Electronic Supplementary Material

The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation

Anders Eriksson, Federico Elías-Wolff, Bernhard Mehlig, and Andrea Manica

Contents

Supplementary Text

Appendix A: Individual-based simulations

In our simulations of the model described in the main text, the populations evolve as follows. First, for each population, we used inverse-transform sampling to generate the number of individuals in each population following recruitment and density-dependent mortality from the distribution of possible population sizes given by Eq. 1 in the main text.

Second, each individual disperses with probability *m*, otherwise remaining in its native population. In the case of the unstructured metapopulation, this is implemented by first moving all dispersing individuals to a common pool, and then moving each dispersing individual to a randomly chosen target population.

The simulations for the spatially explicit metapopulation (Fig. 2 in the main text) differ in the way the destination of the dispersers is chosen. In this case the populations are located in a square grid, where the sides of the squares are of size unity. Consider a dispersing individual leaving a population located in a particular square. Its destination is selected by the following procedure. First, a dispersing distance is chosen by generating an exponentially distributed random number such that the mean distance parameter is $d_{\text{dispersal}}$. Second, a direction is chosen by a randomly generated angle. Third, from the centre of the square a line is drawn with the previously chosen length and angle, and the dispersing individual is placed in the population located at the end of the line (using periodic boundaries where necessary).

Appendix B: Finding the slow mode

The dynamics of the model (Eq. 6 in the main text) is nonlinear in $\boldsymbol{f}$, where $\boldsymbol{f}$ is the distribution of local population sizes in vector form, but the nonlinear term depends only on the dispersal rate *I*. In this appendix we show how to find the local slow mode for a given value of *I* by analysing fast and slow modes of the dynamics. Using Eqs. 1, 2 and 4 in the main text we can write the dispersal rate as $I=\boldsymbol{v}^{\mathrm{T}}\boldsymbol{f}$ where the vector $\boldsymbol{v}$ as elements $v_j = \sum_{i=1}^{\infty} miP_{ij}$ and "T" denotes transpose. The fast and slow modes are found by analysing the eigenmodes of the dynamics linearised around the current population size distribution $\boldsymbol{f}$. This is determined by the Jacobian matrix **J**:

$$\mathbf{J}(\boldsymbol{f}) = \frac{\partial \Delta \boldsymbol{f}}{\partial \boldsymbol{f}} = \frac{\partial}{\partial \boldsymbol{f}}\left[\mathbf{A}\left(\boldsymbol{v}^{\mathrm{T}}\boldsymbol{f}\right)\boldsymbol{f}\right] = \mathbf{A}(I) + \mathbf{A}'(I)\boldsymbol{f}\boldsymbol{v}^{T}, \qquad \text{(Eq. B1)}$$

where **A**′ is the derivative of the matrix **A** with respect to *I*.

Our task is to reconstruct $\boldsymbol{f}$ conditional on the immigration rate *I*. To this end, we express the matrix **A** and the population size distribution $\boldsymbol{f}$ in Eq. B1 in terms of the left and right eigenvectors of **J** (denoted $\boldsymbol{L}_i$ and $\boldsymbol{R}_i$, respectively, for the *i*th eigenvalue). For simplicity, we number the eigenvalues λ_i in order of increasing magnitude ($|\lambda_1|<|\lambda_2|<|\lambda_3|<...$) and take left and right eigenvectors to be bi-orthonormal. Expanding $\boldsymbol{f}$ in the right eigenvectors of **A**, we obtain

$$\boldsymbol{f} = \sum_{i=1}^{\infty} c_i \boldsymbol{R}_i \,. \qquad \text{(Eq. B2)}$$

We note that the constant vector of ones is the left eigenvector for **J** corresponding to eigenvalue zero (this simply reflects that ***f*** is normalised to unity). Hence, the corresponding eigenvector $\boldsymbol{R}_1$ enters in ***f*** with coefficient c_1 = 1. The remaining coefficients are determined from the constraint $I=\boldsymbol{v}^{\mathrm{T}}\boldsymbol{f}$,

$$I = \boldsymbol{v}^{\mathrm{T}} \boldsymbol{f} = \sum_{i=1}^{\infty} c_i \boldsymbol{v}^{\mathrm{T}} \boldsymbol{R}_i \qquad \text{(Eq. B3)}$$

and the adiabatic principle that the change in the population size distribution along the third and higher eigenmodes should vanish, i.e.

$$0 = \boldsymbol{L}_i^{\mathrm{T}} \Delta \boldsymbol{f} = \sum_{j=1}^{\infty} \boldsymbol{L}_i^{\mathrm{T}} \mathbf{A} \boldsymbol{R}_j c_j \ \text{ for } i \geq 3. \qquad \text{(Eq. B4)}$$

Together, these constraints gives a linear system of equations from which the coefficients c_2, c_3, c_4, ... that we solve numerically (in practice we normally truncate the system, taking only the c_1, ..., c_{10} into account). This ties ('slaves') the coefficients of the higher-order modes to the first and second eigenmodes.

Since the Jacobian **J** depends explicitly on the population-size distribution ***f***, and not only on the rate of immigration *I*, we must find ***f*** in a self-consistent manner. In the first iteration we calculate **J** from Eq. B1 using the given value of *I* and take ***f*** to be zero, and use Eqs. B3 and B4 to determine the coefficients c_i and thereby ***f***. We then repeat these steps, using the latest estimate of the population-size distribution as input to each iteration, until convergence. Although there is in general no guarantee of convergence, we have found this approach to be quite stable for a wide range of parameters (5-10 iterations have been sufficient for the parameter combinations explored in this paper).

Appendix C: Simple approximation

In this appendix we derive a simple, explicit approximation for the dynamics of the dispersal rate *I*. As in Appendix B, we use spectral analysis to identify fast and slow mode. Here, however, we will make two simplifying assumptions: first, that the second term in Eq. B1 is small enough that **A** can be used to approximate **J**; second, that it is sufficient to keep only the first and second eigenvalues (c_1 and c_2) in the expansion of ***f*** (Eq. B2), setting all other coefficients to zero. Both of these assumptions are valid if, for example, there is a separation of time scale between the local population dynamics and the global dynamics of *I*, but also when this is not the case the approximation can be used qualitatively.

Using these assumptions, we can write the dynamics of *I* as

$$\Delta I = \boldsymbol{v}^{\mathrm{T}} \Delta \boldsymbol{f} = \boldsymbol{v}^{\mathrm{T}} \mathbf{A}(I)\left(c_1 \boldsymbol{R}_1 + c_2 \boldsymbol{R}_2\right) = c_2 \lambda_2 \boldsymbol{v}^{\mathrm{T}} \boldsymbol{R}_2, \qquad \text{(Eq. C1)}$$

where we have used that $\boldsymbol{R}_1$ and $\boldsymbol{R}_2$ are eigenvectors of **A** and that c_1=1 (since all columns of **A** sum to zero, we find again that c_1=1 for all *I*). Using equation B3, we obtain

$$I = \boldsymbol{v}^{\mathrm{T}} (c_1 \boldsymbol{R}_1 + c_2 \boldsymbol{R}_1) = D(I) + c_2 \boldsymbol{v}^{\mathrm{T}} \boldsymbol{R}_2, \qquad \text{(Eq. C2)}$$

where $D(I) = \boldsymbol{v}^T \boldsymbol{R}_1$ can be interpreted as the rate of dispersal from a population in the steady state determined by the immigration rate *I*. Thus, solving Eq. C2 for c_2 and inserting it into Eq. C1 we obtain Eq. 7 in the main text. In addition, the population size distribution ***f*** predicted from the immigration rate *I* is given by

$$\boldsymbol{f} = \boldsymbol{R}_1 + \frac{I - D(I)}{\boldsymbol{v}^{\mathrm{T}} \boldsymbol{R}_2} \boldsymbol{R}_2. \qquad \text{(Eq. C3)}$$

We conclude this section with a couple of comments on the relation between the simple approximation and the full adiabatic treatment in Appendix B. First, because of the constraint $I=\boldsymbol{v}^{\mathrm{T}}\boldsymbol{f}$ and Eq. B2, the coefficients c_2, c_3, ... are all approximately proportional to I-$\boldsymbol{v}^{\mathrm{T}}\boldsymbol{R}_1$. Because the local steady-state changes only slowly with *I*, this factor is very close to *I*-*D*(*I*), the corresponding factor in the simple approximation. Thus, also the full adiabatic treatment supports the interpretation, from the simple approximation, that the metapopulation dynamics is equivalent to a single population that is continuously approaching the steady state given by the current immigration rate, but prevented from reaching it because the immigration rate changes in the very process, until the metapopulation reaches the global steady state.

Supplementary Figures

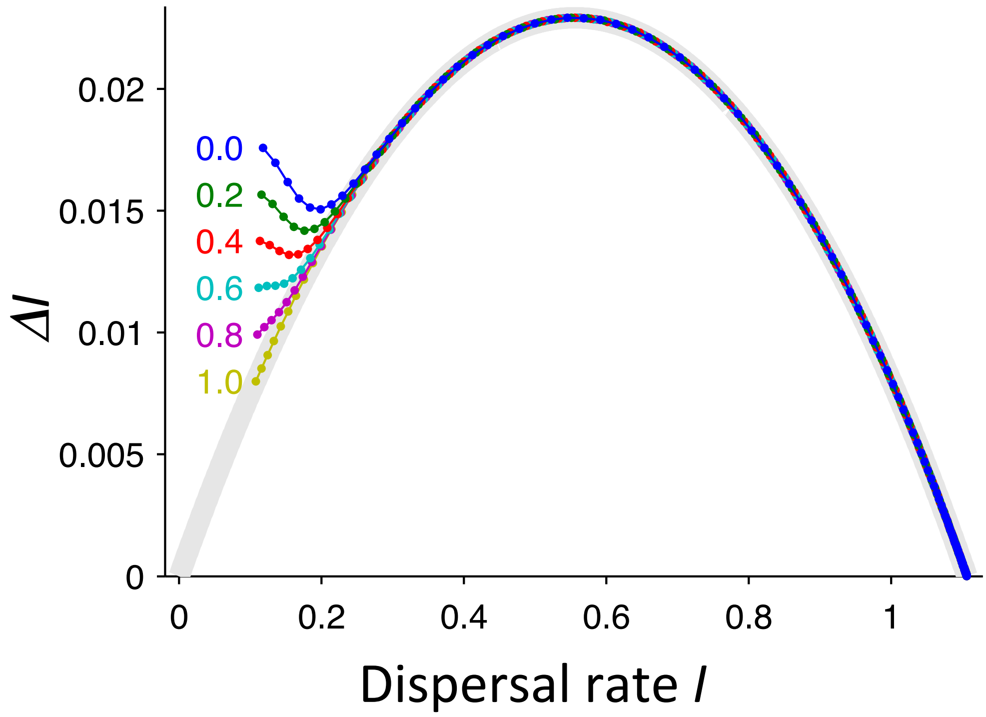

Figure S1: Illustration of convergence to the slow mode. We started simulations (Eq. 6, dotted lines, one dot for each time step) from distributions of patch occupancy that are linear mixes of two distributions with the same mean local population size (equal to one), such that 1 is the slow-mode distribution, and 0 is the Poisson distribution. Because of linearity, all intermediate distributions have the same mean population size. The grey thick line is the relationship between dispersal rate *I* and ΔI predicted by theory. Even when the simulations start far away from the slow mode, they trajectories converge to the slow mode within a few time steps. Parameter values: R=1.2, α=0.01, m=0.1, k_D=1, k_E=10 (environmental recruitment stochasticity).

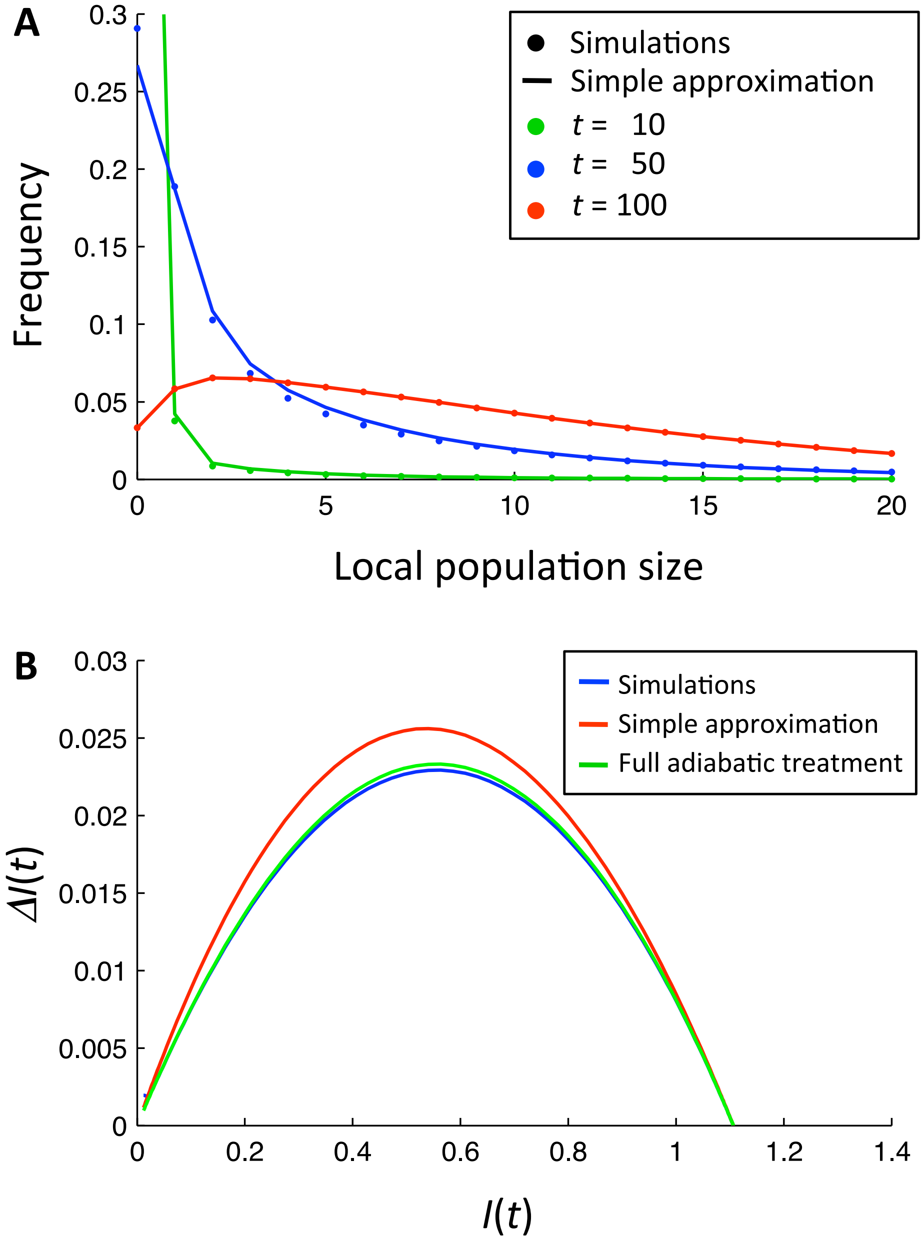

Fig S2: Comparison of the simple approximation (Eq. 7) to simulations (Eq. 6) and the full adiabatic treatment (Appendix B). Panel A compares the distribution of local population sizes from the simulations (points) to the simple approximation, at three different points in time (t=10, 50, 100). Panel B compares the change in dispersal rate, I, as a function of I, in the simulations to the simple approximation and the full theory. Parameter values: R=1.2, α=0.01, m=0.1, k_D=1, k_E=10 (environmental recruitment stochasticity).

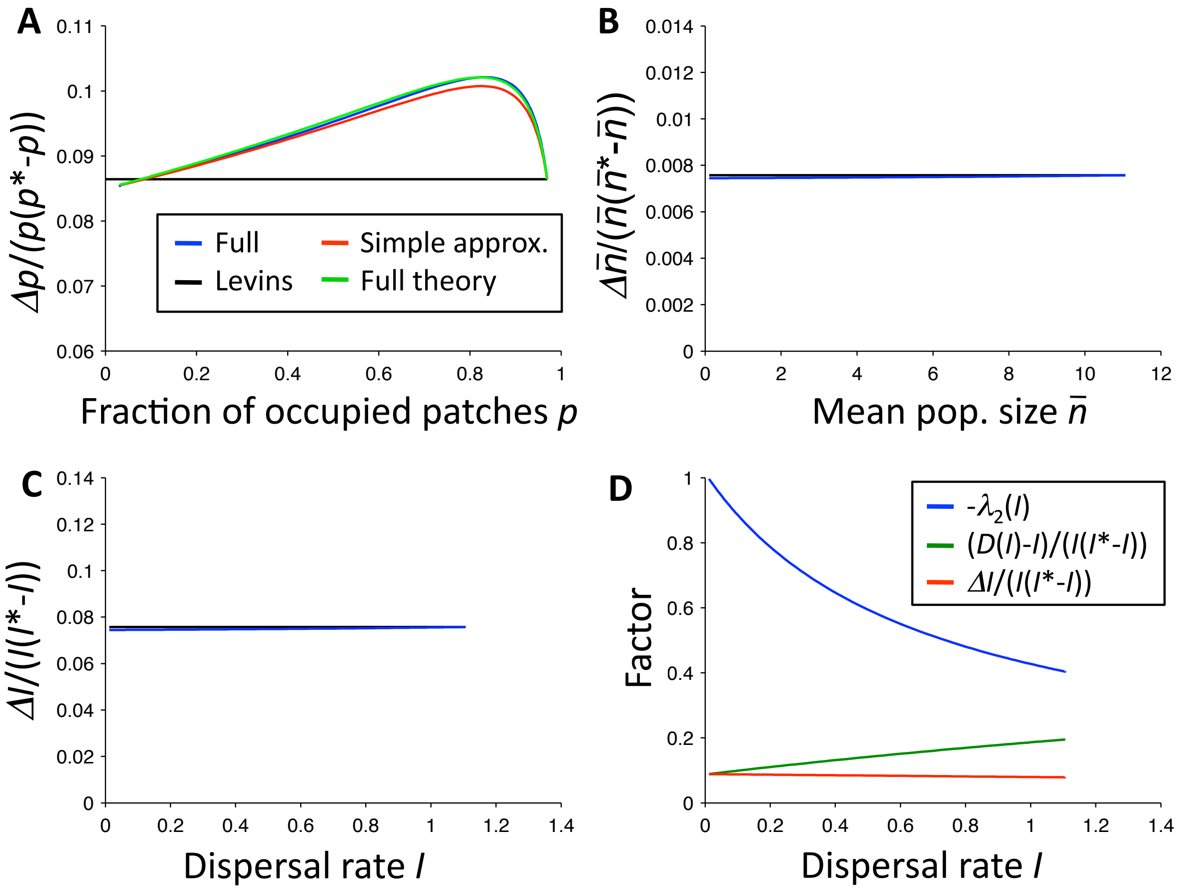

Fig. S3: Comparison of our model to Levins' model. A: In Levins' model the change in fraction of occupied patches (Δp) is proportional to $p(p^*-p)$ where p^* is the value of p in the stationary state of the metapopulation (c.f. Eq. 8 in the main text). According to Levins' simple equation, in the absence of a rescue effect, $\Delta p/p(p^*-p)$ is constant (black line). Deviations of $\Delta p/p(p^*-p)$ from the constant value reveal how the rescue effect emerges from the local population dynamics in our model. We show the full deterministic dynamics (Eq.6, blue line) for a trajectory starting from mean population size 0.1, and the corresponding curves for the slow-mode theory (Appendix B, green line) and the simple approximation (Eq. 7, red line). We observe a strong rescue effect and excellent agreement between the analytical approximations and the full dynamics. In contrast, the corresponding analysis for the mean population size ($\bar{n}$, panel B) and dispersal rate (I, panel C) shows that the dynamics of these observables is very close to Levin's model (after a short transient). D: The two factors determining the change in dispersal rate, ΔI, in the simple approximation, as a function of I. As can be seen in panel C and from the red line, ΔI is approximately proportional to $I(I^*-I)$, where I^* is the steady-state dispersal rate. This would seem to imply an absence of rescue effect, but plotting the two factors in the simple approximation of ΔI (Eq. 6) separately reveals that the effect of an increasing trend in the excess emigration rate ($D(I)-I$, green line) is offset in ΔI by a corresponding decreasing trend in the elasticity ($-\lambda_2(I)$, blue line). Parameter values: R=1.2, α=0.01, m=0.1, k_D=1, k_E=10 (environmental recruitment stochasticity).

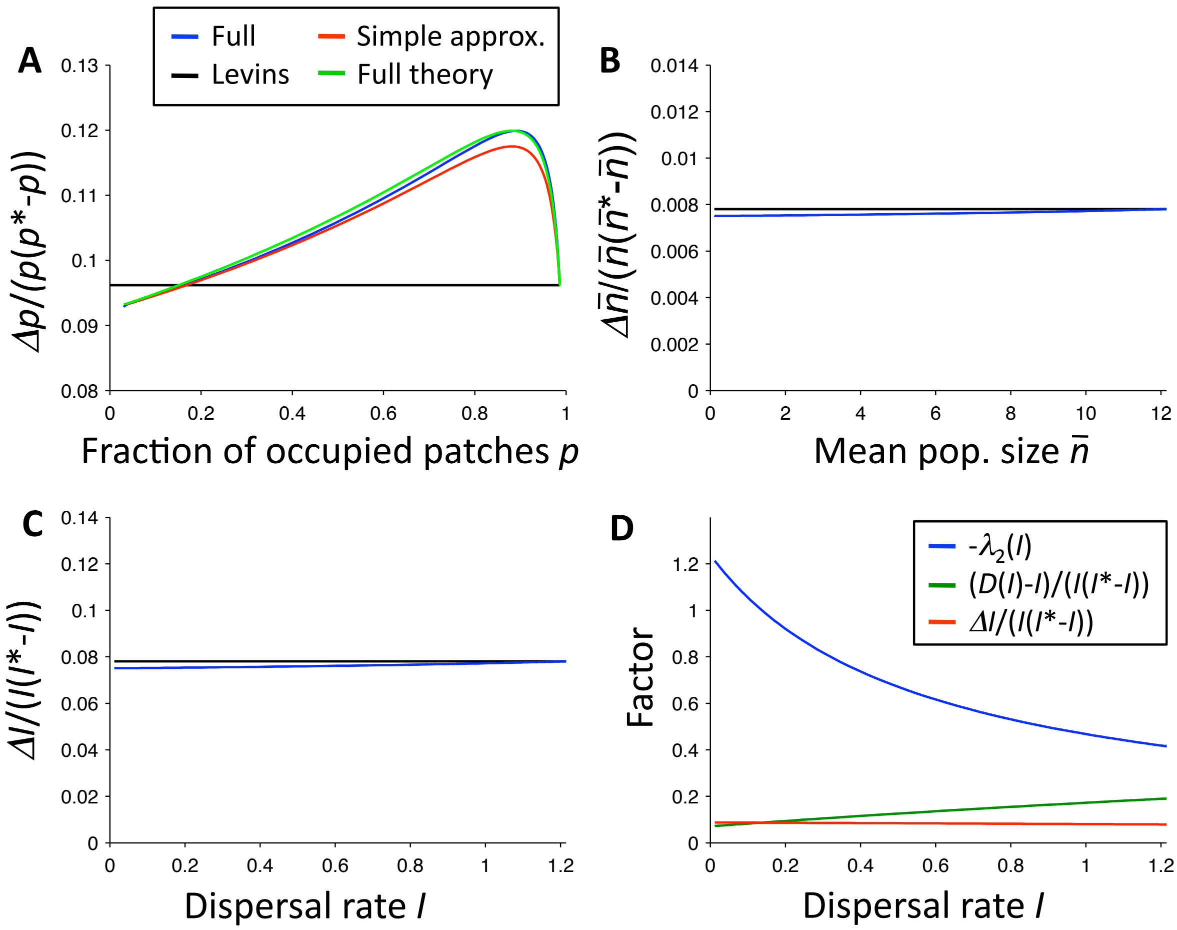

Fig. S4: Comparison of our model to Levins' model for environmental survival stochasticity (Eq. 1b), analogous to Figure S3. A: Comparison to Levins' model for the fraction of occupied patches. B,C: Levins' model is a good fit of the dynamics of the mean population size and of the dispersal rate. D: The two factors determining the change in dispersal rate, ΔI, in the simple approximation, as a function of I. Parameter values: R=1.2, α=0.01, m=0.1, k_D=1, k_A=10. For a more full explanation of each panel, see caption of Figure S3.