

A mesoscale approach to extinction risk in fragmented habitats

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Assessing the fate of species endangered by habitat fragmentation^{1–3} using spatially explicit and individual-based models^{4–7} can be cumbersome and requires detailed ecological information that is often unavailable. Conversely, Levins-like⁸ macroscale models^{9,10} neglect data on the distribution of local numbers, which are frequently collected by field ecologists^{11–13}. Here we present an alternative, mesoscale approach for metapopulations that are subject to demographic stochasticity, environmental catastrophes and habitat loss. Starting from a model that accounts for discrete individuals in each patch and assumes a birth–death stochastic process with global dispersal^{14,15}, we use a negative-binomial approximation¹⁶ to derive equations for the probability of patch occupancy and the mean and variance of abundance in each occupied patch¹⁷. A simple bifurcation analysis¹⁸ can be run to assess extinction risk. Comparison with both the original model and a spatially explicit model with local dispersal proves that our approximation is very satisfactory. We determine the sensitivity of metapopulation persistence to patch size, catastrophe frequency and habitat loss, and show that good dispersers are affected more by habitat destruction than by environmental disasters.

We consider an infinite network of equal patches with a uniform rain of propagules. We define $p_i(t)$ as the probability that, at time t , an integer number i of individuals is present in a patch; ν_i , μ_i and D_i as the birth, death and dispersal rates per capita in a patch containing i individuals; and m as the occurrence rate of catastrophes that wipe out a whole patch^{19,20}. Because of dispersal mortality and/or inability to colonize, only a fraction a of the average number of

dispersers per patch ($S_p = \sum_{i=1}^{\infty} D_i p_i(t)$) will end up in a patch. Habitat loss can reduce a , which may be thus multiplied by a factor u .

By using Poisson-like assumptions^{14,15,21}, we can stipulate an infinite number of equations for $p_i(t)$, $i = 0, 1, 2, \dots$ and test whether the p_i values converge to some distribution. With constant dispersal ($D_i = D$), no environmental catastrophes ($m = 0$), no habitat loss ($u = 1$) and local logistic dynamics, that is, $v_i - \mu_i = r(1 - i/K)$ with $v_i + \mu_i = \beta + \gamma i$, there is a unique stable probability distribution corresponding to either metapopulation persistence ($p_0 < 1$) or extinction ($p_0 = 1$). Figure 1a shows the boundary line in parameter space (D, r) between persistence and extinction. It was obtained by determining whether there are multiple probability distributions (stable or unstable) at equilibrium (see ref. 21 for another criterion). Persistence corresponds to intermediate D : too little dispersal prevents the rescue of patches that become extinct (see ref. 22 for extinction times) because of demographic stochasticity, whereas too much dispersal disproportionately increases the probability of ending up in an unsuitable habitat. The dark grey region corresponds to extinction as predicted by the deterministic model describing the overall balance of birth, death and dispersal for the metapopulation, namely $dM/dt = rM(1 - M/K) - D(1 - a)M$, where M is the abundance per patch.

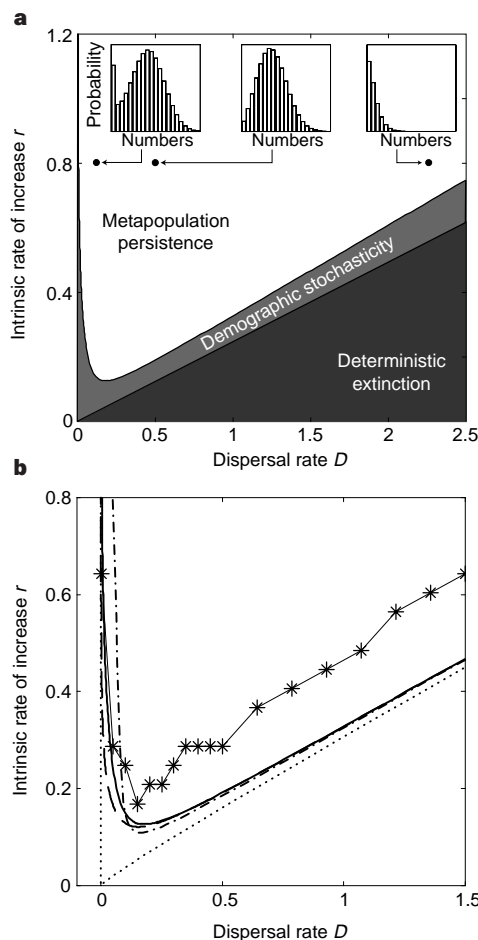


Figure 1 Boundaries separating persistence from extinction in parameter space (D, r) without catastrophes or habitat destruction ($m = 0, u = 1$). **a**, Functioning modes of model (1). The boxes show equilibrium distributions for p_i . Grey areas correspond to global extinction; dark grey $D > r/(1 - a)$, deterministic model; light grey, effect of demographic stochasticity. **b**, Mesoscale models versus the original model (solid line) and a spatially explicit model (asterisks). Mesoscale models are based on Poisson distribution (dotted line), negative binomial distribution with fixed (dash-dotted line) and varying (dashed line) clumping.

The set of infinite equations is not very manageable, because studying the conditions for persistence under different assumptions may be impractical. Deriving the persistence–extinction boundary with non-vanishing catastrophe frequency ($m > 0$) requires a computer-intensive numerical analysis, because there is no closed form for the probability distribution at equilibrium. We thus advocate the use of a sparing and ecologically meaningful approximation of the original model. This approximation is obtained by introducing the probabilities $\delta_i = p_i/(1 - p_0)$, conditional on a patch being occupied, so that the birth–death–dispersal–colonization process is given by

$$\frac{dp_0}{dt} = [-auS_\delta p_0 + (\mu_1 + D_1)\delta_1 + m](1 - p_0) \quad (1)$$

$$\begin{aligned} \frac{d\delta_i}{dt} = & [v_{i-1}(i - 1) + au(1 - p_0)S_\delta]\delta_{i-1} + \\ & - [(v_i + \mu_i + D_i)i + auS_\delta - (\mu_1 + D_1)\delta_1]\delta_i \\ & + (\mu_{i+1} + D_{i+1})(i + 1)\delta_{i+1} \end{aligned} \quad (2)$$

where $S_\delta = S_p/(1 - p_0)$. Equation (1), describing the dynamics of empty patches, is Levins-like^{8–10} and incorporates the rescue effect and the extinction, due to death or emigration, of local populations consisting of one individual. From equation (2), describing the dynamics of numbers in occupied patches, we derive the dynamics of the mean and the variance of local abundance. Making specific assumptions about the density dependence of v_i , μ_i and D_i , we obtain equations for the moments of δ_i , in particular the conditional mean $M_\delta = \sum_{i=1}^{\infty} i\delta_i(t)$ and conditional variance σ_δ^2 . We reduce model (1) to two or three equations by assuming that, at any t , the δ_i values are approximated by a theoretical discrete distribution²³. Using distributions characterized by the first moment only provides δ_1 , σ_δ^2 and the skewness A_δ as functions of M_δ . Thus, two equations can specify the dynamics of local extinction frequency and of average abundance in non-empty patches (see Box 1 for examples). If we select a theoretical distribution characterized by the second moment as well, we obtain a three-dimensional model including the

Box 1 Two-dimensional mesoscale model describing the dynamics of patch occupancy and local mean abundance

Mesoscale metapopulation models

$$\begin{cases} \dot{p}_0 = (1 - p_0)[(\mu_1 + D)\delta_1 - auDp_0\Phi + m] \\ \dot{M}_\delta = M_\delta R(M_\delta) - \frac{r}{K}\Psi + (\mu_1 + D)\delta_1 M_\delta + \\ - [D(1 - au) + auDp_0 M_\delta]\Phi \end{cases}$$

Constant dispersal ($D_i = D$)

Logistic Allee effect

$$\begin{aligned} \Phi &= M_\delta & \Phi &= M_\delta \\ R &= r\left(1 - \frac{M_\delta}{K}\right) & R &= r\left(1 - \frac{M_\delta}{K}\right)\left(\frac{M_\delta}{\epsilon} - 1\right) \end{aligned}$$

$$\Psi = \sigma_\delta^2 \quad \Psi = \frac{A_\delta}{\epsilon} + 3\frac{M_\delta}{\epsilon}\sigma_\delta^2 - \left(1 + \frac{K}{\epsilon}\right)\sigma_\delta^2$$

Density dependent dispersal ($D_i = D_i$)

$$\begin{aligned} \Phi &= M_\delta^2 + \sigma_\delta^2 & \Phi &= M_\delta^2 + \sigma_\delta^2 \\ R &= r\left(1 - \frac{M_\delta}{K}\right) & R &= r\left(1 - \frac{M_\delta}{K}\right)\left(\frac{M_\delta}{\epsilon} - 1\right) \end{aligned}$$

$$\Psi = \sigma_\delta^2 \quad \Psi = \frac{A_\delta}{\epsilon} + 3\frac{M_\delta}{\epsilon}\sigma_\delta^2 - \left(1 + \frac{K}{\epsilon}\right)\sigma_\delta^2$$

As an example, we show analytical expressions for different types of density dependence and dispersal. See text for definition of δ_i , σ_δ^2 and A_δ . They depend on average abundance according to different theoretical distributions (see Methods).

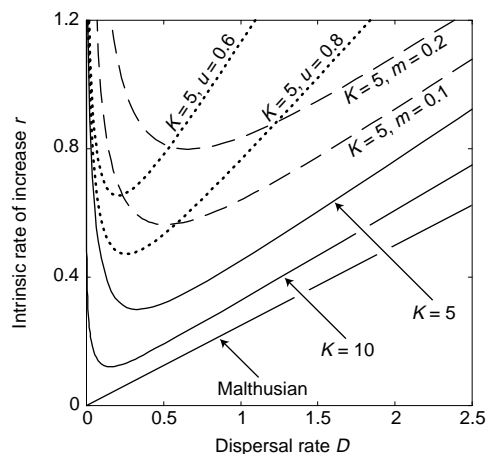


Figure 2 The influence of key ecological parameters on persistence–extinction boundaries (calculated by bifurcation analysis) for three-dimensional mesoscale models (negative binomial with varying clumping). Shown are the effect of decreasing local carrying capacities K (solid line); the further effect of different occurrence rates m of environmental disasters (dashed line) and levels of habitat loss (dotted line, u = fraction of undestroyed patches).

dynamics of abundance variance. Figure 1b compares the performance of the original and the approximate models in terms of extinction–persistence boundaries. Those of reduced models follow from a simple stability analysis. Although the Poisson approximation is too crude, the negative binomial with fixed (varying) clumping can satisfactorily (well) mimic the properties of the original model. Fixed clumping might be estimated from distributional data^{11,12}.

Explorations with stochastic cellular automata²⁴, considering a finite, two-dimensional array of patches and local dispersal, show that the basic features of stability boundaries obtained by the negative-binomial approximation are unchanged (Fig. 1b). Thus, of the two properties ‘being discrete’ and ‘being spatial’²⁵, the first is indeed crucial if we aim to assess metapopulation persistence in a simple, effective and flexible way. With the mesoscale models we can greatly reduce computation times and readily establish the sensitivity of results to different metapopulation parameters, because bifurcation analysis¹⁸ of three ODEs requires a few seconds. For instance, Fig. 2 shows the impact on extinction risk of patch size K , catastrophe frequency m and percentage of preserved habitat u .

We summarize the contribution of the different forces driving extinction in Fig. 3. If, besides demographic stochasticity, environmental catastrophes occur at a substantial rate, the lower dispersal

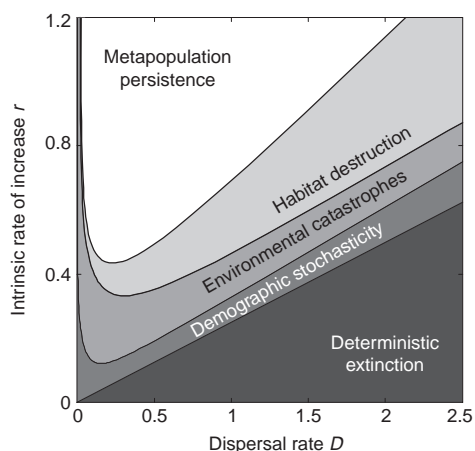


Figure 3 Summary of various contributions to metapopulation extinction in parameter space (D , r). Carrying capacity $K = 10$, environmental disaster rate $m = 0.1$ and fraction of undestroyed habitat $u = 0.8$.

threshold necessary for persistence increases conspicuously, and the upper threshold decreases. If man destroys suitable habitat, this reduces the upper dispersal threshold. Organisms that would survive in a pristine but patchy habitat by their evolved ability to disperse will become extinct in a partly destroyed landscape because they are lost to unsuitable habitat by that very ability. In fact, studies on bird conservation in Europe²⁶ show that modification of the agricultural landscape is one of the most relevant causes of declining populations. □

Methods

We obtain the boundary lines shown in Figs 1, 2 and 3, where not specified otherwise, by setting: $a = 0.75$, $K = 10$, $\beta = 2$, $\gamma = 0.001$, $m = 0$ and $u = 1$. For the Poisson distribution, $\sigma_\delta^2 = M_\delta$ and $\delta_1 = e^{-(M_\delta - 1)}$; for the negative binomial distribution, $\sigma_\delta^2 = (M_\delta - 1) + ((M_\delta - 1)^2/h)$ and $\delta_1 = (1 + (M_\delta - 1/h))^{-h}$, where the clumping h is either fixed ($h = 0.7$) or varying according to the relationship linking the third moment with the first two moments²⁷. The spatially explicit model is a 6×6 cellular automaton with local dispersal (four neighbours on a torus). For each patch, we draw dispersal, birth and death at random. Birth and death probabilities are logistically dependent upon local abundance. For each point of a grid in parameter space, we run simulations several times over a time horizon equal to $100/r$. The stopping rule for the simulations (metapopulation is considered either persistent or prone to extinction and no further simulation is run) is given by a sequential statistical test²⁸ (100% persistence probability is tested against 80% persistence probability, type I error = 5%, type II error = 10%).

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