

# Patchy Populations in Stochastic Environments: Critical Number of Patches for Persistence

Jordi Bascompte,<sup>1,\*</sup> Hugh Possingham,<sup>1,2</sup> and Joan Roughgarden<sup>1,3</sup>

1. National Center for Ecological Analysis and Synthesis,  
University of California, Santa Barbara, California 93101-3351;

2. Departments of Zoology and Mathematics, University of  
Queensland, Saint Lucia, Queensland 4072, Australia;

3. Department of Biological Sciences, Stanford University,  
Stanford, California 94305

Submitted August 25, 2000; Accepted July 30, 2001

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**ABSTRACT:** We introduce a model for the dynamics of a patchy population in a stochastic environment and derive a criterion for its persistence. This criterion is based on the geometric mean (GM) through time of the spatial-arithmetic mean of growth rates. For the population to persist, the GM has to be  $\geq 1$ . The GM increases with the number of patches (because the sampling error is reduced) and decreases with both the variance and the spatial covariance of growth rates. We derive analytical expressions for the minimum number of patches (and the maximum harvesting rate) required for the persistence of the population. As the magnitude of environmental fluctuations increases, the number of patches required for persistence increases, and the fraction of individuals that can be harvested decreases. The novelty of our approach is that we focus on Malthusian local population dynamics with high dispersal and strong environmental variability from year to year. Unlike previous models of patchy populations that assume an infinite number of patches, we focus specifically on the effect that the number of patches has on population persistence. Our work is therefore directly relevant to patchily distributed organisms that are restricted to a small number of habitat patches.

**Keywords:** environmental stochasticity, extinction, spatially distributed model, reserves, geometric mean fitness.

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How patchily distributed populations persist in stochastic environments is a fundamental question in both basic and applied ecology. A great deal is known about how spatial processes influence the persistence of patchy populations.

\* Corresponding author. Present address: Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apartado 1056, E-41080 Sevilla, Spain; e-mail: bascompte@ebd.csic.es.

Am. Nat. 2002. Vol. 159, pp. 128–137. © 2002 by The University of Chicago. 0003-0147/2002/15902-0002\$15.00. All rights reserved.

For instance, much work has been done on how population persistence is influenced by factors such as dispersal, landscape structure, minimum amount of suitable habitat, and environmental synchronization (Crowley 1981; Harrison and Quinn 1989; Gilpin and Hanski 1991; Hassell et al. 1991; Adler 1993; Allen et al. 1993; Bascompte and Solé 1995, 1998; Grenfell et al. 1995; Hanski et al. 1996). In contrast, relatively little is known about the number of patches required for the long-term persistence of a spatially distributed population. Most existing models assume an infinite number of patches, which is clearly unrealistic for most patchily distributed organisms that are constrained to live in a finite number of habitat patches. Investigating how the effects of such factors as dispersal and environmental stochasticity on persistence change with the number of patches is therefore an issue of high priority.

Quite a large number of species have spatially distributed populations whose dynamics are affected by severe, density-independent environmental fluctuations (Andr wartha and Birch 1954). For example, many butterfly species reproduce in discrete patches of suitable habitat. One of the best-studied examples is *Melitaea cinxia*, a butterfly inhabiting the Åland Islands in southwest Finland (Hanski et al. 1995; Lei and Hanski 1997; Hanski 1999). This butterfly breeds on discrete patches of dry meadows. Because there are local extinctions and subsequent colonizations from other patches, regional persistence depends on the total number of patches (Hanski et al. 1996). Let us now imagine that the species has some economic value. In our example, the butterfly species can be harvested to sell specimens to collectors. Because harvesting imposes an additional source of mortality, population persistence would require a larger number of patches than in the absence of harvesting.

In marine ecosystems, several commercially exploited species have patchily distributed populations. Examples range from invertebrates (e.g., red sea urchin *Strongylocentrotus franciscanus* [Quinn et al. 1993] and queen conch *Strombus gigas* [Stoner and Ray 1996]) to vertebrates (different reef fish stocks [Colin 1996]). In these cases, individuals spawn in specific areas that serve as permanent

spawning sites (Colin 1996), producing large numbers of pelagic larvae that disperse large distances. After developing, the juvenile or adults recruit back to the spawning areas. Since high levels of harvesting are superimposed on these life cycles, persistence of stocks requires an adequate number of reproductive areas. The actual number of such sites will depend crucially on harvesting rates.

In the above examples, the problems are population preservation and sustainable population management. However, some patchy populations are crop pests (Levins 1969*b*). Pests with a patchy distribution are also becoming an increasing problem in marine ecosystems. Two examples are the black-striped mussel and the polychaete worm *Terebrasabella heterouncinata* (see Myers et al. 2000 and references therein). Similarly, some infectious diseases have a patchy distribution (Grenfell and Harword 1997). In these cases, the goal is the extermination of the population. However, there is a lack of simple analytical theory predicting how many patches have to be destroyed or what level of human-induced mortality has to be reached to eradicate the pest. The theory we present is very general and can be applied to all these scenarios.

In this article, we develop a model for a spatially distributed population. Our approach is based on the geometric mean fitness (GMF), a concept widely used in population genetics and ecology to understand persistence in fluctuating environments (Levins 1969*a*; Lewontin and Cohen 1969; Gillespie 1974; Kuno 1981; Klinkhamer et al. 1983; Metz et al. 1983; Yoshimura and Jansen 1996; Jansen and Yoshimura 1998). Our approach is also related to the problem of optimal harvesting in stochastic environments (e.g., Ricker 1958; Reed 1979; Clark 1985; Lande et al. 1994, 1995, 1997; Saether et al. 1996). We build on this previous work by evaluating persistence from the point of view of the number of patches. This also complements the classical metapopulation framework that assumes an infinite number of patches.

We construct the model and formalize a criterion for persistence based on the geometric mean of the spatial-arithmetic mean of the growth rates. From this criterion, we derive analytical approximations to answer these questions: What is the maximum human-induced mortality rate a patchy population can sustain? How many patches are needed to sustain a given harvesting rate? We conclude by discussing the robustness of our approach when some of our initial assumptions are relaxed.

### A Patchy-Population Model

Our model is in spirit similar to early population genetic models assuming a mating pool and dispersal into separate demes (Levene 1953; Dempster 1955) and to models developed in relation to the evolution of dispersal (Kuno

1981; Metz et al. 1983). We assume spatial structure and geometric growth. Since we are looking for basic criteria for persistence, rather than predicting long-term population dynamics, we have kept our model simple by ignoring density dependence. Models by Chesson (1981) and others (reviewed in Tuljapurkar 1989) account for density dependence. Our model describes a spatially structured population that occupies a finite number of patches. It also assumes nonoverlapping generations (but see "Discussion" section for a generalization).

Dispersal in this model operates according to the island model with individuals entering a common migrant pool. A fraction ( $h$ ) is removed (or subject to human-induced mortality; e.g., harvesting), while the rest will be distributed evenly into a set of patches ( $n$ ) within which they undergo reproduction. We consider human-induced mortality to be a fixed fraction. The growth rate at each patch is a random variable with some stationary probability-density function. This introduces environmental stochasticity to the model. After reproduction, offspring (e.g., larvae) disperse to the pool where they develop as adults. For simplicity, we assume perfect mixing and an even distribution among the patches (below we discuss the robustness of our approach when these assumptions are relaxed).

Let  $N_0$  be the initial population size before the annual harvesting and  $R_{i,j}$  be the growth rate of patch  $i$  at year  $j$ . Given the above assumptions, the population size in the next generation is given by

$$N_1 = \frac{1}{n}(1-h)N_0 \sum_{i=1}^n R_{i0} = (1-h)N_0 \bar{R}_0, \quad (1)$$

where  $\bar{R}_0$  is the arithmetic mean of growth rates among the  $n$  patches in year 0. Similarly, the population size one generation later will be

$$N_2 = (1-h)N_1 \bar{R}_1 = (1-h)^2 N_0 \bar{R}_0 \bar{R}_1. \quad (2)$$

One can then generalize an expression for the population size after  $t$  generations:

$$N_t = N_0 \prod_{j=0}^{t-1} (1-h) \bar{R}_j. \quad (3)$$

Let  $\bar{R}'_j \equiv (1-h)\bar{R}_j$  be the spatial-arithmetic mean of the growth rates times the fraction escaping harvesting. If we denote the geometric mean (GM) of  $\bar{R}'_j$  by  $G(\bar{R}') = (\prod_{j=0}^{t-1} \bar{R}'_j)^{1/t}$ , then equation [3] can be written as

$$N_t = N_0 G(\bar{R}')^t. \quad (4)$$

Then, the population will persist in the long term ( $N_t \geq N_0$ ) if

$$G(\bar{R}') \geq 1 \quad (5)$$

(Lewontin and Cohen 1969; Kuno 1981; Yoshimura and Jansen 1996). The above criterion is equivalent to the criterion for invasibility widely studied by Chesson (1990, 1994), Chesson and Ellner (1989), and Sasaki and Ellner (1995) in the context of the coexistence of competing species.

Kuno (1981) studied a similar model in the context of the evolution of dispersal. He concluded that by “spreading the risk” (i.e., by dispersing evenly to all patches), the population maximizes the geometric mean of growth rates. Jansen and Yoshimura (1998) analyzed a two-patch model in the context of optimum offspring allocation into two different habitats to maximize the GMF. Chesson (1981), however, studied the effect of within-patch variability and its role in maintaining spatial and temporal variability. Our goal is to build on this basic body of theory. We derive simple rules of thumb for the minimum number of patches required for population persistence as a function of harvesting and environmental stochasticity.

#### The Variance-Discount Approximation to Geometric Mean Fitness

We can approximate the GM in equation (5) by using Taylor expansions (i.e., by the so-called variance-discount approximation [VDA]; Gillespie 1974; Yoshimura and Jansen 1996). This will allow us to relate  $G(\bar{R}')$  to the number of patches and to the level of environmental fluctuations. The VDA has been used for the simplified case in which there is only one patch and the population is not harvested ( $n = 1$ ;  $h = 0$ ). In this case, equation (5) becomes  $G(\bar{R}') = G(R) \geq 1$ , and  $G(R)$  can be approximated as follows:

$$G(R) \approx \bar{R} - \frac{\sigma^2}{2\bar{R}}, \quad (6)$$

where  $\bar{R}$  and  $\sigma^2$  are the arithmetic mean and variance, respectively, of  $R$  (i.e., the mean and variance of growth rates within patches). A complete derivation of this approximation can be found in Yoshimura and Jansen (1996).

Now, we want to extend the VDA to our multiple-patch situation depicted by equation (5). If  $R$  is a random variable with mean  $\bar{R}$  and variance  $\sigma^2$ , then  $\bar{R}' = \sum_{i=1}^n (1-h)R_i/n$  is a new random variable with mean  $(1-h)\bar{R}$  and variance  $(1-h)^2[\sigma^2 + (n-1)\text{cov}]/n$ , where  $\text{cov} \equiv \text{cov}(R_i, R_k)$  is the spatial covariance between any pair of

growth rates (we assume for simplicity that the covariance function is homogeneous among all the possible pairs  $R_i, R_k$ ). If we substitute this mean and variance into equation (6), then the temporal geometric mean of the spatial-arithmetic mean of growth rates can be approximated by

$$G(\bar{R}') \approx (1-h) \left[ \bar{R} - \frac{\sigma^2 + (n-1)\text{cov}}{2n\bar{R}} \right]. \quad (7)$$

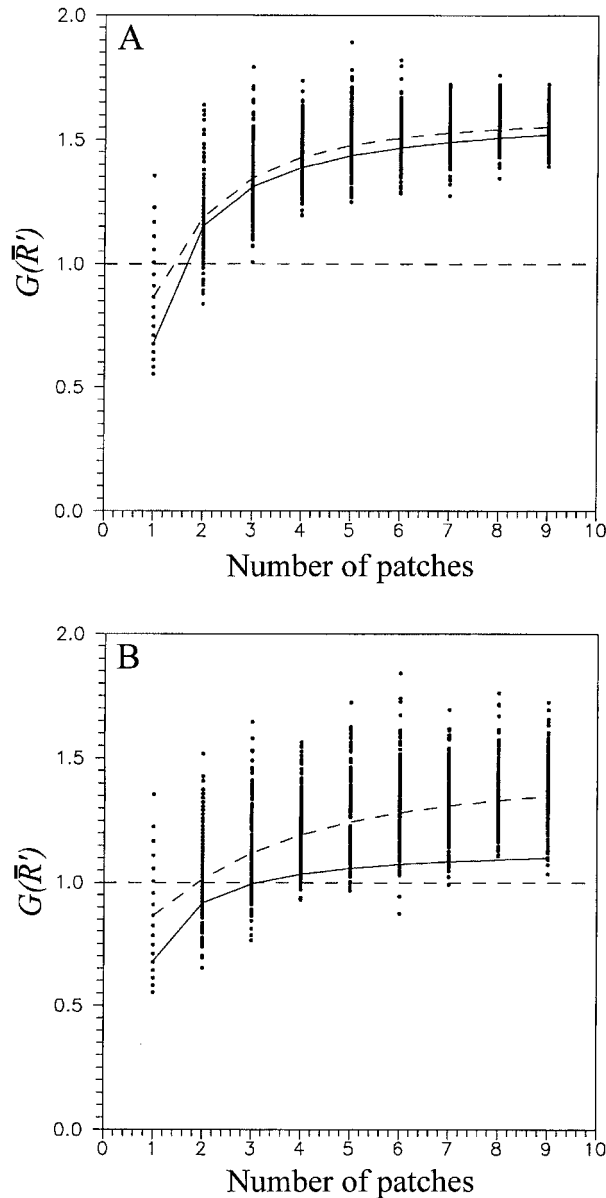
Our goal is to provide rules for the critical number of patches and maximum human-induced mortality consistent with sustainability. Hence, we want to ensure that our estimate is a conservative one. After studying the behavior of several approximations, we found that a reasonably accurate approximation to the GM is

$$G(\bar{R}') \approx (1-h) \left[ \bar{R} - \frac{\sigma^2 + (n-1)\text{cov}}{2n} \right]. \quad (8)$$

This approximation of the GM converges with equation (7) when  $\bar{R} = 1$ , when  $n$  is large, or for a combination of these conditions. For other situations, equation (7) sets a lower bound to equation (8), making it a conservative estimate. As can be observed from equation (8), increasing the covariance between patches (or increasing the variance in environmental fluctuations) decreases the geometric mean and so makes persistence more difficult. The fit of equation (8) to the real geometric mean value is illustrated in figures 1 and 2.

The key to our approximation lies in the concept of sampling error and the difference between the geometric mean and the arithmetic mean in variable environments. The error in estimating the spatial-arithmetic mean of growth rates diminishes with sample size (i.e., the number of patches). In other words, the variability between the  $\bar{R}'_i$ s decreases as  $n \rightarrow \infty$ . Let us assume that the expectation of  $R$  is  $E(R) = 2$ . We can imagine two different situations. In the first one,  $n$  is infinite. In this case, there would be no sampling error in estimating  $\bar{R}$  and so no year-to-year variability. A temporal series of  $\bar{R}$  would be 2, 2, 2. Here  $G(\bar{R}) = (2 \times 2 \times 2)^{1/3} = 2$ , which coincides with the temporal-arithmetic mean. Now, consider another situation involving a small value of  $n$ . Due to sampling error, the temporal series could be 3, 2, 1. In this case, the geometric mean is  $G(\bar{R}) = (3 \times 2 \times 1)^{1/3} = 1.817$ , which is smaller than the arithmetic mean. Thus, the lower the value of  $n$ , the higher the sampling error and the lower the temporal geometric mean of spatial-arithmetic means of growth rates.

In the following examples, we assume that each patch can have either a low or a high growth rate with the same



**Figure 1:** Value  $G(\bar{R})$  is plotted as a function of the number of patches.  $\bar{R} = R(1 - h)$ ,  $h$  being the fraction of the metapopulation harvested. Each point corresponds to one of 100 replicates of a simulation. Patches can have a high ( $R = 3$ ) or a low ( $R = 0.25$ ) growth rate with the same probability. At each generation, the effective arithmetic mean of growth rates  $\bar{R}$  is calculated, and the temporal geometric mean of such values is calculated for a time window of 50 generations. The discontinuous line plots the exact value, and the continuous line represents the approximation given by equation (8).  $G(\bar{R}) = 1$  delimits the condition for the long-term persistence of the population. Spatial correlation is  $\rho = 0$  (A) and  $\rho = 0.5$  (B);  $h = 0$ .

probability. We assume that there can be spatial correlation in environmental fluctuations, but there is no temporal correlation. We complement our analytical results with numerical simulations. In the latter, the arithmetic mean of  $R'$  is estimated every year, and the geometric mean of such values is calculated over a time span of 50 yr. One hundred replicates are plotted. The exact analytical values are calculated in the following way. For each number of patches, all the possible combinations of high and low growth rate values are considered. For each scenario ( $k$ ), the arithmetic mean of growth rates ( $\bar{R}'_k$ ) is calculated. Each scenario occurs with a probability ( $P_k$ ) given by the binomial distribution. The exact geometric mean is then  $G(\bar{R}') = \prod_{k=1}^n \bar{R}'_k^{P_k}$ . The dependence between  $G(\bar{R}')$  and the number of patches is shown in figures 1 and 2.

If there is no spatial correlation among patches, then we assign a low or high value independently for each patch. If  $\text{cov} > 0$ , we apply standard Markov chain theory to calculate the relationship between spatial correlation and the probability of high and low for the successive patches once we assign the value for the first one. This set of probabilities will be used to calculate both the exact analytical value and the simulation. The procedure is the same as used in the case of temporal correlation (see Roughgarden 1991), but now we look at the successive state transitions through space instead of through time. If  $P_{12}$  and  $P_{21}$  are the respective probabilities of low following high and of high following low, the respective stationary probabilities of high ( $\pi_1$ ) and low ( $\pi_2$ ) are easily derived (Cox and Miller 1965):

$$\pi_1 = \frac{P_{21}}{P_{12} + P_{21}}, \quad \pi_2 = \frac{P_{12}}{P_{12} + P_{21}}. \quad (9)$$

The serial correlation between consecutive states (i.e., the spatial correlation) is

$$\rho = 1 - (P_{12} + P_{21}). \quad (10)$$

By rearranging equation (9) and introducing equation (10), we have that

$$P_{21} = \pi_1(1 - \rho), \quad P_{12} = \pi_2(1 - \rho). \quad (11)$$

In our case, high and low are equally likely ( $\pi_1 = \pi_2 = 0.5$ ), so  $P_{12} = P_{21}$ . If we define  $P_{\text{change}}$  as the transition probability (i.e., the probability of changing from low to high or from high to low when moving to the next patch), we end up with the following expressions for assigning the appropriate status to the next patch:

$$P_{\text{change}} = \frac{1 - \rho}{2}, \quad P_{\text{same}} = 1 - P_{\text{change}} = \frac{1 + \rho}{2}. \quad (12)$$

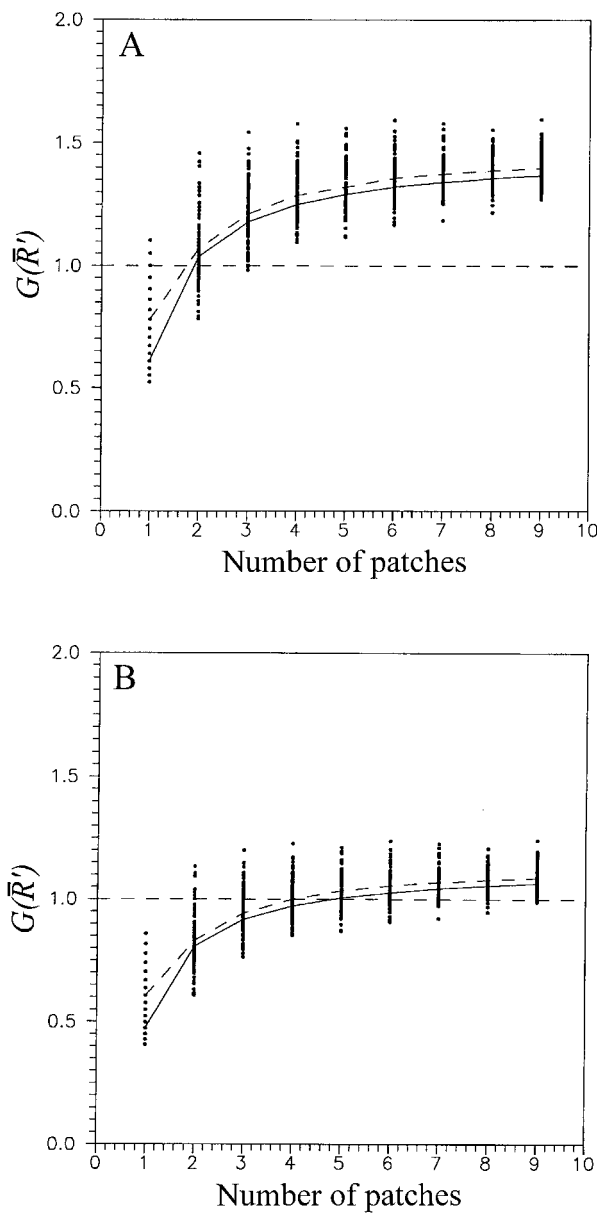


Figure 2: Similar to figure 1, but now  $\rho = 0$  and the fraction harvested is  $h = 0.1$  (A) and  $h = 0.3$  (B).

As seen here, if there is no spatial correlation, then  $P_{\text{change}} = P_{\text{same}} = 0.5$  (i.e., each patch's state is independent of those of the other patches).

In our simulations, the first patch is assigned randomly to high or low with the same probability. Then we use equation (12) to assign the subsequent patches. In a similar way, we use equation (12) to assign the probability of each possible scenario when calculating the analytical value for the geometric mean.

We plot in figure 1A and 1B the exact value of  $G(\bar{R}')$ , its approximation given by equation (8), and a set of numerical simulations as a function of the number of patches. As can be seen by comparing figure 1A and 1B, spatial correlation decreases the value of  $G(\bar{R}')$ . In other words, if environmental fluctuations are spatially correlated,  $G(\bar{R}')$  increases much slower with  $n$ . We would need more patches to attain a specific  $G(\bar{R}')$  value.

Figure 2A and 2B is equivalent to figure 1, but now we compare the effect of increasing harvesting. As when increasing spatial correlation, increasing harvesting reduces the value of  $G(\bar{R}')$  for a specific number of patches.

Finally, both figures 1 and 2 illustrate the dependence of  $G(\bar{R}')$  on  $n$  and show that the behavior of our approximation (eq. [8]) provides a conservative estimate of the exact geometric mean.

### Critical Harvesting and Critical Number of Patches

Two interesting questions can be answered by using equation (8). First, what is the maximum human-induced mortality rate ( $h_c$ ) compatible with the persistence of the population for a specific number of patches? Second, what is the minimum number of patches ( $n_c$ ) needed for any given human-induced mortality rate? These critical values can be obtained from equation (8) after setting  $G(\bar{R}') = 1$  (the population neither increases nor decreases). The critical harvesting rate is

$$h_c \approx 1 - \left( \frac{\bar{R} - \frac{\sigma^2 + (n-1)\text{cov}}{2n}}{\bar{R}} \right)^{-1}, \quad (13)$$

defined for  $n > \sigma^2 + \text{cov}/(2\bar{R} + \text{cov})$ .

Inspection of equation (13) suggests that it can have negative solutions. This happens when the number of patches is insufficient to maintain the population even in the absence of harvesting. A negative harvesting rate could be interpreted as the fraction of individuals that should be introduced every year into the pool to assure long-term persistence of the population. If we are dealing with a crop pest, we would have to kill a higher fraction than equation (13) to have a good chance of eradication. Similarly,  $h_c$  is the minimum fraction of individuals we should vaccinate to eradicate an infectious disease.

In a similar way, the critical number of patches ( $n_c$ ) necessary to sustain a population harvested at a rate  $h$  is provided by

$$n_c = \frac{(1-h)(\sigma^2 - \text{cov})}{(1-h)(2\bar{R} - \text{cov}) - 2}, \quad (14)$$

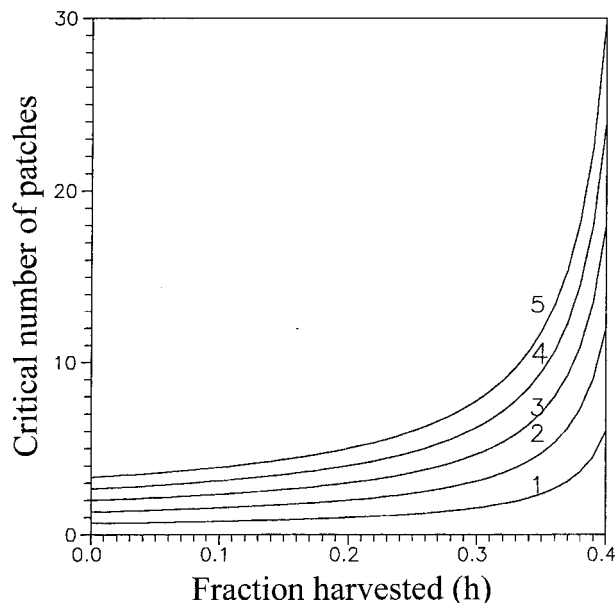
defined for  $h < 2(\bar{R} - 1)/(2\bar{R} - \text{cov})$ .

The critical number of patches for persistence ( $n_c$ ) is plotted in figure 3 as a function of the harvesting rate. The different curves correspond to a fixed arithmetic mean of growth rates but different variances. The curves are highly nonlinear, with a slow increase in  $n_c$  for low to moderate  $h$  values, followed by a fast increase for higher  $h$  values. Also, the critical number of patches increases with the variance in growth rates. The shape of the curves in figure 3 would be important in determining the economic benefit of harvesting the population if this benefit is defined as a trade-off between the gross benefit of exploitation and the cost of maintaining the patches (protect them as reserves).

### Robustness of the Model: Relaxing Some Assumptions

Two of the key assumptions in our model are that individuals are uniformly distributed among patches and that all individuals migrate into a common pool. This, in principle, could restrict the potential number of examples at which our approach could be applied, so it is worthwhile relaxing these assumptions. First, we will assume an uneven distribution among patches. Then, we will assume that a fraction of the recruits is retained locally.

Kuno (1981) considered the case of an uneven distribution in his study of the evolution of dispersal. Here, we will work through his reasoning. For purposes of clarity, let us assume that both  $h$  and  $\text{cov}$  are 0. In this case,



**Figure 3:** Critical number of patches to sustain a patchy population as a function of harvesting according to equation (14).  $\bar{R} = 1.75$ ;  $\sigma^2 = 1$ , 2, 3, 4, and 5.

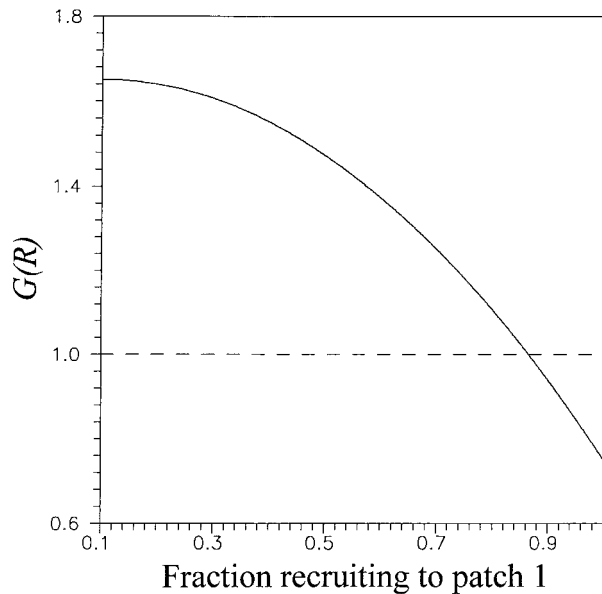
$\bar{R}'_j \equiv (1-h)\bar{R}_j = \bar{R}_j$ . Then, if  $\alpha_i$  is the fraction of individuals in the pool that migrate to patch  $i$ ,  $\bar{R} = \sum_{i=1}^n \alpha_i R_i$  is a random variable with mean  $\bar{R}$  (it coincides with the mean for an even distribution) and variance  $\sigma^2 \sum_{i=1}^n \alpha_i^2$  (instead of  $\sigma^2/n$  for the case of an even distribution). Our approximation to the geometric mean would be

$$G(\bar{R}) \approx \bar{R} - \frac{\sigma^2 \sum_{i=1}^n \alpha_i^2}{2}. \quad (15)$$

Since  $1/n \leq \sum_{i=1}^n \alpha_i^2 \leq 1$ , it is clear that the previous equation is  $\leq \bar{R} - \sigma^2/2n$  (see eq. [8]). So, by departing from the even distribution, the geometric mean of arithmetic means of growth rates is reduced. Other things being equal, we would need a larger number of patches to sustain the population. In other words, an uneven distribution diminishes the risk-spreading benefits of uniform dispersal.

Let us imagine that a fraction ( $\alpha_1$ ) of the individuals present in the pool recruit to patch 1, while the rest recruit evenly among the remaining  $n-1$  patches ( $\alpha_1 \geq \alpha^* = \alpha_2 = \dots = \alpha_n$ ). We can have, for example, one large patch and a set of small ones. Another possibility would be to have one patch located closer to the larval pool and the remaining patches being at a larger distance. Under such a scenario, one can compare the implications of many small versus a few large patches of habitat. Let us suppose that there are 10 patches, and let's allow  $\alpha_1$  to range from 0.1 (all patches are equal as assumed by our model) to 1 (there is only one effective patch). The value  $G(\bar{R})$  is plotted versus  $\alpha_1$  in figure 4. Interestingly, the decline in  $G(\bar{R})$  is small for values of  $\alpha_1$  close to an even situation, the curve becoming steeper for larger  $\alpha_1$  values. For example, moving from a situation with 10 patches of the same size ( $\alpha_1 = \alpha^* = 0.1$ ), to a situation with one big patch comprising 30% of the total area and nine small patches, each one comprising 7.8% of the total area, represents only a decrease in  $G(\bar{R})$  of 2.42%. Consequently, for small to moderate deviations from the even assumption, our approach could still be applied (remember that we deliberately made a conservative estimate). The other conclusion from figure 4 is that, other things being equal, having a large number of small patches (as opposed to a few number of big patches) increases the geometric mean fitness and so the chances of population persistence.

Our second assumption is that all the individuals from a patch migrate into the common pool. Metz et al. (1983) and Klinkhamer et al. (1983) have both studied the case in which only a fraction of the local populations disperses. For comparison purposes, we have developed a spatially explicit simulation of our model to explore the effect of the fraction migrating to a common pool ( $m$ ) on popu-



**Figure 4:** Robustness of our results when we depart from our assumption of an even recruitment among patches. Value  $G(R)$  is plotted as a function of  $\alpha_1$  (i.e., the fraction of individuals recruiting back to patch 1). The rest of the individuals recruit evenly among the remaining  $n - 1$  patches. Based on equation (15).  $n = 10$ ;  $R = 1.75$ ;  $\sigma^2 = 2$ .

lation growth. Note that our model is a good approach to predict criteria for persistence but not to predict population density since it assumes unlimited exponential growth. To plot population density, we have used a density-dependent version of our model. Figure 5 shows the population size after a given number of generations as a function of  $m$ . The interesting point here is the shape of figure 5. Population size is almost the same for values of  $m$  between 0.8 and 1, and it declines faster as  $m$  becomes smaller. For this particular example, moving from  $m = 1$  to  $m = 0.8$  implies a reduction in population size of only 1.1%. Even at  $m = 0.6$ , the reduction is only of about 11%. This means that our approach would work quite well for moderate departures from the assumption of total migration.

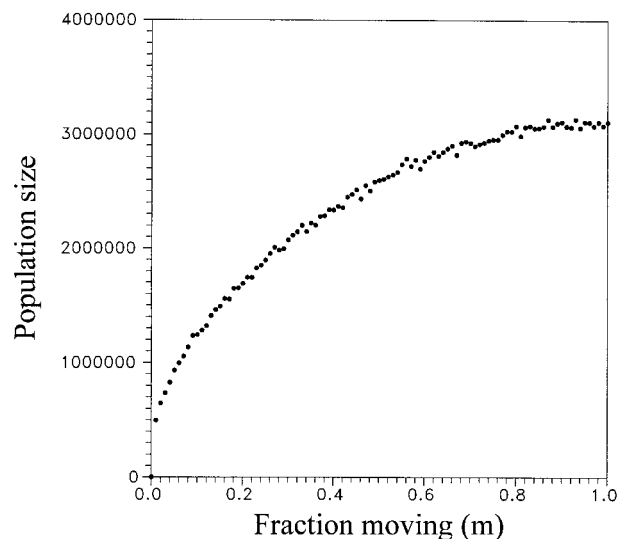
### Discussion

The model we have developed can be used to make predictions about the two case studies mentioned in the introduction, namely, the red sea urchin *Strongylocentrotus franciscanus* and some coral reef fishes. Both have a well-defined patchy distribution and larval dispersal, and both are harvested (Quinn et al. 1993; Mann et al. 1995). In several well-documented reef fish species (i.e., redbelt parrotfish *Sparisoma ribripinne*, striped parrotfish *Sparisoma*

*iserti*, ocean surgeonfish *Acanthurus bahianus*, and blue tang *Acanthurus coeruleus*) reviewed by Colin (1996), spawning areas persisted through time. In the case where spawning sites ceased to exist, overfishing by humans seems to be the most likely cause (Colin 1996).

One could estimate population growth rates at different years and at various of such spawning sites. By only calculating the mean, variance, and spatial covariances of this spatiotemporal data, one could predict the minimum number of patches required for persistence given the current levels of environmental stochasticity. Conversely, one could predict the maximum rate of harvesting for a particular combination of environmental fluctuations and number of patches. One prediction arising from the results shown here is that, other things being equal, one could harvest a larger fraction of individuals (or maintain the population with a smaller number of patches) in places with lower environmental variability. Also, persistence would be more likely if the redistribution of individuals into patches was more equidistant or if we had a larger number of small patches as opposed to a lower number of large patches.

In this article, we have derived simple rules for predicting persistence of a patchy population subject to human-induced mortality. These rules address frequently



**Figure 5:** Robustness of our result when we depart from our assumption of total migration into the pool. The figure plots population abundance after 1,000 iterations, according to a numerical simulation of a density-dependent, spatially explicit version of our model, as a function of the fraction of individuals migrating to the common pool ( $m$ ). Each point is the average of 1,000 replicates. The carrying capacity was assumed to be  $10^6$  at each patch. Abundance is quite constant (and so assuming global mixing is acceptable) for moderate departures from  $m = 1$ .  $n = 9$ ;  $\text{cov} = 0$ ;  $h = 0$ ; other parameters as in figure 1.

asked questions: What is the maximum harvesting rate a population can sustain? How many patches are necessary for the persistence of an exploited population? The model is very general and some assumptions can be relaxed to accommodate different case studies. Our conservative approximation is justified since the two most important deviations from our assumptions (namely, an uneven recruitment to patches and partial migration) decrease the geometric mean and thus increase the number of patches required for population persistence. However, as shown before, the decrease in the GM when departing moderately from our assumptions can be as small as 3%. This means that our model, despite its simplicity, is very robust when some of the key assumptions are relaxed and additional detail is introduced.

Our strategy has been to use a simple model to completely understand the relationships between environmental stochasticity, harvesting, and minimum number of patches for population persistence. In this way, we have been able to develop simple analytical expressions. As noted by Lande et al. (1997, p. 1342), “analytical models, although necessarily simplified in some respects, have the advantage of deriving general, robust conclusions.” However, this does not preclude additional levels of complexity if they are considered to be important in particular examples. For example, we have neglected larvae mortality during the dispersal phase. In some situations, a large fraction of larvae can fail to colonize any patch. This can be easily introduced into the model. Mortality can be either a constant or, more realistically, a function of the number of patches since one could imagine that the probability of successfully finding a patch decays as the number of patches decreases. If  $\beta_n$  is the mortality associated to a number  $n$  of patches, then the right-hand side of equation (1) should be multiplied by a term  $(1 - \beta_n)$ . We then can define  $\bar{R}_j \equiv (1 - \beta_n)(1 - h)R_j$  and use the same analytical expressions developed in this article.

In contrast to most harvesting and reserve design theory that focuses on density-dependence and deterministic models (Gerber et al., in press), our focus is on density-independent stochastic population dynamics where long-term population growth is mediated by dispersal of juveniles between patches in a patchy population. By deriving a relationship between persistence and the number of patches, our approximation also departs from traditional metapopulation models that assume an infinite number of patches.

We have assumed nonoverlapping generations. However, the framework described in this article can be easily extended to a situation with overlapping generations. If there is a stable age-structure, it can be proved that the fundamental net reproductive rate ( $R$ ), the basic reproductive rate ( $R_0$ ; a parameter easily estimated from a co-

hort life table), and the generation time ( $T$ ) are related by the following relationship (which is valid for semelparous populations):  $r = \ln R = \ln R_0/T$ , where  $r$  is called the intrinsic rate of natural increase (see Begon et al. 1990). If generations are discrete,  $T = 1$  and  $R = R_0$ . If  $R_0 \approx 1$ , and/or there is little variation in generation time, a good approximation to  $r$  is  $r \approx \ln R_0/T_c$ , where  $T_c$  is the cohort generation time. The value of  $T_c$  can again be obtained from a cohort life table (May 1976).

The theory presented here is particularly relevant to species with weak density dependence, spatial structure, and high dispersal and to species that are also subject to high abiotic environmental variability. While we have stressed the applicability of the model for harvesting a stock, the ideas also apply to the control of patchily distributed pests and diseases that experience environmental variability.

### Acknowledgments

This article originated at the Theoretical Ecological Economics Working Group supported by the National Center for Ecological Analysis and Synthesis (NCEAS), a center funded by the National Science Foundation (DEB-94-21535); the University of California, Santa Barbara; and the State of California. J.B. was a postdoctoral associate and H.P. and J.R. were sabbatical fellows at NCEAS. Funding during the last stages of production of this article was provided by a grant from the Spanish Ministry of Science and Technology (BOS2000-1366-CO2-02) to J.B. We thank P. Amarasekare, S. Andelman, P. Armsworth, R. Burton, L. Gerber, and E. Sala for useful discussion. V. Jansen and H. Metz brought to our attention previous theory on geometric mean fitness. P. Amarasekare read a previous draft and made valuable suggestions.

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Associate Editor: Lenore Fahrig