

1 Description of the analytical model

For a full overview of the modeling approach, one can consult the Supplementary Mathematica sheet. The analysis below is largely based on a previous model [1], which itself has been based on continuous-time models by [2], [3] and, in particular, [4].

1.1 General approach

We first work out the ecological dynamic, which consists of solving for the equilibria of (i) patch frequencies, (ii) reproductive values and (iii) relatedness coefficients between the different types of individuals. Subsequently, we (iv) derive selection gradients which reflect how epigenetic resetting phenotypes are changed through the successive invasion of mutants of slight effect. Here we note that the ecological dynamic is updated upon each successful invasion of a novel epigenetic resetting phenotype. Table 1 provides an overview of the different symbols used.

1.2 Patch frequencies

We consider a population in which there are two breeders per patch, each of which can have one of two different phenotypes $z_i \in \{z_1, z_2\}$. Consequently, there are three configurations of breeder phenotypes in each local environment (both have phenotype z_1 ; one has phenotype z_1 and one has phenotype z_2 ; both have phenotype z_2). Finally, there are two local environmental states $e_i \in \{e_1, e_2\}$, thus resulting in 6 different patch frequencies.

We first derive an expression for the total number of competing juveniles $c(n_a, e_i)$ who compete for a vacant breeding position in a patch which originally contained n_a adapted breeders (preceding mortality events) and $n - n_a$ maladapted breeders in an e_i environment:

$$c(n_a, e_i) = (1-d) [n_a B_{z_i e_i} + (n - n_a) B_{z_j e_i}] + d \sum_{\nu_a=0}^n \sum_{e_k \in \{e_1, e_2\}} f(\nu_a, e_k) [\nu_a B_{z_k e_k} + (n - \nu_a) B_{z_\ell e_k}], \quad (1)$$

where the first part reflects the total number of philopatric offspring born in the n_a, e_i -patch, either born from the n_a adapted parents who have fecundity $B_{z_i e_i}$ or from the $n - n_a$ maladapted parents who have fecundity $B_{z_j e_i}$ ($j \neq i$). The second part reflects the total number of immigrant offspring, born on remote patches containing $0 \leq \nu_a \leq \nu$ adapted breeders (and $n - \nu_a$ maladapted breeders) whilst in environmental state e_k , at frequency $f(\nu_a, e_k)$. Here we denote the phenotype of adapted breeders (matching environment e_k) with z_k , while maladapted breeders are denoted by phenotype z_ℓ .

Next, $l_a(n_a, e_i)$ or $l_m(n_a, e_i)$ reflect the probabilities that local breeders in a n_a, e_i patch produce a offspring that successfully establishes itself as a breeder, and is locally adapted or maladapted respectively:

$$l_a(n_a, e_i) = \frac{(1-d) [n_a B_{z_i e_i} \pi_{z_i \rightarrow z_i} + (n - n_a) B_{z_j e_i} \pi_{z_j \rightarrow z_i}]}{c(n_a, e_i)} \quad (2)$$

$$l_m(n_a, e_i) = \frac{(1-d) [n_a B_{z_i e_i} \pi_{z_i \rightarrow z_j} + (n - n_a) B_{z_j e_i} \pi_{z_j \rightarrow z_j}]}{c(n_a, e_i)}. \quad (3)$$

In the expression above, $\pi_{z_i \rightarrow z_j} \equiv \pi_{z_i \rightarrow z_j}(p_1, p_2)$ is the inheritance function which determines the probability that a z_j offspring is born from an adult breeder with phenotype z_i , which depends on the probability p_i that a z_i breeder produces z_1 offspring in the next generation. We then have

$$\pi_{z_1 \rightarrow z_1} = p_1 \quad (4a)$$

$$\pi_{z_1 \rightarrow z_2} = 1 - p_1 \quad (4b)$$

$$\pi_{z_2 \rightarrow z_1} = p_2 \quad (4c)$$

$$\pi_{z_2 \rightarrow z_2} = 1 - p_2. \quad (4d)$$

Table 1: An overview of the notation used.

symbol	definition
$B_{z_i e_i}$	Fecundity of a locally adapted parent with phenotype z_i in environment e_i , where $B_{z_j e_i} \leq B_{z_i e_i}$ ($i \neq j$)
d	Juvenile migration probability
e_i	State of local environment
$f(n_a, e_i)$	Frequency of patches that contain n_a adapted breeders and are in local environmental state e_i
$M_{z_i e_i}$	Mortality rate of an individual with phenotype z_i in environment e_i , where $M_{z_j e_i} \geq M_{z_i e_i}$ ($i \neq j$)
n	Number of breeders in the local patch, where we assume $n = 2$ throughout.
n_a	Number of adult breeders which have a phenotype that matches local conditions, where $0 \leq n_a \leq n$
\hat{n}_a	Number of nonfocal adult breeders which have a phenotype that matches local conditions, where $0 \leq \hat{n}_a \leq n - 1$
$\pi_{z_j \rightarrow z_i}$	Probability that individual with phenotype z_j produces an individual with phenotype z_i .
p_i	Probability that a breeder with phenotype z_i produces z_1 offspring
$r_{xy}(n_a, e_i)$	Relatedness between an individual in state x and another in state y in patch with n_a locally adapted breeders and in local environmental state e_i . Here, $x, y \in \{a, m\}$ (adapted or maladapted)
$s_{e_j \rightarrow e_i}$	Rate at which any patch changes from environmental state e_j to e_i , $0 \leq s_{e_j \rightarrow e_i} \leq \infty$.
$\psi_{x \rightarrow y}$	probability that an adult breeder in environment e_i and in state x produces offspring in state y
z_i	Individual's phenotype (z_1 or z_2)
$v(x, \hat{n}_a, e_i)$	Reproductive value of a focal individual in locally adapted state $x \in \{a, m\}$ (adapted, maladapted) whilst living with \hat{n}_a nonfocal adapted individuals in patch in environmental state e_i

While eq. (4) considers the transmission probability conditioned on phenotype, sometimes it will be more convenient to consider the probability $\psi_{x \rightarrow y}(e_i)$ that a parent living in environment e_i and in state x produces an offspring in state y in that same environment, where $x, y \in \{a, m\}$ (adapted, maladapted). Consequently, we have

$$\psi_{a \rightarrow a}(e_1) = \psi_{m \rightarrow m}(e_2) = \pi_{z_1 \rightarrow z_1} = p_1 \quad (5a)$$

$$\psi_{a \rightarrow m}(e_1) = \psi_{m \rightarrow a}(e_2) = \pi_{z_1 \rightarrow z_2} = 1 - p_1 \quad (5b)$$

$$\psi_{m \rightarrow a}(e_1) = \psi_{a \rightarrow m}(e_2) = \pi_{z_2 \rightarrow z_1} = p_2 \quad (5c)$$

$$\psi_{m \rightarrow m}(e_1) = \psi_{a \rightarrow a}(e_2) = \pi_{z_2 \rightarrow z_2} = 1 - p_2. \quad (5d)$$

Next to the probabilities of successful establishment of locally born offspring in eqns (2,3), $\tilde{l}_a(n_a, e_i)$ or $\tilde{l}_m(n_a, e_i)$ reflect the probabilities that a remotely born offspring successfully establishes itself as a breeder in a n_a, e_i -patch, to which it is locally adapted or maladapted respectively:

$$\tilde{l}_a(n_a, e_i) = \frac{d \sum_{\nu_a=0}^n \sum_{e_k \in \{e_1, e_2\}} f(\nu_a, e_k) [\nu_a B_{z_k e_k} \pi_{z_k \rightarrow z_i} + (n - \nu_a) B_{z_\ell e_k} \pi_{z_\ell \rightarrow z_i}]}{c(n_a, e_i)} \quad (6)$$

$$\tilde{l}_m(n_a, e_i) = \frac{d \sum_{\nu_a=0}^n \sum_{e_k \in \{e_1, e_2\}} f(\nu_a, e_k) [\nu_a B_{z_k e_k} \pi_{z_k \rightarrow z_j} + (n - \nu_a) B_{z_\ell e_k} \pi_{z_\ell \rightarrow z_j}]}{c(n_a, e_i)}. \quad (7)$$

We then have the following differential equation reflecting the instantaneous change in the frequency $f(n_a, e_i)$ of patches containing n_a adapted breeders and currently in state e_i :

$$\begin{aligned} \frac{df(n_a, e_i)}{dt} = & s_{e_j \rightarrow e_i} f(n - n_a, e_j) - s_{e_i \rightarrow e_j} f(n_a, e_i) \\ & - f(n_a, e_i) n_a M_{z_i e_i} [l_m(n_a, e_i) + \tilde{l}_m(n_a, e_i)] \\ & - f(n_a, e_i) (n - n_a) M_{z_j e_i} [l_a(n_a, e_i) + \tilde{l}_a(n_a, e_i)] \\ & + f(n_a + 1, e_i) (n_a + 1) M_{z_i e_i} [l_m(n_a + 1, e_i) + \tilde{l}_m(n_a + 1, e_i)] \\ & + f(n_a - 1, e_i) (n - n_a - 1) M_{z_j e_i} [l_a(n_a - 1, e_i) + \tilde{l}_a(n_a - 1, e_i)], \end{aligned} \quad (8)$$

where the first line reflects any changes due to switches in patch environment, the next two lines reflect removal of n_a, e_i due to a death of an adapted breeder (at rate $M_{z_i e_i}$) or a maladapted breeder (at rate $M_{z_j e_i}$, where $i \neq j$) respectively. The adapted breeder is then replaced by a maladapted breeder at probability $l_m(n_a, e_i) + \tilde{l}_m(n_a, e_i)$, while the maladapted breeder is replaced by an adapted breeder at probability $l_a(n_a, e_i) + \tilde{l}_a(n_a, e_i)$. Note that cases where a dead breeder is replaced by a juvenile of the same phenotype have no effect on the resulting dynamics.

Similarly, the last two lines reflect the case where the number of n_a, e_i patches is increased. This can either be due to a death of an adapted breeder and replacement by a maladapted individual in a patch containing $0 \leq n_a + 1 \leq n$ adapted breeders, or by the death of a maladapted breeder and replacement by an adapted individual in a patch containing $0 \leq n_a - 1 \leq n$ adapted breeders. Equation (8) then results in a system of $(n + 1) \times 2$ differential equations denoted by $\dot{\mathbf{f}}$ for all possible combinations of $0 \leq n_a \leq n$ adapted breeders and $e_i = \{e_1, e_2\}$ patch environments. As noted in the main text, these differential equations are then numerically solved for the point where $\dot{\mathbf{f}} = 0$.

1.3 Reproductive values

Similarly, we can derive the dynamics of the reproductive value $v(x, \hat{n}_a, e_i)$ necessary to derive selection gradients. The arguments of $v(x, \hat{n}_a, e_i)$ denote, respectively, the state $x \in \{a, m\}$ of the focal individual, where a denotes adapted and m denotes maladapted, $0 \leq \hat{n}_a \leq n - 1$ the number of adapted breeders other than the focal, where the focal lives in a e_i -patch. Let $L_{x \rightarrow y}(\hat{n}_a, e_i)$ then reflect the probability that the focal in state x produces a philopatric offspring in state y who successfully establishes itself in the local patch, conditional upon the availability of a breeding position. We then have

$$L_{x \rightarrow y}(\hat{n}_a, e_i) = \frac{(1 - d) B_{x e_i} \psi_{x \rightarrow y}(e_i)}{c(\hat{n}_a + \delta_{x=a}, e_i)}, \quad (9)$$

where the total number of competing juvenile offspring $c(\hat{n}_a + \delta_{x=a}, e_i)$ is again given by eq. (1), where $\delta_{x=a} = 1$ when the focal breeder is maladapted and $\delta_{x=a} = 0$ otherwise.

Similarly, let $\mathcal{O}_y(\hat{n}_a, e_i)$ reflect the probability that any non-focal breeder produces an offspring in state y who successfully establishes itself in the local patch, conditional upon the availability of a breeding position. We then have

$$\begin{aligned} \mathcal{O}_y(\hat{n}_a, e_i) = & (1-d) \frac{\hat{n}_a B_{z_i e_i} \psi_{a \rightarrow y}(e_i) + (n-1-\hat{n}_a) B_{z_j e_i} \psi_{m \rightarrow y}(e_i)}{c(\hat{n}_a + \delta_{x=a}, e_i)}, \\ & + d \frac{\sum_{\nu_a=0}^n \sum_{e_k=\{e_1, e_2\}} f(\nu_a, e_k) [\nu_a B_{z_k e_k} \psi_{a \rightarrow y}(e_k) + (n-\nu_a) B_{z_\ell e_k} \psi_{m \rightarrow y}(e_k)]}{c(\hat{n}_a + \delta_{x=a}, e_i)}, \end{aligned} \quad (10)$$

where the first part reflects the successful establishment of philopatric offspring in state y born from the \hat{n}_a locally breeding (nonfocal) adapted breeders and maladapted breeders. The second part reflects the production of immigrant offspring in state y born from adapted and maladapted parents in remote patches.

As an example, we provide a differential equation describing the instantaneous change in reproductive value of a focal adapted individual (state a), living in a patch with $0 \leq \hat{n}_a \leq n-1$ adapted nonfocal neighbours, which is in environmental state e_i . Following [4], we have

$$\begin{aligned} \frac{dv(a, \hat{n}_a, e_i)}{dt} = & \Delta_1 v(a, \hat{n}_a, e_i) + \Delta_2 v(a, \hat{n}_a, e_i) + \Delta_3 v(a, \hat{n}_a, e_i) \\ & + \Delta_4 v(a, \hat{n}_a, e_i) + \Delta_5 v(a, \hat{n}_a, e_i) + \Delta_6 v(a, \hat{n}_a, e_i) \end{aligned} \quad (11)$$

where the $\Delta_i v(a, \hat{n}_a, e_i)$ s indicate the six different events that result in an instantaneous changes of a focal's reproductive value. These events are: 1. environmental change; 2. death of focal; 3. death of a nonfocal who is adapted and replacement by one of the focal's offspring; 4. death of a neighbour who is maladapted and replacement by one of the focal's offspring; 5. death of a neighbour and replacement by nonfocal offspring in a different state than its predecessor; 6. changes in reproductive value due to establishment of focal offspring in remote patches.

The first event is environmental change, so that

$$\Delta_1 v(a, \hat{n}_a, e_i) = s_{e_j \rightarrow e_i} [v(m, n - \hat{n}_a - 1, e_j) - v(a, \hat{n}_a, e_i)], \quad (12)$$

reflecting the change in reproductive value due to environmental switching $s_{e_j \rightarrow e_i}$, resulting in a change in reproductive value from $v(a, \hat{n}_a, e_i)$ to $v(m, n - \hat{n}_a - 1, e_j)$ as the adapted focal now becomes maladapted, its \hat{n}_a adapted neighbours become maladapted, while the focal's $n - \hat{n}_a - 1$ maladapted neighbours (all individuals minus the focal (-1) minus the \hat{n}_a adapted neighbours) become adapted and the environmental state changes to e_j .

The second event is the change in reproductive value due to death (and subsequent replacement) of the adapted focal individual:

$$\begin{aligned} \Delta_2 v(a, \hat{n}_a, e_i) = & M_{z_i e_i} L_{a \rightarrow m}(\hat{n}_a, e_i) [v(m, \hat{n}_a, e_i) - v(a, \hat{n}_a, e_i)] \\ & + M_{z_i e_i} [\mathcal{O}_a(\hat{n}_a, e_i) + \mathcal{O}_m(\hat{n}_a, e_i)] [-v(a, \hat{n}_a, e_i)], \end{aligned} \quad (13)$$

where the focal adapted breeder dies (at rate $M_{z_i e_i}$) after which it is either replaced by one of the focal's own maladapted offspring (first line) or a nonfocal offspring (second line), that is either adapted (with probability $\mathcal{O}_a(\hat{n}_a, e_i)$) or maladapted (with probability $\mathcal{O}_m(\hat{n}_a, e_i)$). In case the dead focal is replaced by any nonfocal offspring, the focal's new reproductive value is 0, so the effective change in reproductive value is $-v(a, \hat{n}_a, e_i)$.

Next, $\Delta_3 v(a, \hat{n}_a, e_i)$ reflects the change of a focal's reproductive value due to the death of any nonfocal adapted individual, at rate $\hat{n}_a M_{z_i e_i}$ and replacement by one of the focal's offspring:

$$\begin{aligned} \Delta_3 v(a, \hat{n}_a, e_i) = & \hat{n}_a M_{z_i e_i} \{ L_{a \rightarrow a}(\hat{n}_a, e_i) v(a, \hat{n}_a - 1 + \delta_{x=a}, e_i) \\ & + L_{a \rightarrow m}(\hat{n}_a, e_i) [v(m, \hat{n}_a - 1 + \delta_{x=a}, e_i) + v(a, \hat{n}_a - 1, e_i) - v(a, \hat{n}_a, e_i)] \}. \end{aligned} \quad (14)$$

With probability $L_{a \rightarrow a}(\hat{n}_a, e_i)$ the focal's offspring is adapted, and this newly established offspring has reproductive value $v(a, \hat{n}_a - 1 + \delta_{x=a}, e_i)$. Here, $\hat{n}_a - 1 + \delta_{x=a}$ reflects the total number of other adapted breeders in the patch apart from the focal's offspring itself, which is \hat{n}_a minus the adapted nonfocal breeder who died, plus the phenotype $\delta_{x=a}$ of the focal breeder. Note that the reproductive value of the focal breeder itself is unchanged, because the successful establishment of its adapted offspring results in the same number of \hat{n}_a adapted nonfocal breeders as experienced by the focal breeder. Alternatively, with probability $L_{a \rightarrow m}(\hat{n}_a, e_i)$ the focal's offspring is maladapted. In this case the reproductive value of this offspring is $v(m, \hat{n}_a - 1 + \delta_{x=a}, e_i)$ while the reproductive value of the focal itself is now $v(a, \hat{n}_a - 1, e_i)$ where $\hat{n}_a - 1$ is now the total number of nonfocal adapted individuals.

Next, $\Delta_4 v(a, \hat{n}_a, e_i)$ reflects the change of a focal's reproductive value due to the death of any nonfocal maladapted individual, at rate $(n - 1 - \hat{n}_a)$ and replaced by a focal's offspring:

$$\begin{aligned} \Delta_4 v(a, \hat{n}_a, e_i) = & (n - 1 - \hat{n}_a) M_{z_i e_i} \{ L_{a \rightarrow a}(\hat{n}_a, e_i) [v(a, \hat{n}_a + \delta_{x=a}, e_i) + v(a, \hat{n}_a + 1, e_i) - v(a, \hat{n}_a, e_i)] \\ & + L_{a \rightarrow m}(\hat{n}_a, e_i) [v(m, \hat{n}_a - 1 + \delta_{x=a}, e_i) + v(a, \hat{n}_a - 1, e_i)] - v(a, \hat{n}_a, e_i) \}, \end{aligned} \quad (15)$$

where the derivation follows the same logic as for eq. (14).

Next, $\Delta_5 v(a, \hat{n}_a, e_i)$ reflects the change in a focal's reproductive value by the death of a nonfocal adult breeder (either one of the \hat{n}_a nonfocal adapted breeders or one of the $n - 1 - \hat{n}_a$ maladapted breeders respectively), while being replaced by a nonfocal offspring who is maladapted or adapted respectively:

$$\begin{aligned} \Delta_5 v(a, \hat{n}_a, e_i) = & \hat{n}_a M_{z_i e_i} \mathcal{O}_m(\hat{n}_a, e_i) [v(a, \hat{n}_a - 1, e_i) - v(a, \hat{n}_a, e_i)] \\ & + (n - 1 - \hat{n}_a) M_{z_i e_i} \mathcal{O}_a(\hat{n}_a, e_i) [v(a, \hat{n}_a + 1, e_i) - v(a, \hat{n}_a, e_i)], \end{aligned} \quad (16)$$

where change in reproductive value occurs as the focal now experiences a different number of nonfocal adapted breeders than before.

Finally, $\Delta_6 v(a, \hat{n}_a, e_i)$ reflects the increase in reproductive value due to the focal's offspring taking up breeding positions in remote patches, where positions are vacated by mortalities of adapted and maladapted breeders in remote patches containing ν_a adapted breeders in environmental state e_k :

$$\begin{aligned} \Delta_6 v(a, \hat{n}_a, e_i) = & dB_{z_i e_i} \sum_{\nu_a=0}^n \sum_{e_k=\{e_1, e_2\}} \frac{f(\nu_a, e_k)}{c(\nu_a, e_k)} \\ & \times \{ \nu_a M_{z_k e_k} [\psi_{a \rightarrow a}(e_i) v(a, \nu_a - 1, e_k) + \psi_{a \rightarrow m}(e_i) v(m, \nu_a - 1, e_k)] \\ & + (n - \nu_a) M_{z_j e_k} [\psi_{a \rightarrow a}(e_i) v(a, \nu_a, e_k) + \psi_{a \rightarrow m}(e_i) v(m, \nu_a, e_k)] \}, \end{aligned} \quad (17)$$

where d reflects the probability that a focal's offspring migrates to any remote patch, $B_{z_i e_i}$ the adapted focal's fecundity. The probability of arriving on a e_k -patch containing ν_a adapted breeders is then given by the patch frequency $f(\nu_a, e_k)$, where we take averages by summing over all possible patch combinations. On the remote ν_a, e_k -patch, juvenile offspring successfully compete with a total number of $c(\nu_a, e_k)$ offspring (see eq. [1]). At rate $\nu_a M_{z_k e_k}$, one of the adapted breeders dies in the remote patch: in this case, the focal's offspring is adapted to the remote site with probability $\psi_{a \rightarrow a}(e_i)$ or maladapted with probability $\psi_{a \rightarrow m}(e_i)$, resulting in the respective reproductive values $v(a, \nu_a - 1, e_k)$ and $v(m, \nu_a - 1, e_k)$ (the $\nu_a - 1$ denotes the fact that due to the mortality event, one fewer adapted breeder accompanies the focal's offspring in the remote site). Similar arguments ensue in case one of the $n - \nu_a$ maladapted breeders dies in the remote site.

In total, the Mathematica sheet describes a system of $2 \times n \times 2$ equations for the instantaneous change in reproductive value, reflecting the two different states $x \in \{a, m\}$ of a focal individual, times the total number of combinations of nonfocal adapted individuals (where $\hat{n}_a \in \{0, 1, \dots, n - 1\}$) times the two environments e_1, e_2 .

1.4 Relatedness

As we deal with populations characterized by limited dispersal, we need to consider relatedness among interacting individuals. To this end, $r_{xy}(n_a, e_i)$ tracks relatedness between two adapted individuals (one

in state $x \in \{a, m\}$, the other in state $y \in \{a, m\}$) in a patch containing a total of n_a adapted individuals and in environmental state e_i .

To arrive at expressions for the relatedness coefficients, we first derive the probability $\mathcal{L}_{a \rightarrow y}(n_a, e_i)$ (or $\mathcal{L}_{m \rightarrow y}(n_a, e_i)$) that a newly established individual in state y is born from one of the locally adapted (or maladapted) breeders:

$$\mathcal{L}_{a \rightarrow y}(n_a, e_i) = \frac{(1-d)n_a B_{z_i e_i} \psi_{a \rightarrow y}(e_i)}{c(n_a, e_i)} \quad (18)$$

$$\mathcal{L}_{m \rightarrow y}(n_a, e_i) = \frac{(1-d)(n-n_a) B_{z_j e_i} \psi_{m \rightarrow y}(e_i)}{c(n_a, e_i)}. \quad (19)$$

We then provide an equilibrium condition for the instantaneous change in relatedness $r_{aa}(n_a, e_i)$ between two adapted individuals, with similar expressions for $r_{am}(n_a, e_i)$ and $r_{mm}(n_a, e_i)$ provided in the online Mathematica sheet. At equilibrium, the instantaneous change in relatedness, given by rather of change of in total four events should vanish, or

$$\frac{dr_{aa}(n_a, e_i)}{dt} = \Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 = 0, \quad (20)$$

where the first event reflects the instantaneous change due to environmental switching

$$\Delta_1 = s_{e_j \rightarrow e_i} f(n-n_a, e_j) [r_{mm}(n-n_a, e_j) - r_{aa}(n_a, e_i)], \quad (21)$$

where a gain in relatedness among maladapted individuals in an e_j environment, $r_{mm}(n-n_a, e_j)$, occurs due to environmental change of e_j to e_i . However, as we are at equilibrium (i.e., $dr_{aa}(n_a, e_i)/dt = 0$), this gain has to be matched by an equal loss in relatedness $-r_{aa}(n_a, e_i)$.

Next, change in $r_{aa}(n_a, e_i)$ occurs to the death of a maladapted individual and replacement by an adapted individual in a $n_a - 1, e_i$ patch:

$$\begin{aligned} \Delta_2 = & f(n_a - 1, e_i)(n - (n_a - 1)) M_{z_j e_i} [l_a(n_a - 1, e_i) + \tilde{l}_a(n_a - 1, e_i)] \\ & \times \left\{ \frac{n_a - 2}{n_a} r_{aa}(n_a - 1, e_i) \right. \\ & + \frac{2}{n_a} \left[\mathcal{L}_{a \rightarrow a}(n_a - 1, e_i) \left(\frac{1}{n_a - 1} + \frac{n_a - 2}{n_a - 1} r_{aa}(n_a - 1, e_i) \right) + \mathcal{L}_{m \rightarrow a}(n_a - 1, e_i) r_{ma}(n_a - 1, e_i) \right] \\ & \left. - r_{aa}(n_a, e_i) \right\} \end{aligned} \quad (22)$$

Deaths of maladapted individuals in a $n_a - 1$ patch occur at rate $(n_a - 1) M_{z_j e_i}$. Replacement by a newly established adapted individual occurs with probability $l_a(n_a - 1, e_i) + \tilde{l}_a(n_a - 1, e_i)$, see eqns. [2,6]. With probability $(n_a - 1)/n_a \times (n_a - 2)/(n_a - 1) = (n_a - 2)/n_a$ one samples a pair of adapted individuals which do not involve the newly established breeder, in which case relatedness among sampled individuals is given by $r_{aa}(n_a - 1, e_i)$. Alternatively, with probability $1 - (n_a - 2)/n_a = 2/n_a$ one samples any pair involving the newly established adapted breeder. This newly established breeder is born from one of the $n_a - 1$ locally adapted breeders with probability $\mathcal{L}_{a \rightarrow a}(n_a - 1, e_i)$: with probability $1/(n_a - 1)$ the breeder's mother is sampled together with the newly established breeder, and hence relatedness among both is 1. Alternatively, with probability $(n_a - 2)/(n_a - 1)$ a non-parental breeder is sampled, so that relatedness between the newly established breeder and the non-parental breeder is equal to the relatedness between the non-parental breeder and the adapted parent of the newly established individual: $r_{aa}(n_a - 1, e_i)$. Finally, with probability $\mathcal{L}_{m \rightarrow a}(n_a - 1, e_i)$ the newly established adapted breeder is born from one of the maladapted breeders, so that relatedness between a sampled adapted individual and the newly established adapted individual is then equal to the relatedness between the maladapted parent of the newly established individual and a randomly sampled adapted breeder, or $r_{ma}(n_a - 1, e_i)$. Finally, near equilibrium, gains have to be matched by an equal loss in relatedness $-r_{aa}(n_a, e_i)$.

Next, change occurs due to the death of an adapted individual and replacement by an adapted individual in a n_a, e_i patch:

$$\Delta_3 = f(n_a, e_i) n_a M_{z_i e_i} [l_a(n_a, e_i) + \tilde{l}_a(n_a, e_i)] \left\{ \frac{n_a - 2}{n_a} r_{aa}(n_a, e_i) + \frac{2}{n_a} \left[\mathcal{L}_{a \rightarrow a}(n_a, e_i) \left(\frac{1}{n_a} + \frac{n_a - 1}{n_a} r_{aa}(n_a, e_i) \right) + \mathcal{L}_{m \rightarrow a}(n_a, e_i) r_{ma}(n_a, e_i) \right] - r_{aa}(n_a, e_i) \right\}, \quad (23)$$

where deaths of adapted individuals occur at rate $n_a M_{z_i e_i}$. The equation above can be derived in a similar fashion as the preceding eq. (22).

Next, change occurs due to the death of an adapted individual and replacement by an maladapted individual in a $n_a + 1, e_i$ patch:

$$\Delta_4 = f(n_a + 1, e_i) (n_a + 1) M_{z_i e_i} [l_m(n_a + 1, e_i) + \tilde{l}_m(n_a + 1, e_i)] [r_{aa}(n_a + 1, e_i) - r_{aa}(n_a, e_i)], \quad (24)$$

again the equation above can be derived in the same way as eq. (22), where $l_m(n_a + 1, e_i) + \tilde{l}_m(n_a + 1, e_i)$ reflect the total probability that a maladapted individual establishes itself in the local patch. In this case, pairs of adapted individuals can only be sampled among previously established adapted adult breeders, so the gain in relatedness is identical to $r_{aa}(n_a + 1, e_i)$.

Finally, equilibrium values $\hat{r}_{aa}(n_a, e_i)$, $\hat{r}_{ma}(n_a, e_i)$, $\hat{r}_{mm}(n_a, e_i)$ are found by solving expression 20 and their equivalents in the Mathematica sheet.

1.5 Selection gradients

Based on a derivation in the Supplement of [1], we then derive the change in fitness of a slightly different mutant with phenotype $\mathbf{p}^{\text{mut}} = [p_1^{\text{mut}}, p_2^{\text{mut}}]$ who invades in a population playing the resident strategy \mathbf{p} [5]. To this end, we calculate how the actions of a focal mutant affect the change $dW(\cdot)/dt$ in fitness over time, where changes in fitness come about through changes in reproductive value (e.g., [2, 4]).

By means of example, we focus in the remainder of this section on an adapted focal mutant (hence having state $x = a$) who lives in a patch with \hat{n}_a adapted others and in a local environment in state e_i . The total change in fitness is given by

$$\begin{aligned} \frac{dW(a, \hat{n}_a, e_i)}{dt} &= \Delta_2 W(a, \hat{n}_a, e_i) + \Delta_3 W(a, \hat{n}_a, e_i) + \Delta_4 W(a, \hat{n}_a, e_i) \\ &\quad + \Delta_5 W(a, \hat{n}_a, e_i) + \Delta_6 W(a, \hat{n}_a, e_i) \end{aligned} \quad (25)$$

where each of the ΔW_i reflect how the action of the mutant results in a change in reproductive value for event i , where the event numbers follow the order as in section 1.3 for the reproductive values and a listing is given in eqns. (27-34) below. The direction of evolutionary change in the phenotype p_i due to a focal mutant in state a who lives in a patch with \hat{n}_a adapted others and in a local environment in state e_i is then proportional to (eg., see eq. A6 in [4])

$$\left. \frac{\partial}{\partial p_i^{\text{mut}}} \frac{dW(a, n_a - 1, e_i)}{dt} \right|_{p_i^{\text{mut}} = p_i},$$

while the overall change in the phenotype p_i is a weighted average over all the different states that a focal mutant can attain, or

$$\Delta p_i = \sum_{n_a=0}^n \sum_{e_i=\{e_1, e_2\}} f(n_a, e_i) \left\{ \frac{n_a}{n} \left[\left. \frac{\partial}{\partial p_i^{\text{mut}}} \frac{dW(a, n_a - 1, e_i)}{dt} \right|_{p_i^{\text{mut}} = p_i} \right] + \frac{n - n_a}{n} \left[\left. \frac{\partial}{\partial p_i^{\text{mut}}} \frac{dW(m, n_a - 1, e_i)}{dt} \right|_{p_i^{\text{mut}} = p_i} \right] \right\}, \quad (26)$$

which reflects the change in p_i due to successive invasion of mutants. When $\Delta p_1 = 0, \Delta p_2 = 0$, we have a candidate evolutionarily stable value \mathbf{p} , numerical values of which are highlighted in the main text.

1.5.1 Selection gradient: components

The first component ΔW_1 reflects the change in the focal mutant's fitness due to environmental change. However, the mutant's phenotype \mathbf{p}^{mut} does not affect environmental change, so this term would vanish and hence is omitted from eq. (26).

The second component $\Delta_2 W(a, \hat{n}_a, e_i)$ reflects the change in the focal mutant's fitness due to the death of an adapted focal and replacement by its own offspring that are of a different type than the original focal. It is analogous to eq. (13), but only considers changes actions of the focal mutant, rather than replacement of the focal by nonfocal individuals. Hence,

$$\Delta_2 W(a, \hat{n}_a, e_i) = M_{z_i e_i} L_{a \rightarrow m}^{\text{mut}}(\hat{n}_a, e_i) [v(m, \hat{n}_a, e_i) - v(a, \hat{n}_a, e_i)], \quad (27)$$

where $L_{x \rightarrow y}^{\text{mut}}(\hat{n}_a, e_i)$ reflects the probability that a slightly different mutant focal breeder in state x produces a philopatric offspring in state y who successfully establishes itself in the local patch, conditional upon the availability of a breeding position (see eq. 9):

$$L_{x \rightarrow y}^{\text{mut}}(\hat{n}_a, e_i) = \frac{(1-d) B_{x e_i} \psi_{x \rightarrow y}^{\text{mut}}(e_i)}{c(\hat{n}_a + \delta_{x=a}, e_i)}, \quad (28)$$

and $\psi_{x \rightarrow y}^{\text{mut}}(e_i)$ is the state-dependent phenotype switch function (see eq. [5]), except that the phenotype switch function is itself a function of the mutant switch rates $p_1^{\text{mut}} = p_1 + \delta$ and $p_2^{\text{mut}} = p_2 + \delta$, rather than of the resident traits.

Next, we have $\Delta_3 W(a, \hat{n}_a, e_i)$, which is the change in fitness due to the death of any nonfocal *adapted* individual, at rate $\hat{n}_a M_{z_i e_i}$ and subsequent replacement by one of the focal's offspring, who is either adapted or maladapted respectively (see eq. 14):

$$\begin{aligned} \Delta_3 W(a, \hat{n}_a, e_i) = & \hat{n}_a M_{z_i e_i} \left\{ L_{a \rightarrow a}^{\text{mut}}(\hat{n}_a, e_i) [v(a, \hat{n}_a - 1 + \delta_{x=a}, e_i) \right. \\ & \left. + L_{a \rightarrow m}^{\text{mut}}(\hat{n}_a, e_i) [v(m, \hat{n}_a - 1 + \delta_{x=a}, e_i) + v(a, \hat{n}_a - 1, e_i) - v(a, \hat{n}_a, e_i)] \right\}. \end{aligned} \quad (29)$$

Next, we have $\Delta_4 W(a, \hat{n}_a, e_i)$, reflecting the change of a focal mutant's fitness due to the death of any nonfocal *maladapted* individual, at rate $(n - 1 - \hat{n}_a)$ and replaced by a focal's offspring, who is either adapted or maladapted respectively (see eq. 14):

$$\begin{aligned} \Delta_4 W(a, \hat{n}_a, e_i) = & (n - 1 - \hat{n}_a) M_{z_j e_i} \left\{ L_{a \rightarrow a}^{\text{mut}}(\hat{n}_a, e_i) [v(a, \hat{n}_a + \delta_{x=a}, e_i) + v(a, \hat{n}_a + 1, e_i) - v(a, \hat{n}_a, e_i)] \right. \\ & \left. + L_{a \rightarrow m}^{\text{mut}}(\hat{n}_a, e_i) [v(m, \hat{n}_a - 1 + \delta_{x=a}, e_i) + v(a, \hat{n}_a - 1, e_i)] - v(a, \hat{n}_a, e_i) \right\}, \end{aligned} \quad (30)$$

Next, we have $\Delta_5 W(a, \hat{n}_a, e_i)$, reflecting the change of a focal mutant's fitness by the death of a nonfocal adult breeder (either one of the \hat{n}_a nonfocal adapted breeders or one of the $n - 1 - \hat{n}_a$ maladapted breeders respectively), while being replaced by a nonfocal offspring who is maladapted or adapted respectively:

$$\begin{aligned} \Delta_5 W(a, \hat{n}_a, e_i) = & \hat{n}_a M_{z_i e_i} \mathcal{O}_m^{\text{mut}}(a, \hat{n}_a, e_i) [v(a, \hat{n}_a - 1, e_i) - v(a, \hat{n}_a, e_i)] \\ & + (n - 1 - \hat{n}_a) M_{z_j e_i} \mathcal{O}_a^{\text{mut}}(a, \hat{n}_a, e_i) [v(a, \hat{n}_a + 1, e_i) - v(a, \hat{n}_a, e_i)], \end{aligned} \quad (31)$$

where $\mathcal{O}_y^{\text{mut}}(x, \hat{n}_a, e_i)$ is analogous to the expression in eq. (10) and reflects the probability that – given a focal neighbour in state $x \in \{a, m\}$ – any related nonfocal breeder produces an offspring in state $y \in \{a, m\}$ who successfully establishes itself in the local patch, conditional upon the availability of a breeding position. We then have

$$\begin{aligned} \mathcal{O}_y^{\text{mut}}(a, \hat{n}_a, e_i) = & (1-d) \frac{\hat{n}_a B_{z_i e_i} \psi_{a \rightarrow y}^{\text{mut,rel}}(a, e_i) + (n - 1 - \hat{n}_a) B_{z_j e_i} \psi_{m \rightarrow y}^{\text{mut,rel}}(a, e_i)}{c(\hat{n}_a + \delta_{x=a}, e_i)}, \\ & + d \frac{\sum_{\nu_a=0}^n \sum_{e_k \in \{e_1, e_2\}} f(\nu_a, e_k) [\nu_a B_{z_k e_k} \psi_{a \rightarrow y}(e_k) + (n - \nu_a) B_{z_\ell e_k} \psi_{m \rightarrow y}(e_k)]}{c(\hat{n}_a + \delta_{x=a}, e_i)}, \end{aligned} \quad (32)$$

where $\psi_{x \rightarrow y}^{\text{mut,rel}}(z, e_i)$ is the phenotype switch probability expressed by relatives (in state x) of the focal (in state $z \in \{a, m\}$) to produce an offspring in state y , or

$$\psi_{a \rightarrow a}^{\text{mut,rel}}(z, e_1) = \pi_{z_1 \rightarrow z_1}^{\text{mut,rel}}(z, e_1) = p_1 + r_{za}(\hat{n}_a = 2, e_1)\delta p_1 \quad (33a)$$

$$\psi_{m \rightarrow m}^{\text{mut,rel}}(z, e_2) = \pi_{z_1 \rightarrow z_1}^{\text{mut,rel}}(z, e_2) = p_1 + r_{zm}(\hat{n}_a = 0, e_2)\delta p_1 \quad (33b)$$

$$\psi_{a \rightarrow m}^{\text{mut,rel}}(z, e_1) = \pi_{z_1 \rightarrow z_2}^{\text{mut,rel}}(z, e_1) = 1 - (p_1 + r_{za}(\hat{n}_a = 1, e_1)\delta p_1) \quad (33c)$$

$$\psi_{m \rightarrow a}^{\text{mut,rel}}(z, e_2) = \pi_{z_1 \rightarrow z_2}^{\text{mut,rel}}(z, e_2) = 1 - (p_1 + r_{zm}(\hat{n}_a = 1, e_2)\delta p_1) \quad (33d)$$

$$\psi_{m \rightarrow a}^{\text{mut,rel}}(z, e_1) = \pi_{z_2 \rightarrow z_1}^{\text{mut,rel}}(z, e_1) = p_2 + r_{zm}(\hat{n}_a = 0, e_1)\delta p_2 \quad (33e)$$

$$\psi_{a \rightarrow m}^{\text{mut,rel}}(z, e_2) = \pi_{z_2 \rightarrow z_1}^{\text{mut,rel}}(z, e_2) = p_2 + r_{za}(\hat{n}_a = 1, e_1)\delta p_2 \quad (33f)$$

$$\psi_{m \rightarrow m}^{\text{mut,rel}}(z, e_1) = \pi_{z_2 \rightarrow z_2}^{\text{mut,rel}}(z, e_1) = 1 - (p_2 + r_{zm}(\hat{n}_a = 0, e_1)\delta p_2) \quad (33g)$$

$$\psi_{a \rightarrow a}^{\text{mut,rel}}(z, e_2) = \pi_{z_2 \rightarrow z_2}^{\text{mut,rel}}(z, e_2) = 1 - (p_2 + r_{za}(\hat{n}_a = 2, e_2)\delta p_2), \quad (33h)$$

where relatedness coefficients are derived in section 1.4.

Finally, $\Delta_6 W(a, \hat{n}_a, e_i)$ reflects the change in fitness due to mutant focal offspring taking up breeding positions in remote patches, where positions are vacated by mortalities of adapted and maladapted breeders in remote patches containing ν_a adapted breeders in environmental state e_k :

$$\begin{aligned} \Delta_6 W(a, \hat{n}_a, e_i) = & dB_{z_i e_i} \sum_{\nu_a=0}^n \sum_{e_k=\{e_1, e_2\}} \frac{f(\nu_a, e_k)}{c(\nu_a, e_k)} \\ & \times \left\{ \nu_a M_{z_k e_k} \left[\psi_{a \rightarrow a}^{\text{mut}}(e_i) v(a, \nu_a - 1, e_k) + \psi_{a \rightarrow m}^{\text{mut}}(e_i) v(m, \nu_a - 1, e_k) \right] \right. \\ & \left. + (n - \nu_a) M_{z_j e_k} \left[\psi_{a \rightarrow a}^{\text{mut}}(e_i) v(a, \nu_a, e_k) + \psi_{a \rightarrow m}^{\text{mut}}(e_i) v(m, \nu_a, e_k) \right] \right\}, \end{aligned} \quad (34)$$

where the derivation is similar to eq. (17), with the difference that phenotype switch rates are the result of mutant phenotypes \mathbf{p}^{mut} .

References

- [1] Kuijper, B. & Johnstone, R. A., 2016 Parental effects and the evolution of phenotypic memory. *J. Evol. Biol.* **29**, 265–276. doi:[10.1111/jeb.12778](https://doi.org/10.1111/jeb.12778).
- [2] Härdling, R., Kokko, H. & Arnold, K. E., 2003 Dynamics of the caring family. *Am. Nat.* **161**, 395–412. doi:[10.1086/367587](https://doi.org/10.1086/367587).
- [3] Wild, G., Gardner, A. & West, S. A., 2009 Adaptation and the evolution of parasite virulence in a connected world. *Nature* **459**, 983–986. doi:[10.1038/nature08071](https://doi.org/10.1038/nature08071).
- [4] Alizon, S. & Taylor, P., 2008 Empty sites can promote altruistic behavior. *Evolution* **62**, 1335–1344. doi:[10.1111/j.1558-5646.2008.00369.x](https://doi.org/10.1111/j.1558-5646.2008.00369.x).
- [5] Geritz, S. A. H., Kisdi, É., Meszéna, G. & Metz, J. A. J., 1998 Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**, 35–57. doi:[10.1023/a:1006554906681](https://doi.org/10.1023/a:1006554906681).