

Stability and instability of polymorphic populations and the role of multiple breeding seasons in phase III of Wright's shifting balance theory

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It is generally difficult for a large population at a fitness peak to acquire the genotypes of a higher peak, because the intermediates produced by allelic recombination between types at different peaks are of lower fitness. In his shifting-balance theory, Wright proposed that fitter genotypes could, however, become fixed in small isolated demes by means of random genetic fluctuations. These demes would then try to spread their genome to nearby demes by migration of their individuals. The resulting polymorphism, the coexistence of individuals with different genotypes, would give the invaded demes a chance to move up to a higher fitness peak. This last step of the process, namely, the invasion of lower fitness demes by higher fitness genotypes, is known as phase III of Wright's theory. Here we study the invasion process from the point of view of the stability of polymorphic populations. Invasion occurs when the polymorphic equilibrium, established at low migration rates, becomes unstable. We show that the instability threshold depends sensitively on the average number of breeding seasons of individuals. Iteroparous species (with many breeding seasons) have lower thresholds than semelparous species (with a single breeding season). By studying a particular simple model, we are able to provide analytical estimates of the migration threshold as a function of the number of breeding seasons. Once the threshold is crossed and polymorphism becomes unstable, any imbalance between the different demes is sufficient for invasion to occur. The outcome of the invasion, however, depends on many parameters, not only on fitness. Differences in fitness, site capacities, relative migration rates, and initial conditions, all contribute to determine which genotype invades successfully. Contrary to the original perspective of Wright's theory for continuous fitness improvement, our results show that both upgrading to higher fitness peaks and downgrading to lower peaks are possible.

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In the genomic distribution of an evolving population, there are often several advantageous combinations of alleles, each well adapted. These combinations usually involve alleles at several loci, and the transition from one advantageous combination to another requires multiple allele changes. Changes in a single gene or in a small group of genes lead to less fit individuals. In genomic space, one can imagine a fitness landscape where local maxima are separated by troughs and valleys of varying depths. Crossing from one local maximum to a higher one may be very difficult for large populations, since organisms with small genomic changes are usually less fit, so that the mechanism of sexual reproduction makes the population drift back to the local maximum. Even if a fitter combination arises by chance, it will generally not persist into the next generation. Evolution toward higher fitness peaks becomes nearly impossible. In his famous shifting-balance theory, Wright [1,2] proposed that, by means of random genetic fluctuations, the genotypes of various local maxima could become established in small demes, i.e., small isolated groups in physical space. These demes would then try to spread their genome to nearby demes, or *invade* them, by migration of a few individuals. The resulting polymorphism, mixing of organisms from the different demes, would give the invaded ones a chance to

move up to a higher fitness peak. This last step of Wright's theory is known as phase III. Although there has been a major controversy on the credibility of Wright's theory [3], we are not discussing the theory as a whole in this paper. We are focusing on the understanding of genetic invasion processes (with or without genetic drift) from the viewpoint of stability, which is relevant only to phase III of Wright's theory. In addition, we shall see that it may also be relevant in a much broader ecological and evolutionary contexts. The process of genetic invasion by migration of individuals has been addressed in many recent papers [4–9]. The main question discussed is the calculation of a migration threshold beyond which invasion should occur. The many models considered involve differential migration rates, mutations and different numbers of loci, demes, and dimensions for the population distribution in physical space. The conclusions vary, ranging from very small migration thresholds [4,5,7] to higher migration thresholds [6,8,9] according to the model used for the population dynamics and structure.

For small enough migration rates, invasion cannot happen and polymorphic populations are established [10,9]. In this paper, we are mainly concerned with the stability of these polymorphic populations. Under certain conditions the populations are *stable*: small changes in the migration rates, site

capacities, reproduction rates, death rates, or any other parameter, cause only small changes in the long-term behavior. Under other conditions the populations are *unstable*: they are very sensitive and small changes in the parameters or initial conditions may lead to completely different outcomes. We shall argue that the process of invasion results from destabilization of the polymorphic populations. We shall also argue that iteroparity, or multiple breeding seasons, can play a crucial role in this process. When a polymorphic population becomes unstable, any imbalance between the demes or genotypes may decide the outcome of the invasion. Fitness is just one of many possible parameters that can cause such an imbalance. Any asymmetry in the site capacities, the migration rates, or even the initial conditions, for example, may also have the decisive role, and it is not at all certain that the fitter group always prevails.

In order to study the process of migration between demes, we shall consider the simplest possible case: two initially isolated demes, which we shall refer to as the *left* and *right* demes. We assume that in the left deme a certain combination of alleles has prevailed; we call this particular genome G . In the right deme, on the other hand, a different combination dominates; we call this genome H . Both combinations correspond to fit genotypes, but the offspring resulting from mating between G and H are assumed to be of much lower fitness than both G and H . For simplicity, we shall assume in the following that these cross-breeds are nonviable. Assuming that they are viable but of low fitness does not change the conclusions of this paper, as we discuss later.

Once the left and right demes start exchanging individuals with small migration rates, a polymorphic population is established in both groups. The population will be dominantly of genotype G on the left and of genotype H on the right. For small enough migration rates we expect these polymorphic populations to be stable. We shall actually show that this is the case using a particular model. Therefore, if invasion is to occur, it happens either because the migration rates are very large (and possibly asymmetric between left-to-right and right-to-left), or because the polymorphic populations are really unstable due to some structural property that had not been considered before. Indeed we shall see that the number of breeding seasons is such a property.

We call g_t and h_t the number of individuals at time t with genotypes G and H , respectively. After each breeding season part of the previous population dies and offspring are born. The total population on each deme is limited by an intrinsic site capacity k . The populations are updated according to the following equations:

$$\begin{aligned} g_{t+1} &= \sigma g_t + \lambda' \frac{g_t^2}{(g_t + h_t)} \left[1 - \frac{1}{k} (g_t + h_t) \right], \\ h_{t+1} &= \sigma h_t + \lambda \frac{h_t^2}{(g_t + h_t)} \left[1 - \frac{1}{k} (g_t + h_t) \right], \end{aligned} \quad (1)$$

where σ is the survival rate of the parents. The average number of breeding seasons τ is given by the inverse of the death

rate, $\tau = 1/(1 - \sigma)$. The reproduction rates λ and λ' measure the average number of offspring for each genotype. The terms inside the square brackets restrict the population size, as in the logistic equation. They apply only to the reproductive rate, modeling the fact that adult individuals usually have large advantages when competing with newborns. In what follows, we shall write $\lambda' = \lambda + \epsilon \gg \lambda$, indicating that G is the fitter genotype when $\epsilon > 0$.

The above equations for the population dynamics are the mean field version of a spatially extended model that has been successfully applied to study symmetry breaking and coarsening [11] and pattern formation [12] in spatially distributed populations. Equations (1) describe very accurately the dynamics in regions with uniformly distributed populations, which is the case of isolated demes [12,13]. The dynamics at larger scales, where many such regions coexist and interact, may be treated either by considering individual organisms at each site and resorting to Monte Carlo simulations [14–16], or by diffusive partial differential equations [11–13,17]. In this work, we assume that demes have already been formed and are sufficiently isolated so that the only relevant interaction is through migration.

For a single isolated group, Eqs. (1) possess four, and only four, solutions that are independent of time, or stationary:

1. All individuals have genotype G . The number of individuals is given by $g = k(\lambda + \epsilon + \sigma - 1)/(\lambda + \epsilon) \equiv kg_0$ with $h = 0$. We call this outcome the *high-fitness solution*.
2. All individuals have genotype H . The number of individuals is given by $h = k(\lambda + \sigma - 1)/\lambda \equiv kh_0$ with $g = 0$. This is the *low-fitness solution*.
3. The population goes extinct, i.e., $g = h = 0$.
4. Both genotypes coexist. In this case $g = k[\lambda/(2\lambda + \epsilon) - (1 - \sigma)/(\lambda + \epsilon)]$ and $h = k[(\lambda + \epsilon)/(2\lambda + \epsilon) - (1 - \sigma)/\lambda]$. This is the *mixed solution*.

The mixed solution is always unstable. In this paper, we restrict ourselves to the case $\sigma + \lambda > 1$, where the third solution, corresponding to extinction, is also unstable. For a complete analysis of all stationary points, refer to Ref. [12].

Next, we study the conditions under which an incompletely isolated group *invades* a neighbor population and promotes its change to the genotype carried by the invaders. In order to study this process, phase III of Wright's shifting-balance theory, we assume the existence of two demes coupled by migration in both directions. The main question we want to address here is whether the polymorphic equilibrium promoted by migration may become unstable, thus pulling both populations to the same genotype. We shall see that the number of breeding seasons τ can play a decisive role in this process. We emphasize again that the fitter group is not guaranteed to be the invader.

Let the four-vector $y_t = (g_t^l, h_t^l, g_t^r, h_t^r)$ denote the populations of genotypes G and H on the left and right demes at generation t . Assume a migration rate m from left to right and m^* from right to left. Over the duration of one generation, these rates change the populations from y_t to $M(y_t)$ according to the linear equations

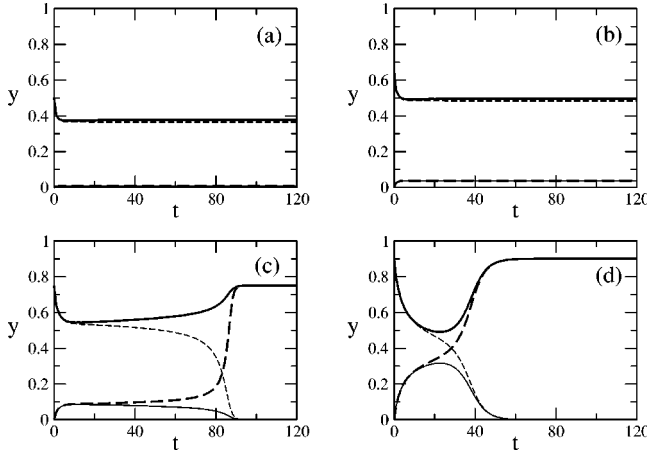


FIG. 1. The role of the number of breeding seasons in the process of invasion. The panels show the time evolution, measured in number of generations t , of the four populations described by the vector y : G (thick lines) and H (thin lines) in the left deme (continuous lines) and in the right deme (dashed lines) for different survival rates. The populations are plotted in units of the site capacity, which is the same for both demes. Genotype G has a slightly larger reproduction rate (larger fitness). The migration rates in both directions are equal to 0.1. Panel (a) shows the populations for $\sigma = 0$ (nonoverlapping generations) evolving to polymorphic equilibrium with low mixing of genotypes. In (b), $\sigma = 0.3$ and more mixing is observed. Panels (c) and (d), for $\sigma = 0.5$ and $\sigma = 0.8$, respectively, show the fitter genotype invading the right deme. For the larger σ the invasion occurs more rapidly.

$$M(y_t) = \begin{pmatrix} g_t^l - m g_t^l + m^* g_t^r \\ h_t^l - m h_t^l + m^* h_t^r \\ g_t^r - m^* g_t^r + m g_t^l \\ h_t^r - m^* h_t^r + m h_t^l \end{pmatrix}. \quad (2)$$

The complete update of the populations after one generation is given by the composite actions of reproduction (1) and migration (2):

$$y_{t+1} = R(M(y_t)), \quad (3)$$

where R represents Eqs. (1) applied to both demes. Equilibrium is reached when $y_{t+1} = y_t$. There are two trivial solutions to this condition, when the populations on both demes are either all of type G or all of type H . The nontrivial polymorphic solution is a complicated function of all the parameters involved and can only be found numerically. For small migration rates, however, an analytic solution is possible. We obtain this solution explicitly in the Appendix.

In order to understand the effect of the number of breeding seasons on the stability of the polymorphic equilibrium, we show in Fig. 1 numerical calculations of the time evolution of the populations for different values of σ . The starting point is the isolated equilibrium $h^l = 0$, $g^l = k^l g_0$ (on the left deme) and $h^r = k^r h_0$, $g^r = 0$ (on the right deme). The site capacities k^r and k^l are set equal and the migration rates in both directions are 0.1. The symmetry between the demes is broken by assigning a slightly higher reproduction rate λ' to

the G genotype, namely, $\lambda' = 2.01$ vs $\lambda = 2.00$. The populations are plotted in units of the common site capacity. For $\sigma = 0$, when all parents die after each generation and the population is totally replaced by the offspring, no invasion occurs and only a very small amount of mixing is observed. This is shown in Fig. 1(a). As σ increases to 0.3 the mixing increases, as shown in Fig. 1(b). For larger σ 's, however, the same rate of migration leads to invasion, as shown in Figs. 1(c) and 1(d) for $\sigma = 0.5$ and 0.8. Notice that $\sigma = 0.5$ corresponds to only two breeding seasons and $\sigma = 0.8$ to five. Notice also that the duration of the invasion process is much longer for $\sigma = 0.5$ than for $\sigma = 0.8$.

To analyze the effect of σ in biological terms, let us see how the few migrants with genotype G manage to fixate at the right deme. The number of G offspring in a dominantly H environment tends to be very small, proportional to $(g^r)^2$. If $\sigma = 0$, all previous g^r parents die leaving very few offspring. The polymorphic character is maintained only because new migrants arrive all the time. However, if σ is large, many parents survive and add to the new migrants. Therefore, although the number of G offspring is initially small, it tends to increase with the increase in the number of parents. When a critical threshold is reached, the population g^r surpasses h^r and invasion occurs.

Figure 1 has shown how a small difference in fitness can result in invasion when the survival rate is sufficiently large. We now argue that fitness is just one among many parameters that may affect invasion. In Fig. 2, we set both λ and λ' equal to 2.00. And, as an example, we discuss the effect of the initial conditions. Figure 2(a) shows the evolution of the populations in perfectly symmetric demes, i.e., with the same reproduction rates, same migration rates, and same site capacities, starting from the symmetric initial conditions $g^l = k g_0$, $h^l = 0$ (on the left deme) and $g^r = 0$, $h^r = k h_0$ (on the right deme). The populations on the figure are again measured in units of k . We take $\sigma = 0.2$ and $m = m^* = 0.1$. After a few generations the populations reach the polymorphic equilibrium, which, as expected, is symmetric between the two demes. Figure 2(b) shows the same situation for $m = m^* = 0.2$. The difference between Figs. 2(a) and 2(b) is that the first is stable, whereas the second is not: perturbing the initial conditions has no effect in the long term behavior for the first case, but it completely changes the outcome in the second case. To see this, we plot in Figs. 2(c) and 2(d) the time evolution with the same parameters as in Fig. 2(b), but starting from slightly asymmetric initial conditions, namely, $g^l = k g_0$, $h^l = 0.01 k$ (left deme) and $g^r = 0$, $h^r = k h_0$ (right deme) for (c), and the opposite for (d), i.e., $g^l = k g_0$, $h^l = 0$ and $g^r = 0.01 k$, $h^r = k h_0$. The result is that, despite the dynamical symmetry, the right deme invades the left one in (c), whereas the opposite happens in (d). This suggests that the polymorphic solution has become unstable and, therefore, any breakdown in the symmetry between the demes will cause one of the two populations to invade the other. Fitness is one possible parameter, but site capacities, differential migration rates, or just simple random fluctuations may do it. In a more complex situation, the balance between these (and possibly other) factors will actually dictate which group does the invading. Figure 3 illustrates the role of the relative deme

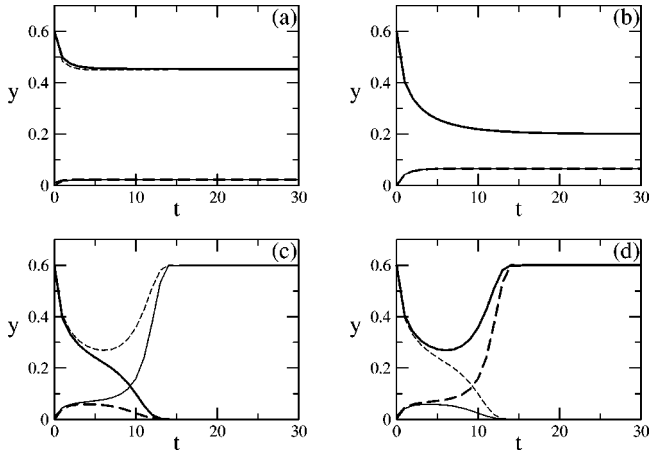


FIG. 2. Stability and instability of the polymorphic populations. Time evolution, in number of generations t , of the populations described by the vector y : G (thick lines) and H (thin lines) in the left deme (continuous lines) and in the right deme (dashed lines) for symmetric dynamics. The populations are plotted in units of the site capacity, which is the same for both demes. In panel (a) the migration rate is small, $m=0.1$, and the polymorphic populations are stable. The initial conditions are $g_0^r=h_0^l=0$. In panels (b) to (d), $m=0.2$: the polymorphic populations are unstable and sensitive to initial conditions. In (b), the initial conditions are symmetric, $g_0^r=h_0^l=0$. This leads to a symmetric, but unstable, evolution: any minor fluctuation along the way can tilt the balance and lead to invasion. In (c), a small imbalance is included from the beginning, $g_0^r=0$, $h_0^l=0.01k$. This is sufficient to decide the invasion in favor of H . In (d), the initial conditions, $g_0^r=0.01k$ and $h_0^l=0$, favor G , which invades the right deme.

size $\alpha=k^r/k^l$ and the relative migration rate $\beta=m^*/m$ in the outcome of the invasion process for three values of the reproduction rate difference ϵ . The populations start from the isolated initial condition, $g^l=k^l g_0$, $h^l=0$ (left deme) and $g^r=0$, $h^r=k^r h_0$ (right deme), as in Figs. 2(a) and 2(b). The left-to-right migration rate m is fixed at 0.15 and σ is 0.5 (two breeding seasons). For $\epsilon=0$ it suffices to have a slightly larger deme or a slightly larger migration rate towards the other deme to guarantee a successful invasion. However, even if the individuals with genotype G are fitter than those with genotype H , a sufficiently larger right deme ($\alpha>1$) or right-to-left migration rate ($\beta>1$) may decide the invasion in favor of the less fit group.

These results can be understood in mathematical terms using linear stability analysis. The polymorphic solution can be constructed explicitly for small migration rates and its stability studied. The calculations are performed in the Appendix. The solution is given by Eq. (A7) and the stability eigenvalues μ_i by Eq. (A9). The polymorphic solution is stable if all four eigenvalues satisfy $|\mu_i|<1$. For $m=m^*=0$ the demes are isolated and their populations are stable. As m or m^* increase, the eigenvalues change. When the first eigenvalue becomes larger than 1, the solution becomes unstable and any perturbation in the symmetry between the demes causes invasion to occur. When m is very small and the populations have only one breeding season ($\sigma=0$), migration cannot overcome selection. This is apparent from the

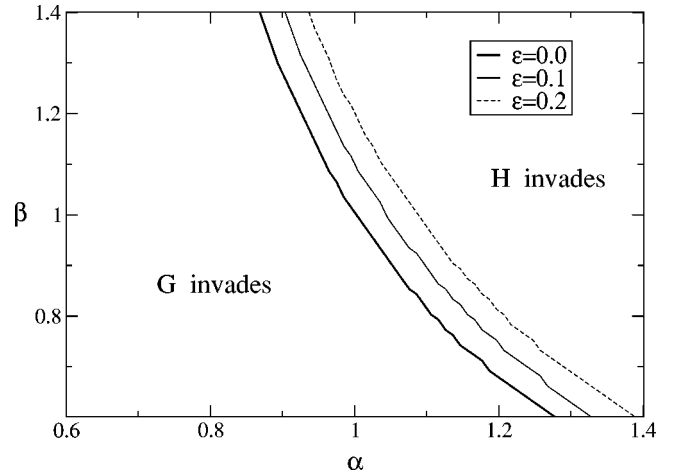


FIG. 3. The role played by relative deme sizes and migration rates in the outcome of the invasion process. The x axis is the relative size of the demes, $\alpha=k^r/k^l$; the y axis is the relative migration rate $\beta=m^*/m$. Each curve corresponds to a different fitness differential parameter ϵ . For scenarios where the point (α,β) lies left of the curve, G invades. For points on the right, H does the invading, even when it is less fit than G .

fact that the stability eigenvalues μ_i are just small perturbations of the original eigenvalues (assumed stable). Therefore, invasion can only occur for substantial migration rates. For σ close to 1, however, the denominators $(1-\sigma)$ occurring in the equilibrium populations, in μ_1 , and in μ_4 , can destabilize the polymorphic equilibrium, even for quite small migration rates. The dotted line in Fig. 4(a), calculated with the equations in the Appendix, divides the m - σ plane into two regions, stable and unstable. This is for the symmetric case, i.e., $m^*=m$, equal size demes, and both genotypes with the same reproduction rate $\lambda=2$. We found the instability threshold by setting the eigenvalues μ_i (A9) equal to 1 and solving for m as a function of σ . This line actually corresponds to the equation $\mu_4=1$, since μ_4 is the first eigenvalue to become unstable as m increases [see Eq. (A11)]. Larger σ 's correspond to a smaller migration threshold for invasion. The dotted line is an approximate curve, obtained from a linear analysis, and it is only valid for small values of m . The actual curve can be computed numerically and is shown by the solid line. Both curves have the same shape and show the same qualitative features. They are displaced by an amount of the order of m^2 , which is consistent with the linear theory employed. Figure 4(b) shows the same data in terms of the number of breeding seasons $\tau=1/(1-\sigma)$. The existence of such a critical curve is not special to the symmetric case. Given any $\alpha=k^r/k^l$, ϵ , and ratio m^*/m , polymorphism is going to be stable for sufficiently small migration rates and a threshold for invasion will exist. Above the threshold, the direction of invasion will depend on all the parameters, as we showed earlier.

Finally, we note that if the intermediate genotypes have low but nonzero fitness, the essential conclusions of the model do not change. These marginal populations turn out to be relevant only in the case of genomes with few loci [6,10], when their offspring may still be of genotypes G or H . Ba-

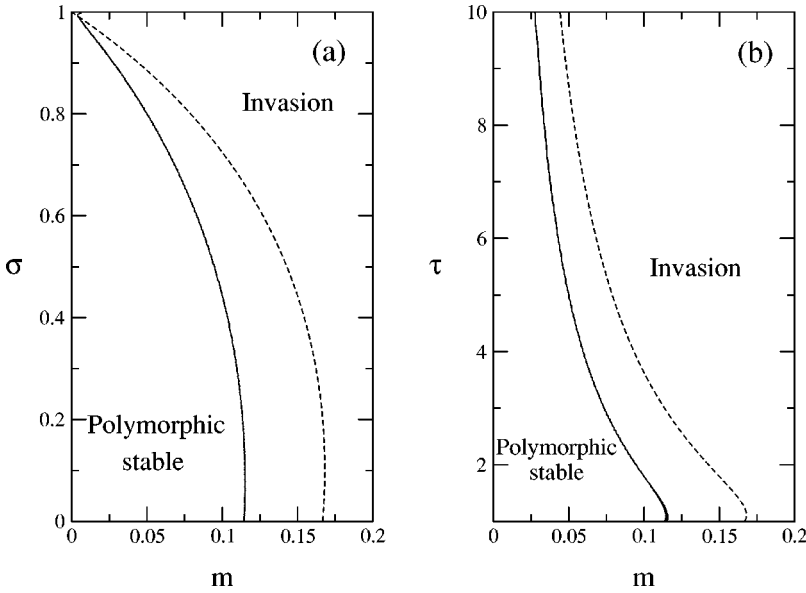


FIG. 4. Stability diagram. Panels show the stability phase diagram for the symmetric case, $m^* = m$, $\epsilon = 0$, and $\alpha = 1$, in terms of the survival rate σ (a) and the number of breeding seasons τ (b). The polymorphic equilibrium is unstable on the right side of the critical curve. There, any imbalance between the two populations results in invasion by one of them. The continuous line is the numerical result, while the dashed line is the approximate result from linear stability analysis (see Appendix).

sically, including such intermediates in a few-loci model lowers the migration threshold and increases the time for invasion. No substantial difference is expected if the number of loci is large.

To summarize, we have shown that the process of invasion by migration of individuals can be understood as the loss of stability of the polymorphic equilibrium. This is a conceptually important result. Among other things, it implies that many factors, not only fitness, combine to dictate the outcome of an invasion process. Downgrades of populations to lower-fitness peaks, as well as upgrades to higher ones, may take place. We, therefore, conclude that Wright's original concept of shifting balance theory as describing a mechanism for systematic fitness improvement does not adequately capture the subtlety of the dynamics of genetic invasion.

We have also shown that iteroparous species, where individuals have more than one breeding season, have lower migration thresholds for the onset of instability. The balance between aging and fertility has been the subject of many papers in the field of life history theory (see, for instance, Ref. [18]). Although iteroparity seems to be a common feature in many species [19], it has not been considered before in this context.

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APPENDIX: STABILITY OF THE POLYMORPHIC SOLUTION

In this appendix, we find the polymorphic solution explicitly by solving Eq. (3) in the approximation of small migration rates. Then we study its stability. Thus, we perform two linearizations in succession. The first one is a linearization with respect to m and m^* . With this approximation, we can deal with Eqs. (1) analytically, though the work is long and

tedious. The results are valid for the small migration rates considered in this paper. The second linearization is a standard linear stability analysis with respect to small changes in the populations.

It is convenient to measure the populations in units of the site capacities. In analogy to the four-vector y_t we define $x_t = (g_t^l/k^l, h_t^l/k^l, g_t^r/k^r, h_t^r/k^r)$ where k^r and k^l are the right and left site capacities respectively. In terms of x_t Eqs. (2) and (3) become

$$M(x_t) = \begin{pmatrix} g_t^l/k^l - m g_t^l/k^l + m^* \alpha g_t^r/k^r \\ h_t^l/k^l - m h_t^l/k^l + m^* \alpha h_t^r/k^r \\ g_t^r/k^r - m^* g_t^r/k^r + m g_t^l/(k^l \alpha) \\ h_t^r/k^r - m^* h_t^r/k^r + m h_t^l/(k^l \alpha) \end{pmatrix} \equiv x_t + F(x_t), \quad (\text{A1})$$

and

$$x_{t+1} = R(M(x_t)) = R(x_t + F(x_t)) \equiv U(x_t), \quad (\text{A2})$$

where $\alpha = k^r/k^l$ represents the relative size of the demes and F is a vector of the order of m or m^* . Equation (A2) defines a four-component, nonlinear evolution operator U .

The first linearization consists in expanding the right-hand side of Eq. (A2) to first order with respect to the migration rates, i.e., to first order with respect to $F(x_t)$. In order to find the stationary solution we also set $x_{t+1} = x_t = x$. This yields

$$x = R(x + F(x)) \approx R(x) + R'(x)F(x), \quad (\text{A3})$$

where $R'(x)$ is a derivative matrix, obtained by differentiating the components of the vector R with respect to x : $R'_{i,j}(x) = \partial R_i / \partial x_j(x)$. A special case of this matrix is shown in Eq. (A6). When no migration is present, $F(x) = 0$ and the solution is $x = x^0 \equiv (g_0, 0, 0, h_0)$. For small migration rates, we write $x = x^0 + x^1$ and substitute this solution in Eq. (A3), keeping only first-order terms in F and x^1 . Solving for x^1 we obtain

$$x^1 = [1 - R'(x^0)]^{-1} R'(x^0) F(x^0). \quad (\text{A4})$$

This expression gives the result of the first linearization (implicitly). It is a correction to the solution x^0 for isolated demes. It accounts for the polymorphism due to migration.

Next, we perform the second linearization, which is the stability analysis. The stability of the polymorphic solution is determined by the linearized dynamics of Eq. (A2) in the vicinity of $x^0 + x^1$. It is given by the matrix $U'(x^0 + x^1)$, which is the derivative of U with respect to each of the four coordinates. When an eigenvalue of $U'(x^0 + x^1)$ is larger than 1 (in absolute value), the equilibrium is unstable: the time evolution from initial conditions close to equilibrium, and in the direction of the corresponding eigenvector, diverges exponentially. If, on the other hand, an eigenvalue has absolute value smaller than 1, under the same conditions the time evolution converges back to the equilibrium point. Only when all the eigenvalues of U' have absolute value smaller than 1 is the equilibrium stable.

We use the result of the first linearization to calculate the stability matrix U' in an approximation valid for small migration rates, and we obtain

$$U'(x^0 + x^1) \approx R'(x^0)(1 + F'(x^0)) + R''(x^0)(x^1 + F(x^0)), \quad (\text{A5})$$

where

$$\begin{pmatrix} 2 - \sigma - \lambda - \epsilon & (\lambda + \epsilon)(1 - m) & \alpha m^*(2 - \sigma - \lambda - \epsilon) & -\alpha m^*(\lambda + \epsilon) \\ -2(\lambda + \epsilon)z_1 & +2(\lambda + \epsilon)z_2/g_0 & 0 & \alpha m^*\sigma \\ -m(2 - \sigma - \lambda - \epsilon) & & 0 & \\ 0 & \sigma(1 - m) & \sigma(1 - m^*) & 0 \\ & +2\lambda(1 - g_0)z_2/g_0 & +2(\lambda + \epsilon)(1 - h_0)z_3/h_0 & \\ m \frac{\sigma}{\alpha} & 0 & -\lambda(1 - m^*) & 2 - \sigma - \lambda \\ -m \frac{\lambda}{\alpha} & m \frac{2 - \sigma - \lambda}{\alpha} & +2\lambda z_3/h_0 & -2\lambda z_4 \\ & & & -m^*(2 - \sigma - \lambda) \end{pmatrix}, \quad (\text{A6})$$

where

$$z = x^1 + F(x^0) = \begin{pmatrix} x_1^1 - m g_0 \\ x_2^1 + \alpha m^* h_0 \\ x_3^1 + m g_0 / \alpha \\ x_4^1 - m^* h_0 \end{pmatrix}. \quad (\text{A8})$$

$$R'(x^0) = \begin{pmatrix} 2 - \sigma - \lambda - \epsilon & -(\lambda + \epsilon) & 0 & 0 \\ 0 & \sigma & 0 & 0 \\ 0 & 0 & \sigma & 0 \\ 0 & 0 & -\lambda & 2 - \sigma - \lambda \end{pmatrix}, \quad (\text{A6})$$

is the stability matrix of the isolated demes solution x^0 . R'' is a tensor with three indices, obtained by differentiating the components of R twice with respect to x : $R''_{ijk} = \partial^2 R_i / \partial x_j \partial x_k$. Explicit evaluations of Eqs. (A4) and (A5) result in

$$\begin{aligned} x_1 &= g_0 - m \frac{2 - \sigma - \lambda - \epsilon}{\lambda + \epsilon} - m^* \frac{h_0}{g_0} \frac{\alpha}{1 - \sigma}, \\ x_2 &= m^* h_0 \frac{\alpha \sigma}{1 - \sigma}, \\ x_3 &= m g_0 \frac{\sigma}{\alpha(1 - \sigma)}, \\ x_4 &= h_0 - m^* \frac{2 - \sigma - \lambda}{\lambda} - m \frac{g_0}{h_0} \frac{1}{\alpha(1 - \sigma)}, \end{aligned} \quad (\text{A7})$$

for x , while U' is given by

The four eigenvalues μ_i of U' , the stability eigenvalues, can be calculated analytically to first order in m and m^* using standard perturbation theory. The result is

$$\begin{aligned} \mu_1 &= (2 - \lambda - \epsilon - \sigma) + m(\lambda + \epsilon + \sigma) \\ &+ m^* \frac{2\alpha(\lambda + \epsilon)^2(\lambda + \sigma - 1)}{(1 - \sigma)\lambda(\lambda + \epsilon + \sigma - 1)}, \end{aligned}$$

$$\begin{aligned}
\mu_2 &= A + \sqrt{A^2 - B}, \\
\mu_3 &= A - \sqrt{A^2 - B}, \\
\mu_4 &= (2 - \lambda - \sigma) + m^*(\lambda + \sigma) \\
&\quad + m \frac{2\lambda^2(\lambda + \epsilon + \sigma - 1)}{\alpha(1 - \sigma)(\lambda + \epsilon)(\lambda + \sigma - 1)}, \quad (\text{A9})
\end{aligned}$$

where

$$\begin{aligned}
A &= -\sigma(m + m^*)/2 + \frac{m}{\alpha} \left(\frac{\lambda + \epsilon + \sigma - 1}{\lambda + \sigma - 1} \right) \\
&\quad + m^* \alpha \left(\frac{\lambda + \sigma - 1}{\lambda + \epsilon + \sigma - 1} \right),
\end{aligned}$$

$$\begin{aligned}
B &= mm^* \left[\sigma^2 + 4 - \left(\frac{\lambda + \epsilon}{2 - \lambda - \epsilon - 2\sigma} \right) \left(\frac{\lambda}{2 - \lambda - 2\sigma} \right) \right] \\
&\quad - \frac{2\sigma m^2}{\alpha} \left(\frac{\lambda + \epsilon + \sigma - 1}{\lambda + \sigma - 1} \right) - 2\sigma m^* \alpha \left(\frac{\lambda + \sigma - 1}{\lambda + \epsilon + \sigma - 1} \right). \quad (\text{A10})
\end{aligned}$$

In the case of symmetric demes, where $m^* = m$, $\alpha = 1$, and $\epsilon = 0$, μ_4 is the first eigenvalue to become larger than 1 as m increases. Setting $\mu_4 = 1$ for this case gives

$$m(\sigma) = \frac{(\lambda + \sigma - 1)(1 - \sigma)}{3\lambda - \sigma(\lambda + \sigma - 1)}, \quad (\text{A11})$$

which is the migration threshold curve shown in Fig. 3.

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