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 extinc-
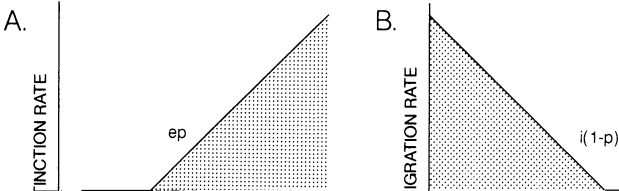
tion events occurring between population sites (Levins 1969a, 1970; den Boer 1981; Hanski 1982, 1989). In this sense, they form a bridge between the tradition-ally separate domains of population ecology (local abundance) and biogeography

(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:

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

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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 ac-

cording 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

model incorporates a rescue effect. Equation numbers refer to the text.

"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

$$\mathrm{d}p/\mathrm{d}t = i(1 - p) - ep, \tag{5}$$

with an equilibrium point at

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

effect:

$$\mathrm{d}p/\mathrm{d}t = i(1 - p) - ep(1 - p), \tag{7}$$

with an equilibrium point at

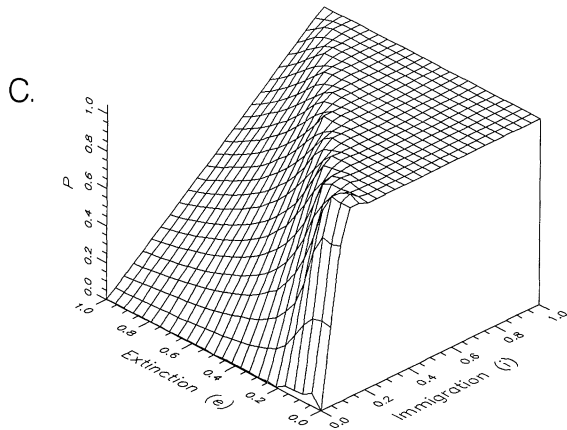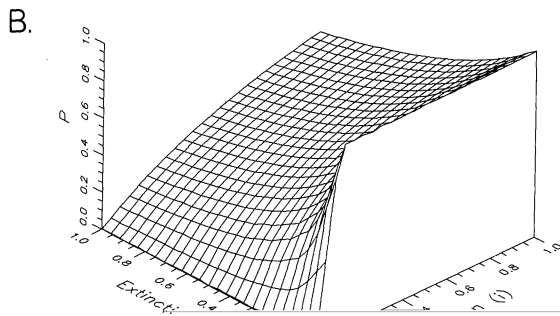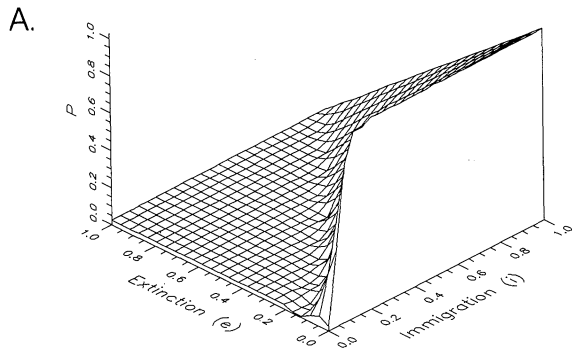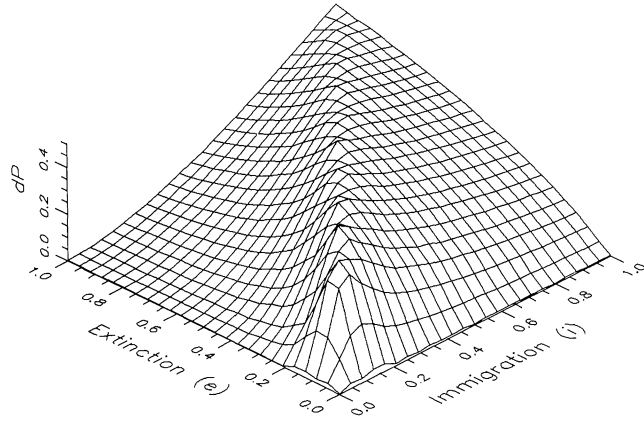$$\hat{p} = i/e. \tag{8}$$

A.

B.

C.

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.
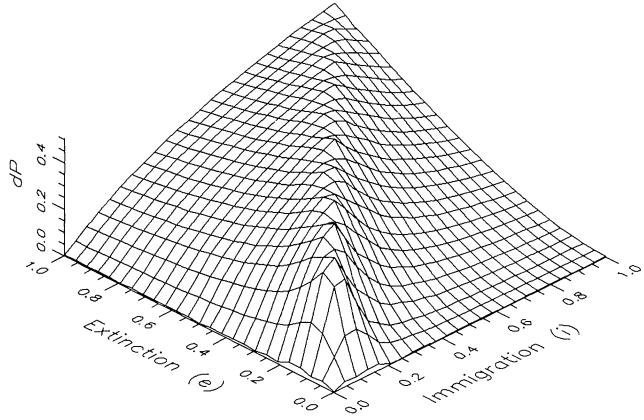
A.

B.

FIG. 4.—A—Increases in *p* due to the rescue effect. In both graphs, *i* and *e* are the probabili

DISCUSSION

Equations (5) and (7) extend the domain of the metapopulation dynamics models and illustrate their relationship to island biogeography models. Equation (5),

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

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

realized. However, any empirical test of metapopulation models will be problem-

species: relation to incidence functions and species colonization curves. Proceedings of the
National Academy of Sciences of the USA 78:392–396.

Gotelli, N. J., and D. Simberloff. 1987. The distribution and abundance of tallgrass prairie plants: a
test of the core-satellite hypothesis. American Naturalist 130:18–35.

38:210–221.
———. 1983. Coexistence of competitors in a patchy environment. Ecology 64:493–500.