Scaling of population resilience with dispersal length and habitat size

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Received 26 May 2021
Accepted for publication 22 December 2021
Published 11 February 2022

Online at stacks.iop.org/JSTAT/2022/023501
https://doi.org/10.1088/1742-5468/ac4982

Abstract. Environmental fluctuations can create population-depleted areas and even extinct areas for the population. This effect is more severe in the presence of the Allee effect (decreasing growth rate at low population densities). Dispersal inside the habitat provides a rescue effect on population-depleted areas, enhancing the population resilience to environmental fluctuations. Habitat reduction decreases the effectiveness of the dispersal rescue mechanism. We report here how the population resilience to environmental fluctuations decreases when the dispersal length or the habitat size are reduced. The resilience reduction is characterized by a decrease of the extinction threshold for environmental fluctuations. The extinction threshold is shown to scale with the ratio between the dispersal length and the scale of environmental synchrony, i.e. it is the dispersal connection between non-environmentally-correlated regions that provides resilience to environmental fluctuations. Habitat reduction also decreases the resilience to environmental fluctuations, when the habitat size is similar to or

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smaller than the characteristic dispersal distances. The power laws of these scaling behaviors are characterized here. Alternative scaling functions with spatial scales of population synchrony are found to fit the simulations worse. These results support the dispersal length as the critical scale for extinction induced by habitat reduction.

**Keywords:** population dynamics, stochastic processes

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1. **Introduction**

Habitat reduction is one of the main causes of danger for population stability (Fahrig 1997). The extinction risk is higher for species that experience (strong) Allee effect (decreasing growth rate at low population densities) (Allee and Schuett 1927, Allee 1931) because habitat reduction emphasizes the harmful phenomena for small population densities. Genetic variability is reduced due to the increasing inbreeding in small habitats (Wagenius et al 2007, Bruggeman et al 2010). The weakest individuals of strongly territorial or intra-competing species can be displaced and die because they

https://doi.org/10.1088/1742-5468/ac4982
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cannot find a place to settle down without being attacked by their congers (Jager et al 2006). Other possible consequences of habitat reduction include species that suffer from lack of food and are forced to change their diet (Araújo et al 2014). Several studies also prove the detrimental effect of fragmentation on populations. For example, stochastic simulations in a bidimensional space in which each individual moves, dies, or procreates randomly every time step (Fahrig 1997) show that fragmentation and even more habitat loss imply a greater extinction risk. Stochastic logistic growth models have also proven that fragmentation reduces population abundance (Herbener et al 2012), i.e. the sum of the population size in two separate patches is always lower than the population when the patches are together. Here, we will mainly explore the impact of habitat size reduction by decreasing the effective dispersal length.

Environmental fluctuations represent stochastic external factors (as weather fluctuations) influencing the population dynamics. Environmental fluctuations typically have spatial synchrony and lead to spatial synchrony on the population fluctuations. These spatially synchronized population fluctuations imply simultaneous population depletions or even local or global extinctions (Heino et al 1997, Engen et al 2002, Engen 2007). The spatial scale of population synchrony is equal (Moran 1953) or larger, due to dispersal (Lande et al 1999), than the spatial scale of synchrony of environmental fluctuations. Interspecies interactions can further increase the spatial scale of population synchrony (Bjørnstad et al 1999, Blasius et al 1999, Cazelles and Boudjema 2001, Ripa and Ranta 2007, Jarillo et al 2018, 2020, Fernández-Grande and Cao-García 2020). Here, we describe the risk of extinction in terms of population resilience to environmental fluctuations. We define the extinction threshold (for the environmental fluctuations) as the value of the amplitude of environmental fluctuations above which environmental fluctuations cause a global extinction of the population (Crespo-Miguel et al 2022). The extinction threshold provides a measure of the resilience to extinction.

In spatially extended populations (also known as metapopulations), dispersal provides a rescue mechanism to prevent local extinction from becoming global. Dispersal allows repopulating depleted regions with individuals from the non-depleted areas. Theoretical studies have shown that dispersal is much more effective as a mechanism to enhance resilience to environmental fluctuation if the area occupied by the population is much larger than the scale of population synchrony (Engen et al 2002). In addition, habitat fragmentation or habitat reduction effectively decreases dispersal as it has been observed in field studies for animals such as squirrels (Antolini et al 2001) and in simulations that mimic the natural growth of populations of different species of plants (Collingham and Huntley 2000, Dullinger et al 2015).

Here, we study the impact on resilience to environmental fluctuations due to reducing the dispersal length. We also investigate the harmful consequences of habitat reduction as an effective limiter of dispersal length. See section 3. The study is performed with the spatially extended population model (with Allee effect, dispersal, and stochastic environmental fluctuations) introduced in section 2.
2. Methods: spatially extended population model for finite and infinite habitats

To study the effects of habitat size in population dynamics, we introduce a spatially extended population model with Allee effect, dispersal, and environmental stochasticity. Dispersal provides the population with resilience to environmental stochasticity for infinite habitats (Crespo-Miguel et al 2022). Here, we check how this resilience is limited when the population is confined to a finite habitat, implemented through a finite simulation box with reflecting boundary conditions.

2.1. Infinite habitat

The evolution equation has both a deterministic and a stochastic part (caused by environmental stochasticity), giving the dynamics of the population density $N(x,t)$ as a function of the spatial location $x$ for future times $t$. The local deterministic dynamics is described by an Allee growth equation (Allee and Rosenthal 1949). Additionally, environmental stochasticity is added as a multiplicative noise, so the local dynamics of the population is described by

$$
\frac{dN}{dt}_{\text{local}} = rN \left( \frac{A}{N} - 1 \right) \left( 1 - \frac{N}{K} \right) dt + \sigma N dB.
$$

Here, $r$ is the population’s characteristic extinction rate (at low populations) and $K$ is the population’s carrying capacity (the stable, viable local population density). $A$ is the population’s Allee threshold, the minimum viable population density (i.e. the minimum local population density that gives a deterministic positive growth). The environmental stochastic term $\sigma N dB$ is proportional to the population density $N$. The amplitude of environmental fluctuations is given by $\sigma$, and $dB$ is a normalized Gaussian random field with zero mean $\langle dB(x,t) \rangle = 0$, and a spatial scale of synchrony of the fluctuations equal to $l_e$, which means that the environmental fluctuations are correlated within a length $l_e$ (Lande et al 2003). This Gaussian field is uncorrelated in time and has an exponentially decreasing spatial correlation function

$$
c_{dB dB}(y) = e^{-\frac{2|y|}{l_e}}.
$$

This means $\langle dB(x,t) dB (x+y,t+\tau) \rangle = c_{dB dB}(y) \delta(\tau) dt$, with $\delta(\tau)$ the Dirac delta.

Dispersal is also considered, as it plays a crucial role in the persistence of a spatially extended population (Crespo-Miguel et al 2022). If we consider individuals dispersing with a dispersal rate $m$ to a mean characteristic distance equal to $l_m$, then the dispersal term can be described by

$$
\frac{dN}{dt}_{\text{dispersal}} = -mN dt + m dt \int N(y,t) f(x-y) dy,
$$

where the function $f(x-y)$ is a Gaussian function with mean zero and variance equal to $l_m^2$. This equation describes that individuals leave from a particular point $y$ with probability $m dt$, and they disperse with probability $f(x-y)$ to a distance $x-y$, usually of the order of $l_m$, coupling the population densities over space.

https://doi.org/10.1088/1742-5468/ac4982
Combining equations (1) and (3), we get the dynamical equation of a spatially extended, non-confined population,

\[ \frac{dN}{dt} = rN \left( \frac{N}{A} - 1 \right) \left( 1 - \frac{N}{K} \right) dt - mN dt + m \int N(y,t) f(x-y) dy + \sigma N dB. \tag{4} \]

This non-confined population equation simulates a population on an infinite habitat, corresponding to an infinite confinement size, \( L = \infty \). In practice, this corresponds to cases where the size of the habitat is much larger than the characteristic scales of the systems (in particular, larger than the population synchrony scales). Numerically, we considered large confinement size \( L \), and periodic boundary conditions to reduce the border effects. (Our results revealed that border effects are negligible for values of \( L \gg l_m \) as we discuss later in detail in the results section.)

The deterministic local term, the first term in equation (4), has two stable population densities, \( N = 0 \) (extinction) and \( N = K \) (carrying capacity). For small population fluctuations, the rates of return to the extinction or the carrying capacity states are given by \( \gamma_0 = r \) and \( \gamma_K = r \left( \frac{K}{A} - 1 \right) \), respectively (Crespo-Miguel et al 2022). For populations close to a stable equilibrium point, small environmental fluctuations lead to a spatial scale of population synchrony \( l \) greater than the spatial scale of synchrony of environmental fluctuations \( l_e \), with \( l = \sqrt{l_e^2 + m l_m^2 / \gamma} \) and \( \gamma \) the rate of return to the stable equilibrium (Lande et al 1999). Therefore, in the present case, we can define two characteristic scales of population synchrony around extinction and around carrying capacity, \( l_0 \) and \( l_K \), respectively, defined as

\[ l_0 = \sqrt{l_e^2 + \frac{m \cdot l_m^2}{\gamma_0}}, \tag{5} \]

\[ l_K = \sqrt{l_e^2 + \frac{m \cdot l_m^2}{\gamma_K}}, \tag{6} \]

corresponding to the different return rates to extinction and carrying capacity, \( \gamma_0 \) and \( \gamma_K \), respectively (Crespo-Miguel et al 2022).

### 2.2. Finite habitat

Here we aim to address the effects of habitat size on ecosystem resilience to environmental fluctuations. This provides very relevant information on the impact of habitat reduction or habitat fragmentation in ecosystems.

We consider a population confined between the Frontier positions \( x = a \) and \( x = b \), i.e. in the interval \( x \in [a, b] \), which means a confinement length of \( L = b - a \). We consider reflecting boundary conditions in these two Frontier positions. One of the possible ways to introduce these reflecting boundary conditions is to generalize the convolution \( \int N(y,t) f(x-y) dy \) in equation (4) to a convolution \( F^{(a,b)}(x) \) defined by the following
Table 1. Variables used in this article, definitions, and units.

| Variables | Description                                                                 |
|-----------|-----------------------------------------------------------------------------|
| $N(x,t)$  | Population density at a given position $x$ and time $t$. Units of space$^{-1}$|
| $A$       | Allee threshold of the species. Species with a population density lower than $A$ has negative growth in a deterministic system. Units of space$^{-1}$|
| $K$       | Carrying capacity of the species. Units of space$^{-1}$                     |
| $r$       | Extinction rate of the species (at low population). Units of time$^{-1}$     |
| $\gamma_0$| Rate of return to extinction, $\gamma_0 = r$. Units of time$^{-1}$           |
| $\gamma_K$| Rate of return to carrying capacity, $\gamma_K = r(K/A - 1)$. Units of time$^{-1}$|
| $m$       | Dispersal rate of the species. Units of time$^{-1}$                         |
| $l_e$     | Spatial scale of synchrony of environmental fluctuations. Units of length    |
| $l_m$     | Characteristic dispersal distances of the population. Units of length        |
| $L$       | Confinement size. Units of length                                           |
| $\sigma$  | Amplitude of the environmental fluctuations. It is equal to the standard deviation of the environmental fluctuations. Units of time$^{-1/2}$|
| $\sigma_{\text{extinction}}$ | Extinction threshold for the amplitude of environmental fluctuations (minimum amplitude of the environmental fluctuations that ensures global extinction). Units of time$^{-1/2}$ |

iterative process. We start computing

$$F_{0}^{[a,b]} (x) = \int_{a}^{b} N(y,t) f(x-y) \, dy.$$  
(7)

in an interval wider than $[a,b]$ by several $l_m$, for example $[a - 3l_m, b + 3l_m]$. Then, we alternatively reflect the dispersal tails outside each of the sides of the interval to the interior. Alternatively, applying the right Frontier reflection transformation

$$F_{2n+1}^{[a,b]} (x) = \begin{cases} 
F_{2n}^{[a,b]} (x) + F_{2n}^{[a,b]} (2b - x) & \text{if } x \leq b \\
0 & \text{if } x > b 
\end{cases}$$
(8)

and the left Frontier reflection transformation

$$F_{2n+2}^{[a,b]} (x) = \begin{cases} 
F_{2n+1}^{[a,b]} (x) + F_{2n+1}^{[a,b]} (2a - x) & \text{if } x \geq a \\
0 & \text{if } x < a 
\end{cases}$$
(9)

The process finally converges to a convolution $F_{\infty}^{[a,b]} (x)$, which gives the dispersal of the population confined in the interval $[a,b]$ with reflecting boundary conditions. The
dynamical equation for the population confined in this interval is given by

\[ \frac{dN}{dt} = rN \left( \frac{N}{A} - 1 \right) \left( 1 - \frac{N}{K} \right) dt - mN dt + mF_{\infty}^{(a,b)} dt + \sigma N dB. \]  (10)

Numerical simulations have been performed for finite habitat (finite \( L \)) using equation (10) with reflecting boundary conditions, and for infinite habitat (\( L = \infty \)) using equation (4) with periodic boundary conditions. Spatial and temporal resolutions are implemented in the same way for both cases. We consider the environmental synchrony scale, \( l_e \), as the reference length, and set the spatial resolutions to have at least 20 lattice nodes per minimum parameter length (i.e. the smallest parameter among \( l_e, l_m, \) and \( L \)). The time resolution has been set as 50 times smaller than the minimum of the two characteristic time scales, \( r^{-1} \) and \( m^{-1} \) (the inverses of the extinction rate \( r \) and the dispersal rate \( m \) respectively). The extinction threshold for the amplitude of environmental fluctuations is obtained from several simulations stopping at 100 times \( r^{-1} \) (which is also a large time compared to the characteristic dispersal time, as for the simulations performed \( r^{-1} \sim 10m^{-1} \)). (The extinction threshold mildly depends on the logarithm of the maximum simulation time as discussed in appendix C. Increasing the maximum simulation time one order of magnitude, from \( t = 100r^{-1} \) to \( t = 1000r^{-1} \), only implies a change of the order of 10% in the extinction threshold.) Table 1 summarizes the variables used in this article, their definitions and units.

3. Resilience to environmental fluctuations

Environmental fluctuations can lead an otherwise stable population to global extinction. Here, we address how large are the environmental fluctuations that a population can endure without going extinct. We define the extinction threshold \( \sigma_{\text{extinction}} \) as the minimum amplitude of environmental fluctuations that ensures global extinction (see appendix D). The extinction threshold provides a measure of the resilience of the population to environmental fluctuations.

Dispersal plays an essential role in making the populations more resilient to environmental fluctuations, recovering depleted or extinct populations in one location through the dispersal of the individuals from nearby non-depleted areas (Gotelli 1991, Hanski and Gyllenberg 1993, Crespo-Miguel et al 2022). Habitat reduction (or habitat fragmentation) confines the population to a smaller region, where, therefore, the population fluctuations are more correlated. This higher population correlation reduces the effectiveness of this dispersal recovery mechanism. As a result, habitat reduction decreases the resilience of the population to environmental fluctuations. See figures 1 and 2. Reductions in the dispersal length \( l_m \) also lead to reductions in the resilience of the population to environmental fluctuations, as we see in figure 2, and we study below in more detail in section 3.1, where we show the scaling of the extinction threshold \( \sigma_{\text{extinction}} \) with the dispersal length \( l_m \). In section 3.2, we characterize the scaling of the extinction threshold \( \sigma_{\text{extinction}} \) with habitat size \( L \). Finally, in section 3.3, we show how we can define an effective dispersal length \( l_{m,\text{effective}}(L) \) to describe how the dispersal length \( l_m \) is effectively reduced as the habitat size \( L \) decreases. This effective reduction in \( l_m \) leads to earlier
Figure 1. Habitat reduction can lead to extinction, as it reduces the resilience to environmental fluctuations. Population density $N(x)$ at long times ($t = 100r^{-1}$) for a huge confinement size, $L = 142$ (blue solid line) and for a medium confinement size, $L = 20$ (red solid line), and for two amplitudes of the environmental noise $\sigma = 0.65$ (upper panel) and $\sigma = 0.70$ (bottom panel). The figure shows an example of how the reduction of confinement size reduces the resilience to environmental fluctuations, leading to the extinction of the more confined population when environmental noise is increased (red solid line of the bottom panel). Horizontal dotted lines represent extinction $N = 0$ (black), Allee threshold $N = A = 0.1$ (red), and carrying capacity $N = K = 1$ (green) population density values. These parameter values are common to all the cases represented in this figure, and also the extinction rate $r = 0.1$, the dispersal rate $m = 1$, and the dispersal length $l_m = l_e$ (with the spatial scale of environmental synchrony $l_e$ chosen as the unit of length $l_e = 1$). Huge confinement size $L = 142$ (blue solid line) was simulated with equation (4) and periodic boundary conditions, while medium confinement size $L = 20$ (red solid line) was simulated with equation (10) and reflecting boundary conditions.

saturation of the extinction threshold as a function of $l_m$ for smaller confinement sizes $L$, as figure 2 shows.

3.1. Greater dispersal lengths increase the resilience to environmental fluctuations

Increasing the dispersal length $l_m$ favors the dispersal rescue effect for the population. This enhanced rescue effect enlarges the extinction threshold $\sigma_{\text{extinction}}$ (see figure 2)
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Figure 2. Extinction threshold $\sigma_{\text{extinction}}$ as a function of the ratio $l_m/l_e$ for different confinement sizes $L$. X-shaped points indicate simulations with a huge confinement size $L = 100\sqrt{l_e^2 + l_m^2}$ and periodic boundary conditions, whereas diamond-shaped points indicate simulations with a finite confinement size and reflecting boundary conditions. Vertical bars indicate uncertainty in the simulation result (see appendix D). All simulations are for Allee threshold $A = 0.1$, carrying capacity $K = 1$, extinction rate $r = 0.1$, dispersal rate $m = 1$, and spatial scale of synchrony of environmental fluctuations $l_e = 1$. The blue solid line represents the result in the limit of infinite habitat size and characteristic dispersal length, $L = \infty, l_m = \infty$ and it has been obtained using the mean-field approximation as described in references (Crespo-Miguel et al 2022).

with $l_m$, until it saturates to the mean-field value ($l_m \to \infty$). Figure 2 also shows that the extinction threshold depends additionally on the habitat size $L$, i.e. $\sigma_{\text{extinction}}(l_m, L)$. However, we will focus first on the dependence on the dispersal length $l_m$ for infinite habitats ($L = \infty$). Therefore, we will study the extinction threshold for infinite habitats $\sigma_{\text{extinction},\infty}(l_m) = \sigma_{\text{extinction}}(l_m, L \to \infty)$. The mean-field value for an infinite habitat is denoted here by $\sigma_{\infty} = \sigma_{\text{extinction}}(l_m \to \infty, L \to \infty)$ and it is computed by the mean-field approximation explained in reference (Crespo-Miguel et al 2022). The ratio of extinction threshold for infinite habitat $\sigma_{\text{extinction},\infty}$ and its respective mean-field value $\sigma_{\infty}$ for each dispersal rate $m$ is plotted as a function of the ratio of the dispersal length and the environmental correlation length, $l_m/l_e$, in figure 3. This two ratios show an approximate scaling of the form

$$\frac{\sigma_{\text{extinction},\infty}(m, l_m)}{\sigma_{\infty}(m)} = M \left( \frac{l_m}{l_e} \right) = \left( \frac{1}{1 + \left( b_M \frac{l_m}{l_e} \right)^{n_M}} \right)^{1/d_M}. \quad (11)$$

A maximum likelihood fit (see appendix A) of this scaling form to the simulation results leads to the values of the fitting parameters: $d_M$, $n_M$, and $b_M$ indicated in table 2. Plots of $\sigma_{\text{extinction},\infty}/\sigma_{\infty}$ as a function of the ratios $l_m/l_0$ or $l_m/l_K$ do not present this approximate scaling behavior. See figure B1 in appendix B.

The data in figure 3 have a slight dependence in the dispersal rate $m$, showing that points with smaller dispersal rates are higher than those with larger dispersal rate for the same ratio $l_m/l_e$. Thus, the extinction threshold $\sigma_{\text{extinction}}$ divided by its respective
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Figure 3. Extinction threshold for infinite habitat $\sigma_{\text{extinction, } \infty}$ as a function of the dispersal length $l_m$, for various values of the dispersal rate $m$. The figure shows that the extinction threshold for infinite habitat $\sigma_{\text{extinction, } \infty}$ (divided by the respective mean-field value $\sigma_{\infty}$ for each dispersal rate $m$) is fitted by the scaling function in equation (11) with the parameter values in table 2 (solid black line). The dispersal length is expressed in units of the spatial scale of environmental fluctuations $l_e$. Vertical bars indicate uncertainty in the simulation results (see appendix D). All simulations are for Allee threshold $A = 0$, carrying capacity $K = 1$, extinction rate $r = 0.1$, and spatial scale of synchrony of environmental fluctuations $l_e = 1$.

Table 2. Parameters giving the maximum likelihood fit for the 42 points in figure 3 to equation (11). Uncertainties have been calculated with a confidence interval of 68%, i.e. at one-sigma level. SE, logarithm of the likelihood ($-\ln \mathcal{L}$) and Akaike information criterion AIC$_C$ are also included (see appendix A for their definitions).

| $n_M$  | $d_M$  | $b_M$  | SE   | $-\ln \mathcal{L}$ | AIC$_C$ |
|--------|--------|--------|------|--------------------|---------|
| 1.9 ± 1.4 | 8.0 ± 6.8 | 10.1 ± 3.2 | 0.105 | 146                | 298     |

The mean-field value $\sigma_{\infty}$, has a better fit with a function scaling with $(\frac{m}{r})^{s_M}(\frac{l_m}{l_e})$, where $s_M$ is an additional fitting parameter,

$$\frac{\sigma_{\text{extinction, } \infty}(m, \frac{l_m}{l_e})}{\sigma_{\infty}(m)} = M(\frac{m}{r}, l_m, l_e) = \left( \frac{1}{1 + (b_M l_m (\frac{r}{m})^{s_M})^{n_M}} \right)^{1/d_M}.$$  (12)

The fit to the numerical results of this scaling law, equation (12), is better than for the previous one, equation (11), even taking into account the AIC penalty for the additional parameter ($s_M$). See figure 4 and table 3. The significant difference in AIC$_C$ yielded by fitting equations (11) and (12), $\Delta$AIC$_C = 481 \gg 10$, implies that the model with higher AIC$_C$, given by equation (11), can be discarded entirely (appendix A). The best-fitting model (the model with the lowest AIC$_C$), equation (12), indicates that the mean-field value is reached for long dispersal distances $l_m$, but more slowly for higher dispersal rates $m$.
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Figure 4. Extinction threshold for infinite habitat $\sigma_{\text{extinction, }\infty}$ scales as a function of the ratio $(m/r)^{s_M} \left(\frac{L}{l_e}\right)^{s_M}$, with $s_M = -0.667$. The figure shows that the extinction threshold for infinite habitat $\sigma_{\text{extinction, }\infty}$ (divided by the respective mean-field value $\sigma_{\infty}$ for each dispersal rate $m$) is fitted by the scaling function in equation (12) with the parameter values in table 3 (solid black line). Vertical bars indicate uncertainty in the simulation results (see appendix D). All simulations are for Allee threshold $A = 0.1$, carrying capacity $K = 1$, extinction rate $r = 0.1$, and spatial scale of synchrony of environmental fluctuations $l_e = 1$.

Table 3. Parameters giving the maximum likelihood fit for the 42 points in figure 4 to equation (12). Uncertainties have been calculated with a confidence interval of 68%, i.e. at one-sigma level. SE, logarithm of the likelihood ($-\ln \mathcal{L}$) and Akaike information criterion (AIC$_C$) are also included (see appendix A for their definitions).

| $n_M$   | $d_M$ | $b_M$ | $s_M$       | SE    | $-\ln \mathcal{L}$ | AIC$_C$ |
|---------|-------|-------|-------------|-------|--------------------|---------|
| 1.26 ± 0.21 | 5.0 ± 1.1 | 1.57 ± 0.36 | −0.667 ± 0.049 | 0.0120 | −96.0              | −183    |

3.2. Habitat reduction decreases resilience to environmental fluctuations

As we explained above, the resilience to environmental fluctuations can be characterized by the minimum amplitude of environmental fluctuations that leads to global extinction, the extinction threshold $\sigma_{\text{extinction}}(m, l_m, L)$. The extinction threshold decreases as the habitat size decreases (for example, due to habitat fragmentation). We characterized in the previous section the dependence of the extinction threshold with the dispersal length $l_m$ for infinite habitats. Using these previous results and an analogous approach, we will find the scaling behavior with the habitat size $L$. We consider the ratio of the extinction threshold for finite and infinite habitat size (see figure 5) and compare fits of the type

$$
\frac{\sigma_{\text{extinction}}(m, l_m, L)}{\sigma_{\text{extinction, }\infty}(m, l_m)} = F\left(\frac{L}{l_i}\right) = \left(\frac{1}{1 + (bk)^{n_M}}\right)^{1/d_M},
$$

where $l_i$ can represent the spatial scale of environmental synchrony $l_e$, the dispersal length $l_m$, the spatial scale of population synchrony close to extinction

https://doi.org/10.1088/1742-5468/ac4982

J. Stat. Mech. (2022) 023501
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Figure 5. Extinction thresholds for fragmented habitats $\sigma_{\text{extinction}}$ as functions of the size of the habitat $L$ divided by the dispersal length of the population $l_m$ (A), the spatial scale of population synchrony around extinction $l_0$ (B), the spatial scale of population synchrony around carrying capacity $l_K$ (C), and the spatial scale of synchrony of environmental fluctuations $l_e$ (D). The figure shows that the extinction threshold for a fragmented habitat $\sigma_{\text{extinction}}$ divided by the respective infinite habitat value $\sigma_{\text{extinction,}\infty}$ (for the same dispersal rate $m$ and dispersal length $l_m$) is fitted by the scaling function in equation (13) with the parameter values in table 4 (solid black line). Vertical bars indicate uncertainty in the numerical results (see appendix D). All simulations are for Allee threshold $A = 0.1$, carrying capacity $K = 1$, extinction rate $r = 0.1$, and spatial scale of synchrony of environmental fluctuations $l_e = 1$.

\[ l_0 = \sqrt{l_e^2 + ml_m^2/\gamma_0}, \]
\[ l_K = \sqrt{l_e^2 + ml_m^2/\gamma_K} \]

(As introduced in equations (5) and (6) above). The maximum likelihood fitting of equation (13) to the simulation results (figure 5) gives the parameter values indicated in table 3, where the AICC results indicate that the best fitting model is that with $l_i = l_m$, closely followed by $l_i = l_0$. The other models can be

https://doi.org/10.1088/1742-5468/ac4982
Table 4. Parameters giving the maximum likelihood fit for the 60 points of figure 5 to equation (13). Uncertainties have been calculated with a confidence interval of 68%, i.e. at one-sigma level. SE, logarithm of the likelihood (− ln L) and Akaike information criterion AIC_C are also included (see appendix A for their definitions).

|                 | nF    | dF    | bF    | SE   | − ln L | AIC_C |
|-----------------|-------|-------|-------|------|--------|-------|
| L/λ_m           | 1.93 ± 0.83 | 8.5 ± 4.0 | 28.7 ± 6.4 | 0.158 | −69.4 | −132 |
| L/λ_0           | 1.84 ± 0.73 | 8.0 ± 3.5 | 6.4 ± 1.5 | 0.193 | −68.9 | −131 |
| L/λ_K           | 2.3 ± 1.6  | 10.1 ± 7.6 | 16.5 ± 4.6 | 0.382 | −21.6 | −36.8 |
| L/λ_e           | 3.0 ± 4.0  | 14 ± 19  | 58 ± 26  | 1.033 | 209    | 424   |

Table 5. Parameters giving the maximum likelihood fit for the 60 points of figure 6 to the equation (14). Uncertainties have been calculated with a confidence interval of 68%, i.e. at one-sigma level. SE, logarithm of the likelihood (− ln L) and Akaike information criterion AIC_C are also included (see appendix A for their definitions).

|                 | nF    | dF    | bF    | sF   | SE   | − ln L | AIC_C |
|-----------------|-------|-------|-------|------|------|--------|-------|
| L/λ_m           | 1.91 ± 0.70 | 8.5 ± 3.4 | 2.5 ± 1.4 | −0.93 ± 0.21 | 0.132 | −89.6 | −170 |
| L/λ_0           | 1.87 ± 0.72 | 8.2 ± 3.5 | 1.6 ± 1.0 | −0.53 ± 0.24 | 0.188 | −75.5 | −142 |
| L/λ_K           | 2.2 ± 1.4  | 9.7 ± 6.6 | 3.1 ± 2.6 | −0.62 ± 0.29 | 0.367 | −31.1 | −53.5 |
| L/λ_e           | 2.5 ± 2.5  | 11 ± 12  | 2.7 ± 3.7 | −1.09 ± 0.48 | 0.963 | 179   | 367   |

discarded as its difference in AIC_C is greater than 10 (Burnham and Anderson 2002). In particular, the model with λ_i = λ_e is completely discarded due to the large value of AICc, and the large uncertainty and instability in the parameter value determination, which is consistent with the dispersal of the values observed in figure 5 for this case.

Additionally, the improved fit found in the previous subsection for the λ_m/λ_e scaling introducing a dependence on the ratio between the dispersal rate m and the extinction rate r motivates us to perform a similar check for the scaling of the habitat size L. We found that the data in figure 5 scale better as a function of \((m/r)^sF(L/λ_i)\),

\[
\sigma_{\text{extinction}}(m, l_m, L) = F(m/r, L/λ_i) = \left(\frac{1}{1 + (bF^L(m/r)^sF)^{nF}}\right)^{1/dF}, \tag{14}
\]

which fits the numerical results with the parameters of table 5 (figure 6). We see, comparing tables 4 and 5, that the AIC_C is much lower for a maximum likelihood fit to equation (14) than to equation (13) (ΔAIC_C > 10), therefore the model with more empirical support is that which follows equation (14) with λ_i = λ_m. The scaling given by equation (14) indicates that the infinite habitat value is reached for long ratios L/λ_i, and that limit is reached slower for higher dispersal rates m.

https://doi.org/10.1088/1742-5468/ac4982
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Figure 6. Extinction thresholds for fragmented habitats $\sigma_{\text{extinction}}$ as functions of the size of the habitat $L$ multiplied by the ratio $(m/r)^{s_F}$ (value of $s_F$ is given in table 5) and divided by the dispersal length of the population $l_m$ (A), the spatial scale of population synchrony around extinction $l_0$ (B), the spatial scale of population synchrony around carrying capacity $l_K$ (C), and the spatial scale of synchrony of environmental fluctuations $l_e$ (D). The figure shows that the extinction threshold for a fragmented habitat $\sigma_{\text{extinction}}$ (divided by the respective infinite habitat value $\sigma_{\text{extinction,\infty}}$ for the same dispersal rate $m$ and dispersal length $l_m$) is fitted by an approximate scaling described by equation (14) with the parameter values in table 5 (solid black line). Vertical bars indicate uncertainty in the simulation result (see appendix D). All simulations are for Allee threshold $A = 0.1$, carrying capacity $K = 1$, extinction rate $r = 0.1$, and spatial scale of synchrony of environmental fluctuations $l_e = 1$. https://doi.org/10.1088/1742-5468/ac4982
Putting together the results of this subsection and the previous one provides the complete scaling behavior of the extinction threshold \( \sigma_{\text{extinction}} \):

\[
\sigma_{\text{extinction}}(m, l_m, L) = \sigma_\infty^\infty(m) M \left( \frac{m}{r}, \frac{l_m}{l_e} \right) F \left( \frac{m}{r}, \frac{L}{l_m} \right)
\]

\[
= \sigma_\infty^\infty(m) \left( \frac{1}{1 + \left( \frac{b_M}{l_m} \left( \frac{r}{m} \right)^{s_M} \right)^{n_M}} \right)^{1/d_M} \left( \frac{1}{1 + \left( \frac{b_F}{L} \left( \frac{r}{m} \right)^{s_F} \right)^{n_F}} \right)^{1/d_F},
\]

with the values of the parameters given in the first row of tables 3 and 5.

### 3.3. Habitat reduction decreases the effective dispersal length

From the results in previous subsections, we got that habitat reduction effectively decreases the dispersal length, leading to a detriment in the population’s resilience to environmental fluctuations. Thus, we can define an effective dispersal length \( l_{m,\text{eff}}(m, l_m, L) \), as the dispersal length of a population in an infinite habitat \( (L = \infty) \) that has the same extinction threshold as a population with dispersal length \( l_m \) confined in a fragmented habitat of size \( L \), if all the other parameters affecting both populations are equal. This definition is equivalent to the following equation (expanded using equation (15)):

\[
\sigma_{\text{extinction}}(m, l_{m,\text{eff}}, L \to \infty) = \sigma_{\text{extinction}}(m, l_m, L)
\]

\[
\Rightarrow M \left( \frac{m}{r}, \frac{l_{m,\text{eff}}}{l_e} \right) F \left( \frac{L}{l_m} \to \infty \right) = M \left( \frac{m}{r}, \frac{l_m}{l_e} \right) F \left( \frac{m}{r}, \frac{L}{l_m} \right)
\]

\[
\Rightarrow M \left( \frac{m}{r}, \frac{l_{m,\text{eff}}}{l_e} \right) = M \left( \frac{m}{r}, \frac{l_m}{l_e} \right) F \left( \frac{m}{r}, \frac{L}{l_m} \right).
\]

Thus, we got the following expression for the effective dispersal length \( l_{m,\text{eff}}(m, l_m, L) \),

\[
l_{m,\text{eff}}(m, l_m, L) = b_M l_e \left( \frac{r}{m} \right)^{s_M} \left( 1 + \left( \frac{b_M l_e}{l_m} \left( \frac{r}{m} \right)^{s_M} \right)^{n_M} \right)^{1/n_M}
\]

\[
\times \left( 1 + \left( \frac{b_F l_m}{L} \left( \frac{r}{m} \right)^{s_F} \right)^{n_F} \right)^{1/n_F} - 1 \right)^{-1/n_M},
\]

with the parameters given in the first row of tables 3 and 5. The effective dispersal length, as shown in figure 7, is a monotonously increasing function with the habitat size \( L \), and it tends to the real dispersal length \( l_m \) when the habitat size becomes sufficiently large. Thus, habitat size reduction implies a decrease in the effective dispersal length.
4. Discussion

We have shown that both habitat reduction and dispersal reduction decrease population resilience against environmental fluctuations. We have measured the population resilience with the extinction threshold $\sigma_{\text{extinction}}$, defined as the minimum amplitude of environmental fluctuations that ensures population extinction at long times (appendix D). On the one hand, we have obtained that populations with dispersal distances larger than the scale of synchrony of environmental fluctuations are more resilient to fluctuations, and reach the largest extinction threshold for every confinement size. On the other hand, habitat reduction is found to decrease the resilience to environmental fluctuations, leading to a huge drop in the extinction threshold when the habitat size becomes of the order of the typical dispersal distances of the population.

These results imply that habitat reduction (or habitat fragmentation) causes an effective reduction in dispersal length, thus minimizing dispersal-induced resilience caused by the rescue effect. Dispersal is proved as an essential mechanism against extinction in populations with the Allee effect (Palmqvist and Lundberg 1998, Dennis et al 2016, Crespo-Miguel et al 2022). However, dispersal is not so effective when a smaller habitat size truncates its range. These results further clarify that habitat reduction (or habitat fragmentation) is a problem for endangered populations. Its impact can be much more significant for species that depend on diffusion when the habitat size is reduced close to its typical dispersal length. We can apply this knowledge by making a special effort to develop conservation strategies that include active prevention of habitat destruction, so environmental fluctuations are less likely to destroy endangered species populations. Deeper knowledge of populations’ dynamics helps to optimize species conservation and sustainable exploitation policies.

Synchrony plays an essential role in the regional extinction risk (Heino et al 1997, Engen et al 2002, Engen 2007). However, we found that the decrease of the extinction threshold with habitat size scales better with the ratio of the habitat size to the dispersal length than with the ratio of the habitat size to the spatial scale of synchrony. Thus, we
think that the transition to regional extinction needs further study to achieve a complete
understanding of the interplays among the spatial scale of population synchrony, the
dispersal length, the habitat size, and the transitions to extinction.

Here, we have studied the one-dimensional case. The extension of this study to two
dimensions would be interesting because many natural ecosystems are two-dimensional.
It is known that the shapes of the fragmented patches can affect the survival of many
species (Diamond 1975), favoring connectivity to support recovery by internal migration.
Patch shapes can also determine colonized area expansion or contraction (Lewis and
Kareiva 1993, Keitt et al 2001). Additionally, habitat reduction and fragmentation per
se have slightly different effects on population resilience (Fahrig 1997, 2003). Studying
the one- and two-dimensional patch structure and its connectivity can also provide
insight into the transitions to extinction.

These results have been obtained for one-species systems, for which dispersal is
beneficial, increasing the rescue effect. However, dispersal does not always benefit the
dynamics for multiple-species systems since it can homogenize the habitats, removing
some local species (Mouquet and Loreau 2003). Furthermore, the diversity is expected to
peak at intermediate diffusion (Gravel et al 2016). Additionally, recent work has shown
that coupling between heterogeneous patches can lead to a non-monotonic behavior of
the extinction probability with the dispersal (Agranov and Bunin 2021). This work also
stresses that dispersal from other patches might act as a non-Gaussian noise in the
receiving patch, extending the noise-induced phenomena found in ecosystems (Spagnolo
et al 2004).

Funding

This work was funded by European Regional Development Fund (ERDF) and the
Spanish Ministry of Economy and Competitiveness through Grant RTI2018-095802-
B-I00, and by European Union’s Horizon 2020 through Grant Agreement No. 817578
TRIATLAS. J J was supported by CEFIC under the GETREAL project, and from the
Fund for Scientific Research, FNRS (PDRT.0048.16).

Author contributions

R C M and F J C G conceived the manuscript. J J wrote the original code used for
the stochastic population dynamics. R C M adapted the code to populations with Allee
effect and reflecting boundary conditions. R C M and J J ran the numerical simulations.
R C M and F J C G wrote the first version of the manuscript. R C M prepared the
figures. All authors discussed the results and contributed to the final manuscript.

Appendix A. Maximum likelihood fit and Akaike information criterion (AICc)

The fits used in the main text have been done by maximizing likelihood (Burnham
and Anderson 2002). Likelihood is defined by equation (A1) for a set of n independent

https://doi.org/10.1088/1742-5468/ac4982
measures with equal standard deviation $S$,

$$-\ln L = \frac{n}{2} \ln (2\pi) + \frac{n}{2} \ln S^2 + \frac{1}{2S^2} \text{SE}, \quad (A1)$$

where $\text{SE} = \sum_i^n (f(x_i) - y_i)^2$ is the total squared error (SE), $f(x_i)$ is the value of the fit function for a parameter $x_i$, and $y_i$ its measured value.

This definition can be generalized for a set of measures with different uncertainties $S_i$ (Hogg et al 2010), so that the logarithm of the likelihood in this case becomes

$$-\ln L = \frac{n}{2} \ln (2\pi) + \frac{1}{2} \sum_i^n \ln S_i^2 + \frac{1}{2} \sum_i^n \frac{(f(x_i) - y_i)^2}{S_i^2}. \quad (A2)$$

Thus, maximizing the likelihood is equal to minimizing the right-hand side of equation (A2). In addition, $\frac{n}{2} \ln (2\pi) + \frac{1}{2} \sum_i^n \ln S^2$ is a constant that only depends on the data, not on the model (as a consequence, it is usually omitted when comparing models that depend on the same data, as it cancels out). Then, maximizing the likelihood is equivalent to minimizing $\sum_i^n \frac{(f(x_i) - y_i)^2}{S_i^2}$.

Comparing maximum likelihood of two models is useful if both models have the same number of free parameters. In the other case, we must compare them by the Akaike information criterion (Akaike 1974) defined by

$$\text{AIC} = 2k - 2 \ln L, \quad (A3)$$

where $k$ is the number of free parameters of the model. The definition of equation (A3) supposes a infinitely large number of points to fit by the model, so there is a correction for small size of the sample defined by

$$\text{AIC}_C = \text{AIC} + \frac{2k^2 + 2k}{n - k - 1} = 2k - 2 \ln L + \frac{2k^2 + 2k}{n - k - 1}. \quad (A4)$$

Thus, given two models fitting the same set of points, the model with lower $\text{AIC}_C$ is the best. Nonetheless, models with higher $\text{AIC}_C$ should not always be discarded. If we define the difference between the $\text{AIC}_C$ of the two models, this is

$$\Delta_i = \text{AIC}_{C,i} - \text{AIC}_{C,\text{min}}, \quad (A5)$$

then, a difference $\Delta_i$ between 0 and 2 indicates that the $i$th model has a substantial empirical support (Burnham and Anderson 2002), a difference between 4 and 7 indicates a considerably lesser support of the model, and a difference greater that 10 means that the $i$th model has essentially no empirical support and should be completely discarded.

**Appendix B. Figures of extinction threshold depending on the dispersal distance shown as functions of other parameters**

See figure B1.

https://doi.org/10.1088/1742-5468/ac4982
Appendix C. Extinction threshold and extinction time

In all of the paper we have estimated the extinction threshold $\sigma_{\text{extinction}}$ for a maximum simulation time, or final time for the simulation, of $t = 100r^{-1}$. At this time we considered the population is extinct if all the positions are below the Allee threshold. To determine the extinction threshold we plotted the fraction of the positions with a population density above the Allee threshold $f_A$ as function of the amplitude of environmental fluctuations $\sigma$. The extinction threshold $\sigma_{\text{extinction}}$ and its uncertainty was estimated as the center and the width of the range of values where $f_A$ makes the transition between extinct and non-extinct population. (See figures C1(A) and (B) and appendix D for further details.)

Here, we show that extinction threshold mildly decreases as we increase the maximum simulation time, because the extinction time increases as the amplitude of environmental fluctuations decreases. Figures C1(C) and (D) show that the extinction threshold has a relative decrease of the order of 10% when the maximum simulation time is increased by a factor 10.

In the computations of this article, we have considered ten different realizations for each value of the amplitude of environmental fluctuations $\sigma$. (See, for example, figure C1.) This number of realizations is enough for the required precision. For five and ten realizations, the difference in the results for the mean of $\log_{10}t_{\text{extinction}}$ for five and ten realizations is small enough (4.8% for small habitat size and 2.9% for large habitat),
Figure C1. Extinction threshold for the amplitude of environmental fluctuations $\sigma$ and extinction times $t_{\text{extinction}}$. Upper panels show the fraction of the positions with a population density above the Allee threshold $f_A$ for a small habitat size $L = l_e$ (A) and a large habitat size ($L = 187l_e$) (B) as a function of the amplitude of the environmental fluctuations $\sigma$. Bottom panels show the extinction time (in units of the inverse of the extinction rate $r^{-1}$) for a small habitat size (C) and a large habitat size (D) as a function of the amplitude of the environmental fluctuations $\sigma$. (Triangles indicate the mean and error bars the one-standard deviation interval in $\log_{10}t_{\text{extinction}}$.) (Ten simulations for each value of $\sigma$.) For all panels Allee threshold $A = 0.1$, carrying capacity $K = 1$, extinction rate $r = 0.1$, dispersal rate $m = 1$, and dispersal length $l_m = 0.5l_e$ (with the spatial scale of environmental synchrony $l_e$ chosen as the unit of length).

and even smaller for $\sigma_{\text{extinction}}$ (1% difference). In both cases, the differences are smaller than the uncertainties (see appendix D). Thus, a greater number of realizations would mean only a small difference in the final results.

Appendix D. Calculation of extinction thresholds

In order to obtain the extinction threshold and its uncertainty for given fixed values of the rest of parameters (i.e. for each point in figures 2–6), we have implemented the
following procedure. We chose a set of amplitudes of the environmental fluctuations \( \{\sigma_1, \sigma_2, \ldots, \sigma_s\} \), with \( \sigma_{i+1} = \sigma_i + \Delta \sigma \), using \( \Delta \sigma = 0.01 \), and covering a sufficiently large range (such as realizations with the smaller \( \sigma \) never end in global extinction and those with the larger \( \sigma \) always do). Then, we perform \( R \) realizations for each \( \sigma_i \) and we store the fraction of realizations \( k_i \) which finish in global extinction at the end of the simulation (i.e. those realizations with a fraction of the positions with a population density above the Allee threshold \( f_A = 0 \) at \( t = 100r^{-1} \)). Next, we define the discrete distribution

\[
p(\sigma_i) = \frac{\min (k_i, 1 - k_i)}{\sum_i \min (k_j, 1 - k_j)},
\]

which satisfies \( \sum_i p(\sigma_i) = 1 \). This distribution can be used to calculate the mean extinction threshold

\[
\sigma_{extinction} = \sum_1^s p(\sigma_i) \cdot \sigma_i,
\]

and its standard deviation

\[
\text{sd}_{biased} = \sqrt{\sum_1^s p(\sigma_i) \cdot (\sigma_i - \sigma_{extinction})^2}.
\]

The distribution is discrete and obtained by a finite sample, so the standard deviation is biased. Only \( h \cdot R \) simulations contribute to sampling the distribution \( p(\sigma) \), where \( h \) is the number of \( \sigma_i \) with non-zero \( p(\sigma_i) \) (i.e. with \( k_i \) different to 0 or 1). The unbiased standard deviation is then given by

\[
\text{sd}_{unbiased} = \frac{h \cdot R}{h \cdot R - 1} \text{sd}_{biased}.
\]

Furthermore, the discretization of the \( \sigma \) interval in intervals of \( \Delta \sigma = 0.01 \) can contribute to an underestimation of the standard deviation. To correct this underestimation, we computed the uncertainty \( S \) of the extinction threshold as

\[
S = \sqrt{\text{sd}_{unbiased}^2 + \Delta \sigma^2}.
\]

We verified that the interval value of \( \Delta \sigma = 0.01 \) did not contribute significantly to the uncertainty of the extinction threshold. Thus, the uncertainty \( S \) accurately represented the uncertainty in \( \sigma_{extinction} \) due to the stochastic nature of the dynamics.

We first considered five realizations, \( R = 5 \), for each amplitude \( \sigma_i \), then we compared the results with those obtained with ten realization, \( R = 10 \). The average difference between \( \sigma_{extinction,R=5} \) and \( \sigma_{extinction,R=10} \) was less than 1% and always smaller than the uncertainty \( S \). This result indicates that ten realization for each environmental fluctuations amplitude \( \sigma_i \) (for each fixed group of value of the other parameters) are enough to accurately calculate the extinction threshold and its uncertainty in the range of parameters that we studied.
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