A source-sink patch occupancy metapopulation model

Un modelo metapoblacional de ocupación de parches fuente y sumidero

PABLO A. MARQUET[1] and JORGE X. VELASCO-HERNANDEZ[2]

[1]Departamento de Ecología
P. Universidad Católica de Chile, Casilla 114-D, Santiago, Chile
E-mail: pmarquet@genes.bio.puc.cl
[2]Departamento de Matemáticas,
UAM-Iztapalapa, Apartado Postal 55-534, Iztapalapa, D.F.09340
and Biometrics Unit, Cornell University.
E-mail: jxvh@xanum.uam.mx

ABSTRACT

We consider a model of a heterogeneous and dynamic landscape composed of two different patch types (source and sink) and one type of organism. We incorporate extinction and degradation rates that vary according to patch type (sink versus source). We address the problem of the importance of source and sink patches for metapopulation dynamics under the above conditions. We construct a deterministic mathematical model and compute a threshold parameter that measures invasion and persistence of occupied sink and source patches. The threshold parameter is a convex function of extinction rates and presents an optimum value for invasibility and persistence. Depending on the relationship between propagule production and extinction rates of colonized patches of both types this optimum may or may not be ecologically feasible. Metapopulation models that consider homogeneous patch types do not present this property. We compare our results with Richard Levins' classical metapopulation model to assess the role of heterogeneity and patch degradation in the asymptotic dynamics of our system.

Key words: Metapopulation, patch-occupancy model, habitat degradation, source-sink dynamics.

RESUMEN

En este trabajo analizamos un modelo de un paisaje heterogéneo compuesto por dos tipos de parches (fuente y sumidero) y habitado por un tipo de organismo. En el modelo incorporamos tasas de extinción y degradación que varían de acuerdo al tipo de parche (fuente versus sumidero). Con este modelo nos interesa evaluar la importancia de la existencia de parches fuente y sumidero para la dinámica metapoblacional bajo las condiciones señaladas más arriba. Para esto construimos un modelo matemático determinista y calculamos un parámetro umbral que mide la invasión y persistencia de parches tipo fuente y sumidero. El parámetro umbral es una función convexa de las tasas de extinción y presenta un valor óptimo de invasibilidad y persistencia. Dependiendo de la relación entre las tasas de producción de propágulos y extinción de los parches colonizados de ambos tipos, este óptimo puede o no ser ecológicamente alcanzable. Los modelos metapoblacionales que consideran parches homogéneos no presentan esta propiedad. Comparamos nuestros resultados con el modelo clásico de Richard Levins para evaluar el rol de la heterogeneidad y de la existencia de degradación de los parches en el comportamiento dinámico asintótico de nuestro sistema.

Palabras clave: Metapoblación, modelo de ocupación de parches, degradación del hábitat, dinámica fuente y sumidero.

INTRODUCTION

We consider a heterogeneous and dynamic landscape composed of two different patch types (source and sink) and one type of organism. We address the problem of the importance of sink patches for metapopulation dynamics. Spatial heterogeneity, manifested as spatial variability or a patchy distribution in resource abundance, microclimate condi- tions, and in general, habitat quality for different species is a dominant feature of landscapes. Most populations living in patchy landscapes are not homogeneously distributed across space, but distributed as distinct subpopulations forming an interacting ensemble or metapopulation system (Levins 1970, Hanski 1991, Hastings & Harrison 1994). Colonization and extinction are the two fundamental processes that affect the

dynamics of a metapopulation system (Hanski 1991). The interaction between these two processes results in each demographic unit, or subpopulation, not being independent from the other subpopulations.

Metapopulation theory has become one of the most powerful frameworks for analyzing colonization and extinction processes in natural populations (Hastings & Wolin 1989, Hanski 1991). The first metapopulation model was proposed by Levins (1969, 1970, but see also MacArthur & Wilson 1967). Levins' model assumes a set of identical habitat patches with local subpopulations going extinct and the empty patches being recolonized from the currently occupied ones. This type of patch-occupancy metapopulation model has been extended and modified to describe single-species (Hanski 1985, 1991, Hastings & Wolin 1989; Gotelli 1991, Gyllenberg & Hanski 1992, Hanski & Gyllenberg 1993), competitive (Horn & MacArthur 1972, Slatkin 1974, Hanski 1983, Nee & May 1992), and predator-prey metapopulation dynamics (Vandermeer 1973, Hastings 1977, Zeigler 1977, Sabelis et al. 1991). Some of these models have relaxed some of the assumptions of Levins' original model by incorporating a "rescue-effect," population structure, and differences in patch size. Here, we explore the dynamical consequences of relaxing the assumption that all patches are equally likely to become extinct and that all occupied patches are sources of colonists. In particular, we analyze the effect of distinguishing source and sink patches. In addition, we explicitly consider the dynamics of the species (i.e., how individuals occupy patches), and the dynamics of the patches (i.e., how patches of different type are created, occupied, and go extinct). Our model couple patch and species dynamics.

The paper is organized as follows: in the next section we provide a brief description of the simplest metapopulation model stressing the assumptions under which it holds; next we present a metapopulation model that incorporates source and sink patches and a single organism type, derive a basic threshold parameter for the invasion of an empty habitat, and explore through computer simulations the asymptotic be-

havior of the model. Finally in the last section we give our conclusions.

Basic background and definitions

The pioneer of metapopulation models is the one studied by Levins (1969). This model assumes that N, the total number of available patches, is a constant. Let U and O denote the number of unoccupied and occupied patches respectively. Levins' model assumes that instantly upon colonization of an empty patch the organisms achieve their carrying capacity, thus reaching their demographic equilibrium within each patch. Assume that at this equilibrium, each individual in the patch produces a total of β propagules per unit time. Therefore, βO represents the total number of propagules produced by all the individuals in the occupied patches. These propagules find unoccupied patches at a rate proportional to their frequency U/N, thus unoccupied patches are "lost" to colonization at a rate $-\beta OU/N$ per unit time, and occupied patches increase by the same number per unit time. If we assume that occupied patches go extinct at a rate e then eO is the number of occupied patches that go extinct per unit time. Furthermore, this model assumes that extinct occupied patches become unoccupied and immediately available for colonization at the same rate at which they go extinct, implying a closed system without an independent patch dynamics. The equations that govern this system are (Figure 1a):

$$\frac{d}{dt} U = -\beta O \frac{U}{N} + eO,$$
$$\frac{d}{dt} O = \beta O \frac{U}{N} - eO.$$

Dividing both equations by N and defining $O/N = f$, we note that $U/N = 1 - f$, and the equations reduce to the Levins metapopulation model:

$$\frac{d}{dt} f = \beta f (1 - f) - ef.$$

Levins' model postulates that the total number of patches N is constant and that all

a)

colonization

U ⟶ O

extinction

b)

generation process

generation process

patch degradation

P$_1$ ⟶ P$_2$

patch extinction

patch colonization   population extinction

patch colonization   population extinction

patch extinction

patch degradation
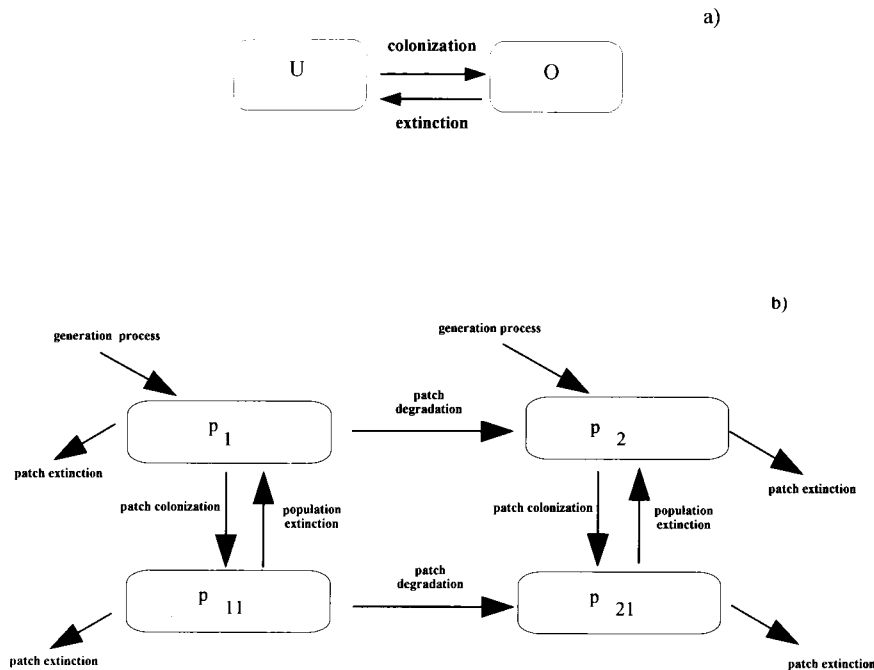
P$_{11}$ ⟶ P$_{21}$

patch extinction

patch extinction

Fig.1: Kinetic diagrams of the Levins' metapopulation model and equation (1): a) In Levins' model there are only two patch states. The total number of patches is constant; b) The model represented by equation (1) assumes that patches can be in four possible states: empty source, empty sink and the corresponding colonized ones for each type.

Diagramas cinéticos de los modelos metapoblacionales de Levins y la ecuación (1): a) En el modelo de Levins existen solamente dos estados posibles de los parches. El número total de parches es constante; b) El modelo representado por la ecuación (1) permite cuatro estados posibles de los parches: fuente vacío, sumidero vacío, y los correspondientes a parches colonizados de ambos tipos.

patches and colonizing individuals are identical. These assumptions allow us to dynamically follow the proportion of occupied patches instead of their actual number; also they allow us to characterize the whole dynamics with two parameters: β and e. It is also important to point out that this model makes no distinction between the dynamics of patches and that of the organisms that occupy them.

Levins' model predicts that colonization of empty patches is successful whenever $\beta/e > 1$. This condition also determines the existence of a nontrivial equilibrium point $f^* = 1 - e/\beta$ that is globally asymptotically stable.

Several models and hypothesis have been proposed for empirical data that contradict the properties of this model (e.g., Hanski 1982, Hanski & Gyllenberg 1993, Lima et al. 1996). In this work, we explicitly concentrate in the role of habitat het-

erogeneity in the time evolution of patches. To begin, we consider two types of *empty* patches, based on the work of Pulliam (1988) and Holt (1985). The first type is a *source* patch, or one where a colonizing organism has, on average, a higher propagule production rate and a minimal natural extinction rate. Likewise a *sink* patch is one where a colonizing organism has, on average, low propagule production rate and an extinction rate higher than in source patches.

We consider a single type of organism characterized by a unique propagule production rate and two extinction rates (associated with the patch type that it colonizes). However, even though propagule production is equal for all individuals, survival ability is not equal and varies depending on the nature of the patch from where the individual is dispersing. In the next section we develop the model.

A model with source and sink patches

Patch suitability for species development may vary enormously and, therefore, it is a main determinant for the success of organisms to establish and reproduce. In this section, we propose a mathematical model where a single type of individual colonizes and disperses in a habitat composed of two types of patches (source and sink). The number of empty source and sink patches are denoted by p_1 and p_2 respectively. Source patches are characterized as being able to sustain subpopulations with a larger propagule production and survival rate and lower extinction rates than subpopulations inhabiting sink patches. In our model, we follow the temporal dynamics of these empty patches since we assume that the total number of patches is not constant but varies with time. The empty patches are colonized by an organism. Through this interaction, two additional patch types are generated, denoted by p_{11} and p_{21} (number of occupied source and sink patches respectively).

As mentioned earlier, we do not consider the total number of patches $p = p_1 + p_2 + p_{11} + p_{21}$ to be constant. We incorporate a dynamic nature to this variable by assuming that there is a generation process of empty patches that models the creation of new patches of both types. Each kind of patch has an extinction rate. Thus, our model explicitly incorporates patch dynamics.

Let $p = p_1 + p_2 + p_{11} + p_{21}$ the total patch population. We have (Figure 1b):

$$\frac{d}{dt} p_1 = q\Lambda - (e + k) p_1 + h_1 p_{11} - \beta \; \frac{p_1}{p} (\sigma p_{21} + p_{11}),$$

$$\frac{d}{dt} p_{11} = -(e + h_1) p_{11} + \beta \frac{p_1}{p} (\sigma p_{21} + p_{11}) - k_1 p_{11},$$

$$\frac{d}{dt} p_2 = (1 - q) \Lambda + kp_1 + h_2 p_{21} - ep_2 - \beta \frac{p_2}{p} (p_{11} + \sigma p_{21}),$$

$$\frac{d}{dt} p_{21} = -(e + h_2) p_{21} + \beta \; \frac{p_2}{p} (\sigma p_{21} + p_{11}) + k_1 p_{11}.$$

Patch dynamics and subpopulation dynamics

Our model incorporates both patch dynamics and the dynamics of the species occupying patches. Patch dynamics is driven by several parameters. Λ is the production rate of uncolonized patches with q representing the fraction of them that generates source p_1 patches. The rates e and k are the extinction and degradation rates of patches. We refer to the extinction rate e as the background extinction rate since it is associated with the empty patches. A degraded source patch becomes a sink patch. Thus, the number of degraded uncolonized source patches per unit time is kp_1.

The dynamics of subpopulations occupying these patches is driven in turn by the following parameters. The constants h_1 and h_2 are the extinction rates of the subpopulations in either patch. Therefore, occupied patches (of both types) are recovered as empty source or sink patches at the same rates h_1 and h_2. Thus, the number of colonized source patches that disappear per unit time is $(e + h_1) p_{11}$. The corresponding rate for colonized sink patches is $(e + h_2) p_{21}$. We also assume that patch degradation from occupied source to occupied sink patches occurs at a rate k_1 per unit time.

This model assumes that the colonization of empty source (or sink) patches is a frequency-dependent process proportional to the relative frequency of empty patches of both types, namely, p_1/p and p_2/p. The colonization or propagule production rates for the organism is higher in the source p_1 than in the sink p_2 patches, that is $\beta p_{11} > \sigma \beta p_{21}$ (the propagule production rate of organisms living on source patches is always greater than the propagule production rate of organisms on sink patches). The coefficient σ measures the reduction in the propagule production or colonization rate for individuals in sink patches ($0 \leq \sigma \leq 1$). It is therefore a measure of "sinkiness".

Thus, the total rate of generation of colonized source patches (or in other words the rate by which empty source patches are lost to colonization) is

$$\beta \; \frac{p_1}{p} (\sigma p_{21} + p_{11}),$$

and that of colonized sink patches (or in other words the rate by which empty sink patches are lost to colonization) is

$$\beta \; \frac{p_2}{p} \; (\sigma p_{21} + p_{11}).$$

The invasion threshold

Threshold parameters are valuable theoretical tools for the qualitative evaluation of key metapopulation processes, and provide a useful and simple way to compare patch occupancy metapopulation models (Marquet, Velasco-Hernández & Hernández-Suarez *ms*). In particular, the invasion threshold we are concerned with provides information on the likelihood of invasion and colonization of empty patches, and the long term occupancy of those patches after invasion.

In many situations, including Levins' model and the one analyzed here, this threshold parameter gives information on both of these processes: the likelihood of successful invasion and the existence and stability properties of equilibrium points where occupied patches are always present. In this later case, they provide information on the persistence of occupied patches and the robustness and resilience of this state when subjected to perturbations.

Levins' metapopulation model

In the metapopulation model of Levins (1969), successful invasion of empty patches takes place only if the threshold parameter β/e is greater than one, where β and e are the propagule production and extinction rates, respectively. We interpret this threshold condition as saying that for a successful invasion of an *empty habitat* to occur, the number of propagules produced by one average occupied patch during its lifetime must be enough to allow for the colonization of more than one empty patch initially (i.e., on average each newly colonized patch gives rise to more than one additional colonized patch). Note that a successful invasion means only that, in the beginning of the process, there is an increase in the number of newly occupied patches. In a longer time lapse, this initial increase may

lead to persistence of occupied patches, or may lead to their extinction. In general, threshold parameters do not give information on this long term dynamic. However, in Levins' model the threshold parameter does.

Note that in Levins' model the parameter β/e is associated with the eigenvalue of the corresponding linearized system at the equilibrium point when the proportion of empty patches is 1. Also, we have that the steady-state with occupied patches is given by

$$f^*_{\text{o}} = 1 - e/\beta.$$

Thus, for values of $\beta/e \le 1$, only the steady-state $f_{\text{e}}^* = 0$ exists and is stable. When $\beta/e > 1$, there is a bifurcation of the previous equilibrium point. The steady-state $f_{\text{e}}^* = 0$ is now unstable and a new equilibrium $f_{\text{o}}^* > 0$ is asymptotically stable. In Figure (2), we present a graphical illustration of this bifurcation phenomena.
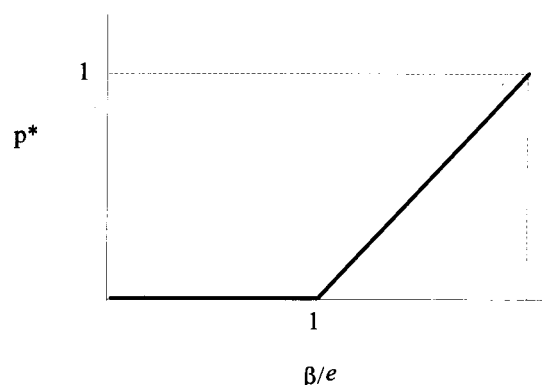

Fig.2: Bifurcation diagram for the Levins' metapopulation model. The graph illustrates the number and value of the possible steady states of the system. For values of $\beta/e < 1$ only the steady-state $p^* = 0$ exists and is stable. For values of the parmeter beyond 1, a second steady-state appears that is asymptotically stable. The other equilibrium $(p^* = 0)$ still exists but is unstable. Note that as β/e increases from 1, the value of the positive steady-state also increases.

Diagrama de bifurcación para el modelo metapoblacional de Levins. El gráfico ilustra el número y la magnitud de los estados estacionarios posibles en el sistema. Para valores de $\beta/e < 1$, $p^* = 0$ es el único estado estacionario que existe. El estado es estable. Para valores del parámetro mayores que 1, un segundo estado estacionario estable aparece. El otro equilibrio $(p^* = 0)$ existe todavía pero es inestable. Nótese que conforme β/e se incrementa desde 1, el valor del estado estacionario positivo también se incrementa.

Threshold parameters for model (1)

In the case of model (1), we find a threshold invasion criterion analogous to the one found for Levins' model. From now on, the threshold parameter for model (1) is denoted by the symbol T. T is found by linearizing the system around the equilibrium $(p_1^*, p_2^*, 0, 0)$, where only empty patches are present, with

$$p_1^* = \frac{q\Lambda}{e+k}, \quad p_2^* = \frac{\Lambda\left(e\,(1-q)+k\right)}{e\,(e+k)}. \tag{2}$$

Thus, we obtain (see Appendix for technical details):

$$T = \frac{\beta eq}{(e+h_1+k_1)\,(e+k)}\left(1 - \sigma\,\frac{e+h_1}{e+h_2}\right) + \frac{\beta\sigma}{e+h_2} \tag{3}$$

T is the equivalent of Levins' threshold parameter. In our case, the existence of two types of patches that differ in both propagule production and extinction properties, makes T an average of two numbers. We discuss this characteristic in the next section. Now, we want to show that T, and thus model (1), are proper generalizations of Levins' model under the assumptions stated in section 3. Note, that if there is no patch degradation $(k = 0)$, if only one type of patch is produced $(q = 1)$, if $\sigma = 1$ (propagule production rates are equal in both patches) and if the extinction rates of sink and source patches are equal $(e + h_1 = e + h_2)$, then T becomes the threshold parameter of Levins' model.

On T and persistence

The quantity $1/(e + k)$ can be interpreted as the average lifetime of a type 1 patch (source) before degrading to the other type (sink). Analogously, the quantities $1/(e + h_1 + k_1)$ and $1/(e + h_2)$ are the average life-time of type 1 and 2 occupied patches be-

fore extinction, respectively. Therefore, $\beta/\,(e + k)\,(e + h_1 + k_1)$ and $\beta\sigma/\,(e + h_2)$ represent the propagule production rate of a p_{11} and p_{21} pair during its lifespan before extinction (when invading an empty habitat) respectively. T is computed by averaging these two parameters that describe each type of patch. Thus, T is the average number of successful colonization attempts of empty patches produced by an average occupied patch during its *average* lifetime when invading an empty habitat. The threshold condition is analogous to that of Levins: if $T > 1$ initially empty patches are invaded successfully.

In Levins' model, the nontrivial equilibrium exists only if invasion is successful $(T > 1)$. In our model, the same property holds. Thus, T is able to describe not only invasion success, but also the existence of an equilibrium point where all patch types are present (it represents an steady-state where the metapopulation shows a mixture of both types of empty patches, and both types of occupied patches). A bifurcation diagram analogous to the one in Figure (2) is shown in Figure (3a) and Figure (3b). In this case we have chosen to plot the equilibrium densities of p_{11} and p_{21} as functions of β and e. It is shown that when T is larger than 1, the equilibrium exists. Otherwise, the equilibrium state where all patches are empty is the only one that exists. In this case, it is also asymptotically stable.

In Figure (4), we show the level curve $T = 1$ using β and e as parameters, that is $T = T\,(\beta, e)$, all other parameter values are fixed. The values of β and e that give $\beta/e = 1$ in the Levins' model are on the line $\beta = e$. Note that the level curve of $T = 1$ is always to the left of the line $\beta = e$. This means that for a given value of e, the magnitude of β required to put the threshold parameter above 1 in our model must be always higher than the one required by Levins' model. Therefore, an increase in patch heterogeneity increases the propagule production rate needed to achieve $T > 1$ (successful colonization). In this regard, the presence of sink patches have diluted the quality of the landscape.
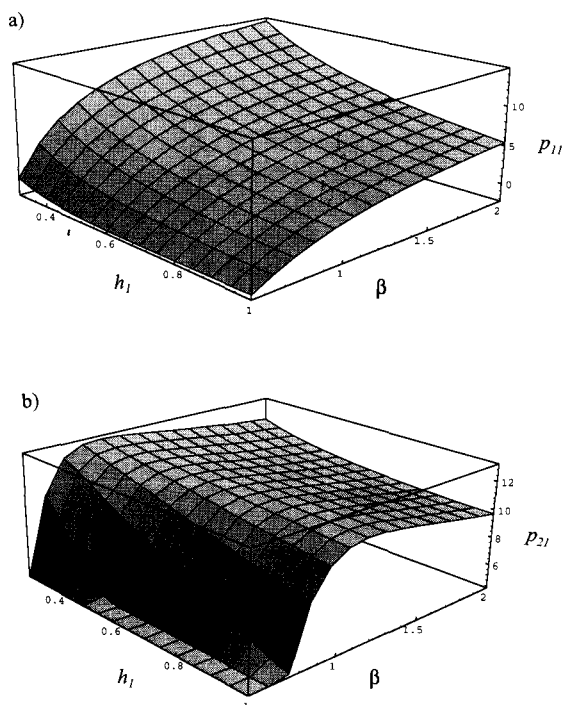
a)

b)

Fig.3: Diagrams for the equilibrium points of equation (1). The diagrams illustrate the value of the colonized patch densities at equilibrium when T is greater than 1. a) Equilibrium density of p_{11} as a function of β and h_1. b) Equilibrium density of p_{21} as a function of β and h_1.

Diagramas para los puntos de equilibrio de las ecuaciones (1). Los diagramas ilustran los valores de las densidades en parches colonizados en equilibrio cuando T es mayor que 1. a) Densidad en equilibrio de p_{11} como función de β y h_1. b) Densidad en equilibrio de p_{21} como función de β y h_1.

Fig.4: Contour plot of T for $T = 1$. Contour plot as a function of β and e. The line β = e represents Levins' threshold parameter. The line above is the contour plot predicted by T.

Curva de nivel de para T =1. Curva de nivel como función de β y e. La línea β = e representa el parámetro umbral de Levins. La línea superior es la curva de nivel predicha por T.

DISCUSSION

Spatial heterogeneity is a very important ecological factor affecting the persistence, diversity, and composition of ecological communities. Our model, equations (1), represents a generalization of Levins' metapopulation model when a) the total number of patches available for colonization is not constant but has an intrinsic dynamic, and b) the patches are not homogeneous. Thus, patch dynamics and heterogeneity are explicitly included.

We have concentrated our analysis in the study of the role of source and sink patches on the invasibility and persistence of a metapopulation. We have found that the threshold parameter (3) has a straightforward interpretation. This parameter deter-
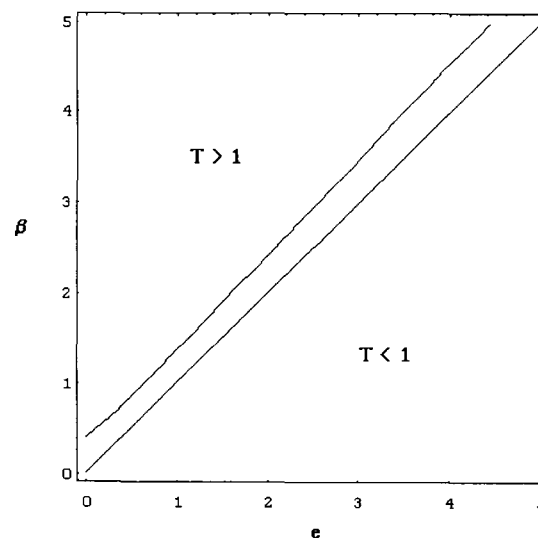
mines, not only the possibility of the successful invasion of a set of patches, but also governs the long term persistence of the metapopulation. Its properties are very similar to those of the Levins' model. The threshold parameter T can be rewritten in the following way:

$$T = T_1 \frac{e}{e + k} \left(1 - \sigma \frac{e + h_1}{e + h_2} \right) + T_2,$$

where $T_1 = \beta q/(e + h_1 + k_1)$ and $T_2 = \beta \sigma/(e + h_2)$.

Several comments can be made here. We start by noticing that it is an average of the colonization potential of the two patch types represented by T_1 and T_2 respectively (equivalent to the ratio β/e of Levins' model). This structure results from the homogeneity imposed on the system by the *single* type of organism that colonizes the patches. Therefore, in model (1) invasibility and persistence ability depend only on the patch type and not on the organism type.

Note also that the average T is weighted by the expression

$$w = \frac{e}{e+k}\left(1 - \sigma\,\frac{e+h_1}{e+h_2}\right).$$

Therefore, if σ, the depression in the propagule production rate imposed on the organism by sink patches, is small, $T_2 \approx 0$ and $w \approx 1$ implying that colonization and persistence dynamics are driven mainly by the source patches through T_1.

Suppose now that $\sigma \approx 1$. The weight w depends now only on the relative difference between extinction rates. If the overall extinction rate of source and sink patches is roughly equal, $w \approx 0$ and the dynamics of the metapopulation is governed by T_2 (the sink patches) but the habitat is essentially homogeneous (source and sink patches are practically the same).

T is foremost an invasion criterion. It indicates whether or not, from a single invasion event, the number of newly colonized patches will increase. For our model, however, we can claim more for T. The existence of a steady-state with a positive number of colonized patches is guaranteed whenever the invasion is successful, that is, whenever $T > 1$.

In Figure (3) we show the densities of colonized patches of type p_{11} and p_{21} as functions of the colonization and extinction rate. For β and e small, T is close to one and the equilibrium value of the two colonized patches is low. This would imply that if T is close to 1, stochastic events are more likely to bring the metapopulation below threshold and thus to extinction. For fixed e, an increase in β increases the value of T with a smooth but sudden in some cases, rise on the value of the equilibrium density. Our diagrams show that sink patch densities are more sensitive to changes on T than source patches are.

In Figure (4) we present a naive but illustrative comparison of our model with Levins'. In Levins' case, the threshold parameter is equal to 1 only when the propagule production rate is exactly equal

to the patch extinction rate. We explored the relationship between propagule production rate and our two types of extinction rates (e and h_1), for $T = 1$. Keeping all other parameters fixed, Figure (4) shows that our model predicts that to invade a heterogeneous environment (two patch types) and for a given extinction rate e, the magnitude of the propagule production rate must be higher than the one required if all patches were equal. Therefore, although it might be easier to persist in a heterogeneous landscape, it is certainly more difficult to colonize it.

Concluding remarks

The consequences of patch heterogeneity for metapopulation dynamics can be profound (Pulliam 1988, Pulliam & Danielson 1991, Holt 1993).

In our model in particular the distinction between source and sink habitat patches affects metapopulation invasion and persistence. In Figure 5, we make this point more clearly, by showing how T, seen as a func-
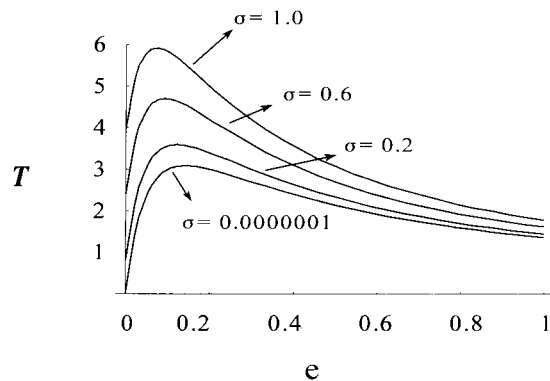

Fig.5: Changes in the threshold parameter T as a function of e. Different curves correspond to different values of the parameter σ ranging form $\sigma \approx 1$ (upper curve) to $\sigma \approx 0$ (bottom curve). Parameter values to calculate T for all simulations were $q = 0.9$, $\beta = 2$, $h_2 = 0.5$, $k = 0.2$, $k_1 = 0.1$, $h_1 = 0$.

Cambios en el valor del parámetro T en función de e. Las distintas curvas corresponden a differentes valores del parámetro σ cubriendo desde 1 (curva superior) hasta $\sigma \approx 0$ (curva inferior). Los valores de T los otros parámetros para el cálculo de T en cada simulación fueron $q = 0.9$, $\beta = 2$, $h_2 = 0.5$, $k = 0.2$, $k_1 = 0.1$, $h_1 = 0$.

tion of e, is a peaked right-skewed function with a maximum at intermediate values of e. Note that, whenever $T_2 < 1$, a window of extinction under which patch invasion and persistence is possible may occur. If $T_2 > 1$ this window does not exist but a maximum value of T still does. The appearance of an optimal value of extinction comes from the introduction of k, the patch degradation rate from source to sink as follows. The propagule production rate of an occupied source patch is βq. An occupied source patch may be lost because of background extinction (e), because while still a source patch, it losses its subpopulation (h_1), or because it degrades and becomes a sink occupied patch (k_1). Therefore, the unadjusted lifetime propagule production of an occupied source patch is $\beta q/(e + h_1 + k_1)$. We have to correct this estimate because once a source patch is degraded, its propagule production rate is not anymore βq. A source patch has an average lifespan of $1/(e + k)$ of which only a fraction $e/(e + k)$ is spent as an occupied, undegraded source patch. Therefore, the discounted propagule production of an occupied source patch is given by

$$\frac{\beta q}{e + h_1 + k_1} \times \frac{e}{e + k}$$

Thus, seen as a function of e, the threshold quantity T is a concave function with a maximum.

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APPENDIX

In this Appendix we derive the threshold parameter T from equations (1).

Define

$$B(t) = \frac{\beta\,(\sigma p_{21} + p_{11})}{p}$$

and then solve the system

$$0 = q\Lambda - (e + k)\,p_1 - Bp_1,$$
$$0 = -\,(e + h_1)\,p_{11} + Bp_1 - k_1 p_{11},$$
$$0 = (1 - q)\,\Lambda + kp_1 - ep_2 - Bp_2,$$
$$0 = -\,(e + h_2)\,p_{21} + Bp_2 + k_1 p_{11}$$

for p_1, p_2, p_{11} and p_{21} in terms of B.

We then use the definition of B to obtain a one-dimensional non-linear map $F(B)$ whose fixed points give the equilibrium densities of (1). It is easy to check that $B = 0$ is a fixed point of $F(B)$ that corresponds to the equilibrium point of (1) where only empty patches are present $((p^*_1, p^*_2, 0, 0))$. Thus, $|dF/dB|$ evaluated at zero determines if the map is locally a contraction in a neighborhood of $B = 0$. It is easy to check that

$$\left|\frac{dF\,(0)}{dB}\right| = T.$$

The properties of T and its consequences for model (1) are discussed in the text.