbf{F}\mathbf{V}^{-1}}{\partial y}\right|_{y=x} \right) u\,(y - x) \tag{C.3}$$

where v and u are the left and right eigenvectors of the matrix $\mathbf{F}\mathbf{V}^{-1}$, associated with the eigenvalue 1 (corresponding to the resident's equilibrium).

C.2 Next-generation method in our model

In our model, the invasion dynamics of a mutant is (the prime $'$ refers to mutant parameters and variables):

$$
\begin{cases}
\dfrac{\mathrm{d}p_{\mathrm{S'}}}{\mathrm{d}t} = B_{\mathrm{S}}{'}\,p_{\mathrm{S'}} + B_{\mathrm{I}}{'}\,p_{\mathrm{I'}} - H'\,p_{\mathrm{S'}} & \text{(C.4a)} \\[2ex]
\dfrac{\mathrm{d}p_{\mathrm{I'}}}{\mathrm{d}t} = H'\,p_{\mathrm{S'}} - D'\,p_{\mathrm{I'}} & \text{(C.4b)}
\end{cases}
$$

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with the following compound variables:

$$
\begin{aligned}
B'_{\mathrm{S}} &= b'_{\mathrm{S}}\left((1-g_{\mathrm{R}})q_{\circ|\mathrm{S}'} + g_{\mathrm{R}}p_{\circ}\right) - d' \\
B'_{\mathrm{I}} &= b'_{\mathrm{I}}\left((1-g_{\mathrm{R}})q_{\circ|\mathrm{I}'} + g_{\mathrm{R}}p_{\circ}\right) + \gamma' \\
H' &= \alpha'\beta\left((1-g_{\mathrm{T}})q_{\mathrm{I}|\mathrm{S}'} + g_{\mathrm{T}}p_{\mathrm{I}}\right) + \alpha'\beta'\left((1-g_{\mathrm{T}})q_{\mathrm{I}'|\mathrm{S}'} + g_{\mathrm{T}}p_{\mathrm{I}'}\right) \\
D' &= d' + \gamma' + \nu'
\end{aligned}
\tag{C.5}
$$

We chose parameters such that B'_{S} is positive. A negative B'_{S} would indeed mean that the mutant population does not persist in the absence of parasites (see appendix B); in this case, the mutant population would *a fortiori* not persist when parasites are present. We therefore do not consider such cases. Note that all mutant parameters are written with a prime $'$, because we do not make any assumption on which parameter evolves at this stage.

We can now linearize system (C.4) near the resident's equilibrium, and we obtain

$$
\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix} p_{\mathrm{S}'} \\ p_{\mathrm{I}'} \end{pmatrix} = \mathbf{A}\begin{pmatrix} p_{\mathrm{S}'} \\ p_{\mathrm{I}'} \end{pmatrix}
\tag{C.6}
$$

with

$$
\mathbf{A} = \begin{pmatrix} B'_{\mathrm{S}} - H' & B'_{\mathrm{I}} \\ H' & -D \end{pmatrix}
\tag{C.7}
$$

We can decompose $\mathbf{A}$ such that $\mathbf{A} = \mathbf{F} - \mathbf{V}$:

$$
\mathbf{F} = \begin{pmatrix} B'_{\mathrm{S}} & B'_{\mathrm{I}} \\ 0 & 0 \end{pmatrix}
\tag{C.8a}
$$

$$
\mathbf{V} = \begin{pmatrix} H' & 0 \\ -H' & D \end{pmatrix}
\tag{C.8b}
$$

and we obtain

$$
\mathbf{F}\,\mathbf{V}^{-1} = \begin{pmatrix} \frac{B'_{\mathrm{I}}}{D} + \frac{B'_{\mathrm{S}}}{H'} & \frac{B'_{\mathrm{I}}}{D} \\ 0 & 0 \end{pmatrix}
\tag{C.9}
$$

The matrix $\mathbf{F}\,\mathbf{V}^{-1}$ is triangular; its leading eigenvalue is therefore the following

$$
R' = \rho(\mathbf{F}\,\mathbf{V}^{-1}) = \frac{B'_{\mathrm{S}}}{H'} + \frac{B'_{\mathrm{I}}}{D'}
\tag{C.10}
$$

The invasion fitness R' is the sum of the contributions of each class (susceptible, S and infected I) to the production of susceptible individuals. Recall indeed that as there is no vertical transmission of the disease, new individuals are always born susceptible. The first term in equation (C.10)

corresponds to the net production of susceptible individuals by susceptible individuals (B'_{S}), during the duration of their stay in the susceptible class ($1/H'$). The second term corresponds to the production of susceptible individuals by infected individuals (B'_{I}, including recovery), during the duration of their stay in the infected class ($1/D'$). Mutant hosts can invade when R' is greater than unity (Hurford et al., 2010). Note that this result is general and does not depend on any specific simplifying hypotheses concerning spatial structure; in particular, we do not need to use the pair approximation. Recall also that the parameters are chosen such that B'_{S} is positive. A negative B'_{S} would indeed mean that mutants cannot persist even in the absence of parasites; hence, these mutant individuals could *a fortiori* not persist when parasites are present.

For the resident or for a neutral mutant, we have $R = 1$, because the resident population is at equilibrium, so using (C.10) we obtain

$$R = 1 = \frac{B^*_{\mathrm{S}}}{H^*} + \frac{B^*_{\mathrm{I}}}{D^*} \tag{C.11}$$

with the following compound variables

$$
\begin{aligned}
B^*_{\mathrm{S}} &= b_{\mathrm{S}} \left((1 - g_{\mathrm{R}}) q^*_{\mathrm{o|S}} + g_{\mathrm{R}} p^*_{\mathrm{o}} \right) - d \\
B^*_{\mathrm{I}} &= b_{\mathrm{I}} \left((1 - g_{\mathrm{R}}) q^*_{\mathrm{o|I}} + g_{\mathrm{R}} p^*_{\mathrm{o}} \right) + \gamma \\
H^* &= \alpha\,\beta \left((1 - g_{\mathrm{T}}) q^*_{\mathrm{I|S}} + g_{\mathrm{T}} p^*_{\mathrm{I}} \right) \\
D^* &= D = d + \gamma + \nu
\end{aligned}
\tag{C.12}
$$

where the q^* correspond to local densities at the resident's equilibrium. Equation (C.11) can also be obtained by solving for the ecological equilibrium of the resident population, using system (1) in the main text. Subtracting equations (C.10) and (C.11), we obtain:

$$R' - 1 = \frac{B'_{\mathrm{S}}}{H'} + \frac{B'_{\mathrm{I}}}{D'} - \frac{B^*_{\mathrm{S}}}{H^*} - \frac{B^*_{\mathrm{I}}}{D^*} \tag{C.13}$$

We now assume that selection is weak, *i.e.*, that the mutant's traits (τ') are close to the resident's (τ), so that all mutant parameters can be written as $\tau' = \tau + \partial\tau$, and so that $\partial R' = R' - 1$ is small. Using this weak selection approximation, we can also Taylor-expand $q_{\mathrm{I|S'}}$ and $q_{\mathrm{I'|S'}}$ in the following way:

$$
\begin{aligned}
q_{\mathrm{I|S'}} &= \bar{q}_{\mathrm{I|S'}} + \partial q_{\mathrm{I|S'}} \tag{C.14} \\
q_{\mathrm{I'|S'}} &= \bar{q}_{\mathrm{I'|S'}} + \partial q_{\mathrm{I'|S'}} \tag{C.15}
\end{aligned}
$$

where the bar (¯) stands for the local densities seen by a neutral mutant (*i.e.,* a mutant with the exact same parameters as the resident, but carrying a cost-free tag); consequently

$$\underbrace{q_{\mathrm{I|S}}^*}_{\text{infecteds seen by the healthy residents}} = \underbrace{\bar{q}_{\mathrm{I|S'}} + \bar{q}_{\mathrm{I'|S'}}}_{\text{infecteds seen by the healthy neutral mutants}} \tag{C.16}$$

where, as mentioned previously, the star $*$ denotes the equilibrium local densities seen by the resident.

With weak selection, equation (C.13) becomes:

$$\partial R' = \frac{\partial B_{\mathrm{S}}'}{H^*} + \frac{\partial B_{\mathrm{I}}'}{D^*} - \frac{B_{\mathrm{I}}^*}{D^*}\frac{\partial D'}{D^*} - \frac{B_{\mathrm{S}}^*}{H^*}\frac{\partial H'}{H^*} \tag{C.17}$$

with, in the general (spatial) model:

$$\partial B_{\mathrm{S}}' = \partial b_{\mathrm{S}}\left((1-g_{\mathrm{R}})q_{\mathrm{o|S}}^* + g_{\mathrm{R}}p_{\mathrm{o}}^*\right) + b_{\mathrm{S}}\left(1-g_{\mathrm{R}}\right)\partial q_{\mathrm{o|S'}} - \partial d \tag{C.18a}$$

$$\partial B_{\mathrm{I}}' = \partial b_{\mathrm{I}}\left((1-g_{\mathrm{R}})q_{\mathrm{o|I}}^* + g_{\mathrm{R}}p_{\mathrm{o}}^*\right) + b_{\mathrm{I}}\left(1-g_{\mathrm{R}}\right)\partial q_{\mathrm{o|I'}} + \partial\gamma \tag{C.18b}$$

$$\partial H' = \alpha\,\beta\,(1-g_{\mathrm{T}})\,\partial(q_{\mathrm{I'|S'}} + q_{\mathrm{I|S'}}) + \partial\alpha\,\beta\left((1-g_{\mathrm{T}})q_{\mathrm{I|S}}^* + g_{\mathrm{T}}p_{\mathrm{I}}^*\right) + \alpha\,\partial\beta\,(1-g_{\mathrm{T}})\,\bar{q}_{\mathrm{I'|S'}} \tag{C.18c}$$

$$\partial D' = \partial d + \partial\gamma + \partial\nu \tag{C.18d}$$

The mutant invades when $\partial R' > 0$.

In the non spatial model (mean-field), where $g_{\mathrm{R}} = g_{\mathrm{T}} = 1$, we have:

$$\partial B_{\mathrm{S}}' = \partial b_{\mathrm{S}}\, p_{\mathrm{o}}^* - \partial d \tag{C.19a}$$
$$\partial B_{\mathrm{I}}' = \partial b_{\mathrm{I}}\, p_{\mathrm{o}}^* + \partial\gamma \tag{C.19b}$$
$$\partial H' = \partial\alpha\,\beta\, p_{\mathrm{I}}^* \tag{C.19c}$$
$$\partial D' = \partial d + \partial\gamma + \partial\nu \tag{C.19d}$$

Note the disappearance of the term with $\partial\beta$ in C.19c, which accounts for the fact that a change in β is neutral in a non-spatial setting.

D Stochastic simulations

Our stochastic simulations are individual-based, and are coded using the Gillespie algorithm (Gillespie, 1977). The simulations presented in this article are run on regular triangular lattices ($n = 6$ neighbors) like the one presented in figure 2.

There is a finite number of possible genotypes (20 in our simulations), each with fixed values of the defense trait and of the cost.

The population is coded as a vector of $nindiv = 900$ individuals; 0 means that the site is empty, $x > 0$ that the site is occupied. The floor of x gives its genotype, and the decimal part of x whether x is infected or not. We allow for mutations; they lead to the $+1$ or -1 neighboring genotype.

We calculate the chances of all possible events on the grid; they are grouped in a $6 * nindiv$-long vector. Each individual indeed can

- reproduce locally, *i.e.,* in one of its n neighboring cells

- die

- infect locally, *i.e.,* one of its n neighboring cells

- recover

- reproduce globally

- infect globally

Events which cannot happen have null probabilities (for instance if the focal individual is surrounded by occupied sites while $g_{\mathrm{R}} = 0$, it cannot reproduce, and the corresponding chances are null).

At each step we

- Draw one event among the $6 * nindiv$ possible events, according to their probabilities. If reproduction or infection is the event, then we also pick the target site.

- Draw which individuals mutate, if any

- Update the population

- Update the vector of chances

- Draw the corresponding time interval

- Update the time vector

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as long as there remain individuals in the population, and as time is below the maximal time.

The simulations are coded in R, and are available upon request.

E Pair equations

We follow the dynamics of all pairs in the system. We first write them up without any approximation. These pair equations are only used to numerically solve the model (using the pair approximation, see section E.2), but they are not used in the derivation of the selection gradient, for which we only need the dynamics of $p_{S'}$ and $p_{I'}$ (singlets).

E.1 Pair equations without pair approximation

Each individual has n neighbors; let ϕ and $\bar{\phi}$ be

$$\phi = \frac{1}{n} \tag{E.1}$$

$$\bar{\phi} = \frac{n-1}{n} \tag{E.2}$$

We write p_{xy} the frequency of the pair xy. Here are some useful relations between pair frequencies:

$$p_{xy} = p_{yx} \tag{E.3}$$

$$\begin{aligned} & p_{\text{oo}} + p_{\text{SS}} + p_{\text{II}} + 2p_{\text{So}} + 2p_{\text{Io}} + 2p_{\text{SI}} \\ & + p_{\text{S'S'}} + p_{\text{I'I'}} + 2p_{\text{S'I'}} + 2p_{\text{I'o}} + 2p_{\text{S'o}} + 2p_{\text{SS'}} + 2p_{\text{SI'}} + 2p_{\text{IS'}} + 2p_{\text{II'}} \\ & = 1 \end{aligned} \tag{E.4}$$

As is the case in the main text, the prime $'$ characterizes a mutant.

Here is the list of all terms which create or destroy a given pair:

Pair oo

Creation	So	$\rightarrow$	oo	$+\,2\,d\,p_{\text{So}}$
	Io	$\rightarrow$	oo	$+\,2\,(d+\nu)\,p_{\text{Io}}$
	S'o	$\rightarrow$	oo	$+\,2\,d'\,p_{\text{S'o}}$
	I'o	$\rightarrow$	oo	$+\,2\,(d'+\nu')\,p_{\text{I'o}}$
Clearance	oo	$\rightarrow$	So	$-\,2\,\bar{\phi}\,b\,p_{\text{Soo}} - 2\,\bar{\phi}\,b_{\text{I}}\,p_{\text{Ioo}}$
	oo	$\rightarrow$	S'o	$-\,2\,\bar{\phi}\,b'\,p_{\text{S'oo}} - 2\,\bar{\phi}\,b'_{\text{I}}\,p_{\text{I'oo}}$

Pair s○

Creation	○○	$\to$	s○	$+\,\bar\phi\,b\,p_{\text{S}\circ\circ} + \bar\phi\,b_{\text{I}}\,p_{\text{I}\circ\circ}$
	ss	$\to$	s○	$+\,d\,p_{\text{SS}}$
	si	$\to$	s○	$+\,(d+\nu)\,p_{\text{SI}}$
	i○	$\to$	s○	$+\,\gamma\,p_{\text{I}\circ}$
	ss'	$\to$	s○	$+\,d'\,p_{\text{SS'}}$
	si'	$\to$	s○	$+\,(d'+\nu')\,p_{\text{SI'}}$
Clearance	s○	$\to$	○○	$-\,d\,p_{\text{S}\circ}$
	s○	$\to$	i○	$-\,\bar\phi\,\beta\,\alpha\,p_{\text{IS}\circ} - \bar\phi\,\beta'\,\alpha\,p_{\text{I'S}\circ}$
	s○	$\to$	ss	$-\,\big(\phi\,b\,p_{\text{S}\circ} + \bar\phi\,b\,p_{\text{S}\circ\text{S}}\big) - \bar\phi\,b_{\text{I}}\,p_{\text{I}\circ\text{S}}$
	s○	$\to$	ss'	$-\,\bar\phi\,b'\,p_{\text{S'}\circ\text{S}} - \bar\phi\,b'_{\text{I}}\,p_{\text{I'}\circ\text{S}}$

Pair ss

Creation	s○	$\to$	ss	$+\,2\,\big(\phi\,b\,p_{\text{S}\circ} + \bar\phi\,b\,p_{\text{S}\circ\text{S}}\big) + 2\,\bar\phi\,b_{\text{I}}\,p_{\text{I}\circ\text{S}}$
	si	$\to$	ss	$+\,2\,\gamma\,p_{\text{SI}}$
Clearance	ss	$\to$	s○	$-\,2\,d\,p_{\text{SS}}$
	ss	$\to$	si	$-\,2\,\bar\phi\,\beta\,\alpha\,p_{\text{ISS}} - 2\,\bar\phi\,\beta'\,\alpha\,p_{\text{I'SS}}$

Pair i○

Creation	s○	$\to$	i○	$+\,\bar\phi\,\beta\,\alpha\,p_{\text{IS}\circ}$
	si	$\to$	i○	$+\,d\,p_{\text{SI}}$
	ii	$\to$	i○	$+\,(d+\nu)\,p_{\text{II}}$
	is'	$\to$	i○	$+\,d'\,p_{\text{IS'}}$
	ii'	$\to$	i○	$+\,(d'+\nu')\,p_{\text{II'}}$
Clearance	i○	$\to$	○○	$-\,(d+\nu)p_{\text{I}\circ}$
	i○	$\to$	si	$-\,\bar\phi\,b\,p_{\text{S}\circ\text{I}} - \bar\phi\,b_{\text{I}}\,p_{\text{I}\circ\text{I}} - \phi\,b_{\text{I}}\,p_{\circ\text{I}}$
	i○	$\to$	s○	$-\,\gamma\,p_{\text{I}\circ}$
	i○	$\to$	is'	$-\,\big(\bar\phi\,b'\,p_{\text{S'}\circ\text{I}} + \bar\phi\,b'_{\text{I}}p_{\text{I'}\circ\text{I}}\big)$

Pair si

Creation	ss	$\to$	si	$+\,\bar\phi\,\beta\,\alpha\,p_{\text{ISS}} + \bar\phi\,\beta'\,\alpha\,p_{\text{I'SS}}$
	○i	$\to$	si	$+\,\bar\phi\,b\,p_{\text{S}\circ\text{I}} + \bar\phi\,b_{\text{I}}\,p_{\text{I}\circ\text{I}} + \phi\,b_{\text{I}}\,p_{\circ\text{I}}$
	ii	$\to$	si	$+\,\gamma\,p_{\text{II}}$
Clearance	si	$\to$	○i	$-\,d\,p_{\text{SI}}$
	si	$\to$	s○	$-\,(d+\nu)\,p_{\text{SI}}$
	si	$\to$	ii	$-\,\big(\bar\phi\beta\,\alpha p_{\text{ISI}} + \phi\,\beta\,\alpha p_{\text{SI}}\big) - \bar\phi\,\beta'\,\alpha\,p_{\text{I'SI}}$
	si	$\to$	ss	$-\,\gamma\,p_{\text{SI}}$

Pair ii

Creation	si	$\to$	ii	$+\,2\,\big(\bar\phi\,\beta\,\alpha\,p_{\text{ISI}} + \phi\,\beta\,\alpha\,p_{\text{SI}}\big)$
Clearance	ii	$\to$	i○	$-\,2\,(d+\nu)\,p_{\text{II}}$
	ii	$\to$	si	$-\,2\,\gamma\,p_{\text{II}}$

Pair s'o

Creation

oo	$\to$	s'o	$+\,\bar\phi\,b'\,p_{\text{s'oo}} + \bar\phi\,b'_{\text{I}}\,p_{\text{I'oo}}$
I'o	$\to$	s'o	$+\,\gamma'\,p_{\text{I'o}}$
ss'	$\to$	s'o	$+\,d\,p_{\text{ss'}}$
Is'	$\to$	s'o	$+\,(d+\nu)\,p_{\text{Is'}}$
s's'	$\to$	s'o	$+\,d'\,p_{\text{s's'}}$
s'I'	$\to$	s'o	$+\,(d'+\nu')\,p_{\text{s'I'}}$

Clearance

s'o	$\to$	I'o	$-\left(\bar\phi\,\beta\,\alpha'\,p_{\text{Is'o}} + \bar\phi\,\beta'\,\alpha'\,p_{\text{I's'o}}\right)$
s'o	$\to$	oo	$-d'\,p_{\text{s'o}}$
s'o	$\to$	s's'	$-\left(\phi\,b'\,p_{\text{s'o}} + \bar\phi\,b'\,p_{\text{s'os'}} + \bar\phi b'_{\text{I}}\,p_{\text{I'os'}}\right)$
s'o	$\to$	ss'	$-\left(\bar\phi\,b\,p_{\text{sos'}} + \bar\phi\,b_{\text{I}}\,p_{\text{Ios'}}\right)$

Pair s's'

Creation

s'o	$\to$	s's'	$+2\left(\phi\,b'\,p_{\text{s'o}} + \bar\phi\,b'\,p_{\text{s'os'}} + \bar\phi\,b'_{\text{I}}\,p_{\text{I'os'}}\right)$
s'I'	$\to$	s's'	$+2\,\gamma'\,p_{\text{s'I'}}$

Clearance

s's'	$\to$	s'o	$-2\,d'\,p_{\text{s's'}}$
s's'	$\to$	s'I'	$-2\left(\bar\phi\,\beta\,\alpha'\,p_{\text{Is's'}} + \bar\phi\,\beta'\,\alpha'\,p_{\text{I's's'}}\right)$

Pair I'o

Creation

s'o	$\to$	I'o	$+\,\bar\phi\,\beta\,\alpha'\,p_{\text{Is'o}} + \bar\phi\,\beta'\,\alpha'\,p_{\text{I's'o}}$
sI'	$\to$	I'o	$+\,d\,p_{\text{sI'}}$
II'	$\to$	I'o	$+\,(d+\nu)\,p_{\text{II'}}$
s'I'	$\to$	I'o	$+\,d'\,p_{\text{s'I'}}$
I'I'	$\to$	I'o	$+\,(d'+\nu')\,p_{\text{I'I'}}$

Clearance

I'o	$\to$	oo	$-(d'+\nu')\,p_{\text{I'o}}$
I'o	$\to$	s'o	$-\gamma'\,p_{\text{I'o}}$
I'o	$\to$	sI'	$-\left(\bar\phi\,b\,p_{\text{soI'}} + \bar\phi\,b_{\text{I}}\,p_{\text{IoI'}}\right)$
I'o	$\to$	s'I'	$-\left(\phi\,b'_{\text{I}}\,p_{\text{I'o}} + \bar\phi\,b'_{\text{I}}\,p_{\text{I'oI'}} + \bar\phi\,b'\,p_{\text{s'oI'}}\right)$

Pair s'I'

Creation

I'o	$\to$	s'I'	$+\,\phi\,b'_{\text{I}}\,p_{\text{I'o}} + \bar\phi\,b'_{\text{I}}\,p_{\text{I'oI'}} + \bar\phi\,b'\,p_{\text{s'oI'}}$
I'I'	$\to$	s'I'	$+\,\gamma'\,p_{\text{I'I'}}$
s's'	$\to$	s'I'	$+\,\bar\phi\,\beta\,\alpha'\,p_{\text{Is's'}} + \bar\phi\,\beta'\,\alpha'\,p_{\text{I's's'}}$

Clearance

s'I'	$\to$	s'o	$-(d'+\nu')\,p_{\text{s'I'}}$
s'I'	$\to$	I'o	$-d'\,p_{\text{s'I'}}$
s'I'	$\to$	I'I'	$-\left(\phi\,\beta'\,\alpha'\,p_{\text{s'I'}} + \bar\phi\,\beta'\,\alpha'\,p_{\text{I's'I'}} + \bar\phi\,\beta\,\alpha'\,p_{\text{Is'I'}}\right)$
s'I'	$\to$	s's'	$-\gamma'\,p_{\text{s'I'}}$

Pair I'I'

Creation

s'I'	$\to$	I'I'	$+2\left(\phi\,\beta'\,\alpha'\,p_{\text{s'I'}} + \bar\phi\,\beta'\,\alpha'\,p_{\text{I's'I'}} + \bar\phi\,\beta\,\alpha'\,p_{\text{Is'I'}}\right)$

Clearance

I'I'	$\to$	I'o	$-2\,(d'+\nu')\,p_{\text{I'I'}}$
I'I'	$\to$	s'I'	$-2\,\gamma'\,p_{\text{I'I'}}$

Pair SS'

Creation	So	$\to$	SS'	$+\,\bar{\phi}\,b'\,p_{\text{S'oS}} + \bar{\phi}\,b'_{\text{I}}\,p_{\text{I'oS}}$

Creation   So $\to$ SS' $+\,\bar{\phi}\,b'\,p_{\text{S'oS}} + \bar{\phi}\,b'_{\text{I}}\,p_{\text{I'oS}}$

  S'o $\to$ SS' $+\,\bar{\phi}\,b\,p_{\text{SoS'}} + \bar{\phi}\,b_{\text{I}}\,p_{\text{IoS'}}$

  SI' $\to$ SS' $+\,\gamma'\,p_{\text{SI'}}$

  IS' $\to$ SS' $+\,\gamma\,p_{\text{IS'}}$

Clearance   SS' $\to$ So $-\,d'\,p_{\text{SS'}}$

  SS' $\to$ S'o $-\,d\,p_{\text{SS'}}$

  SS' $\to$ IS' $-\left(\bar{\phi}\,\beta\,\alpha\,p_{\text{ISS'}} + \bar{\phi}\,\beta'\,\alpha\,p_{\text{I'SS'}}\right)$

  SS' $\to$ SI' $-\left(\bar{\phi}\,\beta\,\alpha'\,p_{\text{IS'S}} + \bar{\phi}\,\beta'\,\alpha'\,p_{\text{I'S'S}}\right)$

Pair SI'

Creation   SS' $\to$ SI' $+\,\bar{\phi}\,\beta\,\alpha'\,p_{\text{IS'S}} + \bar{\phi}\,\beta'\,\alpha'\,p_{\text{I'S'S}}$

  I'o $\to$ SI' $+\,\bar{\phi}\,b\,p_{\text{SoI'}} + \bar{\phi}\,b_{\text{I}}\,p_{\text{IoI'}}$

  II' $\to$ SI' $+\,\gamma\,p_{\text{I'I}}$

Clearance   SI' $\to$ So $-\left(d' + \nu'\right)p_{\text{SI'}}$

  SI' $\to$ SS' $-\,\gamma'\,p_{\text{SI'}}$

  SI' $\to$ II' $-\left(\phi\,\beta'\,\alpha\,p_{\text{SI'}} + \bar{\phi}\,\beta'\,\alpha\,p_{\text{I'SI'}} + \bar{\phi}\,\beta\,\alpha\,p_{\text{ISI'}}\right)$

  SI' $\to$ I'o $-\,p_{\text{SI'}}$

Pair IS'

Creation   Io $\to$ IS' $+\,\bar{\phi}\,b'\,p_{\text{S'oI}} + \bar{\phi}\,b'_{\text{I}}\,p_{\text{I'oI}}$

  II' $\to$ IS' $+\,\gamma'\,p_{\text{II'}}$

  SS' $\to$ IS' $+\,\bar{\phi}\,\beta\,\alpha\,p_{\text{ISS'}} + \bar{\phi}\,\beta'\,\alpha\,p_{\text{I'SS'}}$

Clearance   IS' $\to$ Io $-\,d'\,p_{\text{IS'}}$

  IS' $\to$ II' $-\left(\phi\,\beta\,\alpha'\,p_{\text{IS'}} + \bar{\phi}\,\beta\,\alpha'\,p_{\text{IS'I}} + \bar{\phi}\,\beta'\,\alpha'\,p_{\text{I'S'I}}\right)$

  IS' $\to$ S'o $-\left(d + \nu\right)p_{\text{IS'}}$

  IS' $\to$ SS' $-\,\gamma\,p_{\text{IS'}}$

Pair II'

Creation   SI' $\to$ II' $+\,\phi\beta'\,\alpha\,p_{\text{SI'}} + \bar{\phi}\,\beta'\,\alpha\,p_{\text{I'SI'}} + \bar{\phi}\,\beta\,\alpha\,p_{\text{ISI'}}$

  IS' $\to$ II' $+\,\phi\,\beta\,\alpha'\,p_{\text{IS'}} + \bar{\phi}\,\beta\,\alpha'\,p_{\text{IS'I}} + \bar{\phi}\,\beta'\,\alpha'\,p_{\text{I'S'I}}$

Clearance   II' $\to$ Io $-\left(d' + \nu'\right)p_{\text{II'}}$

  II' $\to$ I'o $-\left(d + \nu\right)p_{\text{II'}}$

  II' $\to$ IS' $-\,\gamma'\,p_{\text{II'}}$

  II' $\to$ I'S $-\,\gamma\,p_{\text{II'}}$

To obtain the dynamics of each pair, we sum up all the terms which create or destroy the pair. For instance (see the bookkeeping for **Pair** oo)

$$\frac{dp_{\text{oo}}}{dt} = +\,2\,d\,p_{\text{So}} + 2\left(d + \nu\right)p_{\text{Io}} + 2\,d'\,p_{\text{S'o}} + 2\left(d' + \nu'\right)p_{\text{I'o}}$$
$$-\,2\,\bar{\phi}\,b\,p_{\text{Soo}} - 2\,\bar{\phi}\,b_{\text{I}}\,p_{\text{Ioo}} - 2\,\bar{\phi}\,b'\,p_{\text{S'oo}} - 2\,\bar{\phi}\,b'_{\text{I}}\,p_{\text{I'o}}$$

(E.5)

E.2 Pair approximation

The above system of pair equations is not closed: there are more unknowns than equations. The pair approximation is a way to close the system. It consists in assuming that $q_{z|xy} \approx q_{z|x}$, *i.e.,* that the local density of z individuals in the neighborhood of the x individual of a xy pair is equivalent to the local density of z individuals in the neighborhood of the x individual of any pair. We use this approximation to simplify the expression of triplets; for instance:

$$
\begin{aligned}
p_{\text{Soo}} &= q_{\text{S}|\text{oo}}\, p_{\text{oo}} \\
&\approx q_{\text{S}|\text{o}}\, p_{\text{oo}} \\
&= \frac{p_{\text{So}}}{p_{\text{o}}}\, p_{\text{oo}} \\
&= \frac{p_{\text{So}}}{p_{\text{oo}} + p_{\text{So}} + p_{\text{Io}} + p_{\text{S'o}} + p_{\text{I'o}}}\, p_{\text{oo}}
\end{aligned}
\tag{E.6}
$$

E.3 Evaluating the q^*, $\bar{q}$ and ∂q

Equilibrium local densities and changes in local densities appear in our expression of the selection gradient for the spatial model (B.17). We estimate them numerically, using the pair approximation.

We first run the pair approximation model with only one host type, and deduce from it the equilibrium local densities q^*. Then, we run the pair approximation model with this host type (resident) at its equilibrium with an initially rare neutral mutant. A neutral mutant has exactly the same traits as the resident, but wears a cost-free tag which makes it different. We deduce from this the local densities $\bar{q}$. Finally, we run the pair approximation model with the resident at its equilibrium and an initially rare non neutral mutant (close to the resident); we estimate the local densities, and using the results with the neutral mutant, we deduce the ∂q.

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