

Metapopulations

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Metapopulations

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A metapopulation is an ensemble of interacting populations connected by dispersal of individuals among them. Many species exist as metapopulations, and more are expected to do so, considering that landscapes are becoming increasingly patchy through habitat loss, degradation, and fragmentation, one of the most important of the many interacting components of global change affecting ecological systems.

In this essay a broad overview of metapopulation models and theory, from an ecological point of view, is presented, with emphasis on those concepts and approaches most important to understand the consequences of changes in the global environment. Global change through fragmentation can increase metapopulation extinction by: (1) destroying key habitat patches, which albeit their low quality (sinks), may be essential to maintain the connectivity of the system or by destroying those of high quality (sources) that are important sources of new colonists; and (2) by altering the natural dynamic regimes of habitat patches within landscapes. The effects of these changes may be subtle, lagged in time, and usually with sharp threshold transitions. Hence it is essential to establish long-term landscape monitoring programs to ensure metapopulation persistence in the face of a global change in the environment.

INTRODUCTION

Individuals and the habitats they occupy are not homogeneously distributed in space. Population ecologists have recognized the importance of spatial heterogeneity for a long time (e.g., Gause, 1935). However, the study of temporal fluctuations in the number of individuals within populations has historically received most attention from both theoretical and empirical ecologists, likely as a result of the complexity involved in the consideration of space in theoretical models and experiments. Researchers following this non-spatial approach pictured populations as closed systems that changed in size as a consequence of births and deaths that occurred locally. However, the observation that populations can go extinct at particular locations and later reappear owing to colonization events, or can persist even if additions of new individuals through births do not compensate for losses through death, pointed to the importance of considering the exchange of individuals among populations in order to account for their dynamics and persistence. Under this view, populations are open systems, not independent from nearby populations with which they interact through the exchange of individuals. This ensemble of interacting

populations (Figure 1) is what is called a *metapopulation* or *population of populations* as epitomized by Richard Levins in two foundational papers (Levins, 1969, 1970). Under the metapopulation paradigm, in addition to the importance of local populations, there is an added emphasis on the dynamics of the ensemble of local populations and the way they interact through migration.

Many species exist as metapopulations, and more are expected to do so, considering that the distribution of habitats within landscapes is becoming increasingly patchy through habitat loss, degradation, and fragmentation. Fragmentation in particular is the largest, and one of the most important, of the many interacting components of global change affecting ecological systems (Vitousek, 1994). Recent analyses of global databases on human disturbance of natural habitats point out that the effects of these degradation processes are acute in different biomes (Groom and Schumaker, 1993; Hannah *et al.*, 1995). Major ecosystems have already been reduced to fragments and numerous species and genetically distinct populations have been lost in the process (Ehrlich and Wilson, 1991). The effects of habitat loss and fragmentation are pervasive, featuring as the primary causes of endangerment of two-thirds of the world's vertebrates categorized as at risk of extinction (Prescott-Allen and Prescott-Allen, 1978) and of 82% of the endangered bird species (Temple, 1986).

Landscapes subjected to change through fragmentation represent one of the real world situations where metapopulation theory and models have been shown to be particularly suited to understand species persistence and population dynamics. The process of habitat fragmentation entails the creation of discrete habitat patches whose effect is that local populations interact with each other through the exchange of dispersing individuals, thus behaving as a metapopulation system (Hanski and Simberloff, 1997). In this essay I will present an overview of metapopulation models and theory from an ecological point of view, emphasizing those concepts and approaches deemed most useful to understand the consequences of changes in the global environment. A more in-depth treatment of metapopulation theory may be found in four recent books on the topic (Gilpin and Hanski, 1991; McCullough, 1996; Hanski and Gilpin, 1997; Hanski, 1999). It should be noted that population geneticists have been analyzing microevolutionary processes within metapopulations or spatially structured populations for a long time (Wright, 1931). The interested reader may refer to Hastings and Harrison (1994) and Harrison and Hastings (1996) for reviews.

METAPOPOPULATION MODELS AND THEORY

The pioneer of metapopulation models is that proposed by Levins (1969). This simple model assumes that N , the total

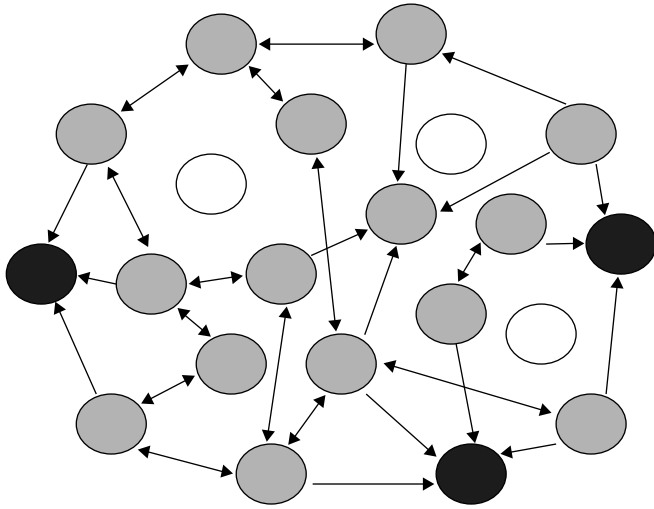


Figure 1 An ideal metapopulation composed of several local populations (or subpopulations) interacting through migration of individuals among them. Empty habitat patches, susceptible to be colonized from nearby local populations, are shown in white. Local populations whose persistence depends on immigration from nearby local populations (sink populations) are shown in black, while sources or immigrants (source populations) are shown in gray

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 $\beta O U/N$ per unit time, and occupied patches increase by the same number per unit time. If we assume that occupied patches become extinct at a rate e , then eO is the number of occupied patches that become extinct per unit time. Furthermore, this model assumes that occupied patches become unoccupied and immediately available for colonization at the same rate at which they become extinct, implying a closed system without an independent patch dynamics. The Equations that govern this system are:

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

Dividing both Equations by N , defining $O/N = p$, and noting that $U/N = 1 - p$, then the Equations reduce to the

Levins metapopulation model (Equation 1):

$$\frac{dp}{dt} = \beta p(1 - p) - ep \quad (1)$$

Because all patches and colonizing individuals are identical, one can dynamically follow the proportion of occupied patches instead of their actual numbers, and characterize the whole dynamics with two parameters: β and e . At equilibrium, the proportion of occupied patches is given by $p^* = 1 - e/\beta$, which is globally asymptotically stable, such that perturbations of this equilibrium as well as all initial conditions converge to this point.

In Levins' model, a positive proportion of occupied patches at equilibrium will exist whenever $\beta/e > 1$ (Figure 2). Taking into account that the average lifetime of an occupied patch is $1/e$, the above expression represents the total number of secondary colonizations produced by an occupied patch during its lifetime. This threshold parameter corresponds to the basic reproductive number used in epidemiology (usually denoted by the symbol R_0) which is a measure of the number of secondary infections that a single infectious individual produces when introduced in a completely susceptible population (Diekmann *et al.*, 1990; Hernández-Suárez *et al.*, 1999). If this number is higher than one, the disease spreads in the host population. Otherwise, no epidemic outbreak ensues and the disease dies out. The basic reproductive number is therefore an invasion criterion: it determines if a pathogen will be able to survive in a host population once it is introduced. In a metapopulation context, it determines if a landscape composed of a set of empty patches will be successfully colonized, and also determines its long-term persistence (Marquet and Velasco-Hernández, 1997). To appreciate the importance of R_0 in affecting metapopulation persistence, we can re-scale time in Equation (1) by taking as a unit the average time to extinction $1/e$. With this re-scaling,

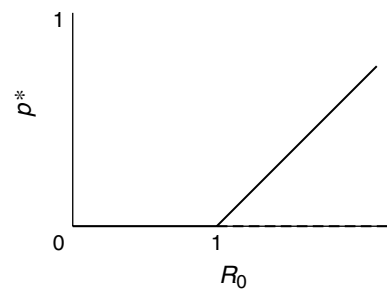


Figure 2 Bifurcation diagram for Levins' metapopulation model. For values of $R_0 < 1$ only the steady-state $p^* = 0$ exists and is stable. For $R_0 > 1$, a second steady-state appears. The other equilibrium still exists but is unstable. Note that the equilibrium proportion of occupied patches increases as R_0 increases. (Reproduced by permission of Sociedad de Biología de Chile in Marquet and Velasco-Hernández, 1997)

Levin's original model becomes (Hernández-Suárez *et al.*, 1999):

$$\frac{dp}{d\tau} = R_0 p(1 - p) - p \quad (2)$$

where τ stands for the new re-scaled time. It is clear that if $R_0 < 1$, $p \rightarrow 0$ and if $R_0 > 1$, $p \rightarrow 1$.

This simple patch-occupancy metapopulation model provides a simple and fruitful way to understand the basic dynamical properties of metapopulations. Its success is reflected in its many subsequent modifications and applications to describe single species, two species, and multi-species interactions (Hanski, 1999). Although the many assumptions made by Levin's model limits its application to understand real world metapopulations, it has been of paramount importance to unveil the existence of important processes affecting species persistence in patchy environments. In retrospect, Levin's simple model is the ancestor of a plethora of more complicated models, some of which are described in Table 1. Among them, spatially explicit models

Table 1 Different types of metapopulation models

Patch occupancy models or patch models

Models where the environment consists of an array of patches in two possible states, occupied or empty. They ignore attributes of local populations such as density and in most cases assume that all patches are equal. This type of model dynamically follows the proportion of patches in each state. Levin's model (Levin, 1969, 1970) is a patch-occupancy model

Structured metapopulation models

Structured metapopulation models explicitly include within-patch dynamics (modeling changes in local population sizes) and allow for the existence of differences in patch quality (reviewed by Gyllenberg *et al.*, 1997)

Spatially implicit metapopulation models

Models that ignore the spatial geometry or arrangement of patches, assuming that all are equally accessible and connected. Levin's model is spatially implicit

Spatially explicit metapopulation models

Models that include space explicitly, usually as a regular lattice of patches. Dispersal is restricted such that the dynamics of each patch in the lattice is a function of the state of the patches in its neighborhood. In this category are Cellular Automata models (e.g., Keymer *et al.*, 1998), coupled map lattice models (Hassell *et al.*, 1991), and interactive particle system models (Durrett and Levin, 1994)

Spatially realistic metapopulation models

These models are spatially explicit, where the lattice of patches is a real landscape (a GIS layer or a remote sensing image). This lattice preserves the relative position of patches, areas and other attributes of the real landscape (Keitt *et al.*, 1997; Schumaker, 1998)

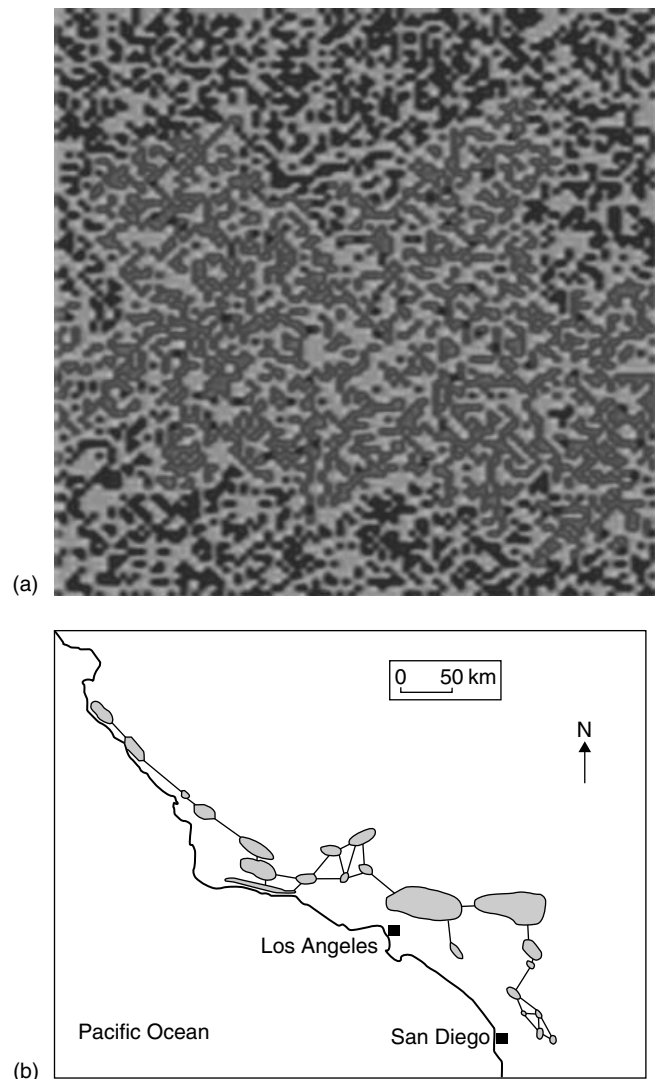


Figure 3 Two types of spatially explicit metapopulation models. (a) Space enters into the model as a regular lattice where each cell can be in a different state. (b) The metapopulation structure of the California spotted owl (*Strix occidentalis occidentalis*) is shown in the Sierra Nevada and in several isolated local populations in the mountains of southern California. (Reproduced with the permission of the British Ecological Society in Lahaye *et al.*, 1994)

have become very important in metapopulation theory (e.g., Keymer *et al.*, 1998) and well grounded in ecology (Durrett and Levin, 1994; Tilman and Kareiva, 1997; Dieckmann *et al.*, 2000). After all, metapopulations as well as ecological systems in general, are spatially extended systems whose dynamics are highly dependent on their topological arrangement, and neighborhood interactions. Two typical spatially explicit metapopulation models are presented in Figure 3. In the first model (Figure 3a) space is included as a regular lattice of patches that can be occupied by

a species. However, most landscapes have a more complex spatial distribution of patches, which have different shapes and are located at different distances from each other. This complexity can be captured in spatially realistic models where a real landscape (in the form of a Geographical Information Systems (GIS) layer or a classified satellite image), instead of an arbitrary lattice, is used to run the model. Examples of this approach are the RAMAS-GIS model developed by Akçakaya (1995), and the PATCH model developed by Schumaker (1998). Figure 3(b) shows the metapopulation structure of the California spotted owl (*Strix occidentalis occidentalis*) in the Sierra Nevada and in several isolated local populations in the mountains of southern California. A metapopulation model run on this patch network would be spatially realistic to the extent that the topology of the real system is preserved and affects its dynamics.

In Levins' patch occupancy model, the dynamics of the metapopulation is the result of the rate at which patches go extinct and the rate at which empty patches are colonized. However, by relaxing some of the assumptions about the source of the colonists, and the effect of migration between extant local populations, more complex and realistic scenarios can be analyzed.

SOME KEY METAPOPOPULATION CONCEPTS

Levins' model assumes that all colonists come from local populations within the system. However, there are other possible formulations (e.g., MacArthur and Wilson, 1967) with colonists coming from outside the system. In this scenario there is a propagule rain (a continuous source of migrants that could potentially colonize an empty site) which implies that the colonization rate depends, linearly on the fraction of empty patches only (Gotelli, 1991):

$$\frac{dp}{dt} = \beta(1 - p) - ep \quad (3)$$

Examples of situations in which the assumption of propagule rain may be appropriate include:

1. a collection of forest fragments separated from a larger expanse of forest which serves as a source of colonizers;
2. an archipelago of islands near a continental source of propagules;
3. intertidal habitats with organisms that are sedentary as adults but have widely dispersed pelagic larvae.

Among metapopulation models that include the colonization process as a propagule rain are the so-called mainland-island metapopulations.

Individuals or propagules produced by a local population may either land in an empty habitat patch, an event

that is called *colonization*, or in an occupied patch where there are already *conspecific* individuals (i.e., that belong to the same species), in which case this event is called *immigration*. Immigration can be of great importance for the persistence of local populations, especially if the population receiving the immigrants is close to extinction. In this case, the genetic and demographic contribution of immigrant individuals may potentially rescue the population from extinction by increasing its population size, thus lowering the chances of disappearing because of demographic or genetic stochasticity. This concept named *rescue effect*, or the effect of immigration on extinction, was elegantly developed by Brown and Kodric-Brown (1977) in the context of the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). It implicitly emphasizes the importance of connectivity among local populations and how this may potentially enhance metapopulation persistence. Clearly, this is of great importance to applied questions such as the maintenance of habitat corridors across landscapes.

Hanski (1982) was the first to include the rescue effect in a metapopulation model. This author reasoned that if rescue effects are operating, then the extinction rate should decrease as the proportion of occupied habitat patches increases. This is because the probability of a local population being rescued from extinction increases as the numbers of potential sources of immigrants to any given local population increases. A simple way to include the rescue effect into Levin's model is (Hanski, 1982):

$$\frac{dp}{dt} = \beta p(1 - p) - ep(1 - p) \quad (4)$$

which reduces to:

$$\frac{dp}{dt} = \lambda p(1 - p) \quad (5)$$

where $\lambda = \beta - e$. This model, which has a stable equilibrium at $p^* = 1$, gives rise to a bimodal distribution of occupied patches when λ is considered to be a random variable. In a multi-species case, this model predicts the existence of two types of species: those found in most of the habitat patches and those found in very few. This is what is known as the *core-satellite species hypothesis* (see Hanski, 1999 for a review and alternative models).

Source-Sink Dynamics

Landscapes are heterogeneous in time and space. Spatial heterogeneity is manifested, among other things, in differences in habitat quality such that the demographic rates of local populations are different in different patches. Extreme cases across a continuum of habitat-specific demographic rates are represented by source and sink populations (Puliam, 1988, 1996). A *source population* is one where births

exceed deaths and emigration exceeds immigration (Pulliam, 1988; see also Roughgarden and Iwasa, 1986). In other words, source populations are net exporters of individuals. In *sink populations*, on the other hand, deaths exceed births and immigration exceeds emigration. By definition, a sink population would not persist if immigration were impeded, because it has a negative rate of population increase (deaths outnumber births). Thus, rescue effects are essential for the persistence of sink populations. Clearly, sink populations will be found to the extent that there are source populations subsidizing them and engaged in source–sink dynamics. According to Pulliam's (1988) definition, real metapopulations should be composed of a mosaic of source and sink local populations. In practical terms, source populations are essential to metapopulation persistence and should be of great conservation concern. But why would some individuals immigrate into low quality patches inhabited by sink populations? There are at least two likely explanations (Dias, 1996). Individuals can occupy low-quality habitats as a result of interference competition whereby juvenile or subordinate individuals are forced to leave high quality (source) habitat patches, or because of passive dispersal as in plants and sessile invertebrates in intertidal habitats. A classical example of the first alternative is Carl's (1971) study on Arctic ground squirrels (*Spermophilus undulatus*). This species lives in breeding colonies where burrowing sites are limited and hence actively defended against conspecifics. Those individuals forced to flee the main breeding colonies occupy low quality (sink) habitat where mortality is high due to predation and environmental perturbations. Virtually all individuals in this population are immigrants in a low quality habitat. An example of a sink population maintained by passive dispersal is that described in Kadmon's (1993) study of the demography of the desert annual herb *Stipa capensis* in three habitats (slopes, depressions, and dry water course—*wadis*). Kadmon estimated that 75–99% of the seeds were produced in the depression and wadis, even though these two habitats represent less than 10% of the area occupied by the species. This evidence and previous results, which indicated that seeds produced in the wadis accounted for more than 90% of the abundance of *Stipa capensis* in the slope habitat, suggest that slope populations are maintained by immigration and correspond to sink populations. Typically sink populations are common at the border of geographic ranges of species. As noted by Lawton (1996), this fact may underlie the observed low success rate in species reintroduction programs at the edge of a species range in comparison with reintroductions in central areas (Griffith *et al.*, 1989).

Source–sink dynamics is an important metapopulation process with profound implications for species conservation in the face of global change. In the first place, it makes clear that the presence of a species in a given habitat is

not proof that the habitat is suitable for its persistence or able to support a locally breeding population in the absence of immigration. Secondly, it suggests that the density of a species may be a misleading indicator of habitat suitability (Pulliam, 1996) because some species can maintain large populations in unsuitable (sink) habitats (Pulliam, 1988).

The previous discussion emphasized the importance of source populations for species persistence. However, sink populations can also be important on ecological and evolutionary grounds. Under some circumstances, sink populations can stabilize interactions between species, can foster coexistence in ecological systems (e.g., Holt, 1985; Loreau and DeAngelis, 1997), and can increase metapopulation persistence (Howe *et al.*, 1991; but see Marquet and Velasco-Hernández, 1997) especially in variable environments (Jansen and Yoshimura, 1998). Sink populations in the periphery of the geographic ranges of species tend to be genetically divergent from central populations and potentially important for future speciation, especially if mutations of large effects on individual fitness occur in these sink populations. If the mutations are large enough, they can overcome the selection bias toward increasing adaptation to source habitats, rather than to sinks (Holt and Gaines, 1992). Thus, under some circumstances peripheral sink populations can be of conservation value (Lesica and Allendorf, 1995), by keeping genetic variability that may be useful for future adaptation, especially in a climate change scenario.

GLOBAL ENVIRONMENTAL CHANGE AND METAPOPOPULATION EXTINCTION

Most species are spatially structured as metapopulations within their geographic ranges, and their global extinction is usually mediated through changes in metapopulation dynamics, as a consequence of habitat loss associated with human encroachment of natural habitats. How these events affect metapopulation extinction depends on three factors: (1) how many local populations or habitat patches are lost; (2) the quality of the remaining patches; and (3) the resulting changes in metapopulation connectivity.

The effect of habitat loss or destruction depends on how many local populations are required to ensure the long-term persistence of the metapopulation or its *minimum viable metapopulation size*. This is equivalent to one of the key concept in population and conservation biology – the *minimum viable population size*, i.e., the minimum number of individuals within an isolated population necessary to guarantee its long-term persistence (Schaffer, 1981). Until recently, this concept remained almost unexplored in a metapopulation context. Following the lead of Lande (1987), Nee and May (1992) proposed a general

model that attempted to understand the effect of habitat destruction upon species interactions and persistence in patchy landscapes. By focusing on patch destruction, this model allows one to estimate the minimum number or fraction of habitable patches required for metapopulation persistence, also known as the *extinction threshold* (Lande, 1987; Lawton *et al.*, 1994; Hanski *et al.*, 1996; Hernández-Suárez *et al.*, 1999). Conceptually, the extinction of a metapopulation following patch destruction is equivalent to the collapse of a disease epidemic following the removal of susceptible hosts (Lawton *et al.*, 1994). The process depends on the *eradication threshold* (Anderson and May, 1991), that is, on the minimum number of susceptible individuals that will enable the disease to persist.

To understand the effect of habitat destruction on metapopulation persistence we can use a simple model. Imagine a metapopulation composed of a finite number (N) of patches and suppose that D patches are destroyed. Now consider the question of how many patches can be destroyed without driving the situation to extinction? In this situation the number of suitable patches is $N - D$, which can be either occupied (O), or empty (U), such that $N - D = O + U$. Dividing by N , defining the proportion of occupied patches as $O/N = p$, the proportion of destroyed patches as $D/N = d$, the proportion of empty patches as $U/N = 1 - d - p$, and then replacing these terms in Equation (1), we arrive at a model equivalent to that proposed by Levins (1969) but now including habitat destruction:

$$\frac{dp}{dt} = \beta p(1 - d - p) - ep \quad (6)$$

In this model the proportion of occupied sites at equilibrium in the face of destruction (p_d^*) is:

$$p_d^* = 1 - \frac{e}{\beta} - d \quad (7)$$

Equation (7) has several implications. First, metapopulation extinction will occur ($p_d^* = 0$) if a critical proportion of habitat (d) is destroyed. This threshold corresponds to

$$d = 1 - \frac{e}{\beta} \quad (8)$$

This implies that species with higher colonization rates or lower extinction rates can sustain higher amounts of habitat destruction (Figure 4). Interestingly, as noted by Tilman *et al.* (1997), this critical threshold corresponds to the equilibrium proportion of occupied patches in the absence of destruction such that a rule of thumb for metapopulation persistence is: A necessary and sufficient condition for metapopulation persistence is that the proportion of destroyed habitat patches should be less than the proportion originally occupied by the species in the

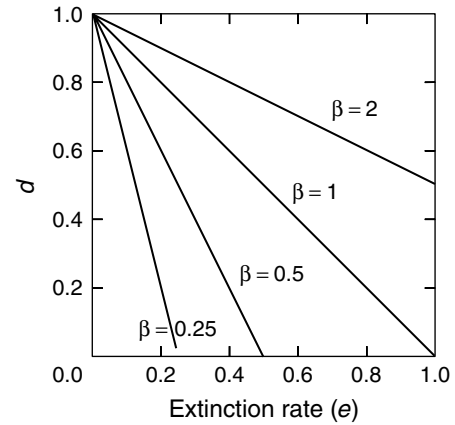


Figure 4 Changes in the critical amount of habitat destruction (d) needed to drive a metapopulation to extinction as a function of the species' extinction rate (e) and for species with different colonization rates (β). Notice that for the same extinction rate, species with higher colonization potential can withstand a higher proportion of habitat destruction before going extinct, and that this critical threshold decreases as extinction rates increases

intact system. Thus, if a species in a pristine habitat occupied 25% of the available patches, then the random destruction of >25% of the patches will result in its extinction. Notice also that Equation (7) can be rearranged as

$$1 - d - p_d^* = \frac{e}{\beta} \quad (9)$$

Noticing that $1 - d$ corresponds to the total amount of suitable habitat left after destruction, an equivalent rule of thumb (see Lawton *et al.*, 1994; Hanski *et al.*, 1996) can be formulated as: A metapopulation will persist if the proportion of suitable habitat patches after destruction exceeds the proportion of empty but suitable habitat patches in the intact system (i.e., $1 - d > e/\beta$). However, there are many other factors not captured by this simple model that can have an effect on metapopulation extinction.

A metapopulation may go extinct well before habitat destruction seriously threatens its persistence, as derived in the models above, because of stochasticity linked to a reduced number of local populations, such that a metapopulations can go extinct simply because all local populations happen to become extinct at the same time. This effect has been termed *extinction-colonization stochasticity* (Hanski, 1991) and is equivalent to the concept of demographic stochasticity for closed populations (May, 1973). But even if there is no habitat destruction and the metapopulation is large enough to escape extinction-colonization stochasticity, large-scale changes in the environment may tend to increase the correlation in local population dynamics, thus increasing the probability that all local populations

become sinks, which can lead to metapopulation extinction. This effect has been termed *regional stochasticity* (Hanski, 1991) and is equivalent to the notion of environmental stochasticity in closed populations (May, 1973). To the extent that local populations are not correlated in their local dynamics, there will always be some local populations acting as sources (and rescue effects operating) to counteract local extinctions.

Finally, the quality of patches lost to destruction can make a big difference in terms of metapopulation persistence. Traditionally, the quality of patches has been assessed in relation to their suitability for population growth (with source and sink being extreme cases). In this context the destruction of a source patch has a higher impact on persistence than the destruction of a sink. However, patches of low quality for population growth can be of paramount importance in maintaining the connectivity of the system by acting as stepping stones between high quality patches; consequently their loss can

have a tremendous impact on persistence. Thus, in terms of connectivity, source patches can be dependent on sink patches. Recently, Keitt *et al.* (1997) proposed a method to quantify habitat connectivity and to assign conservation priority to habitat patches based on their contribution to connectivity. Because connectivity of landscapes depends not only on the spatial configuration of habitat patches but also on the scale at which organisms interact with landscape pattern, e.g., Gardner *et al.* (1989), Keitt *et al.* (1997) quantified connectivity at different scales (Figure 5). Then, for each map, the authors removed patches (one at a time) and recorded the changes in landscape connectivity. This patch removal experiment allowed them to assess the importance of each patch in terms of landscape connectivity. Interestingly, after controlling by area, small patches had a very high contribution to connectivity, which suggest that they may be of high priority for conservation.

This is an important result, provided that small patches are more sensitive to environmental changes and may be the

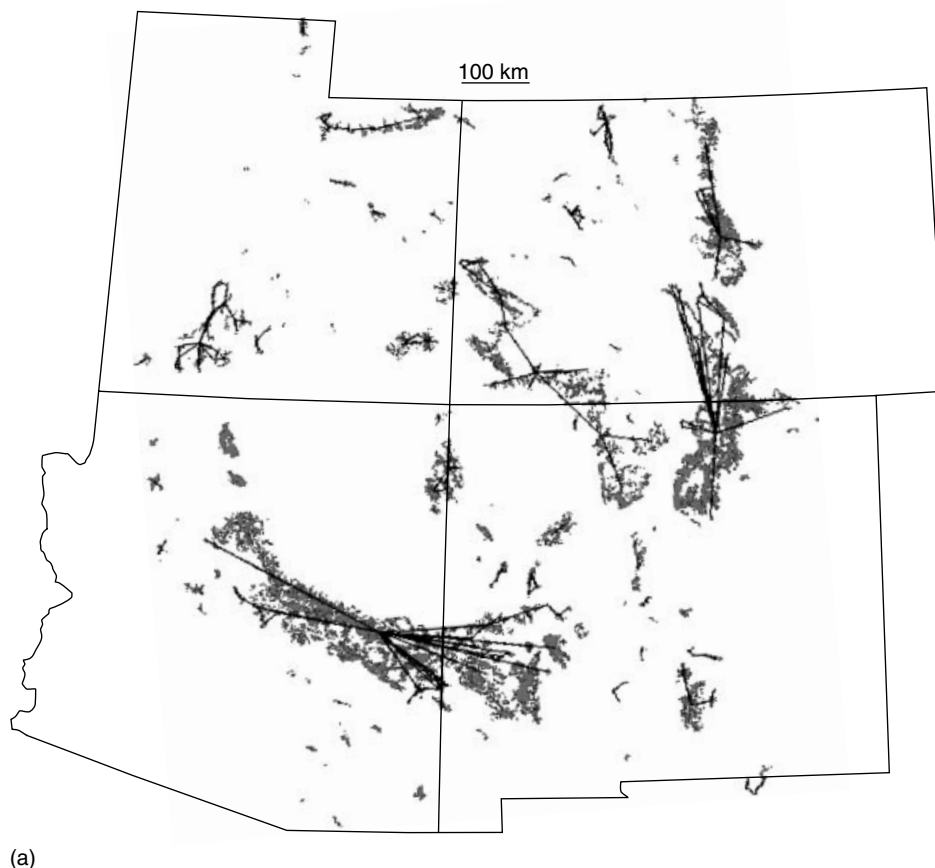
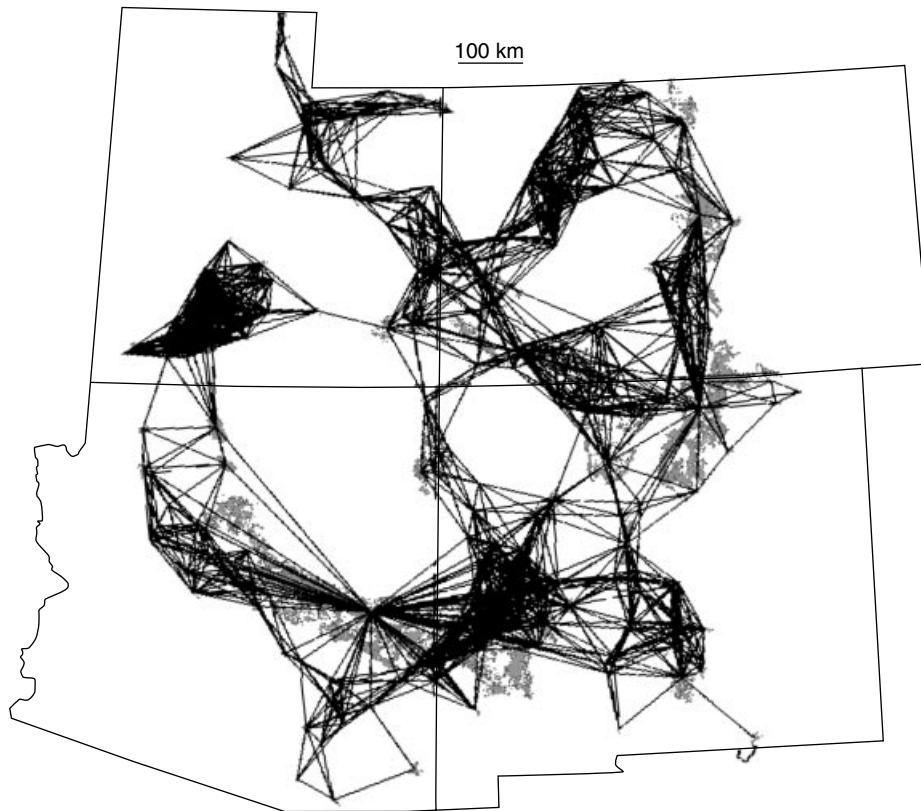


Figure 5 Digital cover map of the southwestern United States showing the spatial distribution of mixed-conifer and ponderosa pine habitat patches and the potential connection among them as a function of the scale at which organisms interact with the landscape pattern. In (a) black lines represent paths along which habitat patches are at a distance less than or equal to a threshold of 10 km, and thus organisms with a dispersal capability <10 km will perceive a highly fragmented landscape with many isolated patches. On the contrary, an organism capable of long distance dispersal [100 km as shown in (b)] will perceive a highly connected landscape. (Reproduced with permission of the Ecological Society of America in Keitt *et al.*, 1997)



(b)

Figure 5 (Continued)

first to disappear. If this is the case, current environmental change may have a strong negative impact on metapopulation persistence even if source patches are not affected. The disappearance of sink populations may trigger a cascade of events such as disruption in connectivity, increase in isolation, limited rescue effects, and loss of useful genetic variability, thus increasing metapopulation extinction risk. Because these effects may be subtle, lagged in time (Tilman *et al.*, 1994), and usually with sharp threshold transitions (Bascompte and Solé, 1996; Keitt *et al.*, 1997), it is essential to establish long-term multi-scale landscape monitoring programs to ensure metapopulation persistence in the face of a global change in the environment.

PATCH DYNAMICS

So far we have discussed the role of landscape pattern and the importance of particular patches for metapopulation persistence. However, Keymer *et al.* (2000) have shown that in addition to the pattern of *patch distribution*, *patch dynamics* (i.e., the creation of extinction and patches) greatly affects metapopulation persistence. Keymer *et al.* (2000) propose that metapopulation persistence is the result of the interaction between landscape pattern, patch dynamics, and species

life history. The inclusion of patch dynamics in metapopulation theory underscores the importance of landscape monitoring, and the need for an adequate characterization of patch dynamic and disturbances regimes in order to gain insight and be able to predict species extinction. In particular, the establishment of monitoring program inside and outside protected areas would be desirable to understand the interaction between direct human impacts and environmental changes upon landscape pattern and dynamics, and how these affects metapopulation extinction.

The effects of global environmental changes upon ecological systems are complex and involve changes in landscape patterns and dynamics. In this context, metapopulation theory provides the theoretical and empirical framework needed to understand and foresee the potential consequences of these changes in the global environment.

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