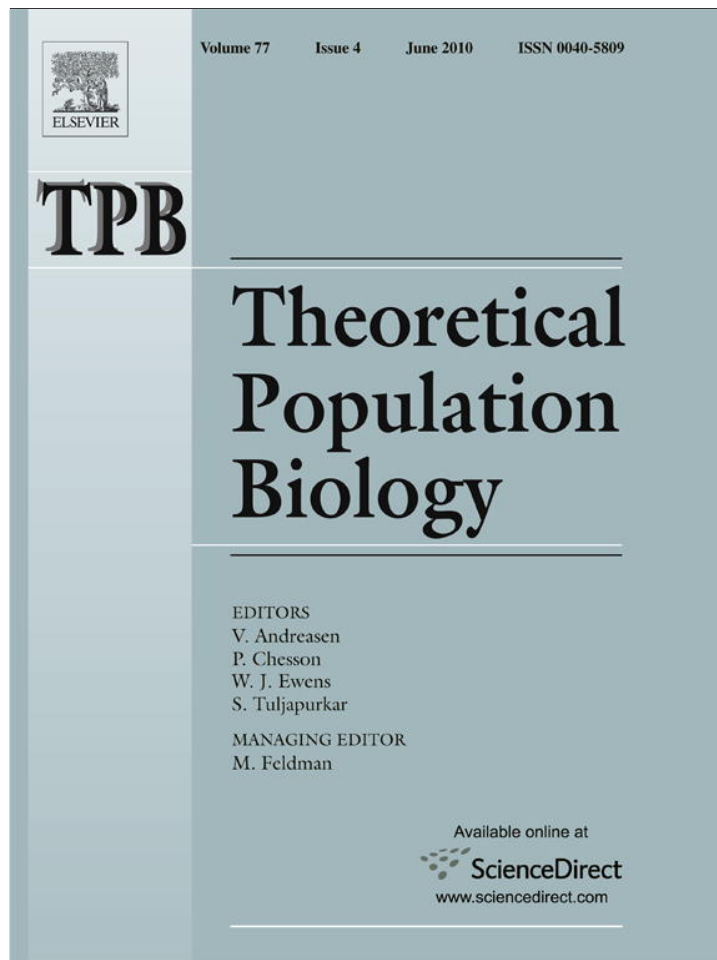


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## Extinction conditions for isolated populations affected by environmental stochasticity

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### ABSTRACT

We determine the critical patch size below which extinction occurs for populations living in one-dimensional habitats surrounded by completely hostile environments in the presence of environmental fluctuations. The population dynamics is reformulated in terms of a stochastic reaction–diffusion equation and is reduced to a deterministic equation that incorporates the systematic contributions of the noise. We obtain bifurcation diagrams and relations for the mean population density at the stationary state, the critical patch size, and the mean number of individuals in the habitat. The effect of the noise differs, depending on whether it affects the net growth rate or the intraspecific competition term. Fluctuations in the net growth rate decrease the critical patch size, whereas fluctuations in the competition term do not change the critical patch size. We compare our analytical results with numerical solutions of the stochastic partial differential equations and show that our procedure proves useful in dealing with reaction–diffusion equations with multiplicative noise.

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### 1. Introduction

A crucial problem in population ecology, both from a theoretical point of view as well as for conservation and management purposes, is to determine the risk of extinction. The latter depends on the internal and external processes that affect the stochastic dynamics of populations (Lande et al., 2003).

A wide variety of models for temporal evolution have developed that incorporate stochasticity to analyze its effects on the probability of extinction and the characteristic time of extinction. Some models treat time in a continuous fashion (Feldman and Roughgarden, 1975; Tuckwell, 1974), while others consider time to be discrete (Schwager et al., 2006; or see for example models based on the Ricker map such as Melbourne and Hastings, 2008, Gao et al., 2007). In general, these models predict that environmental heterogeneity or environmental stochasticity increases the risk of extinction by increasing fluctuations in the population density. There has also been a certain interest in studying the influence of the colour, i.e., the temporal correlations, of the environmental noise on the population dynamics (Kaitala and Ranta, 1996; Kaitala et al., 1997; Ripa and Lundberg, 1996; Xu and Li, 2003; Kamenev et al., 2008). The increase or decrease of the time to extinction as

a function of the noise colour has been studied recently (Schwager et al., 2006).

There are two main sources of stochasticity that modify the risk of extinction: demographic and environmental. Demographic stochasticity occurs in small populations and it increases the extinction risk due to the lack of coincidences in the fate of individuals (Roughgarden, 1975). Environmental stochasticity occurs because external fluctuations introduce fluctuations in birth and death rates (Roughgarden, 1975). While environmental stochasticity introduces random fluctuations at the population level, demographic stochasticity introduces these fluctuations at the individual level.

Most models employed for demographic and environmental stochasticities consider only temporal evolution. However, natural environments are variable not only in time but also in space, and little attention has been paid to spatiotemporal models (Gao et al., 2007). For this reason we study a spatially extended model, namely a stochastic reaction–diffusion equation. The model incorporates environmental stochasticity via an external noise that displays spatial correlations and is white in time. As a result of including space explicitly in our model, we can deal with the problem of extinction from a different perspective, rather than simply finding the probability of extinction and its characteristic time. We consider a linear finite habitat of size  $L$ . The threat of extinction arises from the fact that the surroundings are completely hostile.

Although the assumption of completely hostile surroundings represents an idealization, it has been employed traditionally in

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the literature not only in general theoretical studies (Skellam, 1951; Bradford and Philip, 1970), but also in models of specific populations such as plankton blooms (Kierstead and Slobodkin, 1953), critical plankton filaments (Martin, 2000), fish populations in marine protected areas (Malvadkar and Hastings, 2008), annual plants (Latore et al., 1998) and bacterial colonies under ultraviolet light (Shnerb, 2000). In mathematical language, this assumption implies that the population density vanishes at the boundaries ( $x = 0$  and  $x = L$ ), which corresponds to Dirichlet boundary conditions. If individuals in the course of their diffusive motion through the habitat reach the boundaries, they are absorbed, killed or removed instantaneously. Hostile surroundings favour population extinction. If the net growth rate is high enough to compensate for the losses at the boundaries, persistence is guaranteed. This depends critically on the habitat size. There exists a critical habitat size  $L_c$ , such that if  $L > L_c$  the population survives, but if  $L < L_c$  it goes to extinction (see e.g. Kot, 2003, for a review). This problem is known in the literature as the critical patch size and it has received much attention since the pioneering work by Kierstead and Slobodkin (1953). Their study has been extended in various directions. For example, systems with two or more subpopulations or different boundary conditions have been considered (Cantrell and Cosner, 2001; Cantrell et al., 2001; Kot and Schaffer, 1986; Lutscher et al., 2007).

In a recent paper (Méndez and Campos, 2008), the survival and extinction conditions for a population living in a habitat surrounded by a completely hostile environment were investigated for different models of population growth. In terms of reaction–diffusion equations, it was observed that the population survives for patch lengths larger than a critical value, whereas it becomes extinct for smaller habitats. Chaotic patterns have also been reported and analytically studied (Méndez et al., 2010) for the case where the population dynamics is described by a coupled logistic map.

To investigate the effect of environmental stochasticity, we consider an external noise that gives rise to fluctuations in either the net reproductive rate or the competition term. This paper also addresses the open problem of how to include stochasticity in an analytically tractable model (Melbourne and Hastings, 2008).

As a result of our analysis, we derive analytically the systematic population density profiles within the patch and conditions for population survival. We show that environmental fluctuations in the characteristic growth rate enhance the population survival probability, while fluctuations in the competition term do not affect this probability and lead directly to the results of the classical, non-fluctuating, critical patch size model (Kot, 2003).

## 2. Equation for the systematic population density

Consider a population with density  $\rho(x, t)$ . For simplicity, we assume that the population lives in a one-dimensional (1D) system and evolves dynamically according to the reaction–diffusion equation

$$\frac{\partial \rho(x, t)}{\partial t} = D \frac{\partial^2 \rho(x, t)}{\partial x^2} + F[\rho(x, t), t]. \quad (1)$$

We consider logistic population growth, i.e.,

$$F(\rho, t) = r_1 \rho(x, t) - r_2 \rho(x, t)^2, \quad (2)$$

where  $r_1$  is the net growth rate at low densities and  $r_2$  is the regulation rate of the population due to intraspecific competition or struggle for resources. Traditionally, one writes  $r_1 = r$  and  $r_2 = r/K$ , where  $K$  is the carrying capacity of the environment. In general, we can consider  $r_1(x, t)$  and  $r_2(x, t)$  as functions of space and time, though they are usually treated as constant in

the literature (Murray, 2003). Eq. (1) does not include fluctuations explicitly; environmental fluctuations have been included via  $r$  and  $K$ . Due to the stochastic character of the resulting parameters, Eq. (1) under these conditions is a stochastic partial differential equation (SPDE), and its solution will be a functional of the state of the noise (San Miguel and Toral, 2000).

The presence of an external noise in parameters  $r_1$  or  $r_2$  turns Eq. (1) into an SPDE equation of the general form

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho) + \varepsilon^{1/2} g(\rho) \eta(x, t), \quad (3)$$

where  $\eta(x, t)$  represents the noise and  $\varepsilon$  measures the noise strength. Note that the external noise appears in a multiplicative way in Eq. (3) if  $g(\rho) \neq \text{const}$ . We consider the case that the noise is Gaussian with zero mean,  $\langle \eta(x, t) \rangle = 0$ , and has a correlation function given by

$$\langle \eta(x, t) \eta(x', t') \rangle = 2C(|x - x'| / \lambda) \delta(t - t'). \quad (4)$$

Here  $C(x)$  is the spatial correlation function of the noise and  $\lambda$  its characteristic length. In the numerical simulations  $C(x)$  has been chosen to be Gaussian with variance 1 and  $C(0) = 10$ . Since the noise is white in time, the density is a Markovian stochastic variable. The noise term  $g(\rho) \eta(x, t)$  has a non-vanishing mean value if  $g(\rho)$  is not a constant, which gives rise to systematic (i.e., non-zero mean value) contributions to the dynamics of the density (García-Ojalvo and Sancho, 1999).

We can rewrite Eq. (3) in a form where the noise term has zero mean,

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F_{\text{eff}}(\rho) + \varepsilon^{1/2} \zeta(\rho, x, t). \quad (5)$$

The effective reaction term is defined as

$$F_{\text{eff}}(\rho) = F(\rho) + \varepsilon C(0) \frac{dg(\rho)}{d\rho} g(\rho), \quad (6)$$

and the new noise is given by

$$\zeta(\rho, x, t) = g(\rho) \eta(x, t) - \varepsilon^{1/2} C(0) \frac{dg(\rho)}{d\rho} g(\rho). \quad (7)$$

Let us write the density as

$$\rho(x, t) = \rho_d(x, t) + \sum_n \varepsilon^{n/2} \rho_n(x, t), \quad (8)$$

where the subscript  $d$  stands for “deterministic” and denotes the systematic contributions. This expansion represents an extension of the standard small-noise expansion procedure that keeps the relevant, systematic contribution of the multiplicative noise (see Appendix A for details). It allows us to separate the systematic or deterministic effects from the stochastic effects of the external noise on the population density. We assume that the deterministic contribution dominates, while the stochastic part plays only a small role, and we analyze the extinction conditions for the deterministic part of the population density. We will show by comparing the exact results with numerical simulations that focusing solely on the deterministic density is a good approximation. Substitution of (8) into (5) yields, to lowest order, the equation for the systematic (deterministic) contribution,

$$\frac{\partial \rho_d}{\partial t} = D \frac{\partial^2 \rho_d}{\partial x^2} + F_{\text{eff}}(\rho_d). \quad (9)$$

The equation for the next order (first stochastic contribution) is given by

$$\frac{\partial \rho_1}{\partial t} = D \frac{\partial^2 \rho_1}{\partial x^2} + \frac{dF_{\text{eff}}(\rho_d)}{d\rho_d} \rho_1 + \zeta(\rho_d, x, t).$$

The mean value of the noise  $\zeta(\rho, x, t)$  is zero by construction,  $\langle \zeta(\rho, x, t) \rangle = 0$ , see Eq. (7), and its correlation function can be

obtained from Eqs. (26) and (7),

$$\langle \zeta(\rho, x, t) \zeta(\rho, x', t') \rangle = \rho_d(x', t') \rho_d(x, t) \langle \eta(x, t) \eta(x', t') \rangle.$$

This way of rearranging the noise term has allowed us to separate the systematic contributions of the noise (those with non-zero mean value) from the stochastic contributions (those with zero mean value). The equation for the systematic (deterministic) density, the dominant contribution, reads

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho) + \varepsilon_0 \frac{dg(\rho)}{d\rho} g(\rho), \quad (10)$$

where  $\varepsilon_0 \equiv \varepsilon C(0)$ , and we have omitted the subscript  $d$  for notational simplicity.

We investigate this equation explicitly for two cases: for fluctuations in the net growth rate or in the carrying capacity. Fluctuations in the intrinsic growth rate (Tuckwell, 1974) mean that the difference between births and deaths changes with time, oscillating around a mean value. Fluctuations in the competition term can represent temporal variations in the availability of resources (Feldman and Roughgarden, 1975).

### 2.1. Fluctuating intrinsic net growth rate

If the intrinsic growth rate fluctuates around a mean value  $r_m$ , we can write  $r_1(t) = r_m [1 + \varepsilon^{1/2} \eta(x, t)]$  and  $r_2 = r_m/K$ , with  $r_m$  and  $K$  constants. Introducing the expression for the fluctuations of the intrinsic growth rate into Eq. (1), we obtain the following SPDE:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r_m \rho \left( 1 - \frac{\rho}{K} \right) + \varepsilon^{1/2} r_m \rho \eta(x, t). \quad (11)$$

In this case,  $g(\rho) = r_m \rho$ , as can be seen by comparing Eqs. (11) and (3). According to Eq. (10), the systematic density obeys the reaction–diffusion equation

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r_m (1 + r_m \varepsilon_0) \rho - \frac{r_m}{K} \rho^2, \quad (12)$$

where the systematic effects of the fluctuating net growth rate are represented by the term  $r_m^2 \varepsilon_0 \rho$ . In the following, we will assume that  $K = 1$  for simplicity.

### 2.2. Fluctuating competition term

Consider now Eq. (1) with  $r_2(t) = \frac{r}{K_m} [1 + \varepsilon^{1/2} \eta(x, t)]$  and  $r_1(t) = r$ . Eq. (1) turns into the SPDE

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r \rho \left( 1 - \frac{\rho}{K_m} \right) - \frac{r}{K_m} \varepsilon^{1/2} \rho^2 \eta(x, t). \quad (13)$$

In this case,  $g(\rho) = -r \rho^2 / K_m$ . Making use of Eq. (10), we obtain the following equation for the systematic population density:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r \rho \left( 1 - \frac{\rho}{K_m} \right) + \frac{2r^2}{K_m^2} \varepsilon_0 \rho^3. \quad (14)$$

Note that the systematic contributions of the noise in the competition term give rise to a cubic term in the effective reaction function. Consequently, the range of validity of Eq. (14) is restricted to sufficiently small noise strengths or small densities, respectively. This does not affect our studies, since we are interested in the conditions for extinctions, i.e., situations where the density is indeed small. At higher densities, the model needs to be modified to include higher-order saturation effects. In the following, we will assume that  $K_m = 1$  for simplicity.

## 3. Extinction and survival conditions

In order to analyze the extinction of a population in a 1D habitat, we consider a population with density  $\rho(x, t)$ , growing and

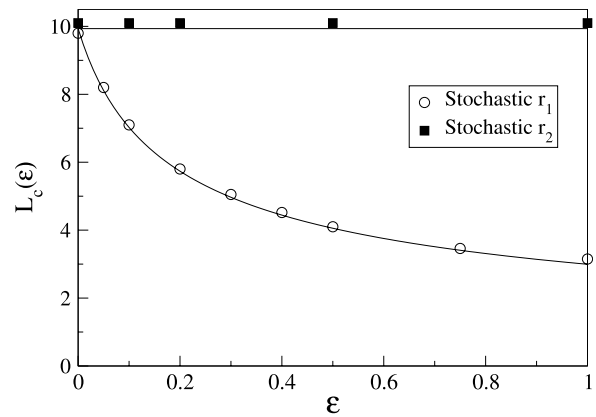


Fig. 1. Critical patch size,  $L_c$ , as a function of the strength of the external noise,  $\varepsilon$ , when the intrinsic net growth rate (circles) or the competition term (squares) fluctuates. Parameter values:  $D = 1$ ,  $r_m = 0.1$  and  $K_m = 1$ .

dispersing according to Eq. (1) and living in a region of size  $L$  surrounded by a completely hostile environment. The corresponding boundary conditions are of Dirichlet type:

$$\rho(-L/2, t) = \rho(L/2, t) = 0, \quad (15)$$

which represent the harshness of the hostile environment.

### 3.1. Critical patch size

One of the relevant questions is whether the population becomes extinct or not as a function of the noise amplitude. The critical patch size  $L_c$  is defined as the minimum patch size required for survival when the environment is hostile. If the patch size  $L$  is lower than  $L_c$ , the population goes to extinction; otherwise it survives. We want to investigate the effect of the stochastic environment on  $L_c$ . The analysis can be carried out by determining the linear stability conditions of the extinction state ( $\rho = 0$ ) or by solving the differential equation for the steady state (Kot, 2003). It can be shown that there exists a critical patch size, given by  $L_c \equiv \pi \sqrt{D/a_1}$ , where  $a_1 = F'_{\text{eff}}(0) > 0$ , i.e., for a population without the Allee effect (Méndez and Campos, 2008) (the prime denotes differentiation with respect to the argument). For a fluctuating intrinsic growth rate, we obtain

$$L_c = \pi \sqrt{\frac{D}{r_m(1 + r_m \varepsilon_0)}}. \quad (16)$$

The critical patch size decreases in the presence of noise in the intrinsic growth rate. The population can survive even in smaller patches, which corresponds to a noise-induced survival. A fluctuating competition term does not change the critical patch size with respect the case without external noise:

$$L_c = \pi \sqrt{\frac{D}{r}}. \quad (17)$$

In Fig. 1 we plot Eqs. (16) and (17) in comparison with their corresponding numerical results obtained by integrating Eqs. (11) and (13), respectively (see Appendix B for details of the numerical algorithm). The agreement is excellent. The critical patch size decreases algebraically with  $\varepsilon_0$  in the case of a fluctuating intrinsic net growth rate ( $r_1$ ) and remains constant when the competition term ( $r_2$ ) fluctuates. This result differs completely from the effect of internal (demographic) fluctuations, where the population has a non-zero probability of extinction for any patch size  $L$  (Escudero et al., 2004).



### 3.2. Spatial patterns

Suppose that the habitat size exceeds the critical patch size and that the population grows. The question then is to evaluate how large it will grow. This can be answered by considering steady-state solutions (spatial patterns). To find exact analytical solutions to the differential equation (12), we assume that the system evolves from an initial condition and reaches the stationary-state solution after a transient. The existence of a steady state reflects the non-homogeneous equilibrium between newborns inside the patch and those individuals killed at the boundaries. The equation to solve is

$$\frac{d^2 \rho_{ss}}{dx^2} + \frac{r_m}{D} [(1 + r_m \varepsilon_0) \rho_{ss} - \rho_{ss}^2] = 0, \quad \rho_{ss}(-L/2) = \rho_{ss}(L/2) = 0. \quad (18)$$

A closed-form solution is given by (see details in Appendix C)

$$\rho_{ss}(\xi) = \frac{1 + r_m \varepsilon_0}{2} \left\{ 1 - \frac{1 + k^2}{\sqrt{1 + k^4 - k^2}} + \frac{3k^2}{\sqrt{1 + k^4 - k^2}} \operatorname{cd}^2 \left[ \frac{\xi L \sqrt{r_m(1 + r_m \varepsilon_0)}}{2\sqrt{D}(1 + k^4 - k^2)^{1/4}}, k \right] \right\}, \quad (19)$$

where  $k$  is the solution to the transcendent equation

$$\operatorname{cd}^2 \left[ \frac{L \sqrt{r_m(1 + r_m \varepsilon_0)}}{4\sqrt{D}(1 + k^4 - k^2)^{1/4}}, k \right] = \frac{1 + k^2 - \sqrt{1 + k^4 - k^2}}{3k^2}. \quad (20)$$

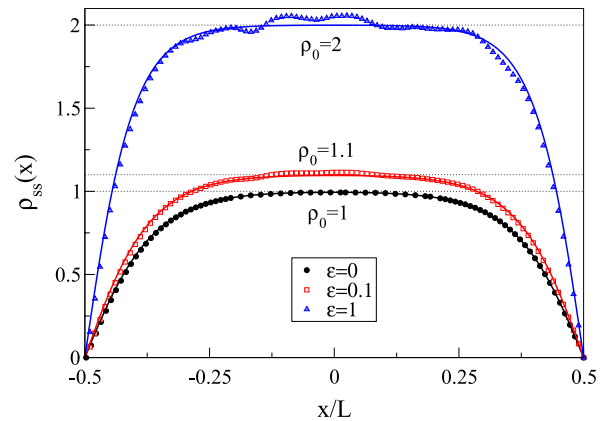
Another interesting quantity is the maximum or central density  $\rho_m = \rho_{ss}(\xi = 0)$ , which is straightforwardly calculated from (19):

$$\rho_m = \frac{1 + r_m \varepsilon_0}{2} \left( 1 - \frac{1 - 2k^2}{\sqrt{1 + k^4 - k^2}} \right). \quad (21)$$

The spatially homogeneous steady states can be found from (12) considering  $\rho$  constant in space and time. Likewise, their stability can be analyzed by considering the temporal part of (12). For a fluctuating intrinsic growth rate, the spatially homogeneous steady states are  $\rho_0 = 0$  (unstable) and  $\rho_0 = 1 + r_m \varepsilon_0$  (stable). This means that when the system evolves from its initial condition, a spatial pattern is formed if the critical patch size is exceeded. The central density  $\rho_m$  tends to  $\rho_0 = 1 + r_m \varepsilon_0$  as  $L \rightarrow \infty$ . So, the condition  $\rho_m < 1 + r_m \varepsilon_0$  must hold, and Eq. (21) implies that  $k < 1$ . However, Eq. (20) has multiple solutions for  $k$  and different profiles  $\rho_{ss}(\xi)$  are mathematically possible. One must specify appropriate criteria in order to choose the actual solution. The population grows to reach the stable state  $\rho_0 = 1 + r_m \varepsilon_0$  in the absence of hostile conditions. Therefore, the actual profile is expected to be that which maximizes the density  $\rho$  at any point of the lattice, and specifically the one that maximizes  $\rho_m$ . This criterion, together with the fact that (21) is an increasing function of  $k$ , leads us to the conclusion that the actual  $k$  must be the largest possible. In summary, the system is expected to choose the maximum  $k$  from the condition (20), provided that  $k < 1$  is satisfied. In Fig. 2, we plot the density profile given by Eq. (19) (solid line) with the maximum value of  $k$  allowed by (20), and compare it with the corresponding numerical solution (symbols), the result of the integration of Eq. (11).

For the case of a fluctuating competition term, it has not been possible to obtain exact analytic solutions for the spatial patterns and one has to resort to other methods such as Galerkin truncation (Méndez and Campos, 2008). In this case, the spatially homogeneous steady states are, from (14),  $\rho_0 = 0$  (unstable) and two other states

$$\rho_0^\pm = \frac{1 \pm \sqrt{1 - 8r\varepsilon_0}}{4r\varepsilon_0},$$



**Fig. 2.** Density profile of the steady state for a fluctuating intrinsic net growth rate for different values of the external noise strength,  $\varepsilon$ . Homogeneous steady states,  $\rho_0$ , are represented by dotted lines. Parameter values:  $L = 40$ ,  $D = 1$ ,  $r_m = 0.1$ ,  $K = 1$ , and initial condition:  $\rho(x) = 0.5 \cos(\pi x/L)$ .

with  $\rho_0^-$  stable and  $\rho_0^+$  unstable. If the critical patch size is exceeded and the noise intensity is small enough ( $\varepsilon_0 < 1/8r$ ), the system evolves towards a spatial pattern, whose central density tends to  $\rho_0^-$  when  $L \rightarrow \infty$ . If the noise intensity is sufficiently high ( $\varepsilon_0 > 1/8r$ ) and the critical patch size is exceeded, the states  $\rho_0^\pm$  do not exist and the population grows without bounds. As discussed above, in this case Eq. (14) is no longer valid, and the population explosion is an artefact of the model. These results are illustrated in Fig. 3, where we plot the density profile obtained from the numerical integration of Eq. (13).

### 3.3. Bifurcation diagrams

We plot diagrams for population persistence/extinction for both Eqs. (20) and (21). A very interesting limiting case is the extinction region which begins when  $\rho_m \rightarrow 0$  and is equivalent to the limit  $k \rightarrow 0$  in (21). Taking the limit  $k \rightarrow 0$  in (20), we obtain  $\operatorname{cd}(\sqrt{a}/4, 0) = 1/\sqrt{2}$ , where  $a = L^2 r_m (1 + r_m \varepsilon_0) / D$ . This can be easily solved to yield  $\sqrt{a} = \pi$ , which is exactly the result given in (16).

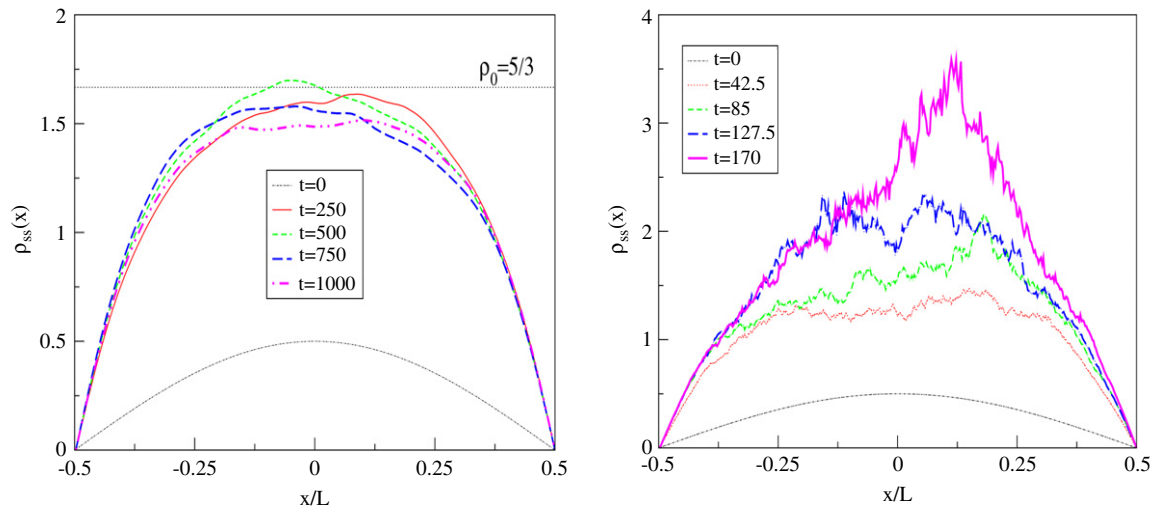
In Fig. 4, we show the bifurcation diagram, i.e., the maximum (central) density of the pattern ( $\rho_m$ ), for different values of the patch size  $L$ , when the intrinsic growth rate fluctuates. For  $L < L_c$ , the only stable solution is  $\rho = 0$ , whereas for  $L > L_c$  the stable solution is the non-trivial one. This behavior corresponds to a forward bifurcation. The bigger  $\varepsilon_0$ , the smaller  $L_c$  and the larger the regime with non-trivial stable solutions. In other words, populations can survive in smaller environments if external noise is present. In Fig. 4, we also compare the analytical solution from Eqs. (20) and (21) (solid curves) with the numerical solutions of Eq. (11).

When the competition term fluctuates, the bifurcation diagram is qualitatively very similar to that of Fig. 4, because in both cases the effective reaction term describes a compensatory growth. To obtain an analytical expression for  $\rho_m$  versus  $L$  one has to make use of approximation methods (Méndez and Campos, 2008).

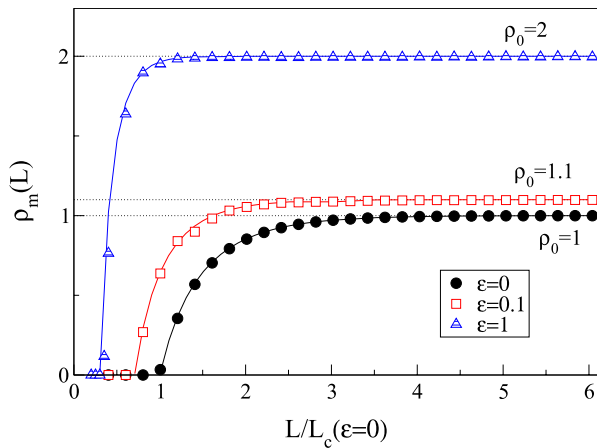
### 3.4. Number of individuals

Another measure for the population is the number of individuals per unit length, i.e., the mean density of individuals in the habitat where they can survive. When the intrinsic growth rate fluctuates, this quantity reads

$$\frac{N}{L} = \frac{1}{L} \int_{-L/2}^{L/2} \rho_{ss}(x) dx$$



**Fig. 3.** Density profile of the steady state at different times for a fluctuating competition term. (a) For  $\varepsilon_0 r = 0.12 < 1/8$ , a steady state exists, where the homogeneous steady state is represented by a dotted line. (b) For  $\varepsilon_0 r = 0.13 > 1/8$ , the population density increases without reaching a steady state. The initial population profile is included in both situations:  $\rho(x) = 0.5 \cos(\pi x/L)$ . Parameter values:  $L = 40$ ,  $D = 1$ ,  $r = 0.1$  and  $K_m = 1$ .



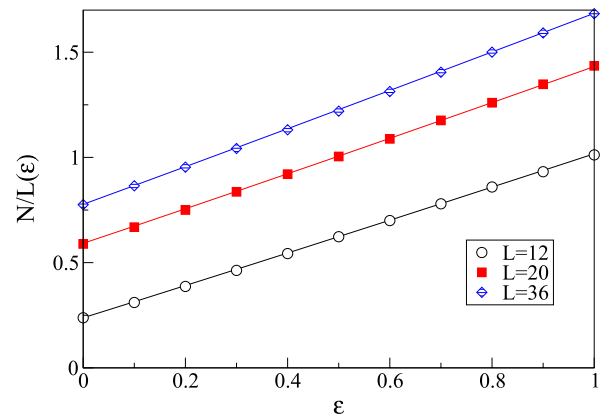
**Fig. 4.** Bifurcation diagram for a fluctuating intrinsic net growth rate. Symbols correspond to numerical integrations of Eq. (3) for different values of the strength of the noise,  $\varepsilon$ . The solid lines are the theoretical results, given by Eqs. (19) and (20). Homogeneous steady states,  $\rho_0$ , are represented by dotted lines. Parameters:  $D = 1$ ,  $r_m = 0.1$  and  $K = 1$ .

$$= \frac{1 + r_m \varepsilon_0}{2} \left\{ 1 - \frac{1 + k^2}{\sqrt{1 + k^4 - k^2}} + \frac{6k^2}{\sqrt{1 + k^4 - k^2}} \int_0^{1/2} cd^2 \left[ \frac{\xi \sqrt{a}}{2(1 + k^4 - k^2)^{1/4}}, k \right] d\xi \right\}. \quad (22)$$

In Fig. 5, we compare the above result (solid curves) with the numerical computations (symbols). This confirms the idea that a fluctuating growth term favours population survival, in agreement with the results for  $L_c$  found above and the general idea throughout the present paper.

#### 4. Discussion

Environmental stochasticity introduces noise at the population level due to fluctuations in exogenous environmental factors such as temperature or other climatic factors. Temporal models predict an increase in extinction risk. We have proposed a continuous model for a population living in a linear finite habitat surrounded by a completely hostile environment. In addition, we consider that environmental stochasticity affects either the net growth



**Fig. 5.** Mean density of individuals in a patch surrounded by a hostile environment as a function of the noise strength,  $\varepsilon$ , for different patch sizes when the intrinsic net growth rate fluctuates. Symbols correspond to numerical integrations of Eq. (3), and lines are the theoretical results, Eq. (22). Parameter values:  $D = 1$ ,  $r_m = 0.1$  and  $K = 1$ .

rate or the carrying capacity. The risk of extinction is due to the loss of individuals that cross the boundaries. Our results can be summarized as follows.

- (i) We have reduced the SPDE to an effective deterministic equation that incorporates the systematic effects of the noise. If the population grows logistically, the systematic contributions of the external noise do not affect the compensatory character of the effective reaction.
- (ii) When the critical patch size is exceeded, the systematic contribution to the density evolves to a stable spatial pattern at random sampling time after the process has reached the stationary state. For the case of a fluctuating net growth rate we have obtained exact analytical solutions for the systematic population density at the steady state, an exact bifurcation diagram for the central density in terms of the habitat size, and the mean density of individuals in the habitat. The exact analytical results have been verified by numerical simulations, which show an excellent agreement. This proves that the effective deterministic equation we have derived captures the essential stochastic dynamics of the system.
- (iii) We have obtained exact analytical results for the critical patch size, both for the case of a fluctuating net growth rate and the case of a fluctuating carrying capacity. In the first case,

the critical patch size is found to be decreased in the presence of noise, so the population can survive in smaller patches. In other words, environmental fluctuations reduces the extinction risk. This difference is due to the fact that the competition term, being nonlinear, has no effect on the critical patch size, which is determined by the dynamics for small densities, where nonlinear terms are negligible.

The result obtained for the first case is in apparent contradiction with previous studies, which claim that environmental fluctuations increase the extinction risk. However, both predictions are compatible if the stochasticity is interpreted as heterogeneity. Actually, the mechanism of extinction we employ here is due to the presence of a hostile environment which can destroy the population if the rate of losses at the boundaries is high enough. In previous studies on extinction due to environmental stochasticity, extinction is not due to an effect of the boundaries but due to fluctuations in population density. The absorbing boundaries are thus a contributor to the environmental heterogeneity. When the habitat is environmentally homogeneous, the environmental variance is highest; that is, there is a high contrast between habitat and boundaries. If the net growth rate fluctuates, the variance of the habitat increases but the total variance experienced by the population is lower because the contrast between habitat and boundaries is smoothed out. Lower variance entails lower extinction risk.

(iv) For a fluctuating carrying capacity, the critical patch size is not affected by environmental fluctuations. When the critical patch size is exceeded, the mean density evolves towards a stable spatial pattern if the noise intensity is smaller than  $1/8r$ . If  $L > L_c$  and noise intensity is higher than  $1/8r$ , the population grows unboundedly, representing an interesting but unrealistic biological behavior. As discussed above, this situation falls outside the range of validity of our model. Another limiting case we have not considered in this paper is when  $r_1$  and  $r_2$  oscillate with the same frequency, i.e., the case of a stochastic  $r$  parameter. The growth and interaction terms fluctuate, and an equation for the systematic density can be written. The critical patch size is also given by Eq. (16), but the spatial patterns and the bifurcation diagram differ considerably from the fluctuating  $r_1$  case. Moreover, the number of individuals increases with respect to the noise amplitude for large patch sizes and decreases for small patch sizes.

Our results can be applied to populations affected by a critical patch size and environmental fluctuations, for example, ecological communities confined to finite habitats or patches surrounded by predators or other adverse environments such as plankton blooms, plankton filaments, fish populations, bacterial colonies or annual plants. In our model, we have considered completely hostile environments, and this is adequate for species where the population is dominated by individuals that have little control over their movement, such as juveniles and larvae.

This work can be extended to other ecological situations by including the Allee effect or by modifying the boundary conditions. For example, if the population disperses towards more favorable environments because of the presence of habitat edges, the boundary conditions must be density dependent (Cantrell and Cosner, 2007). Another example is a fish population living in rivers. The habitat edge may include both a hostile condition and a zero flow condition (Lutscher et al., 2007). From a theoretical point of view, the work can be also modified to analyze the effects of noise with only temporal or spatial correlations.

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### Appendix A. Mean value of the noise term

The mean value can be evaluated as follows:

$$\begin{aligned} \langle g(\rho)\eta(x, t) \rangle &= \int_0^t dt' \int dx' \langle \eta(x, t)\eta(x', t') \rangle \left\langle \frac{\delta g(\rho(x, t))}{\delta \eta(x', t')} \right\rangle \\ &= 2 \int dx' C(|x - x'|/\lambda) \left\langle \frac{dg(\rho)}{d\rho} \frac{\delta \rho(x, t)}{\delta \eta(x', t')} \right\rangle_{t'=t}. \end{aligned} \quad (23)$$

On the other hand, Eq. (3) can be integrated formally to obtain

$$\begin{aligned} \rho(x, t) &= \rho(x, 0) + D \frac{\partial^2}{\partial x^2} \int_0^t ds \rho(x, s) + \int_0^t ds F[\rho(x, s)] \\ &\quad + \varepsilon^{1/2} \int_0^t ds g[\rho(x, s)] \eta(x, s). \end{aligned} \quad (24)$$

Then, from (24)

$$\begin{aligned} \frac{\delta \rho(x, t)}{\delta \eta(x', t')} &= \varepsilon^{1/2} \int_0^t ds g[\rho(x, s)] \frac{\delta \eta(x, s)}{\delta \eta(x', t')} \\ &= \varepsilon^{1/2} \delta(x' - x) g[\rho(x, t')]. \end{aligned} \quad (25)$$

Finally, substituting (25) into (23), we obtain

$$\begin{aligned} \langle g(\rho)\eta(x, t) \rangle &= 2\varepsilon^{1/2} \left\langle \frac{dg(\rho)}{d\rho} g(\rho) \right\rangle \int dx' C(|x - x'|/\lambda) \delta(x' - x) \\ &= \varepsilon^{1/2} C(0) \left\langle \frac{dg(\rho)}{d\rho} g(\rho) \right\rangle, \end{aligned} \quad (26)$$

where in the last equality we have made use of the Stratonovich interpretation of the calculus ( $\int dx' \delta(x' - x) = 1/2$ ). Eq. (26) is Novikov's theorem for spatially extended systems (Novikov, 1965).

### Appendix B. Numerical algorithm

The numerical integration of Eqs. (11) and (13) was performed using the general approach for stochastic partial differential equations (SPDEs) (San Miguel and Toral, 2000). The habitat is simulated as a grid consisting of  $N$  lattice sites of size  $\Delta x$ , such that  $L = N\Delta x$  is the habitat size. Every lattice site  $i$  is identified by its position  $x_i$ , which is a discrete variable. The continuum density,  $\rho(x, t)$ , is replaced by its analogue in discrete space,  $\rho(x_i, t)$ , and the external noise is simulated via the generation of Gaussian numbers, where we replace the white noise  $\eta(x, t)$  by  $\frac{1}{\sqrt{\Delta x}} \eta_i(t)$ , as a result of the relation between the Dirac and the Kronecker delta functions. Now the noise obeys  $\langle \eta_i(t)\eta_j(t') \rangle = \delta_{ij}\delta(t - t')$ . Moreover, the noise amplitude is  $\varepsilon C(0) = \varepsilon/\Delta x$ , using the white noise approximation on a lattice (Santos and Sancho, 1999). Eqs. (11) and (13) can be generalized as

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho) + G(\rho)\eta, \quad (27)$$

where the noise appears in a multiplicative way. Assuming uniform time steps of size  $\Delta t$  and integrating Eqs. (11) and (13) using the Euler algorithm, one obtains the dynamic equation that is discrete in both space and time,

$$\begin{aligned} \rho_{t+\Delta t, i} &= \rho_{t, i} + \Delta t \frac{D}{\Delta x^2} (\rho_{i+1, t} - 2\rho_{i, t} + \rho_{i-1, t}) + \Delta t^{1/2} G(\rho_{i, t}) u_{t, i} \\ &\quad + \Delta t \left[ F(\rho_{i, t}) + \frac{1}{2} G(\rho_{i, t}) G'(\rho_{i, t}) u_{t, i}^2 \right], \end{aligned} \quad (28)$$

where  $\Delta t^{1/2} u_{t, i} = \eta_i(t)$ . Simulations have been performed with  $\Delta x = 0.1$ ,  $\Delta t = 0.0025$  and  $D = 1$ . We have varied the parameters  $r$ ,  $K$ ,  $\varepsilon$  and  $L$  in different simulations.

**Appendix C. Exact solution**

The dimensionless variable  $\xi = x/L$  turns Eq. (18) into

$$\frac{d^2 \rho_{ss}}{d\xi^2} + a\rho_{ss} - b\rho_{ss}^2 = 0, \quad \rho_{ss}(1/2) = \rho_{ss}(-1/2) = 0, \quad (29)$$

where  $a = L^2 r_m (1 + r_m \epsilon_0) / D$  and  $b = L^2 r_m / D$ . Due to the symmetry of Eq. (29) in the variable  $\xi$ , we expect that  $d\rho_{ss}/d\xi = 0$  at  $\xi = 0$ . Eq. (29) admits solutions in terms of Jacobi elliptic functions of the form  $\rho_{ss}(\xi) = A + B \text{cd}^2(C\xi, k)$ , where  $\text{cd}(u, k)$  is the quotient  $\text{cn}(u, k)/\text{dn}(u, k)$ . Substituting this solution into Eq. (29) and grouping in powers of the function  $\text{cd}(u, k)$ , we obtain a set of three algebraic equations that allows us to find the values for the constants  $A, B$  and  $C$  in terms of  $k$ . It is not difficult to check that  $\rho_{ss}(-1/2) = \rho_{ss}(1/2) = 0$  and  $d\rho_{ss}/d\xi = 0$  at  $\xi = 0$ . Then,  $\rho_{ss}$  is

$$\rho_{ss}(\xi) = \frac{1 + r_m \epsilon_0}{2} \left\{ 1 - \frac{1 + k^2}{\sqrt{1 + k^4 - k^2}} + \frac{3k^2}{\sqrt{1 + k^4 - k^2}} \text{cd}^2 \left[ \frac{\xi \sqrt{a}}{2(1 + k^4 - k^2)^{1/4}}, k \right] \right\}, \quad (30)$$

where we obtain the parameter  $k$  from the boundary condition  $\rho_{ss}(1/2) = 0$ ; that is,

$$\text{cd}^2 \left[ \frac{\sqrt{a}}{4(1 + k^4 - k^2)^{1/4}}, k \right] = \frac{1 + k^2 - \sqrt{1 + k^4 - k^2}}{3k^2}. \quad (31)$$

Eq. (30), together with (31), constitutes the solution to (18).

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