

Appendix from M. Roy et al., “Temporal Autocorrelation Can Enhance the Persistence and Abundance of Metapopulations Comprised of Coupled Sinks” (Am. Nat., vol. 166, no. 2, p. 246)

Elaborations and Implementation

This appendix elaborates on points raised at several places in the main text. Section titles in parentheses after each topic name below denote the first time it is referred to in the main text.

Inflation in a Coupled Source-Sink System (“Temporal Variation and Sink Population Dynamics”)

Figure 1E shows a typical time series for population size generated in a sink habitat where local growth rates for a population with discrete generations vary over time (as in fig. 1D), variation is sufficiently large that in some time periods the population can increase, and there is an autocorrelation in the growth rates experienced by successive generations. In the example, a constant environment with the same average growth rate would have a lower equilibrium abundance than does the mean of the observed time series in the variable environment. Autocorrelation permits transient periods of exponential growth, and immigration from the source permits persistence in the sink through periods of low growth rate. The average population size over the time series is increased because of the impact of the outbreaks (which were observed in an experimental microcosm demonstration of the inflationary effect; see Gonzalez and Holt 2002).

Figure A1 depicts a typical example of the magnitude of the inflationary effect for equation (1). The figure shows the time-averaged arithmetic mean abundance \bar{N} as a function of the standard deviation σ_r and correlation coefficient ρ_r in $r = \ln(R)$. Note that \bar{N} increases sharply with both the magnitude of variation in $R(t)$ and with its autocorrelation. (In eq. [1], we set $E(t) = 0$, $I(t) = 1$, and $R(t) = \exp[r(t)]$, where $r(t)$ is an autocorrelated Gaussian sequence.)

At first glance, it might appear from equation (2) that a positive covariance could lead to a positive long-term arithmetic mean abundance in a sink environment even when immigration is zero. But note that in taking the time average, we in effect assume an infinite time horizon. For a population with a time-average arithmetic mean growth rate less than 1, because the geometric mean is less than the arithmetic mean, the population will asymptotically approach zero. As time goes to infinity, the variance in N thus also goes to 0. This in turn implies that the covariance between R and N will go to 0, and so the long-term average population size will also be zero.

A seemingly paradoxical case arises when the geometric mean growth rate is less than 1 but the arithmetic mean exceeds 1. Populations must be positive, yet equation (2) in this case would seem to imply a negative average population size. However, in this case, expression (2) is invalid; the time-average arithmetic mean of $N(t)$ as t goes to infinity is undefined. Numerical studies show that over lengthy but finite time horizons, with time-varying R , the population fluctuates such that the realized average population size over the given time horizon typically exceeds that expected in a constant environment.

Finally, as briefly noted in the main text, we should note that a negative autocorrelation in local growth rates will depress average abundance in a sink habitat. This could arise if a species responds to a periodic forcing function in the environment (e.g., abundance of a generalist predator showing periodic limit cycles). To use consistent terminology, the negative autocorrelation is then said to have a deflationary effect on species abundance. In a metapopulation of coupled sinks of the sort emphasized in the main text, negative autocorrelations in growth rates simply make persistence harder to achieve.

Sink Condition with a Stochastic Growth Rate (“Basic Metapopulation Model”)

Our approach follows that used by Lewontin and Cohen (1969) but also includes an autocorrelation in growth rates between successive generations. Because population sizes in the basic model are continuous variables, populations can only approach extinction but never get there over a finite time horizon (as in a simulation). Therefore, we define a population as a sink if, in isolation, the probability that its size is below an arbitrarily low level approaches 1 as time approaches infinity. For an isolated population with discrete generations defined by $N(t+1) = R(t)N(t)$, where $R(t) = \exp[r(t)]$ and $r(t)$ is a Gaussian series with mean μ_r , variance σ_r^2 , and correlation coefficient between consecutive generations ρ_r , its size at time t is given by

$$N(t) = N(0) \prod_{\tau=0}^{t-1} R(\tau) = N(0) \exp \left[\sum_{\tau=0}^{t-1} r(\tau) \right].$$

Therefore, the logarithm of population size at time t is $\ln N(t) = \ln N(0) + \sum_{\tau=0}^{t-1} r(\tau)$. Because the sum of Gaussian random variables is Gaussian, $\ln N(t)$ is also Gaussian, with arithmetic mean $\ln N(0) + \mu_r t$ and variance $\sigma^2 = \sigma_r^2 [t + 2 \sum_{\tau=1}^{t-1} (t - \tau) \rho_r^\tau]$. The variance is less than $\sigma_r^2 [t + 2 \sum_{\tau=1}^{\infty} t \rho_r^\tau] = \sigma_r^2 t [1 + 2\rho_r/(1 - \rho_r)] = \sigma_r^2 t (1 + \rho_r)/(1 - \rho_r)$ and approaches this limit as t approaches infinity. Subtracting the arithmetic mean from $\ln N(t)$ and dividing by the standard deviation gives a normalized Gaussian random variable z , and one gets the probability

$$P(N(t) < \Omega) = P \left[z < \frac{\ln \Omega - \ln N(0) - \mu_r t}{\sigma_r \sqrt{t + 2 \sum_{\tau=1}^{t-1} (t - \tau) \rho_r^\tau}} \right].$$

If $\mu_r < 0$ and t is sufficiently large, the numerator eventually becomes positive. In this case, we can use the inequality for variance above to get a lower bound on the probability:

$$P(N(t) < \Omega) > P \left[z < \frac{\ln \Omega - \ln N(0) - \mu_r t}{\sigma_r \sqrt{t(1 + \rho_r)/(1 - \rho_r)}} \right].$$

The numerator eventually increases proportionally to t , while the denominator increases only as $t^{1/2}$, and so the probability approaches 1. Therefore, for $\mu_r < 0$, the probability that the population size is lower than any arbitrarily small threshold Ω approaches 1 as t approaches infinity. This makes the population a sink for $\mu_r < 0$, which we assume for all populations.

Generation of an Autocorrelated Growth Rate Sequence (“Basic Metapopulation Model”)

The autocorrelated growth rate sequence $r_i(t)$ is generated from a temporally uncorrelated Gaussian random sequence $\eta_i(t)$ of 0 arithmetic mean and unit variance using

$$r_i(t+1) = \mu_r + \rho_r [r_i(t) - \mu_r] + \sigma_r \sqrt{1 - \rho_r^2} \eta_i(t). \quad (\text{A1})$$

The statistical variance σ_r^2 is generally greater than the variance of a sample of consecutive values (especially if the correlation is high and a short sequence is chosen).

Temporal Correlation ρ_R in Equation (11) (“Basic Metapopulation Model”)

With $R(t) = \exp[r(t)]$, the expectation $E\{R(t)R(t+1)\} = E\{\exp[r(t) + r(t+1)]\}$, where $r(t) + r(t+1)$ is itself Gaussian with arithmetic mean $2\mu_r$ and variance $2\sigma_r^2(1 + \rho_r)$. Thus, $R(t)R(t+1)$ is lognormal with arithmetic mean $\exp[2\mu_r + \sigma_r^2(1 + \rho_r)]$. We also have $E^2\{R(t)\} = \bar{R}^2 = \exp(2\mu_r + \sigma_r^2)$ and $\text{Var}[R(t)] \equiv \sigma_R^2 = \exp(2\mu_r + \sigma_r^2)[\exp(\sigma_r^2) - 1]$. Thus, the correlation coefficient between $R(t)$ and $R(t+1)$ is given by

$$\rho_R = \frac{E\{R(t)R(t+1)\} - E^2[R(t)]}{\text{Var}[R(t)]} = \frac{\exp(\rho_r \sigma_r^2) - 1}{\exp(\sigma_r^2) - 1}.$$

Method and Implementation (“Basic Metapopulation Model”)

The grid size used for computations is $L = 10 \times 10$ unless stated otherwise. For simulations with homogeneous landscapes, initial conditions for $N_i(t)$ involve setting population density $N_i(0) = 10$ on a near-center patch with all other patches empty. Initial conditions for $r_i(t)$ involve assigning $r_i(0) = \mu_r < 0$ to all suitable patches. Note that this procedure initially biases the system against maintenance of species in environments with a high autocorrelation coefficient because most of the environment stays in a sink condition for a number of consecutive generations. Rigid (or reflecting) boundaries are used whenever the near-neighbor dispersal process given by equation (14) is considered (Comins et al. 1992). Each simulation ran for 20,000 generations. Because we are dealing with continuous population sizes most of the time, local extinction is said to occur when the population size on a patch drops below a threshold $\varepsilon = 10^{-20}$ and $N_i(t)$ is set to 0. The parameter K on each patch is 10^{10} (so at the initial population size there is negligible density dependence) unless stated otherwise.

The probability of persistence P is estimated as the fraction of 40 independent runs for which patch-averaged abundance $\langle N(t) \rangle \equiv (1/L) \sum_i N_i(t)$ is above a threshold ε at $t = 20,000$. Arithmetic mean abundance $\langle N \rangle$ is the average $\langle N(t) \rangle$ between generations 10,001 and 20,000, $\langle N \rangle \equiv (1/10,000) \sum_{t=10,001}^{20,000} \langle N(t) \rangle$, for those metapopulations that persist until generation 20,000.

Raising the threshold ε has negligible impact on the dynamics unless it gets within a few orders of magnitude of K . This has been observed by plotting histograms of the time series of abundance drawn from a random patch, $N_i(t)$, and also those of the arithmetic mean per patch abundance, $\langle N(t) \rangle$ (not shown). In both cases, the left tail cutoff of the histogram is only a few orders of magnitude lower than K , indicating local and hence regional persistence provided ε is lower than this. In these numerical studies, recurrent immigration typically greatly boosts the local population size above the threshold value (see fig. A2 for an example). The main text discusses the effects of incorporating demographic stochasticity and imposing strong ceiling density dependence at low densities within patches.

Generation of Spatially Correlated Growth Rates (“Results”)

The spatially correlated (and autocorrelated) growth rate sequences were generated using the following equation:

$$r_i(t+1) = \mu_r + \rho_r [r_i(t) - \mu_r] + \sum_{k=1}^i a_{ik} \eta_k(t), \quad (\text{A2})$$

where $\eta_k(t)$ is a temporally uncorrelated Gaussian random sequence with 0 arithmetic mean and unit variance (as in eq. [A1]).

The coefficients a_{ik} are chosen to introduce a spatial correlation in growth rates. To derive them, we rewrite equation (A2) assuming $\mu_r = 0$ (a nonzero μ_r is introduced in the expression $R(t) = \exp[r(t) + \mu_r]$):

$$r_i(t+1) = \rho_r r_i(t) + \sum_{k=1}^i a_{ik} \eta_k(t). \quad (\text{A3})$$

Each patch has its variance and is spatially correlated to $L - 1$ other patches, giving $L(L - 1)/2$ correlations and L variances, a total of $L(L + 1)/2$ parameters that need to be determined out of potentially L^2 parameters in the matrix of a_{ik} terms. For convenience, we set $a_{ik} = 0$ for $k > i$, which then allows us to solve equation (A3) sequentially for each of the required parameters.

Taking the expected value of $r_i(t+1)r_j(t+1)$ using equation (A3) gives us (assuming $j < i$)

$$\begin{aligned} E\{r_i(t+1)r_j(t+1)\} &= E\left\{\left[\rho_r r_i(t) + \sum_{k=1}^i a_{ik}\eta_k(t)\right]\left[\rho_r r_j(t) + \sum_{k=1}^j a_{jk}\eta_k(t)\right]\right\} \\ &= \rho_r^2 E\{r_i(t)r_j(t)\} + \sum_{k=1}^j a_{ik}a_{jk} E\{\eta_k^2\}. \end{aligned}$$

Other terms in the expansion involve products of the Gaussian random variables with each other or with the growth rates $r_i(t)$. Because these are all independent and have means of 0, the expected values of their products are 0. Assuming the expectation to be time independent, we get

$$E\{r_i(t)r_j(t)\}(1 - \rho_r^2) = \sum_{k=1}^j a_{ik}a_{jk} E\{\eta_k^2\} = \sum_{k=1}^j a_{ik}a_{jk}. \quad (\text{A4})$$

The expected value of $r_i r_j$ is the spatial correlation coefficient between habitats i and j multiplied by the product of their standard deviations σ_r (because the arithmetic means of all r_i are 0). Assuming the spatial correlation to decay with distance d_{ij} as $\rho_s^{d_{ij}}$, equation (A4) becomes

$$\sigma_r^2 (1 - \rho_r^2) \rho_s^{d_{ij}} = \sum_{k=1}^j a_{ik}a_{jk}. \quad (\text{A5})$$

Taking the expected value of $r_i^2(t+1)$ and following similar set of steps gives

$$\sigma_r^2 (1 - \rho_r^2) = \sum_{k=1}^i a_{ik}^2. \quad (\text{A6})$$

Equation (A6) is first solved to get a_{11} . Then, equation (A5) is solved for $i = 2, j = 1$, to give a_{21} . Next, equation (A6) is solved for a_{22} . Then, equation (A5) is solved for $i = 3, j = 1, 2$, and equation (A6) is solved for $i = 3$ and so on through $i = L$.

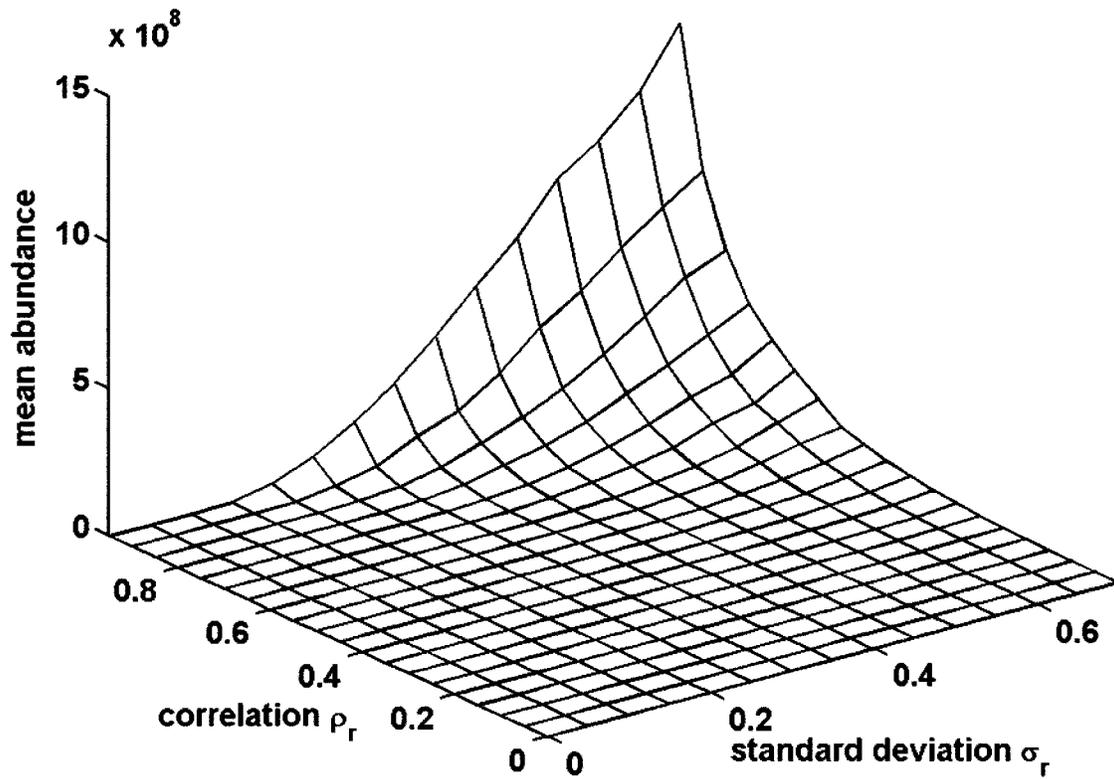


Figure A1: Arithmetic mean abundance \bar{N} given by equation (2) is plotted for the coupled source-sink model presented in the appendix against standard deviation σ_r and correlation ρ_r for $\mu_r = -0.1$. The mean value at each point is estimated after the initial 10,000 generations by time averaging over the next 10,000 generations.

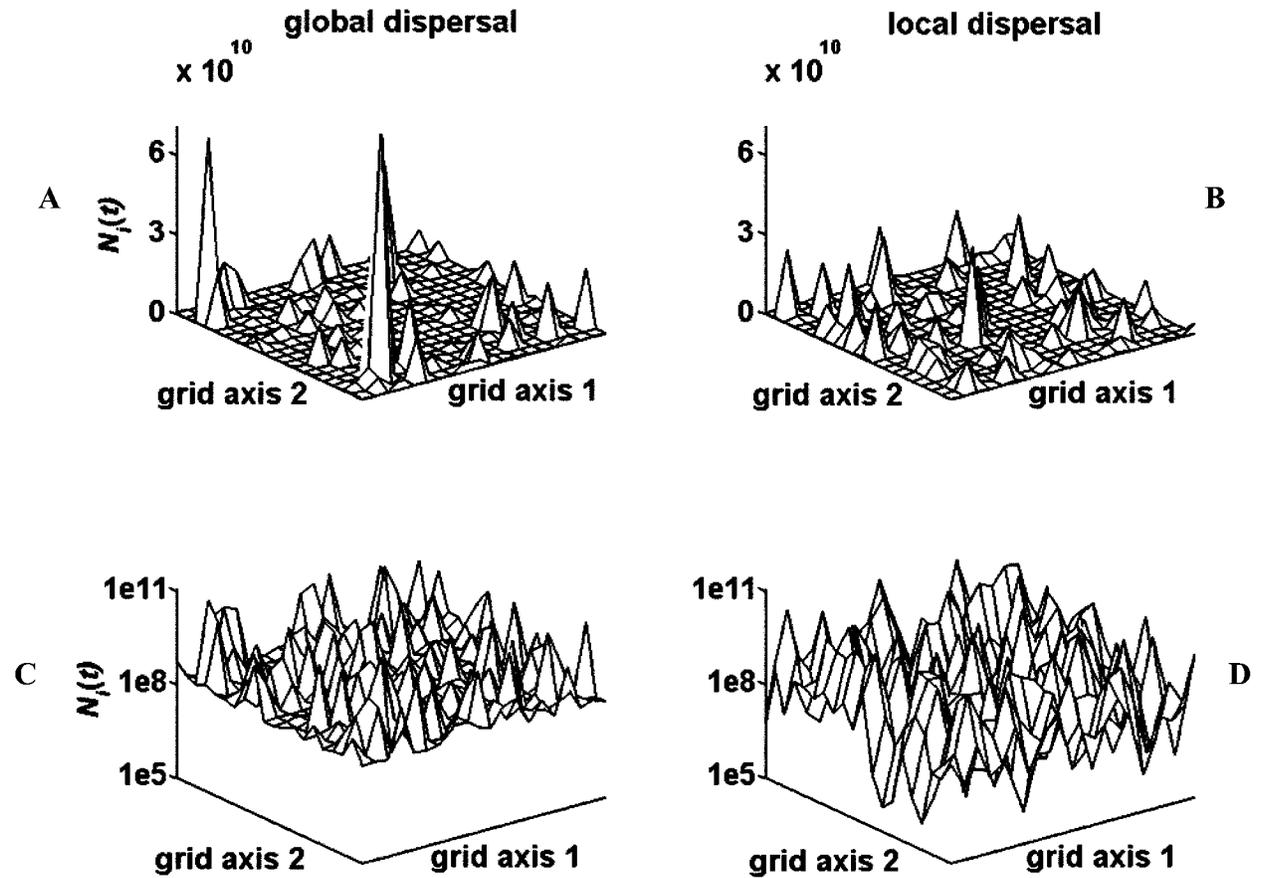


Figure A2: Snapshot patterns of the instantaneous spatial distribution of abundances $N_i(t)$ on a 20×20 grid. *A*, Globally uniform dispersal using equation (10). *B*, Local dispersal using equation (13) with $\alpha = 20$. *C*, *D* are the same plots as *A*, *B* but are displayed on log scales to highlight differences in the baseline population size. The snapshots are recorded at $t = 20,000$. Parameters used are $\mu_r = -1$, $\sigma_r = 1.5$, $\rho_r = 0.9$, $m = 0.05$. Note that in these simulations, because there is immigration, local population sizes are much greater than the threshold values we assume will lead to local extinction (i.e., we do not have “nano-individuals”).