

Supplementary material

A: Population equilibria in the model with one remote habitat

For the system with $N = 1$ and a single sociality $\sigma := \sigma_n$, then the equilibria of the system are

$$(n_0^*, n_1^*) = \begin{cases} (0, 0), \\ \left(\frac{b - \lambda\sigma - \mu}{\delta_0}, 0 \right), \\ (f(\xi_\rho), \xi_\rho), \quad \rho \in \{1, 2, 3, 4\} \end{cases} \quad (\text{A1})$$

where

$$f(z) = (\delta_1(\delta_0\varepsilon\sigma^2 + \delta_1\varepsilon\sigma^2)z^3)/(\delta_0\mu) + ((\delta_0\varepsilon\sigma^2 + \delta_1\varepsilon\sigma^2)(\mu - b + \lambda\sigma)z^2)/(\delta_0\mu) + z + (b - \lambda\sigma - \mu)/\delta_0 \quad (\text{A2})$$

and ξ_ρ are the four roots of the 4th-degree polynomial P with indeterminate z :

$$\begin{aligned} P = & (\delta_0\delta_1^2\varepsilon^2\sigma^4 + \delta_1^3\varepsilon^2\sigma^4)z^4 \\ & + (2\delta_0\delta_1\lambda\varepsilon^2\sigma^5 - 2\delta_0\delta_1b\varepsilon^2\sigma^4 + 2\delta_0\delta_1\varepsilon^2\mu\sigma^4 + 2\delta_1^2\varepsilon^2\mu\sigma^4 + 2\delta_1^2\lambda\varepsilon^2\sigma^5 - 2\delta_1^2b\varepsilon^2\sigma^4)z^3 \\ & - (2\delta_1b\lambda\varepsilon^2\sigma^5 - 2\delta_0b\lambda\varepsilon^2\sigma^5 + 2\delta_0\delta_1\varepsilon\mu\sigma^2 + 2\delta_1\lambda\varepsilon^2\mu\sigma^5 + 2\delta_0\lambda\varepsilon^2\mu\sigma^5 - 2\delta_1b\varepsilon^2\mu\sigma^4 - 2\delta_0b\varepsilon^2\mu\sigma^4 \\ & \quad + \delta_1\varepsilon^2\mu^2\sigma^4 + \delta_0\varepsilon^2\mu^2\sigma^4 + \delta_1\lambda^2\varepsilon^2\sigma^6 + \delta_0\lambda^2\varepsilon^2\sigma^6 + \delta_1b^2\varepsilon^2\sigma^4 + \delta_0b^2\varepsilon^2\sigma^4)z^2 \\ & - (\delta_1\lambda\varepsilon\mu\sigma^3 + 2\delta_0\lambda\varepsilon\mu\sigma^3 - 2\delta_0b\varepsilon\mu\sigma^2 + \delta_1b\varepsilon\mu\sigma^2 - \delta_1\varepsilon\mu^2\sigma^2 + 2\delta_0\varepsilon\mu^2\sigma^2)z \\ & + 2b\lambda\varepsilon\mu\sigma^3 - \lambda^2\varepsilon\mu\sigma^4 - 2\lambda\varepsilon\mu^2\sigma^3 + 2b\varepsilon\mu^2\sigma^2 - b^2\varepsilon\mu\sigma^2 - \varepsilon\mu^3\sigma^2 + \delta_0\mu^2 \end{aligned} \quad (\text{A3})$$

The Jacobian J for the population with $N = 1$ and one strategy is

$$J = \begin{bmatrix} b - \mu - \lambda\sigma - 2\delta_0n_0 - \varepsilon\sigma^2n_1(\delta_0n_0 - \delta_1n_1) - \varepsilon\sigma^2n_0n_1\delta_0 & b - \lambda\sigma - 2\delta_1n_1 - \varepsilon\sigma^2n_0(\delta_0n_0 - \delta_1n_1) + \delta_1\varepsilon\sigma^2n_0n_1 \\ \varepsilon\sigma^2n_1(\delta_0n_0 - \delta_1n_1) + \delta_0\varepsilon\sigma^2n_0n_1 & \varepsilon\sigma^2n_0(\delta_0n_0 - \delta_1n_1) - \mu - \delta_1\varepsilon\sigma^2n_0n_1 \end{bmatrix} \quad (\text{A4})$$

The eigenvalue of the eigenvectors of the Jacobian at equilibrium will determine the stability of that equilibrium; if at least one eigenvalue is positive, then the equilibrium is not stable.

In the case of the equilibrium $(0, 0)$ in (A1), then the eigenvectors are

$$(-1, 1), \quad (1, 0) \quad (\text{A5})$$

with respective eigenvalues

$$-\mu, \quad b - \mu - \lambda\sigma \quad (\text{A6})$$

Since the latter eigenvalue is always positive under the model constraints $\mu > 0, b > \mu, \sigma < \frac{b-\mu}{\lambda}$, then the equilibrium $(0, 0)$ is not stable and a population **close** to $(0, 0)$ has a positive gradient in the direction $(1, 0)$, meaning the non-migrating population will grow.

B: Evolutionary invasion analysis

For the model that accommodates two populations of different sociality, we replace the terms $\delta_i n_i$ with

$$\delta_i(n_i + m_i) \quad (\text{B1})$$

assuming that δ_i is affected equally by all individuals in the habitat h_i regardless of sociality.

Conversely, the negative effects from sociality $\lambda\sigma$ applies to each individual in accordance with their own parameter, meaning residents and mutants have respectively

$$\lambda\sigma_n, \quad \lambda\sigma_m \quad (\text{B2})$$

For the learning rate, the population from h_1 available for a group from h_0 to merge with during the schooling phase will be encountered with a probability proportional to $\sigma_n n_1 + \sigma_m m_1$, when accounting for the groups' probability for accepting a merge. Multiplying with the number of individuals from h_0 and their own probability to accept merging, the learning rates become

$$L_{01}^{(n)} = \varepsilon \sigma_n n_0 (\sigma_n n_1 + \sigma_m m_1) (\delta_0(n_0 + m_0) - \delta_1(n_1 + m_1)) \quad (\text{B3})$$

$$L_{01}^{(m)} = \varepsilon \sigma_m m_0 (\sigma_n n_1 + \sigma_m m_1) (\delta_0(n_0 + m_0) - \delta_1(n_1 + m_1)) \quad (\text{B4})$$

respectively for residents (B3) with sociality σ_n , and mutants (B4) with sociality σ_m . We can ignore the opposite flow direction l_{ji} as $l_{ji}^+ = 0$ in the case with $N = 1$ due to $g_1 > g_0$.

Applying the extensions (B1-B4) to the population model (4-6) with $N = 1$ yields the resident-

invader population model for $N = 1$:

$$\frac{dn_0}{dt} = (b - \delta_0(n_0 + m_0) - \mu - \lambda\sigma_n)n_0 + \max\{0, b - \delta_1(n_1 + m_1) - \lambda\sigma_n\}n_1 - L_{01}^{(n)} \quad (\text{B5})$$

$$\frac{dn_1}{dt} = -\mu n_1 + L_{01}^{(n)} \quad (\text{B6})$$

$$\frac{dm_0}{dt} = (b - \delta_0(n_0 + m_0) - \mu - \lambda\sigma_m)m_0 + \max\{0, b - \delta_1(n_1 + m_1) - \lambda\sigma_m\}m_1 - L_{01}^{(m)} \quad (\text{B7})$$

$$\frac{dm_1}{dt} = -\mu m_1 + L_{01}^{(m)} \quad (\text{B8})$$

with $n_i, m_i \geq 0, \delta_i, \mu, \lambda, \varepsilon > 0, b > \mu, \sigma_n, \sigma_m \in [0, \frac{b-\mu}{\lambda}[$ and $L_{01}^{(n)}$ and $L_{01}^{(m)}$ defined in (B3-B4).

The "invasion fitness" is the fitness of the mutant population as its population is "very small" compared to the resident population, i.e. $0 < \mathbf{m} \ll \mathbf{n}$. The sign of the invasion fitness determines whether the mutant population increases in size and becomes a significant part of the population, moving the average sociality towards that of the mutants (either through interbreeding or by complete takeover by the mutant sociality), i.e. changing the resident sociality ([1]). An ESS is a value of σ_n for which no nearby σ_m has positive invasion fitness, meaning that the greatest real eigenvalue of the population growth linearised at invasion for these σ_m are non-positive ([2]).

Any invasion has the initial state $(n_0, n_1, m_0, m_1) = (n_0^*, n_1^*, 0, 0)$ where n_0^* and n_1^* are the states in a stable equilibrium for the resident population.

The growth rate of invaders $\mathbf{m}$ in the model with $N = 1$ (B7-B8) has

$$J(n_0^*, n_1^*) = \begin{bmatrix} b - \mu - \lambda\sigma_m - \delta_0 n_0^* - \varepsilon\sigma_m\sigma_n(\delta_0 n_0^* - \delta_1 n_1^*)n_1^* & b - \lambda\sigma_m - \delta_1 n_1^* \\ \varepsilon\sigma_m\sigma_n(\delta_0 n_0^* - \delta_1 n_1^*)n_1^* & -\mu \end{bmatrix} \quad (\text{B9})$$

where the Jacobian $J(n_0^*, n_1^*)$ is the growth rate of $\mathbf{m}$ linearised around $(n_0^*, n_1^*, 0, 0)$.

For the equilibrium where the migration is collapsed, i.e. $n_1 = 0$, the Jacobian of the invaders

$$J\left(\frac{b - \lambda\sigma - \mu}{\delta_0}, 0\right) = \begin{bmatrix} \varepsilon\sigma_n - \varepsilon\sigma_m & b - \lambda\sigma_m \\ 0 & -\mu \end{bmatrix} \quad (\text{B10})$$

has the eigenvalues

$$-\mu, \quad \varepsilon(\sigma_n - \sigma_m) \quad (\text{B11})$$

and since $-\mu < 0$ then the Jacobian has a positive eigenvalue if and only if $\varepsilon(\sigma_n - \sigma_m) > 0$ meaning that since $\varepsilon > 0$ then invaders $\mathbf{m}$ will have positive invasion fitness if and only if $\sigma_m < \sigma_n$. Therefore, an individual with lower sociality σ_m than that of the average population σ_n will always have higher fitness than the average population. Hence, when $n_1 = 0$ then any mutation/variation that is less social than average will in general have more expected offspring, meaning such population always adapts towards $\sigma^* = 0$. Conversely, for the equilibria where $n_1 > 0$, the eigenvalues of the Jacobian $J(f(\xi_\rho), \xi_\rho)$ may well be positive for $\sigma_m > \sigma_n$ (though this is too complicated to be shown here analytically) so $\sigma^* > 0$ can exist for these equilibria.

C: Dimensionless model

The model with (4-6) $N = 1$ contains 9 parameters and state variables (table C1) in three dimensions; number of fish in population/contingent: $\#$, time: t , and the measure used for the sociality variable: D . The latter is an arbitrary dimension since sociality is measured as a probability and does not have a dimension in the physical sense. In the mathematical model however, sociality relates to parameters ε and λ in well defined terms equivalently to a physical dimension.

symbol	name	dimension	SI-unit
n_0	Non-migrant number	$\#$	1
n_1	Migrant number	$\#$	1
b	Maximum birth rate	$\frac{1}{t}$	s^{-1}
μ	Mortality rate	$\frac{1}{t}$	s^{-1}
δ_0	Breeding habitat CNDD*	$\frac{1}{t\#}$	s^{-1}
δ_1	Remote habitat CNDD	$\frac{1}{t\#}$	s^{-1}
σ	Sociality	D**	$p.d.u.^{***}$
ε	Learning efficiency	$\frac{1}{D^2\#}$	$p.d.u.^{-2}$
λ	Social cost	$\frac{1}{Dt}$	$s^{-1}p.d.u.^{-1}$

Table C1: Parameters and dimensions in model. *) Con-specific negative density dependence. **) Arbitrary dimension. ***) procedure defined unit.

We can non-dimensionalise, i.e. remove dimensions $t, \#$, and D , by instead of SI-units setting the unit of $t = \frac{1}{b}$, the unit of $\# = \frac{b}{\delta_0}$, and the unit of $D = \frac{b}{\lambda}$. In the model (4-6), parameters b , δ_0 , and λ are set to 1. This leaves a parameter set (table C2) with only 3 free parameters $(\mu, \delta_1, \varepsilon)$.

symbol	name (unit interpretation)	unit
n_0	Non-migrant number (as fraction of breeding habitat capacity as measured by birthrate-equivalent growth loss)	$\frac{b}{\delta_0}$
n_1	Migrant number (as above)	$\frac{b}{\delta_0}$
μ	Mortality rate (fraction of maximum birthrate)	b
δ_1	Remote habitat CNDD (compared to breeding habitat CNDD)	δ_0
σ	Sociality (measured in birthrate-equivalent growth loss)	$\frac{b}{\lambda}$
ε	Learning efficiency (effectiveness of sociality; cost $(\frac{\lambda}{b})^2$ over (potential) benefit $\frac{b}{\delta_0}$ - as measured by birthrate-equivalent growth loss)	$\frac{\lambda^2 \delta_0}{b^3}$

Table C2: Parameters and units in dimensionless model.

Since not all parameter sets contain a non-zero ESS sociality, we can show the span of parameters for which collective migration can possibly occur, and conversely, for which parameters no stable migrating contingents can exist.

For each of the parameters: Mortality rate μ and learning efficiency ε , we show the maximum allowed CNDD of the remote habitat δ_1 (Fig. C1), i.e. the minimum habitat quality, for migration to persist. This graph includes all non-dimensional parameters, and thus globally describes the span of possible social ESS of the system (to the extent of the span of parameters ε and μ in the plot).

We see that populations with lower μ thus higher growth rate $r = b - \mu$ in general have a higher maximal CNDD δ_1 , as these species can utilise a sparsely inhabited habitat proportionally to the cost of sociality needed to go to this location.

The learning efficiency ε increases the maximal CNDD δ_1 . Since ε is directly proportional to higher

learning rates L , any population with a high ε can get away with a lower σ which corresponds to a smaller loss from sociality $\lambda\sigma$.

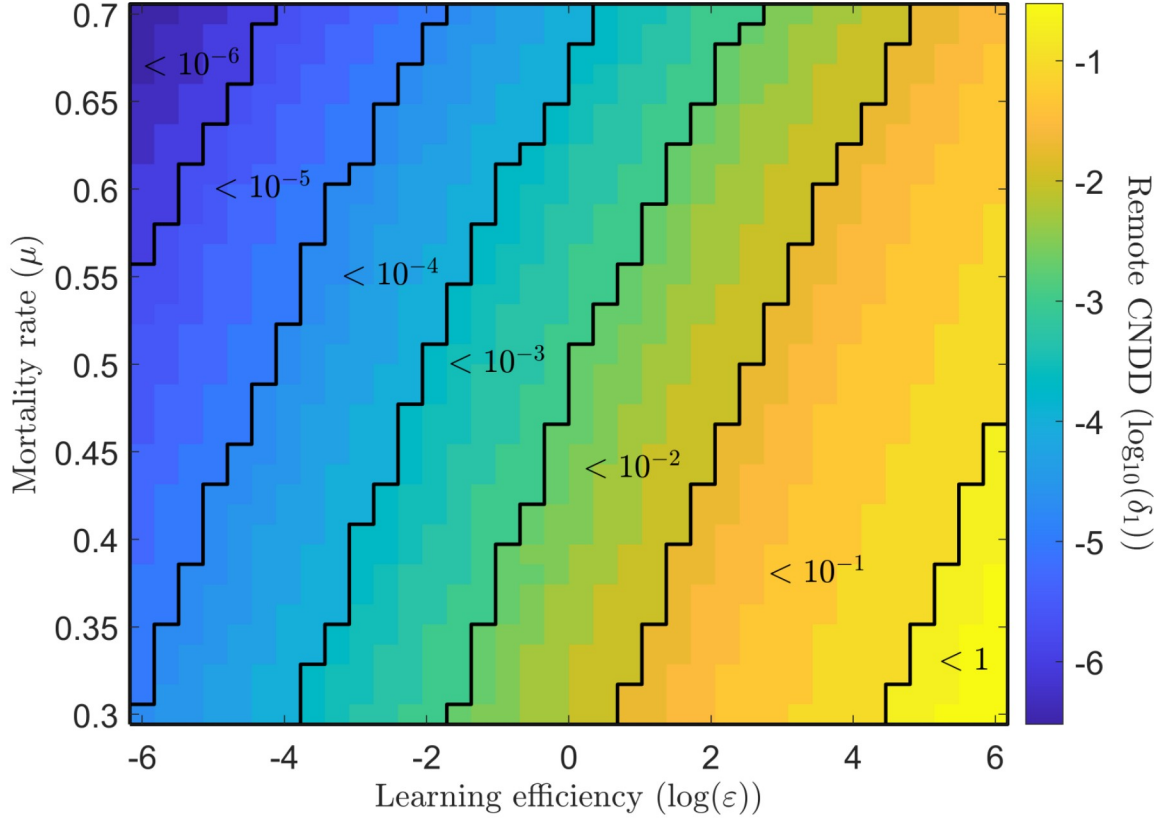


Figure C1: **Non-dimensional ESS bounds.** Critical values (upper bounds) of remote habitat CNDD δ_1 for existence of social ESS $\sigma^* > 0$ given values of mortality rate μ and learning efficiency ε .

Parameters: $\delta_0 = 1; b = 1; \lambda = 1$

D: Evolutionary stable populations

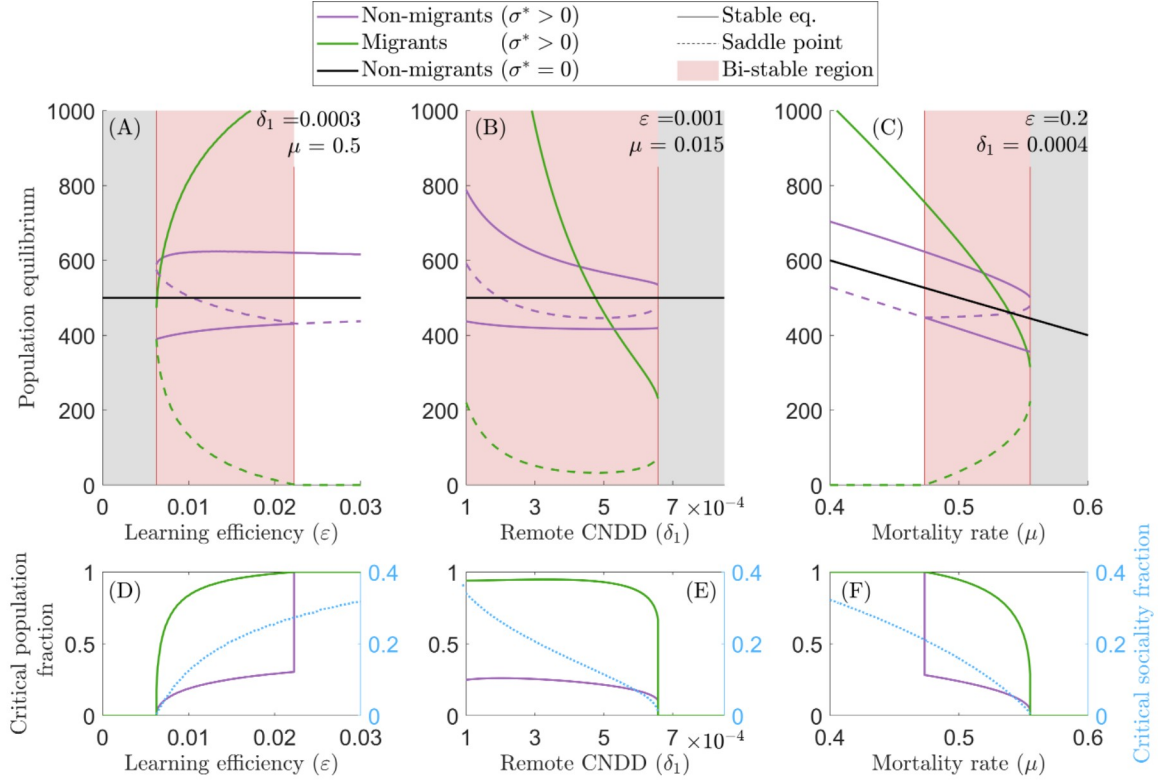


Figure D1: **Bifurcation diagram of population dynamics in ESS.** A-C: Population equilibria for populations following the social ESS $\sigma^* > 0$ (purple: Non-migrants, green: Migrants, grey region undefined) and the non-social ESS $\sigma^* = 0$ (Black: Non-migrants, zero migrants exist) for varied ε , δ_1 , and μ . D-F: Perturbation thresholds for population collapse. Population loss exceeding fraction for both contingents (purple: Non-migrants, green: Migrants) while in the upper equilibrium will cause population to fall to lower equilibrium for a population following the social ESS $\sigma^* > 0$. Blue dots (right axis): Sociality loss exceeding critical fraction of $\sigma^* > 0$ will cause collapse and adaptation to $\sigma^* = 0$. Parameters: $\delta_0 = 0.001$; $b = 1$; $\lambda = 0.2$; $\delta_1 = 0.0003$ (A,C); $\mu = .5$ (A,B); $\varepsilon = 0.15$ (B,C)

As each ESS corresponds directly to a set of population equilibria, we can consider the population's response to parameters (Fig. D1, A-C) without explicitly stating the sociality of the population by always assuming $\sigma = \sigma^*$.

There are one to three stable equilibria for a population depending on parameters. One equilibrium is for the non-social ESS $\sigma^* = 0$ with $(n_0, n_1) = (\frac{b-\mu}{\delta_0}, 0)$ which is always stable as long as $b > \mu$ (Fig. D1, A-C: Black). The social ESS $\sigma^* > 0$ represents zero to two stable equilibria depending on the parameter region; two social stable population equilibria exist in the bi-stable region (Fig. D1, A-C: Purple and green), one with and one without migrants.

Low ε , high δ_1 , and high μ are unfavourable for the population. If either parameter is made sufficiently unfavourable then $\sigma^* > 0$ ceases to exist such that only the non-social equilibrium is stable. Conversely, making parameters sufficiently favourable makes the social ESS robust; its only stable equilibrium has $n_1 > 0$. The remote habitat CNDD (δ_1) is an exception to this. Decreasing δ_1 increases the migrating population significantly, but cannot on its own make the population more robust.

For the given parameters (Fig. D1), the direction of adaptation is entirely given by whether the non-social or social ESS maximises the steady state non-migrant number. Thus if migration collapses in the bi-stable region, then since the number of non-migrants passes below the equilibrium of the non-social ESS, the population will adapt towards σ^* , becoming asocial. We note the opposite is not possible, since there is no bi-stable region for populations in the non-social ESS.

The distance between the unstable and upper stable equilibrium of each contingent corresponds to the magnitude of the perturbation needed for a migrant collapse (Fig. D1, D-F). If both contingents lose more than their respective critical population fraction of their population, then the population enters the basin of attraction to the lower equilibrium and will lose its migration. If only one contingent is perturbed beyond the critical fraction, the dynamics are determined by the trajectory of the slow manifold (Fig. 3, left). For instance, large perturbations of non-migrants may not cause

a migrant collapse. However, if one contingent is forced under the critical fraction for a sustained period of time, the other contingent will follow, eventually crossing the unstable point, leading to a collapse as well.

The bi-stable region is the region where the critical population is above 0, i.e. instantaneous collapse, and below 1 where collapse is impossible (except perturbations of 100% removal of the population).

The critical sociality fraction (Fig. D1, D-F) is the maximal fraction that sociality can be lowered from the social ESS without causing migratory collapse such that adaptation goes toward the non-social ESS. This corresponds to the distance between the social ESS and the maximum sociality in region **I** (Fig. 6).

Note that perturbations of σ of the population may have a compounding effect. The distance between the unstable and upper stable equilibrium of the population dynamics approach one another with lower socialities, decreasing the critical population threshold (Fig. 3, right). Simultaneously, if the non-migrant population is forced below the equilibrium of the non-social ESS, then the critical sociality fraction will temporarily increase to 1, i.e. adaptation will approach $\sigma^* = 0$, lowering the threshold for a behavioural perturbation to cause a collapse.

E: Generalised results

A more general formulation of the model in the main article would be

$$\frac{dn_0}{dt} = g_0 n_0 + \sum_{i=1}^N (\max\{0, g_i + \mu_i\} n_i + L_{i0}) \quad (\text{E1})$$

$$\frac{dn_i}{dt} = -\mu_i n_i + \sum_{j=0}^N L_{ji} \quad i = \{1, \dots, N\} \quad (\text{E2})$$

$$L_{ij} = \varepsilon \sigma^2 n_i n_j (g_i n_i - g_j n_j) \quad i, j = \{0, 1, \dots, N\} \quad (\text{E3})$$

$$g_i = b_i - \delta_i n_i - \lambda_i \sigma - \mu_i \quad i = \{0, 1, \dots, N\} \quad (\text{E4})$$

where b_i , μ_i , and even λ_i are separate for each contingent n_i for $i \in \{0, 1, \dots, N\}$. An equilibrium of this system has

$$g_0 n_0 = \sum_{i=1}^N (\max\{0, g_i + \mu_i\} n_i + L_{i0}) \quad (\text{E5})$$

$$\mu_i n_i = \sum_{j=0}^N L_{ji} \quad (\text{E6})$$

So since $g_i > \mu_i > 0$ if $n_i > 0$ is in equilibrium and because $L_{00} = 0$, then

$$\frac{g_0 - \sum_{i=1}^N g_i \frac{n_i}{n_0}}{\varepsilon \sigma^2} = \sum_{j=0}^N n_j (g_0 - g_j) \quad (\text{E7})$$

$$\frac{\mu_i}{\varepsilon \sigma^2} = \sum_{j=0}^N n_j (g_i - g_j) \quad (\text{E8})$$

Meaning that as $\varepsilon \sigma^2 \rightarrow \infty$ then the solution with all $n_i > 0$ tends towards

$$\sum_{j=0}^N n_j (g_i - g_j) = 0, \quad \forall i \in \{0, 1, \dots, N\} \quad (\text{E9})$$

which is solved simply by $g_i = 0, \forall i \in \{0, 1, \dots, N\}$; the ideal free distribution of the system. As $\varepsilon \sigma^2$ decreases, then remote habitats $n_i, i > 0$ become "under matched" as g_i must increase to match the left hand side equilibrium (E8) which is positive; $\frac{\mu_i}{\varepsilon \sigma^2}$. Conversely, n_0 is "over matched" since g_i will decrease until matching the left hand side of (E8); $g_0 - \sum_{i=1}^N g_i \frac{n_i}{n_0}$ which is negative, as $g_0 > \sum_{i=1}^N g_i \frac{n_i}{n_0}$ would imply $g_0 n_0 > \sum_{i=1}^N g_i n_i \Leftrightarrow \sum_{i=1}^N L_{i0} > 0$ forcing negative total learning rate in at least one remote contingent, the one with lowest g_i , and thus n_i will not be in equilibrium. This means, that equilibria in this system always follow that for all contingents $n_i > 0$, then $g_i \approx 0$ perturbed negatively in relation to $\frac{\mu_i}{\varepsilon \sigma^2}$ for each remote contingent $n_i, i > 0$ and perturbed positively for n_0 .

We switch now to the case from the main article where $b_0 = b_1 = \dots = b_N$ and $\mu_0 = \mu_1 = \dots = \mu_N$. The region of bi-stability in the model with $N = 1$ is equivalent with a bi-stability for any N

(with $\frac{1}{\delta_1}$ for $N = 1$ corresponding to $\sum_{i=1}^n \frac{1}{\delta_n}$ in the N -patch model). This means that for stable equilibria then either all or no migration is occurring, i.e. if a collapse occurs for $N = 1$, it would occur for any N in all remote habitats.

First we consider the conditions for equilibrium of any remote contingent n_i with $i \neq 0$.

$$\frac{dn_i}{dt} = 0 \Leftrightarrow \begin{cases} n_1 = 0 \\ -\mu n_i + \sum_{j=0}^N \varepsilon \sigma^2 n_i n_j (\delta_j n_j - \delta_i n_i) = 0 \Leftrightarrow \frac{\mu}{\varepsilon \sigma^2} = \sum_{j=0}^N n_j (\delta_j n_j - \delta_i n_i) \leq \sum_{j=0}^N n_j^2 \delta_j \end{cases} \quad (\text{E10})$$

where the system is in steady state, so the family $\{n_j\}$ are all equilibria of the system. Disregarding $n_0 = 0$, there are up to 2^N elements of this family, as each contingent n_j , $j \in \{1, 2, \dots, N\}$ may either be present or extinct. If we set $\bar{n}_j = \max\{n_j^*\}$ for every j , i.e. all populations present, then the lower bound for n_i to be non-zero is

$$\frac{\mu}{\varepsilon \sigma^2} = \sum_{j=0}^N \bar{n}_j^2 \delta_j \quad (\text{E11})$$

which we notice is equivalent for any n_i , $i \in \{1, 2, \dots, N\}$, hence all remote habitats share this lower bound.

We observe, without proving rigorously, that since $\bar{n}_j = \max\{n_j^*\}$ is the highest equilibrium value for any state variable, no limit cycles appear, and $n_i \rightarrow \infty$ is repelling, then $\bar{n}_j$ must be attracting, i.e. stable whenever it exists.

The breeding habitat can satisfy (E11) alone when the collapsed population $\mathbf{n} = n_0^*$, i.e. $(n_0, n_1, n_2, \dots) = (\frac{b-\mu-\lambda\sigma}{\delta_0}, 0, 0, \dots)$, is above

$$\frac{\mu}{\varepsilon \sigma^2} = \sum_{j=0}^0 n_j^2 \delta_j + \sum_{j=1}^N 0 = n_0^2 \delta_0 = \frac{(b - \mu - \lambda\sigma)^2}{\delta_0} \quad (\text{E12})$$

$$\begin{aligned} & \Updownarrow \\ \sigma &= \frac{b - \mu \pm \sqrt{(b - \mu)^2 \varepsilon \pm 4\lambda \sqrt{\mu \varepsilon d_0}}}{2\lambda} \end{aligned} \quad (\text{E13})$$

, which real positive value forms an analytic upper bound for the non-existence of non-zero equilibria for n_i , $i \in \{1, \dots, N\}$.

The Jacobian of the system in the collapsed equilibrium $J|_{i=0}$, $i = \{1, 2, ..\}$, i.e $J_{ij} = \frac{\partial \frac{dn_i}{dt}}{\partial n_j}$ in $(n_0, n_1, n_2, ..) = (\frac{b-\mu-\lambda\sigma}{\partial\delta_0}, 0, 0, ..)$, has the elements

$$J_{00}|_{i=0} = b - \mu - \lambda\sigma - 2n_0\delta_0 \quad (\text{E14})$$

$$J_{0i}|_{i=0} = b - \lambda\sigma - \varepsilon\sigma^2\delta_0^2n_0 \quad (\text{E15})$$

$$J_{ii}|_{i=0} = -\mu + \varepsilon\sigma^2n_0^2\delta_0 \quad (\text{E16})$$

$$J_{ij}|_{i=0} = 0 \quad (\text{E17})$$

Since $\frac{dn_0}{dt}$ is not dependent on any n_i after a 1st order linearisation, but $\frac{dn_i}{dt}$ is dependent only on n_0 with the relation $\frac{\partial \frac{dn_i}{dt}}{\partial n_0} = -\mu + \varepsilon\sigma^2n_0^2\delta_0$, then this equilibrium is stable if and only if $-\mu + \varepsilon\sigma^2n_0^2\delta_0 < 0 \Leftrightarrow \frac{\mu}{c\sigma^2} > \sum_{j=0}^N \bar{n}_j^2\delta_j$, i.e. the upper threshold (E13).

Thus, the interval of σ in between the bounds (E11) and (E13) is the bi-stable region. Since these thresholds are simultaneously shared between all remote habitats, there is only one bi-stable region present for any N in the N -patch model.

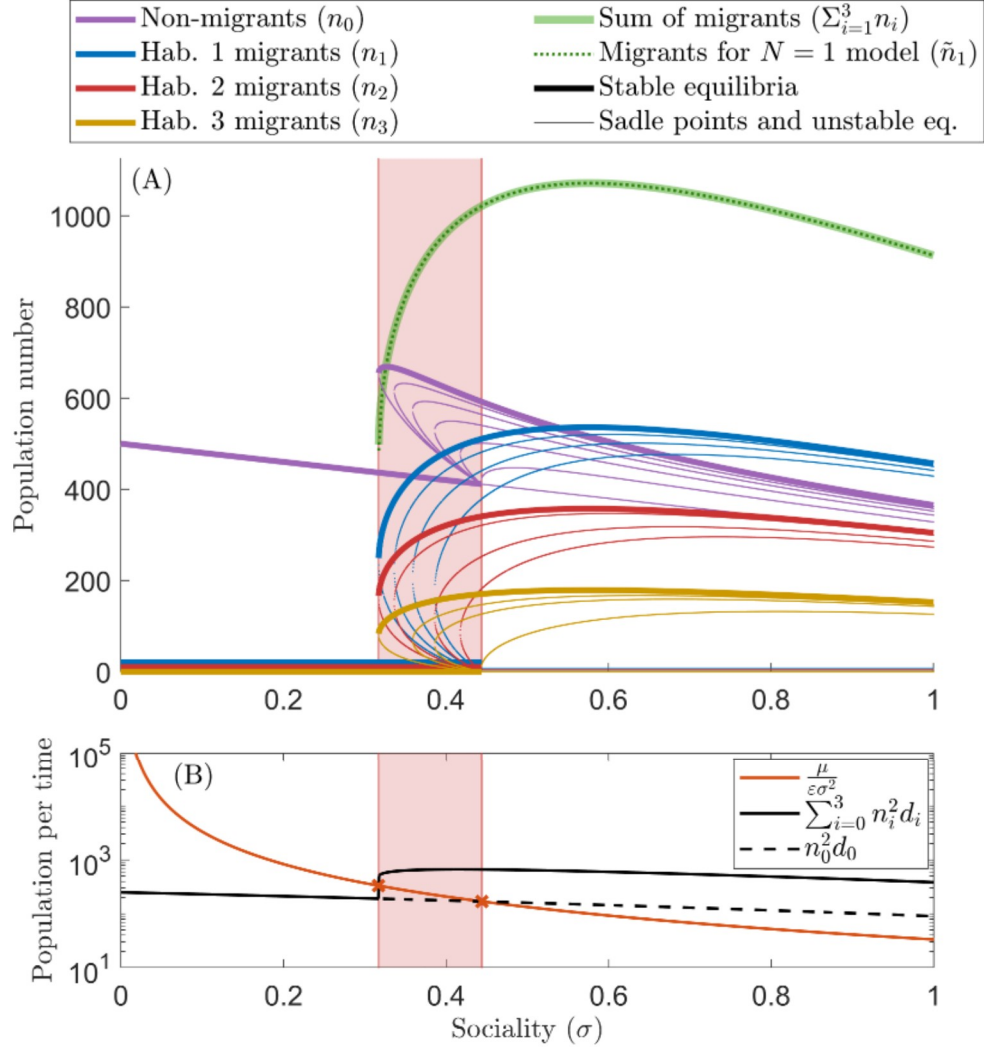


Figure E1: **Four-patch population equilibria.** A: Bifurcation diagram of the stable equilibrium (thick) and saddle points (thin) for the contingents in the 4-patch system as a function of σ . Green transparent line is $n_1 + n_2 + n_3$, green dots on top are $\tilde{n}_1$ in the equivalent model with $N = 1$. B: $\frac{\mu}{\varepsilon\sigma^2}$ of the system intersecting with the maximum (filled) and minimum (dashed) stable pop. equilibria, respectively (E11) and (E13), delimiting the bi-stable region (logarithmic plot).

Parameters: $\delta_0 = 0.001$; $\delta_1 = 0.0006$; $\delta_2 = 0.0009$; $\delta_3 = 0.0018$; $b = 1$; $\lambda = 0.2$; $\varepsilon = 0.015$; $\mu = 0.5$

The equilibria and threshold values of remote habitats are determined by model parameters including those of the breeding habitat, but in terms of remote habitat parameters, only by $\sum_{j=1}^N n_j^2 \delta_j$. Consider the dimension $[n_1] = [\frac{b}{\delta_1}]$ (table C2) implies that n_1 scales inversely with δ_1 for fixed b . Expanding to the N -patch case, we find that in a non-dimensional model we have $n_j \propto \frac{1}{\delta_j}$. Intuitively then $\sum_{j=1}^N n_j^2 \delta_j \propto \sum_{j=1}^N \frac{1}{\delta_j}$, so we may split one remote contingent n_i into an arbitrary number of sub-contingents n_j as long as $\sum_{j=1}^N \frac{1}{\delta_j} = \frac{1}{\delta_i}$.

We can confirm this by considering the 4-patch case (Fig. E1) in which $\delta_1 = 0.0006$, $\delta_2 = 0.0009$, and $\delta_3 = 0.0018$ for which the inverses adds to $\sum_{i=1}^3 \frac{1}{\delta_i} = 0.0003 = d_1$ where d_1 is the CNDD of the remote habitat used in the main article (Fig. 2,3,4 A,6 A). We see that not only does this result in the same bi-stable region, but the stable equilibria of n_0 are exactly the same as in the model with $N = 1$, and the sum $\sum_{i=1}^3 n_i = \tilde{n}_1$ of stable equilibria of remote habitats are exactly the same as with $N = 1$.

F: Period of reproduction

In the main article, we have not discussed the dynamics of the contingents in between the events of spawning and knowledge exchange, but rather considered the overall distribution and size of the contingents over an entire breeding period, adding effects of all rates uniformly in time.

We here attribute τ (dimension t) as the time in-between spawning and knowledge exchange events. Firstly if τ is large in comparison to the birth and mortality rate, then the solution to (4-6) diverge from the dynamics implied by the model equivalently to how it diverges from the difference equation $\mathbf{n}^{t+1} = \mathbf{n}^t + f(\mathbf{n}^t)\tau$ with step size τ , where f is the model equations.

Secondly, the specific mortality in one period $\mu\tau$ should be below 1, so an additional upper bound for the mortality rate $\mu < \frac{1}{\tau}$ now exists.

Lastly, the total number of individuals transferred from n_i to other contingents is $\sum_{j=0}^N L_{ij}$. This is an event that only occurs once every period, the learning "impulse" $\tau \sum_{j=0}^N L_{ij}$ can never be larger than n_i . A contingent population immediately after knowledge exchange impulse, $\tilde{n}_i$, will be

$n_i - \tau \sum_{j=1}^N L_{ij}$, so to ensure this never becomes negative, then

$$\tau \sum_{i=0}^N \varepsilon \sigma^2 n_i n_j M_{ij} \leq n_i \quad (\text{F1})$$

This bound can be enforced by modifying the learning efficiency to have the upper bound

$$\varepsilon \leq \left(\tau \sum_{i=0}^N \sigma^2 n_j M_{ij} \right)^{-1} \quad i = \{0, 1, \dots, N\} \quad (\text{F2})$$

The model will include this restriction if the learning rate (6) is altered to

$$L_{ij} = E_{ij} \sigma^2 n_i n_j (\delta_i n_i - \delta_j n_j) \quad i, j = \{0, 1, \dots, N\} \quad (\text{F3})$$

where E_{ij} is the element-wise ε bounded by either the size of n_i or the size of n_j , since the skew symmetry $L_{ij} = -L_{ji}$ enforces $E_{ij} = E_{ji}$

$$E_{ij} = \min \left\{ \varepsilon, \left| \tau \sum_{k=0}^N \sigma^2 n_k M_{ik} \right|^{-1}, \left| \tau \sum_{k=0}^N \sigma^2 n_k M_{jk} \right|^{-1} \right\} \quad (\text{F4})$$

defined as ε in the case $M_{ij} = 0$. Inserted in an $N = 1$ case with parameters resulting in a large learning rate (Fig. F1), we see that contingents with learning efficiencies at this bound, that are leaving, all vacate their contingent such that the contingent immediately after knowledge exchange impulse $\tilde{n}_i$ is 0.

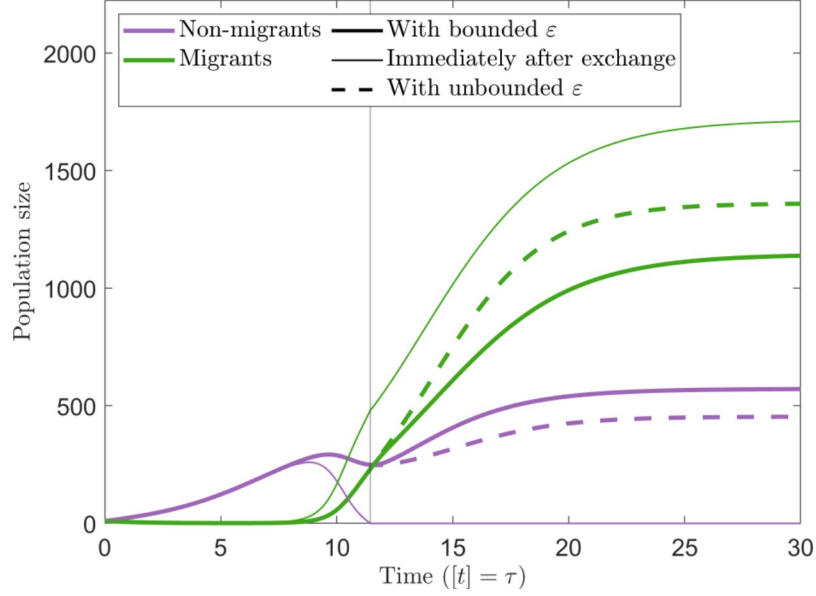


Figure F1: **Time-series with bounded learning efficiencies.** Filled lines are the contingent population distributions with learning rates (F3-F4) bounded such that, immediately after knowledge exchange (thin lines), non-migrants $\tilde{n}_0 = n_0 - \tau L_{01}$ never become negative (reaching 0 at dotted black line). Dashed lines are distributions following equations (4-6) of main article.

Parameters: $\delta_0 = 0.001$; $\delta_1 = 0.0003$; $b = 1$; $\lambda = 0.2$; $\varepsilon = 0.15$; $\sigma = 0.4$; $\tau = 1$

References

- [1] Sarah P Otto and Troy Day. *A biologist's guide to mathematical modeling in ecology and evolution*. 2011. Chap. 12.
- [2] Paul David Williams and Stephanie Jill Kamel. “Evolutionary Invasion Analysis in Structured Populations”. In: *Evolutionary Biology* 48.4 (2021), pp. 422–427.