

A SOURCE-SINK PATCH OCCUPANCY METAPOPULATION MODEL
UN MODELO METAPOBLACIONAL DE OCUPACIÓN
DE PARCHES FUENTE Y SUMIDERO

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Abstract

We consider an 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-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 trade-off 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.

Introduction

We consider an 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 patchy distribution in resource abundance, microclimate conditions, 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 and 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 and Wolin 1989, Hanski 1991). The first metapopulation model was proposed by Levins (1969, 1970, but see also MacArthur and Wilson 1967). Levins' model assumes a set of equal habitat patches with local populations 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 and Wolin 1989; Gotelli 1991, Gyllenberg and Hanski 1992, Hanski and Gyllenberg 1993), competitive (Horn and MacArthur 1972, Slatkin 1974; Hanski 1983, Nee and 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. or how individuals occupy patches), and that of the patches (i.e. how patches of different type are created, occupied and go extinct). Our models 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 behavior 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 immediately 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 represent 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 $-\beta O U/N$ 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):

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

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

$$\frac{d}{dt}p = \beta p(1 - p) - ep.$$

Levins' model postulates that the total number of patches N is constant, that all unoccupied patches are equal, that all colonizing organisms are equal too (therefore implying that all occupied patches are equal). 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 non-trivial equilibrium point $p^* = 1 - e/\beta$ 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 and Gyllenberg 1993, Lima et al. *in press*). In this work we explicitly concentrate in the role of habitat heterogeneity 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 the organism has, on average, a higher propagule production rate and where natural extinction is minimal (that is, source patches are net exporters of individuals). Likewise a *sink* patch is one where the organism has, on average, a low propagule production rate and the extinction rate is always higher than in source patches (these patches are net importers of individuals).

We consider a single type of organism that can be characterized by a single propagule production rate and two extinction rates (associated with each patch type). However, we assume that even though propagule production is equal for all individuals, dispersal 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

Habitat is heterogeneous. 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 an habitat composed of two types of patches. Source and sink patches are denoted by p_1 and p_2 respectively. In our model we follow the temporal dynamics of these empty patches since we assume that the total population 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} (occupied source and sink patches respectively).

As mentioned earlier, we do not consider the total number of patches p to be constant. We incorporate a dynamic nature to this variable by assuming that there is a generation process of empty patches that aggregates two main mechanisms: the actual creation of new patches of both types, and the recovery of previously occupied patches whose populations went extinct. 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):

$$\begin{aligned}\frac{d}{dt}p_1 &= q\Lambda - (e + k)p_1 - \beta\frac{p_1}{p}(\sigma p_{21} + p_{11}), \\ \frac{d}{dt}p_{11} &= -(e + h_1)p_{11} + \beta\frac{p_1}{p}(\sigma p_{21} + p_{11}) - k_1p_{11}, \\ \frac{d}{dt}p_2 &= (1 - q)\Lambda + kp_1 - ep_2 - \beta\frac{p_2}{p}(p_{11} + \sigma p_{21}), \\ \frac{d}{dt}p_{21} &= -(e + h_2)p_{21} + \beta\frac{p_2}{p}(\sigma p_{21} + p_{11}) + k_1p_{11}.\end{aligned}\tag{1}$$

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. 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 constants h_1 and h_2 are extinction rates induced by the presence of individuals in either patch. Thus the number of colonized source patches that become extinct per unit time is $(e + h_1)p_{11}$. The corresponding rate for colonized sink patches is $(e + h_2)p_{21}$.

We assume that patch degradation from source to sink types is independent of its status as colonized or empty. Therefore, a colonized source patch

degrades to a colonized sink patch 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 colonization rate for individuals in sink patches ($0 \leq \sigma \leq 1$).

Thus, the total rate of generation of colonized source patches is

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

and that of colonized sink patches 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 (Velasco-Hernández and Marquet *ms*). In particular the invasion threshold we are concerned with provide 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 dynamics. 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

$$p_o^* = 1 - e/\beta.$$

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

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 \mathcal{T} . \mathcal{T} is found by linearizing the system around the equilibrium $(p_1^*, p_2^*, 0, 0)$, where only empty patches are present, with

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

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

$$\mathcal{T} = \frac{\beta eq}{(e+h_1+h_2)(e+k)} \left(1 - \sigma \frac{e+h_1}{e+h_2}\right) + \frac{\beta \sigma}{e+h_2}. \quad (3)$$

\mathcal{T} is the equivalent to Levins' threshold parameter. In our case, the existence of two types of patches that differ in both propagule production

and extinction properties, makes \mathcal{T} an average of two numbers. We discuss this characteristic in the next section. Now we want to show that \mathcal{T} , and thus model(1) are proper generalization 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 ($e + h_1 = e + h_2$), then \mathcal{T} becomes the threshold parameter of Levins' model.

On \mathcal{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 $1/(e + h_1 + k_2)$ and $1/(e + h_2)$ are the average lifetime of type 1 and 2 occupied patches before 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. \mathcal{T} is computed by averaging these two parameters that describe each type of patch. Thus, \mathcal{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 $\mathcal{T} > 1$ initially empty patches are invaded successfully.

In Levins' model the nontrivial equilibrium exists only if invasion is successful ($\mathcal{T} > 1$). In our model, the same property holds. Thus \mathcal{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 \mathcal{T} is larger than 1, the equilibrium exists. Otherwise the equilibrium state where all patches empty is the only one that exists. In this case it is also asymptotically stable.

In Figure (4) we show the level curve $\mathcal{T} = 1$ using β and e as parameters, that is $\mathcal{T} = \mathcal{T}(\beta, e)$, 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 $\mathcal{T} = 1$ 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 habitat heterogeneity increases the propagule production rate to achieve $\mathcal{T} > 1$ (successful colonization).

Discussion

Equations (1) represent a generalization of Levins' metapopulation model when a) the total number of patches available for colonization is not constant but has an intrinsic dynamics, and b) the patches are not homogeneous. Spatial heterogeneity is a very important ecological factor affecting the persistence, diversity, and composition of ecological communities (citation).

We have concentrated our analysis in the study of the role of source and sink patches in the invasibility and persistence of a metapopulation. We have found that the threshold parameter (3) has a straightforward interpretation. This parameter determines, 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 \mathcal{T} can be rewritten in the following way:

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

where $T_1 = \beta q / (e + h_1 + h_2)$ 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). The reason of this structure comes 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 \mathcal{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 governed 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).

\mathcal{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 \mathcal{T} . The existence of a steady-state with a positive number of colonized patches is guaranteed whenever the invasion is successful, that is, whenever $\mathcal{T} > 1$.

In Figure (3) we show the densities of colonized patches of type p_{11} and p_{21} as function of the colonization and extinction rate. For β and e small, \mathcal{T} is close to one and the equilibrium value of the two colonized patches is low. This would imply that if \mathcal{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 \mathcal{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 \mathcal{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 $\mathcal{T} = 1$. Keeping all other parameters fixed, Figure (4) shows that our model predicts that to invade and 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 habitat, it is certainly more difficult to colonize it.

Concluding remarks

The consequences of habitat heterogeneity for metapopulation dynamics can be profound (Pulliam 1988, Pulliam and 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 \mathcal{T} , seen as a function of e , the background extinction rate, changes from monotonically decreasing to a peaked right skewed function with a maximum at intermediate values of e . This shift is accomplished by modulating the value of σ and h_1 . Varying σ from a value close to one (when sink and source patches are equal in terms of propagule production) to a value close to 0 (when sinks produce no propagules) \mathcal{T} changes from monotonically decreasing to concave. Similarly, changing h_1 from values close to zero up to higher values also induces concavity, for fixed values of σ . In summary, whenever $T_2 < 1$, \mathcal{T} will be concave as a function of the background extinction rate. Thus, the presence of sink

patches defines a window of extinction under which patch invasion and persistence is possible. The appearance of an optimal value of extinction comes from the introduction of k , the patch degradation rate from source to sink. Essentially, what degradation and habitat heterogeneity introduce is an implicit dependence between propagule production, a property of the organism type, and extinction, a patch property (independent of its occupancy status). The degradation rate shortens the period of time during which propagule production is possible. Recall that in Levins' model the threshold parameter is a monotonically decreasing function of e , meaning that the greater the extinction rate, the less likely invasion and persistence are.

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References

- GOTELLI NJ (1991) Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist* 138:768-776
- GYLLENBERG M & I HANSKI (1992) Single-species metapopulation dynamics: a structured model. *Theoretical Population Biology* 42:35-61.
- HANSKI I (1982) Dynamics of regional distribution: the core satellite species hypothesis. *Oikos* 38:210-221.
- HANSKI I (1983) Coexistence of competitors in a patchy environment. *Ecology* 64: 493-500.
- HANSKI I (1985) Single species spatial dynamics may contribute to long term rarity and commonness. *Ecology* 66:335-343.
- HANSKI I (1991) Single-species metapopulation dynamics: concepts, models and observation. *Biological Journal of the Linnean Society* 42:17-38.
- HANSKI I & M GYLLENBERG (1993) Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist* 142:17-41.
- HASTINGS A (1977) Spatial heterogeneity and the stability of predator-prey systems. *Theoretical Population Biology* 12:37-48.
- HASTINGS A & CL WOLIN (1989) Within-patch dynamics in a metapopulation. *Ecology* 70: 1261-1266
- HASTINGS A & S HARRISON S (1994) Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics* 25: 167-188
- HOLT RD (1985) Populations dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181-208.
- HOLT RD (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs RE & D Schluter (eds) *Species diversity in ecological communities. Historical and geographical perspectives*: 77-88. The University of Chicago Press.
- HORN HS & RH MACARTHUR (1972) Competition among fugitive species in a harlequin environment. *Ecology* 53:749-752.
- LEVINS R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of The Entomological Society of America* 15:237-240.

LEVINS R (1970) Extinction. Lectures on mathematics in the life sciences 2. American Mathematical Society, Providence, Rhode Island.

LIMA M, PA MARQUET & FM JAKSIC (In press) Extinction and colonization processes in subpopulations of five sympatric small mammals. *Oecologia*.

MACARTHUR RH & EO WILSON (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

NEE S & RM MAY (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37-40.

PULLIAM H R (1988) Sources, sinks, and population regulation. *American Naturalist* 132:267-274.

PULLIAM H R & BJ Danielson (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137: 50-66.

SABELIS MW, O DIEKMANN & VAA JANSEN (1991) Metapopulation persistence despite local extinction: predator-prey patch models of the Lotka-Volterra type. *Biological Journal of the Linnean Society* 42: 267-283.

SLATKIN M (1974) Competition and regional coexistence. *Ecology* 55: 128-134.

Appendix

In this Appendix we derive the threshold parameter \mathcal{T} from equations (1).

Define

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

and then solve the system

$$\begin{aligned} 0 &= q\Lambda - (e + k)p_1 - Bp_1, \\ 0 &= -(e + h_1)p_{11} + Bp_1 - k_1p_{11}, \\ 0 &= (1 - q)\Lambda + kp_1 - ep_2 - Bp_2, \\ 0 &= -(e + h_2)p_{21} + Bp_2 + k_1p_{11}. \end{aligned}$$

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 F is locally a contraction in a neighborhood of $B = 0$. It is easy to check that

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

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

Figure Captions

FIGURE 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.

FIGURE 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 parameter 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. Notese que conforme β/e se incrementa desde 1, el valor del estado estacionario positivo también se incrementa.

FIGURE 3 Diagrams for the equilibrium points of equation (1). The diagrams illustrate the value of the colonized patch densities at equilibrium when \mathcal{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 \mathcal{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 .

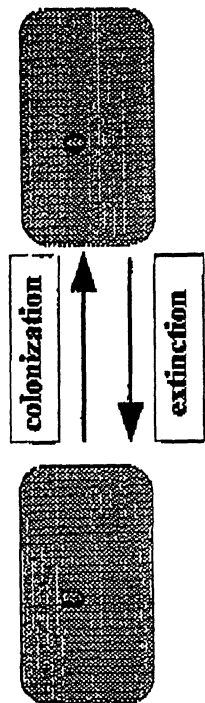
FIGURE 4 Contour plot of \mathcal{T} for $\mathcal{T} = 1$. Contour plot as a function of β and e . The line $\beta = e$ represents Levins' threshold parameter. The line above is the contour plot predicted by \mathcal{T} .

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

FIGURE 5 Changes in the threshold parameter \mathcal{T} as a function of e . Different curves correspond to different values of the parameter σ ranging from $\sigma \approx 1$ (upper curve) to $\sigma \approx 0$ (bottom curve).

Cambios en el valor del parámetro \mathcal{T} en función de e . Las distintas curvas corresponden a diferentes valores del parámetro σ cubriendo desde $\sigma \approx 1$ (curva superior) hasta $\sigma \approx 0$ (curva inferior).

a)



b)

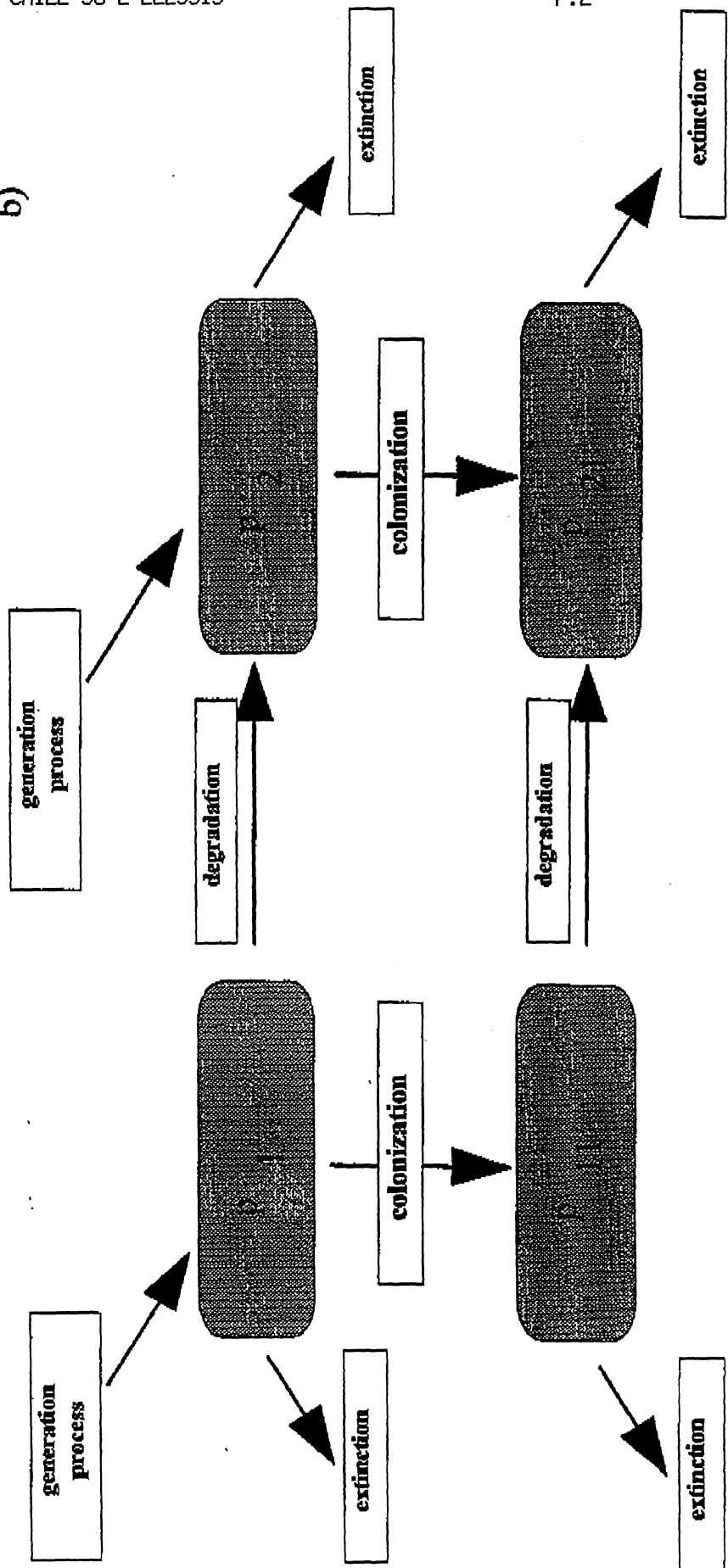


Fig 4

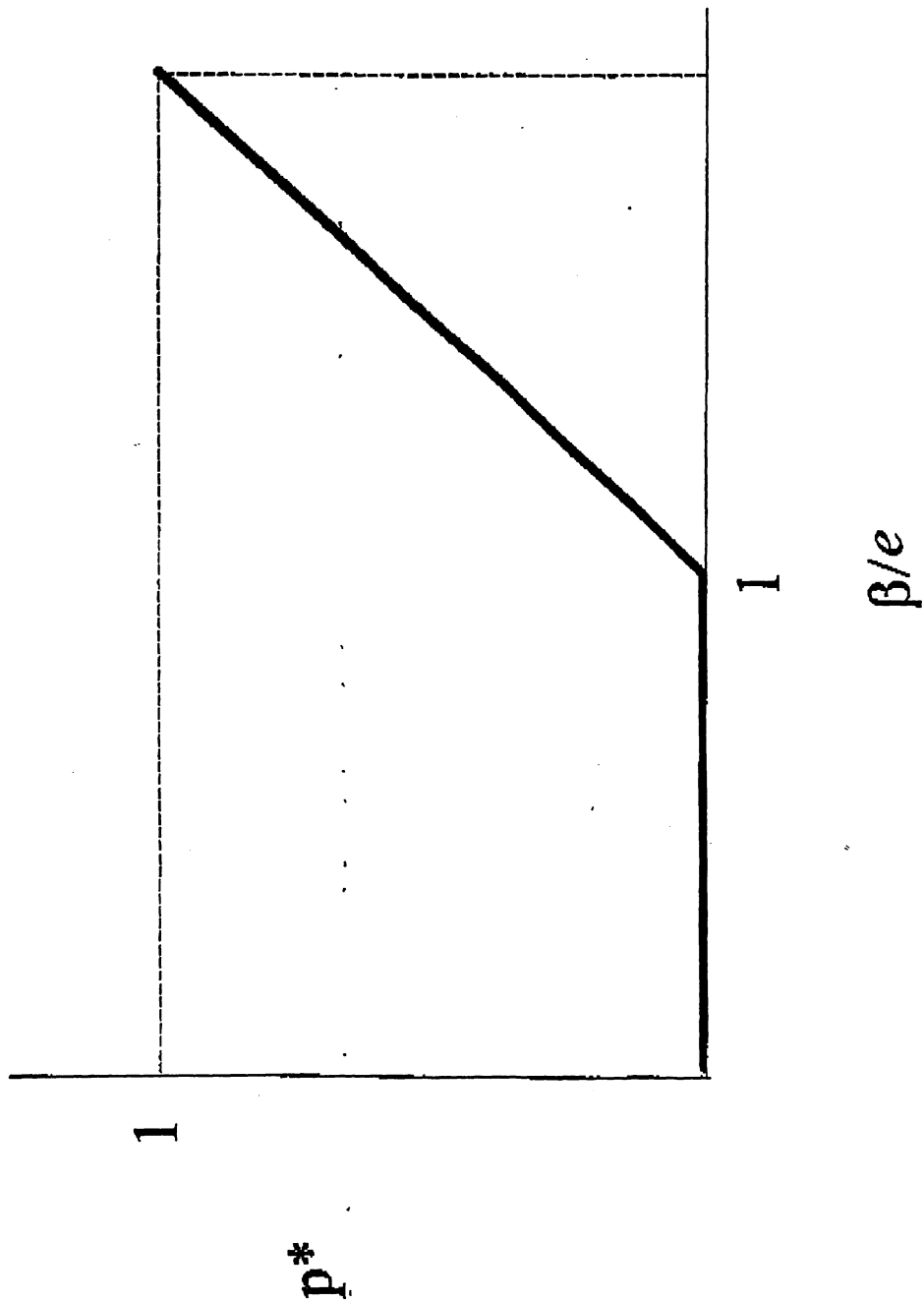
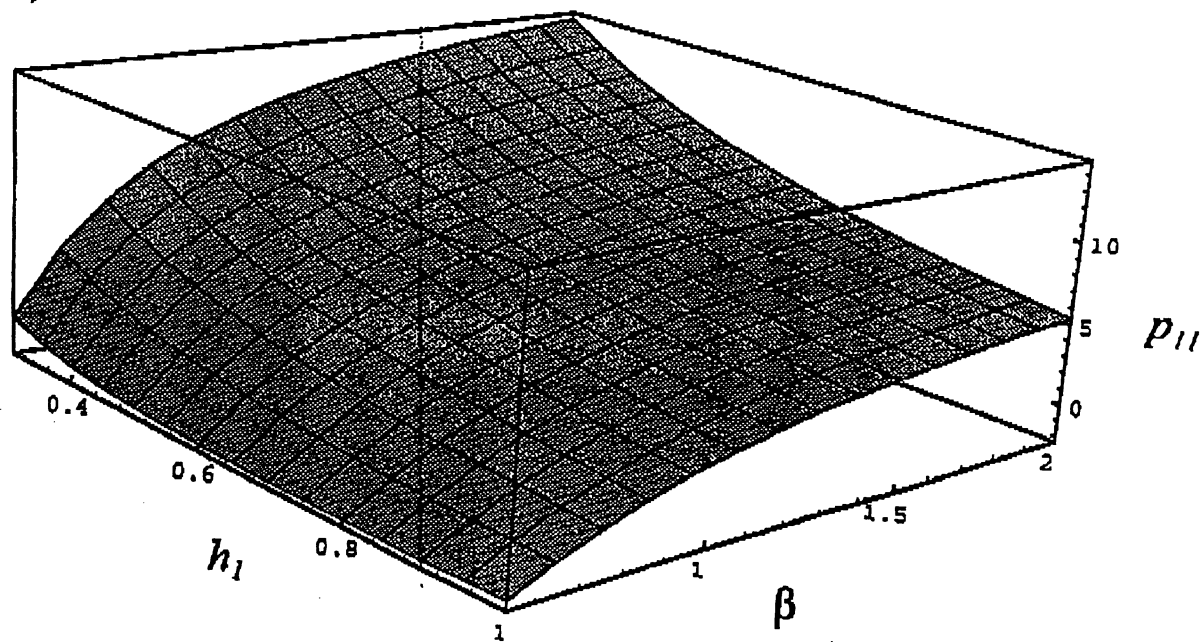


Fig 2

a)



b)

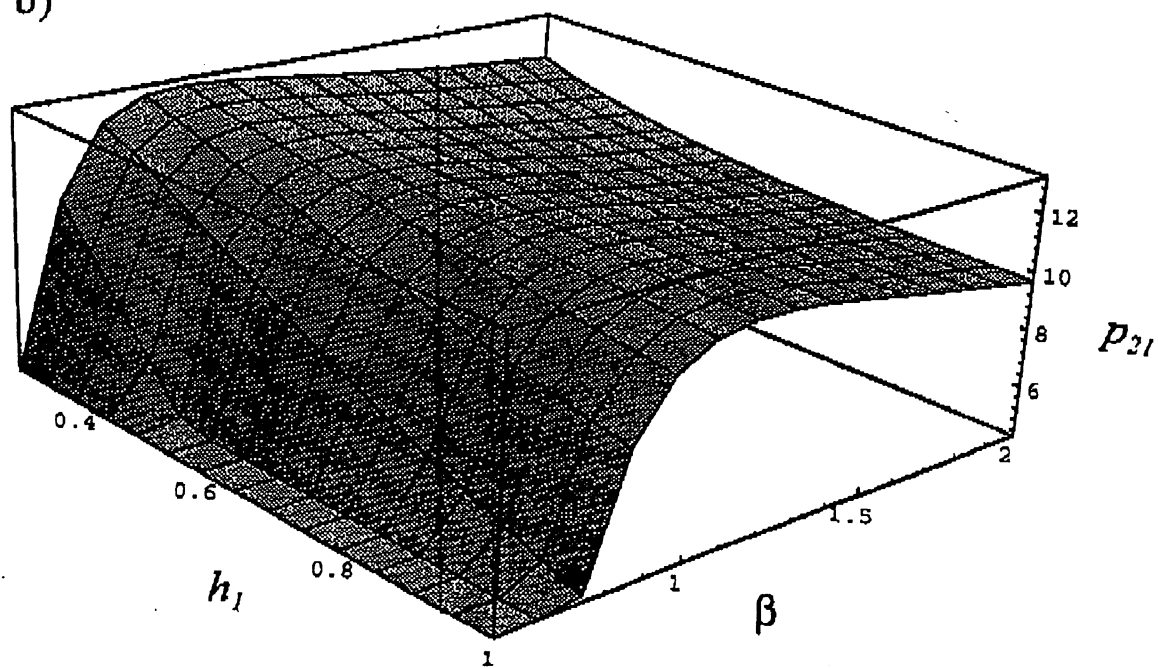


Fig 3

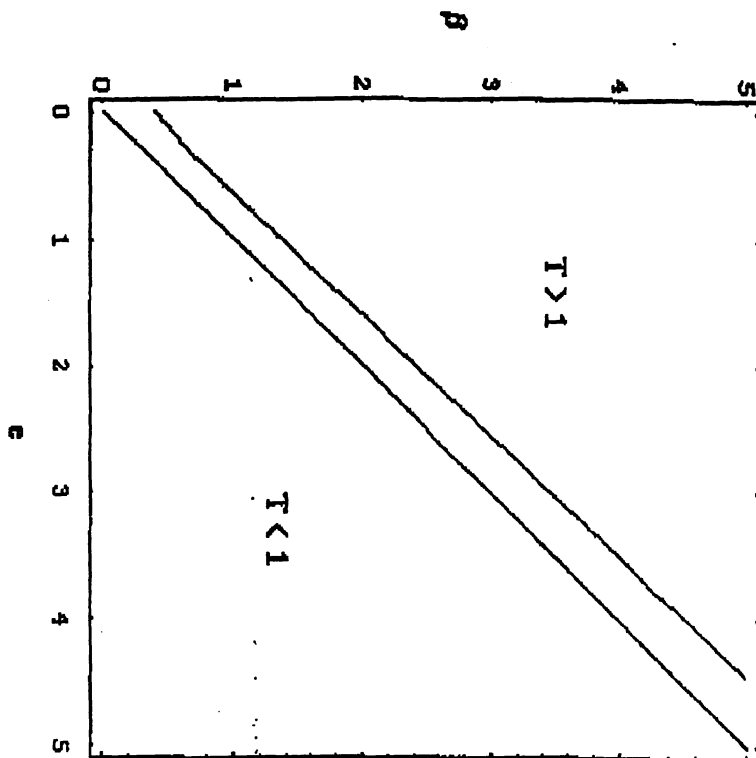


Fig 4

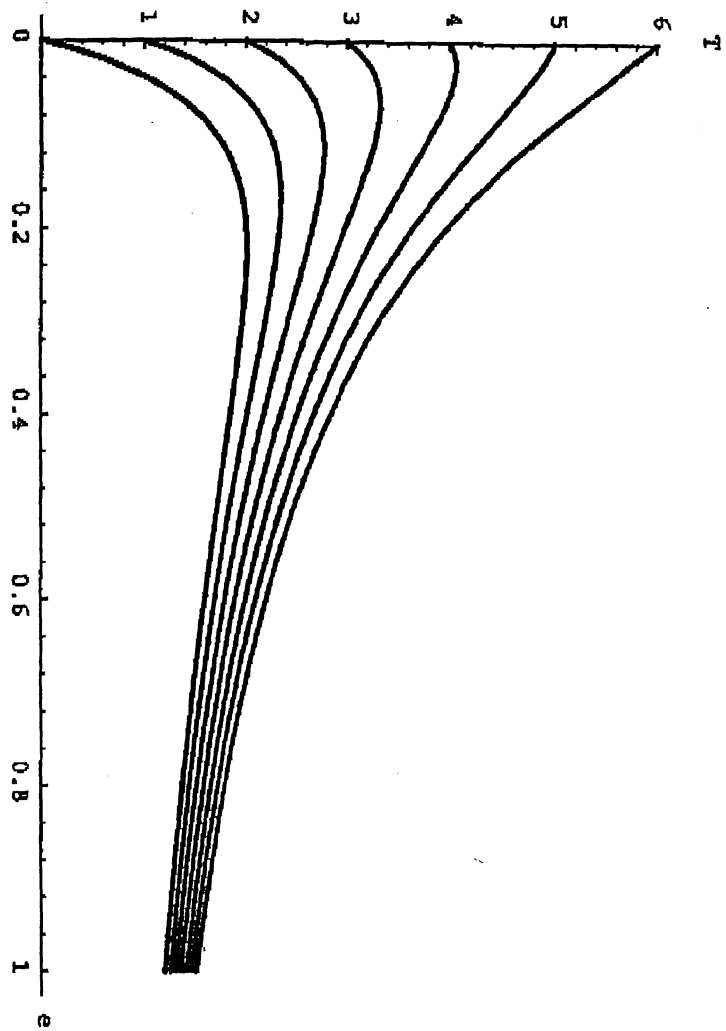


Fig 5