A general model of metapopulation dynamics

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Metapopulation models describe the colonization and extinction of populations in a landscape of connected patches. Levins modeled the fraction of population sites occupied as a balance between the rate of successful immigration into empty sites and the rate of extinction in occupied sites. Several variants of Levins' model have been proposed that assume the probability of local colonization or extinction is either dependent or independent of regional occurrence. We show that the models of Levins, Hanski, and Gotelli are extreme cases of a single metapopulation model, which predicts the equilibrium fraction of sites occupied as a function of 4 parameters, 2 for colonization and 2 for extinction. We tested this model using single-species and multi-species data on patch occupancy.

For the single-species test, we analyzed the distribution of fishes at 10 sites on the Cimarron River, Oklahoma, U.S.A. Significant metapopulation effects (correlations between the fraction of sites occupied and the probability of local colonization or extinction) were not detected in the distributions of carp, the Red River shiner, and the Arkansas River shiner. Instead, the best-fitting model was one of independent colonizations and extinctions among sites (island-mainland model). This model accurately predicted the fraction of sites occupied by carp and the Red River shiner. However, probabilities of colonization and extinction varied significantly among sites (carp, Red River shiner) and years (Arkansas River shiner).

For the multi-species test, we used Simberloff's data on annual colonization of 9 mangrove islands by 254 insect species. These data revealed a significant metapopulation effect and were best fit by a linear extinction function and a quadratic colonization function. However, a Monte Carlo simulation using these functions failed to predict the observed species-occurrence distribution; there were too few insect species that occurred on no islands and too many species that occurred on most islands (bimodality). The explanation may be that species differed in their probabilities of colonization and extinction.

Neither data set provided a fully satisfactory test of the metapopulation model. However, both analyses revealed the importance of spatial and temporal variation of colonization and extinction probabilities in a patchy landscape.

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The persistence of local populations may be affected by immigration and extinction in connected population sites. The concept of a metapopulation, "a population of populations" (Levins 1970), is of current interest from both theoretical (Hanski and Gilpin 1991, Hastings 1991, Gyllenberg and Hanski 1992) and empirical (Sjögren 1991, Verboom et al. 1991) perspectives.

Levins (1969, 1970) introduced an important set of metapopulation models of the general form:

$$\frac{dp}{dt} = I - E \tag{1}$$

p is the fraction of homogenous patches occupied by a single species ($0 \le p \le 1$). The immigration and extinction rates, I and E, are regional, and are measured across the entire set of patches. We use this terminology for consistency with the MacArthur and Wilson (1967)

model. Levins (1970) and Hanski (1982) have analyzed stochastic versions of metapopulation models, and Levins' (1969) initial model has been extended to two-species interactions (Horn and MacArthur 1972, Slatkin 1974, Hanski 1983, Sabelis et al. 1991). We have restricted this analysis to deterministic, single-species forms of eq. (1).

The regional immigration and extinction rates in eq. (1) can be represented as follows:

$$I = g(p)(1 - p) \tag{2}$$

$$E = h(p)p \tag{3}$$

Here $g(p)$ and $h(p)$ are functions that describe the probability per unit time of local colonization and local extinction, respectively, as a function of p. This interpretation is not strictly correct, because probabilities of extinction and immigration imply a discrete time interval, whereas the model is formulated in continuous time. A small correction term could be added to the model (Ray et al. 1991), but we have retained the simple model for heuristic purposes. Regardless of the particular form of $g(p)$ and $h(p)$, the immigration rate I falls to zero when all sites are occupied ($p = 1$) and the extinction rate E falls to zero when all sites are empty ($p = 0$). The probability of local colonization and local extinction will depend on a variety of factors, but a true metapopulation model envisions that the probabilities will be influenced by p, the fraction of sites occupied. If we substitute (2) and (3) into (1), we then obtain a general metapopulation model

$$\frac{dp}{dt} = g(p)(1 - p) - h(p)p = f(p) \tag{4}$$

The simplest functions that have been proposed for the probability of local colonization and extinction are a constant (i or e) and a probability function that is directly proportional to the number of occupied (or unoccupied) sites (ip or $e(1 - p)$). A constant implies that local colonization or extinction probabilities are independent of regional occurrence, whereas a proportional probability implies that these processes are affected by the metapopulation. Recently, Hanski (1991) and Hanski and Gyllenberg (unpubl.) have introduced nonlinear functions for $g(p)$ and $h(p)$ to account for variation in area or patch quality.

Levins (1969) assumed that the probability of colonization (ip) was a metapopulation process, whereas the probability of local extinction (e) was independent of regional occurrence. (The probability of colonization was incorrectly identified as i in Gotelli 1991.) The resulting model is:

$$\frac{dp}{dt} = ip(1 - p) - ep \tag{5}$$

Hanski (1982) modified Levins' equation to incorporate a rescue effect (Brown and Kodric-Brown 1977), so that the extinction probability was also a metapopulation process:

$$\frac{dp}{dt} = ip(1 - p) - ep(1 - p) \tag{6}$$

Our use of the term "rescue effect" differs from the original definition of Brown and Kodric-Brown (1977). Those authors used the term to mean a reduction in the species extinction rate caused by a high immigration rate into an occupied site. In the context of metapopulation models, the rescue effect is the reduction in the probability of local extinction ($h(p)$) caused by an increase in p. We assume that with an increase in p, more propagules are available to prevent local extinction.

If immigration occurs from outside the dynamic system (a "propagule rain"; Gotelli 1991) and the extinction probability is also independent of the metapopulation, a familiar mainland-island model results:

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

This model is the single-species analog of the MacArthur-Wilson (1967) equilibrium model of island species richness.

Finally, if the system is characterized by a rescue effect and a propagule rain, then

$$\frac{dp}{dt} = i(1 - p) - ep(1 - p) \tag{8}$$

Both the propagule rain and the rescue effect enhance metapopulation persistence. For a given set of parameters, this model yields the largest equilibrium value for $\hat{p}$. Thus, 4 metapopulation models are possible, depending on whether the immigration and extinction probabilities are dependent or independent of regional occurrence (Gotelli 1991).

However, these 4 models represent unrealistic endpoints along a continuum of metapopulation models (Hanski and Gyllenberg, unpubl.). For example, eq. (8) implies that only external colonization of empty sites occurs, but that dispersal among occupied sites prevents local extinctions. These processes are contradictory, and it seems unlikely that a real metapopulation will be described by eq. (8). Eq. (5) implies that the system is entirely closed, because colonists can originate only from occupied sites within the metapopulation. Although this assumption is realistic for isolated archipelagoes, many systems are probably characterized by at least some external colonization (Brown 1984). Similarly, eq. (6) implies that the rescue effect is so strong that the probability of local extinction approaches zero
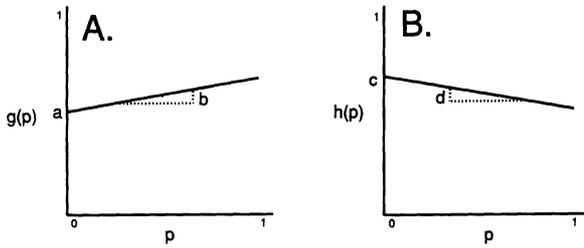
Fig. 1. A) The relationship between $g(p)$, the probability of local colonization and p, the fraction of sites occupied. In this linear model, a is the probability of colonization when $p = 0$, and b is the slope of the line and a measure of the strength of the metapopulation effect on colonization. B) The relationship between $h(p)$, the probability of local extinction, and p. c is the probability of extinction of an isolated patch, and d is the absolute value of the slope and a measure of the strength of the rescue effect in reducing local extinction.

as all the metapopulation sites are filled. It is more realistic to envision that each site has an intrinsic probability of extinction that cannot be reduced further by a rescue effect, even in a saturated landscape (Harrison 1991).

The purpose of this paper is to construct a general metapopulation model that incorporates more realistic functions for the probability of local colonization and extinction. The models of Levins (1969), Hanski (1982) and Gotelli (1991) represent specific cases of this general model. We describe the conditions that insure regional persistence in this model ($p > 0$) and discuss, with empirical examples, two approaches to testing metapopulation models.

A general metapopulation model

Assume that the probability of local colonization is a simple linear function of p, the fraction of sites occupied:

$$g(p) = a + bp \qquad (9)$$

Thus, the chance that an unoccupied site will be successfully colonized in the next time period depends on two parameters, a and b (Fig. 1A). a represents the contribution of external propagules to colonization, because a is the probability of local colonization when the metapopulation is regionally extinct ($p = 0$). b is an indicator of the strength of metapopulation influences on colonization; b measures the increase in the probability of colonization caused by adding another occupied site. b is positive to reflect the fact that occupied sites serve as additional colonization sources in the metapopulation.

In a similar fashion, assume that the probability of local extinction is also a linear function:

$$h(p) = c - dp \qquad (10)$$

Again, 2 parameters describe the extinction process. c measures the intrinsic propensity for extinction of a single occupied site (Fig. 1B). d measures the reduction in the probability of local extinction caused by adding another occupied site (the "rescue effect"). Hanski (1985) presented a similar metapopulation model with a 2-parameter extinction term.

Substituting eqs (9) and (10) into eq. (4) yields:

$$\frac{dp}{dt} = (a + bp)(1 - p) - (c - dp)(p) = f(p) \qquad (11)$$

This general model of metapopulation dynamics describes the change in the occupied fraction of sites as a function of 4 parameters, 2 for immigration (a and b) and 2 for extinction (c and d). If $a = 0$ and $d = 0$, eq. (11) reduceds to Levins' (1969) model (eq. (5)). If $a = 0$ and $c = d$, eq. (11) reduces to Hanski's (1982) model (eq. (6)).

Persistence

Under what conditions will a metapopulation, obeying the dynamics of eq. (11), persist? We can answer this question by constraining the parameters of eq. (11) as follows:

$$a, b, c, d \geq 0$$

$$c \geq d$$

These constraints are biological, rather than mathematical. If $a \geq 0$, then the probability of colonization is non-negative when no patches are occupied ($p = 0$). Similarly, if c and d are both non-negative and $c \geq d$, the probability of extinction is non-negative when all patches are occupied ($p = 1$). The most important assumptions are that $b \geq 0$ and $d \geq 0$. A non-negative value for b implies that an increase in patch occupancy has a positive (or zero) effect on the immigration probability. A non-negative value for d implies that an increase in patch occupancy has a negative (or zero) effect on the extinction probability (i.e. a "rescue effect"). These two mechanisms are central to most metapopulation models (Hanski 1991).

At $p = 0$, $f(0) \geq 0$ because p cannot become negative. Substituting $p = 0$ into eq. (11) implies that:

$$f(0) = a \leq 0$$

Similarly, at $p = 1$, $f(1) \leq 0$ because p cannot increase above 1. Substituting $p = 1$ into eq. (11) implies that:

$$f(1) = d - c \geq 0$$

Four possible cases must be analyzed for the existence of equilibria.

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Case 1. $a > 0$, $d - c < 0$. This is the most general case because it encompasses the widest range of parameters. Because f is a quadratic function, it has at most 2 roots. Since $f(0) > 0$ and $f(1) < 0$, f has exactly one root $\hat{p}$ between zero and 1, and it is stable.

The roots of eq. (11) are:

$$p = \frac{-(b - a - c) \pm \sqrt{(b - a - c)^2 - 4a(d - b)}}{2(d - b)}.$$

If $d > b$, $\hat{p}$ equals the smaller root and if $d < b$, $\hat{p}$ equals the larger root. If $d = b$, the island-mainland model results, with a unique stable root at:

$$\hat{p} = \frac{a}{a + c}$$

Case 2. $a > 0$, $d - c = 0$. In this case, $f'(1) = c - b - a$, which determines whether the function achieves a value of zero between $p = 0$ and $p = 1$. If $c - b - a > 0$ then f has a unique, stable root at:

$$\hat{p} = \frac{a}{c - b}$$

If $c - b - a \leq 0$ then $p \to 1$. If $b = 0$, the model with a propagule rain and rescue effect results (Gotelli 1991).

Case 3. $a = 0$, $d - c < 0$. In this case, $f(1) < 0$, so the solution depends on $f'(0) = b - c$. If $b - c > 0$ there is a single, stable root in (0,1) at:

$$\hat{p} = \frac{b - c}{b - d}$$

If $b - c \leq 0$, then $p \to 0$ (regional extinction). Levins' (1969) model corresponds to the case where $d = 0$ and yields the same equilibrium solutions.

Case 4. $a = 0$, $d - c = 0$. This case corresponds to Hanski's (1982) model. If $d > b$ then $p \to 0$ (regional extinction). If $d < b$ then $p \to 1$, and if $d = b$, p has an arbitrary, neutral equilibrium (i.e., no dynamics).

To summarize, eq. (11) is a general model that encompasses the specific cases described by Levins (1969), Hanski (1982), and Gotelli (1991). For a metapopulation model that follows the dynamics of eq. (11), if there is at least some external colonization ($a > 0$), then p will always achieve a stable equilibrium > 0. If there is no external colonization, an equilibrium may be achieved if the internal colonization (b) is large enough to outweigh the extinction parameters (c, d). This qualitative analysis is valid for any function f, such that $f(0) \geq 0$, $f(1) \leq 0$, and f is unimodal.

Testing the model

To test metapopulation models such as eq. (11), we require empirical data for $g(p)$ and $h(p)$. That is, we need to quantify the probability of local colonization and local extinction as a function of the fraction of sites occupied. Ideally, these data should be gathered for a single species, observed at a set of population sites across time. The analysis assumes that any variation observed in $g(p)$ and $h(p)$ is stochastic. In other words, $g(p)$ and $h(p)$ are not consistently different among times or among sites. Once $g(p)$ and $h(p)$ have been estimated, eq. (11) can be used to predict the equilibrium fraction of sites occupied.

A second approach to testing single-species metapopulation models is to determine $g(p)$ and $h(p)$ for a set of "similar" species that inhabit an archipelago (Hanski 1982). This analysis assumes that all species share the same functions $g(p)$ and $h(p)$. For the purposes of examining qualitative predictions of metapopulation models, such as bimodality vs unimodality, the species do not have to be identical in their colonization and extinction probabilities (Gaston and Lawton 1989). However, if the model is going to be used to make quantitative predictions about the equilibrium value of p, the parameters of the model (a, b, c, and d) should be identical for all species. A final assumption of the multi-species test is that $g(p)$ and $h(p)$ are not influenced by other species. In other words, the probability of colonization or extinction of a species in a site is independent of local species composition.

The single-species approach is the most straight-forward way to test metapopulation models. Unfortunately, long-term data sets on the persistence of a species across a set of similar population sites are scarce. The advantage of the multi-species approach is that, provided its assumptions are met, each species may serve as a replicate, making it possible to estimate $g(p)$ and $h(p)$ fairly easily. The disadvantage of the multi-species approach is the restrictive (and often unrealistic) set of assumptions that must be met.

However, both approaches allow important assumptions of the metapopulation model to be tested empirically. To test the assumption of site homogeneity, the sites can be ordinated on the basis of area, suitability, or location within an environmental gradient. Averaging across time (single-species approach) or species (multi-species approach) yields site-specific probabilities of colonization and extinction. These probabilities should be uncorrelated with the site rankings, if the sites do not differ consistently in the probability of colonization or extinction.

Table 1. Correlations between the yearly probability of colonization (Pr_c) and extinction (Pr_e), and the fraction of sites occupied (p), year of the census (time), and position of the site in an ecological gradient (location) for 3 fish species in the Cimarron River, Oklahoma, 1976–1986. Each entry is the correlation coefficient (Pearson's r); the value in parentheses is the probability the correlation does not differ from 0.0 (one-tailed).

Species	Independent variable	Pr_c	Pr_e
carp	p	−0.516 (0.152)	−0.387 (0.304)
	time	−0.644 (0.061)	0.145 (0.710)
	location	0.745 (0.013)	−0.733 (0.038)
Arkansas River shiner	p	−0.204 (0.572)	0.214 (0.611)
	time	−0.023 (0.950)	0.715 (0.020)
	location	0.169 (0.664)	−0.646 (0.083)
Red River shiner	p	−0.058 (0.874)	0.437 (0.206)
	time	0.247 (0.491)	0.174 (0.631)
	location	0.549 (0.159)	−0.734 (0.024)

For the multi-species approach, it is possible to test whether species differ in their probabilities of colonization and extinction. If there is a positive correlation (among species) between the fraction of sites occupied at two different times, then some species may be consistently widespread and others consistently sparse. Such a result suggests that probabilities of colonization and extinction are not similar among species. Alternatively, if there is no correlation between the fraction of sites occupied at different times, then species are not consistently sparse or widespread in occurrence (core-satellite switching; Gaston and Lawton 1989). However, multi-species tests of core-satellite switching may be problematic, for reasons discussed below. Finally, for the single-species model, summing across sites yields probabilities of colonization and extinction at different time periods. If the metapopulation has achieved a stationary equilibrium distribution, these probabilities should not vary systematically through time.

Single-species test: fishes of the Cimarron River

A long-term study of fishes of the Cimarron River, Oklahoma, U.S.A. (Pigg 1988) was used to test our metapopulation model. From 1976 to 1986, 10 stations on the Cimarron River were sampled with seines and gill nets two to three times yearly. This sampling schedule insured that missing species were not the result of seasonal migrations or transient absences. The 10 stations span nearly the entire length of the 1117 km river, along an ecological gradient from low rainfall, high evaporation rate and little runoff near the headwaters to relatively high rainfall, low evaporation and stable stream flow at the confluence with the Arkansas River. Sampling over this 10-year period yielded a total of 50 species and 347 902 individuals. From this collection, we chose 3 species for analysis: carp (*Cyprinus carpio*), the Arkansas River shiner (*Notropis girardi*), and the Red River shiner (*Notropis bairdi*). These three species were selected because they frequently colonized and disappeared from individual sampling stations on a yearly time scale. As a consequence, there was substantial variation in p, the fraction of sites occupied. Such variation allows us to estimate $g(p)$ and $h(p)$. Species with static distributions may have achieved a stable equilibrium, but do not provide much information for testing metapopulation models.

For each species, we calculated the yearly probabilities of colonization and extinction, respectively, and correlated these probabilities with the fraction of sites occupied in a linear regression. Only 5 to 6 stations were sampled from 1976 to 1980. These small sample sizes contributed variation to the data, but results did not appear appreciably different when the early samples were deleted from the analyses. To examine temporal trends, we also correlated these probabilities with time. Finally, we calculated, across time, probabilities of colonization and extinction for each station and correlated these with position in the ecological gradient (1 = river headwater; 10 = river mouth). Note that it is not possible to examine interactions between time and space because the probability of colonization or extinction for each time period is calculated across sites, and the probability for each site is calculated across time periods.

Table 1 summarizes the results of these correlations. For all 3 species, there was never a significant correla-

Table 2. Predicted vs observed fraction of sites occupied for 3 fish species of the Cimarron River, Oklahoma 1976–1986. For each species, the average probabilities of colonization (Pr_c) and extinction (Pr_e), standard deviations (in parentheses) and predicted fraction of sites occupied ($\hat{p}$, mainland-island model, eq. 7) are given. The observed fraction of sites occupied (p) is calculated across all years and sites.

Species	Pr_c	Pr_e	$\hat{p}$	p
carp	0.540 (0.249)	0.705 (0.275)	0.434	0.405
Arkansas River shiner	0.118 (0.161)	0.323 (0.332)	0.268	0.400
Red River shiner	0.183 (0.246)	0.077 (0.136)	0.704	0.652

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Table 3. Summary of stepwise best-fitting regression models of the probability of colonization (Pr_c) and extinction (Pr_e) of mangrove insects (Simberloff 1976) as a function of p, the fraction of islands occupied. Values in parentheses are the probability that a parameter does not differ from 0.0.

Dependent variable	Pr_c	Pr_e
Independent variable	p^2	p
Intercept	0.0421 (0.0362)	0.8375 (0.0001)
Slope	0.5941 (0.0001)	−0.8296 (0.0001)
R^2	0.2899	0.2599

tion between probabilities of colonization and extinction and the fraction of sites occupied. Thus, in eq. (11), parameters b and d are effectively equal to 0, and the model collapses to eq. (7), the island-mainland model. In this system, intervening stretches of river probably function as a "mainland" source of propagules for the 10 censused sites. Using this model, we estimated the probability of colonization and extinction (across all sites and times), predicted the equilibrium fraction of occupied sites, and compared these predictions to the observed fraction of occupied sites. For carp and the Red River shiner, observed values are within 5% of the model predictions (Table 2). For the Arkansas River shiner, the model substantially underestimated the observed fraction of sites occupied.

For all 3 species, at least one of the assumptions for the metapopulation model was violated. The assumption of patch homogeneity was violated for carp and the Red River shiner. In both cases, the probability of extinction was significantly lower for stable downstream sites than for unstable upstream sites. The probability of successful colonization by carp was also significantly higher for downstream sites. For the Arkansas River shiner, the assumption of time-invariant colonization and extinction probabilities was violated. Specifically, the probability of local extinction increased significantly from 1976 to 1986. In fact, the Arkansas River shiner underwent a regional extinction and disappeared from all sites on the Cimarron River in 1986. This species has recently disappeared from several other river drainages in the midwestern United States. In the Cimarron River, variability in river discharge and extreme water temperatures are thought to be responsible for the demise of the Arkansas River shiner (Pigg 1991).

Multi-species test: insects of mangrove islands

Simberloff (1976) provided a large data set on annual colonization and extinction of 254 insect species on 9
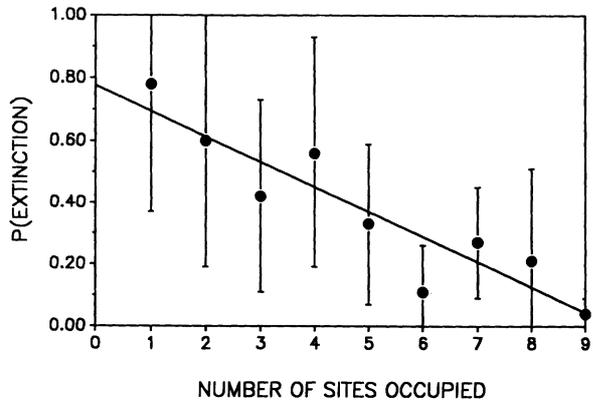

Fig. 2. The annual probability of extinction, averaged across all species of mangrove insects, as a function of the number of sites occupied. Vertical bars are 1 standard deviation. Data in Figs 2–5 from Simberloff (1976).

mangrove islets in the Florida Keys from 1969 to 1971. Only 6 of the islands were censused in 1971, so we have calculated extinction and immigration probabilities based only on the 1969–1970 data. However, species that occurred in any of the three years were considered part of the potential colonization pool. Hanski (1982) used this same data set to confirm a negative, linear relationship between p and the probability of extinction, one of the most important assumptions of his original model. Here, we analyze the same data set in more detail and describe the shape of the immigration function as well. We used a stepwise multiple regression to choose the best linear or nonlinear model describing the relationship between p and the probability of extinction or immigration.

For the extinction function, the results are in accord with Hanski's model: the best-fitting model is linear, with a negative slope (Table 3, Fig. 2). Moreover, at $p = 1$, the 95% confidence interval for the predicted value encompasses 0 (−0.134–0.150) implying that $c = d$
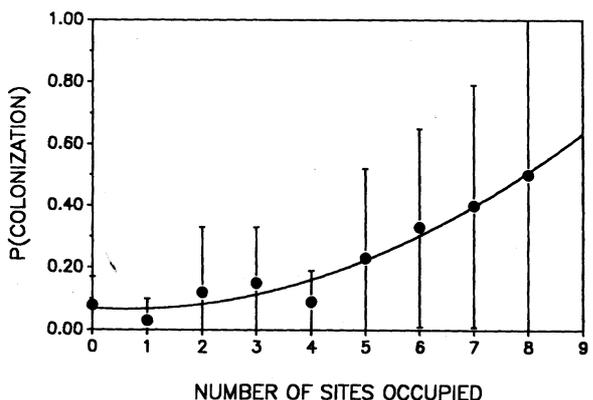

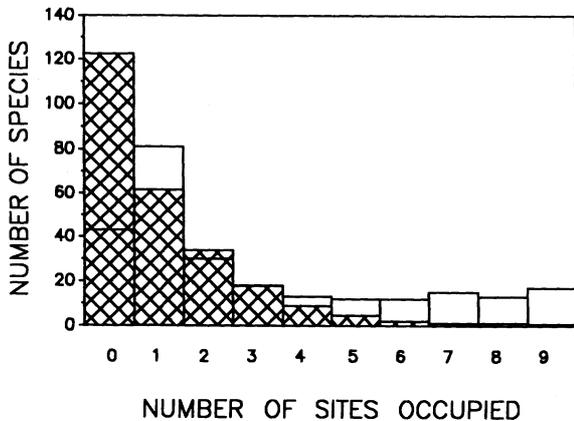Fig. 3. The annual probability of colonization of mangrove insects as a function of the number of sites occupied.

Fig. 4. The distribution of species of mangrove insects ($n = 254$) across sites ($n = 9$ islands). Open bars = observed distribution (1969 data); hatched bars = expected distribution, based on a Monte Carlo simulation of observed extinction (Fig. 2) and colonization probabilities (Fig. 3).

in eq. (11). Biologically, this result means that the rescue effect is so strong that the probability of local extinction approaches 0 when all sites are occupied.

For the colonization data, a quadratic model best fits the data (Table 3, Fig. 3). The predicted value for the intercept is significantly different from 0, implying that $a > 0$ in eq. (11). Biologically, this result means that some external colonization occurs even when no sites are occupied. None of these islands were more than 500 m from other large mangrove islands (Simberloff 1976), so colonization from external sources seems probable. For both the colonization and extinction functions, the amount of variation explained by the model is small. This result is due to small sample size ($n = 9$ islands) and to other sources of variation in the probability of colonization and extinction.

Thus, the best-fitting metapopulation model for Simberloff's mangrove insect data is:

$$\frac{dp}{dt} = (a + bp^2) - cp(1 - p) = F(p) \qquad (12)$$

with the parameter estimates:

$a = 0.0421$, $b = 0.5941$, and $c = 0.8296$.

Hanski (1991) has shown that non-linear metapopulation models may lead to multiple equilibria and bimodal distributions. Before comparing the predictions of eq. (12) with the observed distribution of mangrove insects, we briefly consider the mathematical properties of eq. (12).

The equilibria for eq. (12) are given by

$$\hat{p} = 1, \quad \frac{c \pm \sqrt{c^2 - 4ab}}{2b}$$

The dynamics of eq. (12) may be determined by considering the sign of $F'(1) = c - (a + b)$. If $c - (a + b) > 0$, there is a single stable equilibrium $\hat{p}$ in $(0,1)$. If $c - (a + b) < 0$, then there are three cases to consider:

a) $c^2 - 4ab < 0$

b) $c^2 - 4ab > 0$ and $c > 2b$

In these two cases, there is a single stable equilibrium at $\hat{p} = 1.0$.

c) $c^2 - 4ab > 0$ and $c < 2b$

In this case, there are three equilibrium points in the interval [0,1]: 2 stable points at 1.0 and $\hat{p}$, and an intermediate, unstable point. Bimodality may arise if the system fluctuates stochastically between the 2 stable equilibria. For the mangrove data, $c - (a + b) > 0$, yielding a single, stable equilibrium point at $\hat{p} = 0.05271$.

Next, we ask whether a stochastic analog of eq. (12) can predict the frequency distribution of mangrove insects. We used a Monte Carlo simulation, taking as inputs the mean and variance of the probability of extinction and immigration as a function of site occupancy (Figs 2 and 3). At each time step, we sampled extinction and immigration probabilities from a normal distribution, and then used these probabilities to increase or decrease site occupancy. The simulation began with $p = \frac{5}{9} = 0.56$ and was replicated 10000 times. Results were not sensitive to the initial value of p. The expected frequency distribution was compared to the observed data from 1969 with a χ^2 test, pooling adjacent cells with expectations < 5.0 (Sokal and Rohlf 1981). Results were similar for a comparison with the 1970 data.

The prediction from the metapopulation model is significantly different from the observed ($\chi^2 = 416.33$, $p < 0.001$). Specifically, there are too few species found on few sites and too many species found on several sites
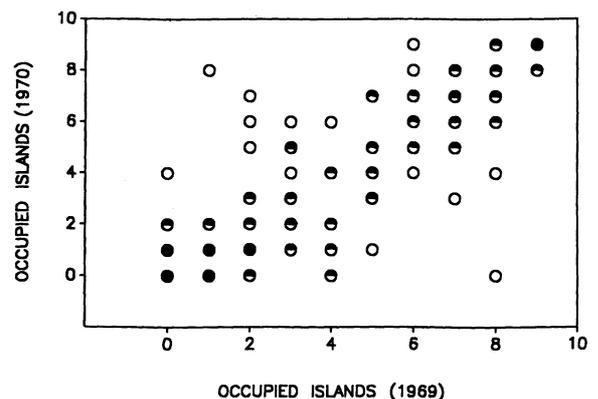

Fig. 5. Number of islands (0–9) occupied by different mangrove insect species in 1969 and 1970. Each point is a different species ($n = 254$, $r = 0.88$, $Pr < 0.0001$). Open circle = 1 point; half-filled circle = 2–9 points; filled circle = >9 points.

(the bimodal tail), compared to the predictions of the model (Fig. 4). Why are these two distributions so different, given that the same data were used to estimate extinction and colonization probabilities and to construct the frequency distribution?

The answer is that one or more of the assumptions underlying eq. (12) was probably violated. One important assumption is that the species are "similar" to one another: i.e. the probabilities of immigration and extinction do not vary substantially from one species to the next. However, Fig. 5 shows that the frequency of occurrence of each species was highly correlated from one year to the next. That is, certain species were consistently widespread and others were consistently sparse on mangrove islands, in spite of substantial turnover in species composition between years. Gaston and Lawton (1989) obtained a similar result for insect herbivores that colonize bracken. Of course, it is certainly possible that a stochastic metapopulatioan model may explain distribution within a species, even though such a model is not successful at the community level.

However, there are two problems with testing the assumption of similarity among species by using data as in Fig. 5. The first problem is that shifts in distribution may not be apparent with only 2 consecutive years of data. The appropriate time scale for metapopulation dynamics may be on the order of decades (Harrison et al. 1988), so the data in Fig. 5 do not necessarily indicate that species differ consistently in their probabilities of local immigration or local extinction.

The second problem is that the model itself may generate the pattern seen in Fig. 5. Hanski's original model (eq. (6)) and a number of other equations (Hanski and Gyllenberg, unpubl.) predict a bimodal distribution of species on sites. Bimodality is apparent in these data (Fig. 4) when compared to the predictions of eq. (12) (see Gotelli and Simberloff (1987) for other tests for bimodality). The two modes (core and satellite species) correspond to two stable, positive equilibrium points. These points function as attractors; once a species becomes widespread ($p \approx 1.0$) or sparse ($p \approx 0.0$), dp/dt will change relatively slowly. Consequently a correlation between years in the fraction of sites occupied by different species may be a consequence of bimodality (we thank R. Holt for this insight).

As in the single-species model, it is possible to test for differences among sites in probabilities of colonization and extinction. Averaging of these probabilities across species, island area was uncorrelated with colonization ($r = 0.39$, $Pr = 0.31$) and only weakly correlated with extinction ($r = -0.59$, $Pr = 0.09$). A negative correlation between island area and the probability of local extinction is one of the important assumptions underlying the MacArthur-Wilson (1967) equilibrium model.

In spite of the fact that both data sets represent some of the best long-term studies of patch occupancy, neither provided a fully satisfactory test of the metapopulation model. The single-species tests for fishes of the Cimarron River failed to reveal any metapopulation effects on the probability of colonization, although there was spatial and temporal variation in these parameters. The best-fitting model for all 3 species was a simple island-mainland model, which generated adequate predictions for two of the 3 species. The multispecies analysis of insects on mangrove islands revealed significant metapopulation effects on both the average probability of local colonization and local extinction. However, a stochastic version of the best-fitting model failed to predict the frequency distribution of occupied sites, possibly because of consistent differences among species in colonization and extinction probabilities. For both systems, patches of intervening habitat (other regions of the Cimarron River and other mangrove islands) undoubtedly contributed to the pattern of patch occupancy. Consequently, the best-fitting metapopulation model may depend on the spatial and temporal scale of the analysis (Collins and Glenn 1990).

We have developed a model that incorporates four important metapopulation processes: external and internal colonization sources, intrinsic risk of extinction, and the rescue effect. The strength of these four mechanisms corresponds, respectively, to the magnitude of parameters a, b, c, and d in eq. (11). The model is simple and generates testable predictions that can be compared to empirical data. Future studies should determine $g(p)$ and $h(p)$ for other data sets, and quantify the effects of sites, species, and time on the probability of local colonization and local extinction in metapopulations.

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