METAPOPULATION MODELS: THE RESCUE EFFECT, THE PROPAGULE RAIN, AND THE CORE-SATELLITE HYPOTHESIS

Metapopulation models are important tools for understanding distribution and abundance of organisms on large spatial scales (Levins 1969a; Hanski 1989). These models integrate local population dynamics with immigration and extinction events occurring between population sites (Levins 1969a, 1970; den Boer 1981; Hanski 1982, 1989). In this sense, they form a bridge between the traditionally separate domains of population ecology (local abundance) and biogeography (regional occurrence) (Andrewartha and Birch 1954; Hanski 1982).

Metapopulation models provide a useful framework for understanding both correlative (Gill 1978; Hanski and Ranta 1983; Harrison et al. 1988) and experimental (Bengtsson 1989) data on distribution and abundance of natural populations. Extensions to the optimal design of subdivided nature reserves are also promising (Quinn and Hastings 1987).

Levins (1969a, 1970) introduced an important class of metapopulation models of the following form:

$$dp/dt = \text{immigration rate} - \text{extinction rate}, \tag{1}$$

in which p is the fraction of occupied population sites in a homogeneous habitat. Thus, $0 \leq p \leq 1$. If $p = 1$, all population sites are occupied and if $p = 0$, regional extinction has occurred. The immigration rate is the number of successfully colonized empty sites/time and the extinction rate is the number of extinctions in occupied sites/time. This type of model is analogous to population models in which the rate of change of abundance is expressed as the difference between birth and death rates (Hutchinson 1978). In Levins's initial model:

$$dp/dt = ip(1 - p) - ep, \tag{2}$$

in which i and e are the probabilities of local immigration and extinction, respectively. At equilibrium:

$$\hat{p} = 1 - e/i. \tag{3}$$

Thus, if i exceeds e, there is a single, internal equilibrium for p. Levins (1970) also considered a stochastic version of equation (3) in which e is not a constant but a random variable. If $i > \bar{e} + \sigma_e^2$, the model predicts a unimodal distribution with a peak at $p = 1 - (\bar{e} + \sigma_e^2)/i$.

Hanski (1982) objected to Levins's model on the grounds that the probability of local extinction (e) was independent of regional occurrence (p). Hanski formu-
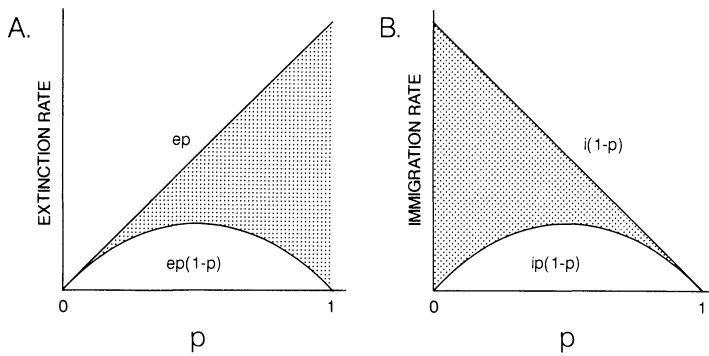
FIG. 1.—A, Extinction rates in Levins's (ep) and Hanski's [$ep(1 - p)$] models; p is the fraction of sites occupied. The difference between these two curves (*shaded region*) constitutes the rescue effect. B, Immigration rates in Levins's and Hanski's models [$ip(1 - p)$] and in eqq. (5) and (7) [$i(1 - p)$]. The difference between these two curves constitutes the propagule rain.

lated an alternative model:

$$dp/dt = ip(1 - p) - ep(1 - p).\qquad(4)$$

Hanski's model incorporates the "rescue effect," the idea that emigrants from surrounding population sites may reduce the probability of local extinction (Brown and Kodric-Brown 1977). Hanski suggested that the extinction rate [ep $(1 - p)$] is a quadratic function: when p is small, the extinction rate increases as more sites are occupied, but when p is large ($p > .5$), the extinction rate decreases as a result of the rescue effect. In Levins's model, the extinction rate (ep) always increases as more population sites are occupied. Thus, the rescue effect decreases the extinction rate by the quantity ep^2 and is most important at large values of p (fig. 1a).

In contrast to Levins's model (eq. [2]), the deterministic version of Hanski's model (eq. [4]) is unstable. If $i > e$, p goes to 1, and if $i < e$, p goes to 0. The stochastic version of equation (2) behaves similarly: if variation in rates of colonization and/or extinction is sufficiently large, the model predicts a bimodal distribution of species occurrence, with a species' being either widespread ($p \sim 1$) or sparse ($p \sim 0$) and occurring rarely at intermediate frequencies. Hanski's dynamic model thus predicts a bimodal distributional pattern, which he terms the *core-satellite hypothesis*. Other ecological models, such as Raunkiaer's (1934) habitat adaptation hypothesis and Williams's (1950, 1964) random sampling hypothesis also predict bimodal distributions (Gotelli and Simberloff 1987).

Hanski makes one additional assumption (which is not critical to the model): the probability of local extinction is a function of local population size (MacArthur and Wilson 1967; Leigh 1981). This assumption, combined with the rescue effect, leads to the prediction of a positive correlation between distribution (p) and average local population size (Bock and Ricklefs 1983). Because Levins's model

EXTINCTION RATE

(rescue effect)

		D	**I**
IMMIGRATION RATE	**D**	$dp/dt = ip(1-p) - ep(1-p)$ (Hanski 1982) equation(4)	$dp/dt = ip(1-p) - ep$ (Levins 1969a) equation(2)
	(propagule rain) **I**	$dp/dt = i(1-p) - ep(1-p)$ equation(7)	$dp/dt = i(1-p) - ep$ equation(5)

FIG. 2.—A dichotomy of metapopulation models. These models can be categorized according to whether immigration and extinction rates are dependent (D) or independent (I) of regional occurrence. If the immigration rate is independent of regional occurrence, the model incorporates a propagule rain. If the extinction rate is dependent on regional occurrence, the model incorporates a rescue effect. Equation numbers refer to the text.

does not incorporate the rescue effect, it does not predict a correlation between distribution and abundance.

In a nutshell, Hanski's model assumes a quadratic function for both immigration and extinction rates. It predicts a bimodal frequency distribution and a positive correlation between distribution and abundance. Levins's model assumes a quadratic function for the immigration rate and a linear function for the extinction rate. It predicts a unimodal distribution and no correlation between distribution and abundance (Gotelli and Simberloff 1987).

It is interesting that both Hanski and Levins implicitly assume a quadratic function for the immigration rate [$ip(1 - p)$]. When p is large, the immigration rate is low because there are very few unoccupied sites. But the immigration rate is also low when p is small, because there are very few population sites from which colonists can originate (fig. 1b).

In this analysis, I begin with a simpler assumption: the immigration rate is linear and does *not* depend on regional occurrence (MacArthur and Wilson 1967). Thus, four different metapopulation models are possible, depending on whether or not immigration and extinction rates are a function of regional occurrence (fig. 2). Hanski and Levins have modeled two of the possibilities, and here I present the two alternative models in which immigration is uncoupled from regional occurrence. These models lead to new quantitative predictions about p and reveal the importance of the rescue effect to patterns of regional occurrence. Finally, these models provide insight into the origins of bimodality in Hanski's model.

THE PROPAGULE RAIN

Assume that the immigration of individuals to new population sites does not depend on regional occurrence. Instead, the immigration rate depends only on the number of unoccupied sites (1 − p). Such a scenario amounts to a constant

"propagule rain" (cf. Harper 1977; Rabinowitz and Rapp 1980). At the community level, this assumption of external species immigration is an important component of MacArthur and Wilson's (1967) equilibrium model. A propagule rain may also arise from a long-lived seed bank or some comparable internal storage mechanism (Warner and Chesson 1985). The propagule rain increases the immigration rate by the amount $i(1 - p)^2$ and is most important when p is small (fig. 1b).

If the extinction rate is also independent of regional occurrence, the dynamics are described by

$$dp/dt = i(1 - p) - ep,\tag{5}$$

with an equilibrium point at

$$\hat{p} = i/(i + e).\tag{6}$$

An alternative model incorporates both the propagule rain and the rescue effect:

$$dp/dt = i(1 - p) - ep(1 - p),\tag{7}$$

with an equilibrium point at

$$\hat{p} = i/e.\tag{8}$$

Figure 3 shows the equilibrium values of p (bounded by 0 and 1) for equations (2), (5), and (7) and illustrates the importance of the rescue effect and the propagule rain on regional occurrence. For example, if i equals e, and both i and $e > 0$, Levins's model (eq. [2], no propagule rain and no rescue effect) predicts regional extinction, equation (5) (propagule rain, no rescue effect) predicts a 50% occupancy of available sites, and equation (7) (propagule rain and rescue effect) predicts 100% occupancy.

I have not presented an analysis of the stochastic versions of equations (5) and (7). Instead, I assume that, if the deterministic model yields a single, internal equilibrium point, the corresponding stochastic model yields a unimodal distribution of occupied sites for most parameter values (see also Levins 1969b; May 1974). Numerical simulations of the stochastic versions of equations (5) and (7) suggest that this is usually true. The only exception is the stochastic version of equation (5), which shows evidence of bimodality when the variances of i and e are large. However, the bimodality is weak compared to that predicted by Hanski's model (eq. [4]) for the same parameter values.

Quantifying the Rescue Effect and the Propagule Rain

Unlike Hanski's model (eq. [4]), equations (2), (5), and (7) predict a single equilibrium point for all possible values of i and e. Therefore, by comparing these equations, it is possible to quantify the change in equilibrium due to the rescue effect and the propagule rain. For example, equation (7) includes the rescue effect, but equation (5) does not. So the increase in p is given by the difference between their equilibrium values (eq. [8] − eq. [6]):

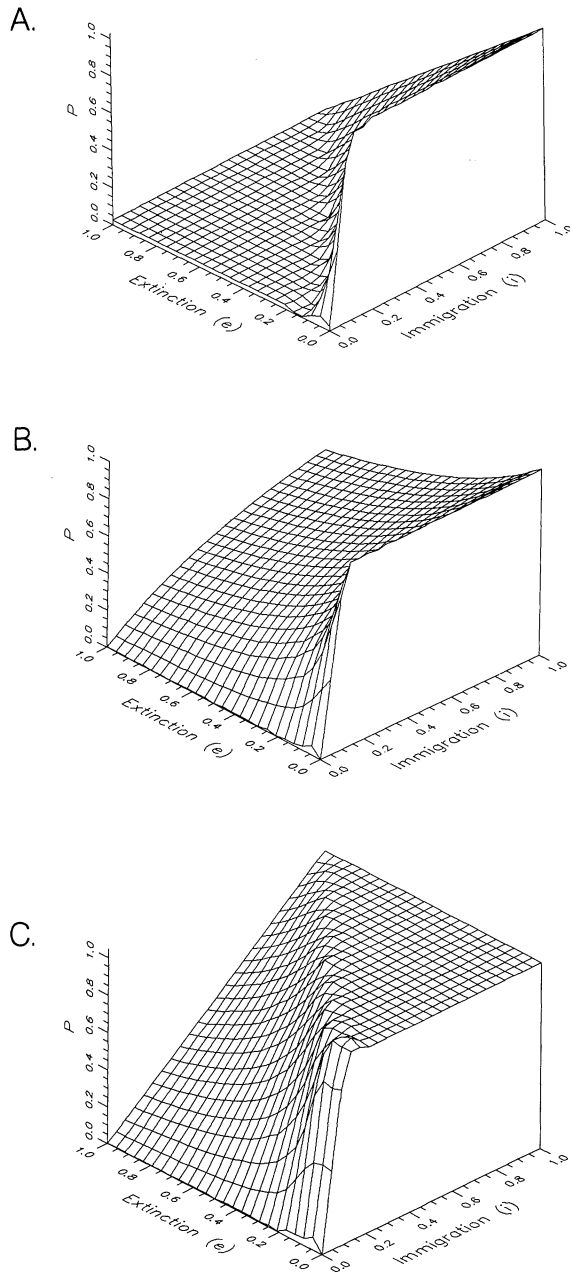$$\Delta p = i^2/[e(i + e)].\tag{9}$$

FIG. 3.—Values of p, the fraction of sites occupied for three metapopulation models at equilibrium; i and e are the probabilities of local immigration and extinction, respectively. A, Equilibrium for eq. (2) (Levins 1969a). This model includes neither the rescue effect nor the propagule rain. B, Equilibrium for eq. (5). This model incorporates the propagule rain. C, Equilibrium for eq. (7). This model incorporates both the rescue effect and the propagule rain.
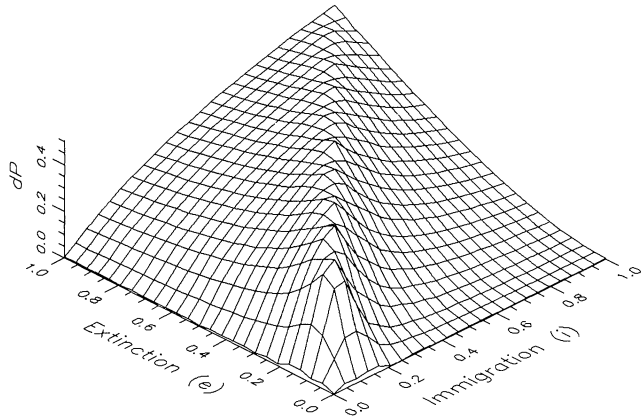
A.
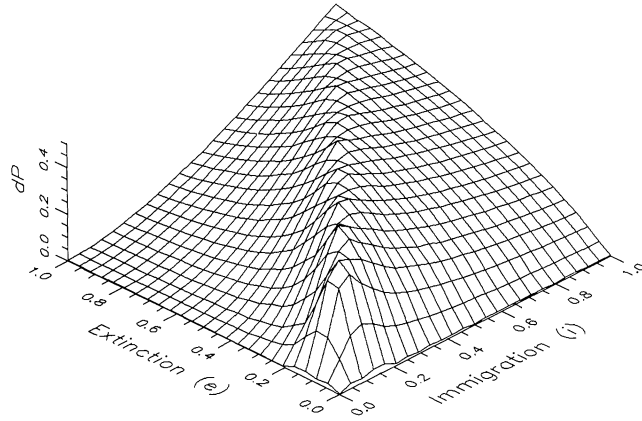
B.

Fig. 4.—*A*, Increases in *p* due to the rescue effect. In both graphs, *i* and *e* are the probabilities of local immigration and extinction, respectively. The increase in *p* is shown as the difference between eqq. (8) and (6). *B*, Increases in *p* due to the propagule rain. The increase in *p* is shown as the difference between eqq. (6) and (3).

Similarly, equations (2) and (5) differ by the presence of the propagule rain. The increase in *p* due to the propagule rain is given by (eq. [6] − eq. [3]):

$$\Delta p = e^2/[i(i + e)]. \tag{10}$$

Figure 4 plots both response surfaces, for values of *p* bounded by 0 and 1. The two surfaces are mirror images of one another with a maximum ridge where *i* = *e*. The rescue effect and the propagule rain contribute equally to *p*. Their effects are greatest when immigration and extinction probabilities are approximately equal. All three models show the most rapid change in *p* in this region of the parameter space.

Equations (5) and (7) extend the domain of the metapopulation dynamics models and illustrate their relationship to island biogeography models. Equation (5), in particular, describes the frequency of occurrence of a species when neither immigration nor extinction probabilities are affected by regional occurrence. At the community level, these assumptions form the basis for MacArthur and Wilson's (1967) equilibrium model of island biogeography.

The equilibrium for equation (5) has been derived in several island models (e.g., Simberloff 1983). For example, Gilpin and Diamond (1981) followed the approach taken here and determined the equilibrium when immigration and extinction rates are equal. Alternatively, Simberloff (1969) arrived at the same result with a Markov model of species occurrence based on constant probabilities of colonization and extinction (see also Bossert 1968 and Holland 1968 cited in Simberloff 1969). Because the equilibrium is not affected by local population processes, equation (5) may be taken as a simple "null model" for measuring metapopulation effects on regional occurrence.

Models that incorporate a propagule rain answer an important criticism of metapopulation models. Brown (1984) objected to Hanski's model because it implies frequent regional extinction ($p \sim 0$) and therefore requires a source of external colonization for long-term persistence of a species. A similar criticism applies to Levins's model if the peak of the frequency histogram is close to zero. Equations (5) and (7) answer these criticisms by assuming that colonists originate outside the system.

Equations (5) and (7) also generate novel predictions that can be compared to empirical data. For example, equation (7) (propagule rain, rescue effect) predicts a single internal equilibrium, as does Levins's original model. Because it incorporates the rescue effect, equation (7) also predicts a positive correlation between distribution and abundance.

Gotelli and Simberloff (1987) found both these patterns in a large data set on the distribution of tallgrass prairie plants and pointed out that these patterns contradicted some of the predictions of both Hanski's and Levins's models. However, equation (7) probably does not account for the prairie plant distributions either, because the assumption of site homogeneity was violated: the unimodal distribution resulted when frequency of occurrence data from seven soil series were pooled. When the data for each soil series were plotted separately, the bimodality predicted by Hanski's model was apparent.

Herbivorous insect species feeding on bracken also show a unimodal distribution of species occurrence and a positive correlation between distribution and abundance (Gaston and Lawton 1989). Gaston and Lawton noted that the frequency of occurrence of most bracken insects was stable through time. That is, most species were either consistently widespread or consistently sparse in their frequency of occurrence. In contrast, Hanski's model predicts major shifts in the occurrence of a single species through time (core-satellite switching; Gaston and Lawton 1989).

Unfortunately, the data presented by Gaston and Lawton (1989, fig. 6) are a weak test of core-satellite switching. Gaston and Lawton plotted abundance of each species (number of individuals per frond) through time, whereas core-satellite switching should be tested directly with a histogram for each species of the frequency of occurrence (fraction of population sites occupied) at different times. It would be very interesting to construct such histograms for the insects of bracken. If a unimodal curve arises, the predictions of equation (7) would be realized. However, any empirical test of metapopulation models will be problematic at best. Metapopulations are replicated at local, but not regional, spatial scales, and the relevant time scale for metapopulation dynamics may be on the order of decades (Harrison et al. 1988).

Finally, models that incorporate a propagule rain provide insight into the origin of bimodality in Hanski's model. Bimodality is not simply a result of incorporating the rescue effect into a model of regional occurrence. For example, equation (7) incorporates the rescue effect, but does not yield a bimodal distribution. Rather, the bimodality in Hanski's model arises because both the immigration rate *and* the extinction rate depend on regional occurrence. If either the immigration rate is uncoupled from regional occurrence (by incorporating a propagule rain) or the extinction rate is uncoupled (by eliminating the rescue effect), a unimodal distribution results.

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NICHOLAS J. GOTELLI

DEPARTMENT OF ZOOLOGY
   UNIVERSITY OF OKLAHOMA
   NORMAN, OKLAHOMA 73019