METAPOPULATION MODELS: AN EMPIRICAL TEST OF MODEL ASSUMPTIONS AND EVALUATION METHODS

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Abstract. Patch occupancy models provide a simple phenomenological approach to evaluating ecological questions on a metapopulation scale. In this study, I use and modify a patch occupancy model to evaluate the effects of synchronous extinctions correlated with flooding and patch-size-dependent migration on the regional dynamics of a neotropical beetle, *Cephaloleia fenestrata*. Various methods have been used to evaluate patch occupancy models. Previous authors most commonly have evaluated patch occupancy models by logistic regression of incidence functions. Likelihoods produced from regression methods, however, neglect autocorrelation in spatial occupancy patterns even though spatial autocorrelation is common in ecological data. In this study, I used a Monte Carlo method of model evaluation, which accounts for spatial autocorrelation. Results suggest that patches undergo synchronous extinctions correlated with flooding and this affects regional dynamics of *C. fenestrata*. Immigration probability positively correlated with patch size, and emigration probability negatively correlated with patch size, also affecting *C. fenestrata* regional dynamics. The patch occupancy pattern was positively spatially autocorrelated at only two of the sites, but was nearly significant at another. The logistic regression method was a reasonable alternative to the Monte Carlo method for model evaluation. Other model evaluation methods (fits to model development data, proportion of occupied patches, and turnover rates) were inconsistent (at best) quantitative measures of a model's fit to independent data. When used to select among competing models, however, the fits to model development data were reasonably good indicators of fits to independent data. Given the increased complexity involved in using the Monte Carlo method, the simpler logistic regression method may be a preferable alternative, especially when spatial autocorrelation is minimal.

Key words: Cephaloleia fenestrata; *logistic regression; Monte Carlo Markov chain; patch occupancy model; patch-size-dependent migration; spatial autocorrelation.*

INTRODUCTION

In recent years, metapopulation modeling has demonstrated the strong effects that spatial processes can have in shaping population dynamics and increasing regional persistence (Hanski and Gilpin 1997). As habitats continue to be fragmented by human activity, the metapopulation approach may prove increasingly useful in conservation efforts. Currently in vogue are patch occupancy models, which are forms of metapopulation models that ignore local population dynamics, instead categorizing patches as being either occupied or empty (Levins 1969, Hanski 1994). The advantage of patch occupancy models is that they require a relatively small amount of empirical data compared to models with local population dynamics. Hanski's (1994) incidence function model (IFM) is perhaps the most utilized patch occupancy model, being used to investigate regional dynamics of a range of organisms. Two possible criticisms of Hanski's basic IFM are, first, that the methods

used to validate patch occupancy models are lacking in various ways and, second, that the model is too simplistic, lacking biotic and abiotic ecological interactions that may be important in shaping regional dynamics. The present study addresses the above two criticisms of an IFM using a Neotropical beetle as a model system.

Various methods have been used to validate patch occupancy models. For example, independent data often are lacking, thus, model evaluation is based on the same data used to build the model (Hanski 1994, Moilanen et al. 1998, Lindenmayer et al. 2001), hereon referred to as ''model development data.'' The predictive power of such models is highly suspect. When independent data are available, criteria for evaluating the fit of a model have been based either on metapopulation-level statistics such as the proportion of occupied patches (Wahlberg et al. 1996) or turnover rates (a summation of colonization and extinction rates; Hanski et al. 1996). In these cases, seemingly good fits at the metapopulation level may be a poor fit on a patch-by-patch basis. Other methods have been based on patch-level statistics such as patch-specific colonization and extinction probabilities (Verboom et al. 1991). These

methods require observations at multiple censuses, thus, large amounts of data are necessary. Logistic regression is a commonly used method of model fitting that requires only one census of patch occupancy data. This method, however, relies on ''pseudo-likelihoods'' meaning that, even though the empirical data and model simulations can contain spatial autocorrelation, ''autocorrelation among the spatial occupancy data is neglected'' in the likelihood value (ter Braak et al. 1998). By spatial autocorrelation, I refer to a higher correlation of population dynamics between spatially proximate populations than between spatially distant populations. Thus, all of the above methods are suboptimal in various ways. Alternatively, a Monte Carlo method of patch occupancy model fitting is superior to the other methods because it requires only one census of occupancy data and the likelihoods it produces do not neglect a form of endogenous spatial autocorrelation (due to dispersal limitation) in the occupancy data (Moilanen 1999). In this study, I compare the predictive values of competing patch occupancy models using the Monte Carlo method on independent data. Moreover, I ask whether the other methods listed above produce quantitatively similar results as the Monte Carlo method in comparing competing patch occupancy models. Finally, I test for spatial autocorrelation in the empirical patch occupancy patterns.

For this study, I use *Cephaloleia fenestrata* Weise (Chrysomelidae: Hispinae), a so-called rolled-leaf beetle, as a model system (see Plate 1). *C. fenestrata* is a specialist herbivore, feeding in the rolled leaves of the 2–3 m high monocot *Pleiostachya pruinosa* (Regel) K. Schum. (Marantaceae: Zingiberales), commonly known as prayer plants, in tropical lowland wet forests of Central America. *P. pruinosa* grows in discrete patches of 1–735 ramets, primarily in and near the flood zone of the Puerto Viejo River at La Selva Biological Station in Costa Rica. Previous studies have demonstrated the following interactions between *C. fenestrata* and its environment. First, stochastic flooding of the Puerto Viejo River completely inundated a subset of *P. pruinosa* patches, causing high beetle mortality (Johnson 2004b). Second and third, immigration and emigration rates of adult *C. fenestrata* were dependent on patch size, where larger patches acted as greater attractors to immigrants and stronger adherents of potential emigrants (Johnson 2003). The above ecological interactions are assumed to be unimportant to regional dynamics in Hanski's basic IFM. Herein, the effects of these abiotic and biotic ecological interactions on the regional dynamics of *C. fenestrata* are examined through modification and analysis of the IFM.

Spatial autocorrelation in population dynamics is common in ecological data (Lichstein et al. 2002). Spatial autocorrelation can be caused by exogenous or endogenous factors. For example, an exogenous factor is the Moran effect, which is spatial synchrony in dynamics caused by climatic events (Moran 1953). Al-

PLATE 1. Adult *Cephaloleia fenestrata* on the host plant, *Pleiostachya pruinosa*. Adults average 8 mm in length. The five dark dots on the elytra (three in the upper left region in the shape of a triangle, one in the upper right, and one in the lower right) are from a concurrent mark–recapture study in which beetles were individually marked with a series of punctures to the elytra using an insect pin. Photo by D. M. Johnson.

ternatively, theoretical analyses of spatially explicit models demonstrate that endogenous factors, such as limited dispersal or conspecific attraction, are sufficient to cause spatial autocorrelation in population distributions (De Roos et al. 1991). Likewise, in a metapopulation context, patch occupancy patterns can be spatially autocorrelated (Smith and Gilpin 1997). In this study, I use empirical data to detect spatial autocorrelation in the occupancy patterns of *C. fenestrata*. I then compare the predicted likelihoods from independent data (data not used to parameterize the model) using logistic regression (neglects spatial autocorrelation) versus the Monte Carlo technique (accounts for endogenous spatial autocorrelation). I also test the ability of model fits derived from model development data, and other model evaluation methods (based on turnover rates and mean patch occupancy), to act as surrogates for the more complex Monte Carlo method of model evaluation.

STUDY SITES

This study was conducted at four study sites. La Selva Biological Station, Heredia Province, Costa Rica

(10°26′ N, 83°59′ W), covers 1510 ha of lowland wet forest on the Caribbean slope of Northeastern Costa Rica. La Selva receives 4000 mm of precipitation per year with no month receiving less than 100 mm. The two study sites at La Selva, referred to as La Selva I and La Selva II, lie along the Puerto Viejo River, on and near the river floodplain.

Corcovado National Park, Puntarenas Province, covers 43 735 ha on the Osa Peninsula of southern Costa Rica on the Pacific side. The study was conducted at Sirena Station (8°29′ N, 83°35′ W), which is located on the Corcovado plain and receives 3000–3800 mm of precipitation per year (Hartshorn 1983). The study site is located approximately 1 km from the ocean. The patches at Corcovado lie above the floodplain of local rivers and streams.

Hacienda Baru, Punterenas Province, covers 320 ha in the coastal lowland of the Pacific slope in Costa Rica (9°15′ N, 84°14′ W). The climate is similar to that of Corcovado, but perhaps a bit drier. The study site is located approximately 1 km inland from the ocean, where uneven topography gives way to the coastal plain. The study site is on the slope of a hill that does not flood.

DATA COLLECTION

C. fenestrata occupancy and dispersal data were collected in 75 patches of *P. pruinosa* at La Selva I. In addition, three other characteristics were recorded for each patch: size (number of ramets), spatial location, and whether the patch was in the flood zone. The flood zone was defined for this project as the area where a December 1999 flood reached 1.5 m depth, enough water to kill immature beetles and flush out or kill adult beetles. Patch size was defined by the number of ramets that were present in June 1999. Spatial locations of the patches were based on Euclidean distances and compass directions to the nearest grid post on an *x–y* grid system at La Selva. I determined whether a patch was in the flood zone by direct observations during the December 1999 flood, and by examining postflood sediment deposits on leaves of plants following the flood. Seventeen patches were in the flood zone.

Patch occupancy for each of the 75 patches was determined at five censuses conducted at 6-mo intervals, between March 1999 and March 2001. Six months is the approximate generation time of *C. fenestrata* (Johnson 2004*a*). During every census, I thoroughly searched leaf petioles in each patch until either an immature *C. fenestrata* was found, or until the entire patch was censused. If immature beetles were present then I considered a patch occupied; because adults could be transients, unmated females, or solo males, they were not taken as evidence for the presence of breeding populations.

Patch occupancy data at a single census were collected from three other sites: La Selva II (32 patches), Corcovado (42 patches), and Hacienda Baru (41 patch-

es). La Selva II was mapped using the same procedures as used at La Selva I. La Selva II was approximately 1 km to the east of La Selva I. Patch coordinates at Corcovado and Hacienda Baru are relative to grids that I created. Hacienda Baru was censused in November 2000, La Selva II was censused on May 2001, and Corcovado was censused in June 2001. These patch occupancy data were used to test the predictive value of the eight competing IFMs.

INCIDENCE FUNCTION MODEL

The IFM is a Markovian chain model in which patches are viewed as being occupied or empty based on stochastic colonization and extinction events (Hanski 1994). The incidence function (J_i) is the probability that patch i is occupied at a given time. Hanski's original IFM makes specific assumptions about regional dynamics (i.e., exponential decay function of dispersal probability, the Allee effect on patch colonization, extinction probability is a power function of patch size, and the rescue effect), some of which were poor fits to the *C. fenestrata* occupancy pattern at La Selva I (or did not significantly improve the fit); thus, I modified the IFM accordingly when an alternative model structure was a better fit to the *C. fenestrata* system (see Appendix A for analyses). I note all alterations to the IFM when the particular equations are presented below. In addition, because previous analyses indicated that postnatal dispersal (dispersal from the natal patch soon after eclosion) (Johnson and Horvitz 2005) and immigration from outside the study area (Johnson 2003) may be important to the regional dynamics of *C. fenestrata*, I also critically tested their effects on the fit of the IFM, but found that they did not improve the performance of the model (see Appendix A).

In the IFM, the incidence probability (J_i) is a function of the colonization probability (C_i) and the extinction probability (E_i), given by

$$J_i = \frac{C_i}{C_i + E_i}. \tag{1}$$

Note, Eq. 1 lacks the "rescue effect" (where a patch is "rescued" from extinction by a simultaneous colonization event; Brown and Kodric-Brown 1977, Hanski 1994) because the IFM without the rescue effect was a better fit to the *C. fenestrata* occupancy data. The colonization probability (C_i) of patch i is a hyperbolic function of the number of immigrants (M_i) into the patch:

$$C_i = \frac{M_i}{M_i + y} \tag{2}$$

and y is the "half saturation" parameter at which the colonization probability equals 0.5 for y equal to M. The original IFM models colonization as an s-shaped function of the number of immigrants, thus, assuming an Allee effect. The model with the hyperbolic response

was a better fit to the *C. fenestrata* patch occupancy data (Appendix A). The number of immigrants into patch i,

$$M_i = \beta \sum_{j=1}^{n} [p_j A_j d_{ij}^{-\alpha})] \quad \text{where } i \neq j \quad (3)$$

is a summation of the number of migrants from all other patches j in the metapopulation. The number of migrants from patch j to patch i, is a function of three patch characteristics: patch j's occupancy status ($p_j = 1$ if occupied, $p_j = 0$ if empty), patch size (A_j), and the Euclidean distance between patches i and j (d_{ij}) (MacArthur and Wilson 1967, Hanski 1994). The dispersal kernel in this model is a power decay function of the Euclidean distance (d) separating the two patches ($d_{ij}^{-\alpha}$) rather than an exponential decay function as in the original IFM. While I concede that this is a rather phenomenological approach to modeling dispersal, I chose the power decay function because it was a much better descriptor ($\Delta AIC = 12.57$ to 14.78) of the regional dynamics of *C. fenestrata* than other dispersal kernels (see Appendix A), which tended to have too skinny a tail at long distances, thus, more isolated patches were predicted to be greatly under-colonized. β normalizes the number of migrants dispersing out of donor patches (js) so it is consistent with the empirically estimated number of migrants in a concurrent study (Johnson 2003). This function also assumes that the number of beetles in a patch is in direct proportion to the size of the patch, an assumption supported by empirical data (Johnson 2003).

Extinction probability,

$$E_i = \min\left(\frac{\mu}{A_i^x}, 1\right) \quad (4)$$

is inversely related to patch size, which is assumed to be positively related to population size (Boorman and Levitt 1973, Jones and Diamond 1976, Schoener and Spiller 1987). This equation assumes that extinction probability is a decaying power function of patch size (where μ and x are curve shaping parameters). I tested to determine whether an exponential function was a better fit, but it was not (Appendix A); although the low $\Delta AIC = 3.72$ indicates that neither models has strong support over the other. Fundamentally, small populations are most prone to extinction in this model (MacArthur and Wilson 1967). Extinction rate is assumed to be temporally constant and asynchronous among patches.

Model modifications

The IFM was modified to include the following ecological processes: Synchronous extinction caused by flooding, patch-size-dependent immigration, and patch-size-dependent emigration. First, synchronous extinctions caused by flooding, which can be a cause

of exogenous spatial autocorrelation, were added to the IFM by altering the extinction equation to

$$E_i = \min\left(\frac{\omega}{A_i^x}, 1\right) \quad (5)$$

when patch i is flooded. The parameter ω is the effect of flooding on extinction probability. When $\omega > \mu$, flooding increases the probability of extinction. Extinction probabilities of patches in the upland are always governed by the equation with μ because they are assumed to never flood. For patches in the flood zone, the equation with ω applies in time periods with a flood, while the equation with μ applies in periods without a flood. Flooding is a stochastic event determined probabilistically in model simulations. The probability of a flood during one time step was set at 0.5 per 6 mo, an estimate based on the observed frequency of flooding events from 1999 to 2002; a total of four floods over the four year period (D. Johnson, *personal observation*).

Second and third, the patch-size-dependent migration model (PDM) is a modification of the basic model in which patch-size-dependent emigration (PDE) and immigration (PDI) are added through the parameters ζ_{em} and ζ_{im}, respectively:

$$M_i = A_i^{\zeta_{im}}\beta \sum_{j=1}^{n} (p_j A_i^{1-\zeta_{em}} d_{ij}^{-\alpha}) \quad i \neq j \quad (6)$$

when $\zeta_{em} > 0$ per capita emigration is negatively correlated with patch size, and when $\zeta_{im} > 0$ per capita immigration is positively correlated with patch size. This model reduces to Hanski's basic IFM migration equation when $\zeta_{im} = 0$ and $\zeta_{em} = 0$. Again, this equation assumes that population size is in direct proportion to patch size. Adding nonzero values of ζ_{im} and ζ_{em} to the migration Eq. 6 alters the predicted number of migrants in the model compared to Eq. 3. To hold the migration rate in the modified models equal to the empirically observed level, the normalization parameter β was recalculated for each combination of ζ_{im} and ζ_{em} used in this equation. Thus, the total number of migrants was held constant, but the distribution of the migrants was altered by the patch-size-dependent migration parameters.

Eight competing IFMs were created, which are all permutations of the three model modifications outlined above: explicit flooding, PDE, and PDI. The effects of each of these three ecological interactions on the patch dynamics of *C. fenestrata* were assessed by comparing the fits of the modified IFMs (with and without the ecological interactions modeled explicitly) to the empirical occupancy data.

Parameter estimation

The IFMs were parameterized from *C. fenestrata* occupancy and dispersal data collected in 75 patches on *P. pruinosa* at the La Selva I site at La Selva Biological

Station. Population-level parameters (α, ζ_{em}, and ζ_{im}) in the IFM were calculated by maximum likelihood estimation (in the software Matlab [The MathWorks, Natick, Massachusetts, USA]) using migration data from a 1-yr mark–recapture study at La Selva I (at 25-d intervals; Johnson 2003). The metapopulation-level parameters y, x, μ, and ω were estimated from turnover data (extinctions, colonizations, or lack there of) from the five censuses at La Selva I by maximum likelihood estimation in Matlab. In the IFM, the patch occupancy pattern (**O**) is a vector of ps (equals 1 when a patch is occupied and 0 when it is empty), with vector length equal to the number of patches (N). A given transition probability from occupancy pattern $\mathbf{O}_{t-1}$ to $\mathbf{O}_t$ can be calculated analytically, given the vector of model parameters $\mathbf{\Theta}$, by calculating the product of all patch-specific transition probabilities based on the equation

$$P[\mathbf{O}_t | \mathbf{O}_{t-1}, \mathbf{\Theta}]$$

$$= \prod_{i=1}^{N} \begin{bmatrix} C_i(t) & \text{if } p_i(t-1) = 0 \cap p_i(t) = 1 \\ 1 - C_i(t) & \text{if } p_i(t-1) = 0 \cap p_i(t) = 0 \\ E_i & \text{if } p_i(t-1) = 1 \cap p_i(t) = 0 \\ 1 - E_i & \text{if } p_i(t-1) = 1 \cap p_i(t) = 1 \end{bmatrix}. \quad (7)$$

The parameter p_i is defined as in Eq. 3. Because likelihoods are often miniscule, it is traditionally transformed into a negative log-likelihood

$$L(\mathbf{O_t} | \mathbf{\Theta}) = -\ln(P[\mathbf{O_t} | \mathbf{O_{t-1}}, \mathbf{\Theta}]) \quad (8)$$

and is minimized. The $-$log-likelihood was summed for transitions between all five empirical occupancy patterns. Parameter estimation of the metapopulation-level parameters was conducted by the method of simulated annealing (Kirkpatrick et al. 1983). This method is advantageous over iterative improvement methods because it is more likely to find a global maximum likelihood and not get stuck in local maximums. The estimation method was repeated for each parameterization to ensure that the estimations converged on the same values. The values of L were adjusted according to Akaike's information criterion

ASSESSING THE PREDICTIVE VALUES OF COMPETING MODELS

Assessing the predictive value of a model requires empirical data, preferably data not used to parameterize the model (Power 1993). In this study, independent patch occupancy data from four sites were used to compare the predictive values of the eight competing IFMs. Because turnover data from La Selva I was used to parameterize the models, one of the occupancy patterns (in this case the first occupancy pattern) could be used to independently assess the predictive values of the models (known as data splitting). A single occupancy pattern was collected at the other three sites. Predictive values were assessed by comparing the Monte Carlo-derived likelihoods to statistics from the following

methods: likelihoods from model development data, and logistic regression, turnover rates, and mean proportion of patches occupied from independent data.

Logistic regression technique

Assessing the predictive value of a patch occupancy model involves asking what is the probability that the model would produce an empirical occupancy pattern. A traditional method of estimating this probability for patch occupancy models is by calculating a probability of the observed occupancy pattern (where $p = 1$ when a patch is occupied and $= 0$ when it is empty) based on the patch-specific incidence probabilities (J_i):

$$P = \prod_{i=1}^{N} [(p_i)(J_i) + (1 - p_i)(1 - J_i)] \quad (9)$$

(a logistic regression technique). The incidence probabilities (J_i) were estimated by running a long model simulation and calculating the proportion of times that each patch was occupied in that simulation. The parameter N is the number of patches in the metapopulation. The probability P is termed a "pseudo-likelihood" because the "autocorrelation among the spatial occupancy data is neglected" in the likelihood estimation process (ter Braak et al. 1998). For example, if there are two neighboring patches each with $J = 0.5$, then using the logistic regression method we would calculate the probability that both patches are occupied at one time is $P = (0.5)(0.5) = 0.25$. However, this method does not consider the conditional possibility that patch 1 may be more likely to be occupied given that patch 2 is occupied than if patch 2 were empty, because patch 2 would act as a source for colonization (which would create spatially correlated data and, thus, independence among data points would be violated).

The Monte Carlo method

The Monte Carlo method is an alternative to the logistic regression method. This is a novel modification of the Monte Carlo method of parameter estimation (Moilanen 1999). In this method, the empirical occupancy pattern $\mathbf{O}_t$ is known. To estimate the likelihood of the given occupancy pattern $\mathbf{O}_t$, theoretically, one could run a long model simulation and calculate the proportion of times that the simulation produced the pattern. This is impractical, however, with even a moderate number of patches because the state space is too large. Another alternative is to run many replicate Monte Carlo simulations, stopping at a given time (t) to create occupancy pattern $\mathbf{X}_t$, and calculating the proportion of times $\mathbf{X}_t = \mathbf{O}_t$. This method is fundamentally the same as the previous, also suffering from the chance that $\mathbf{X}_t = \mathbf{O}_t$ is miniscule except when there are only a few patches in the metapopulation. With a minor modification, however, this method is useful. Instead of naming the simulated pattern $\mathbf{X}_t$, it is named $\mathbf{X}_{t-1}$. We can then calculate the exact transition probability from $\mathbf{X}_{t-1}$ to $\mathbf{O}_t$. By repeating this many times (N will
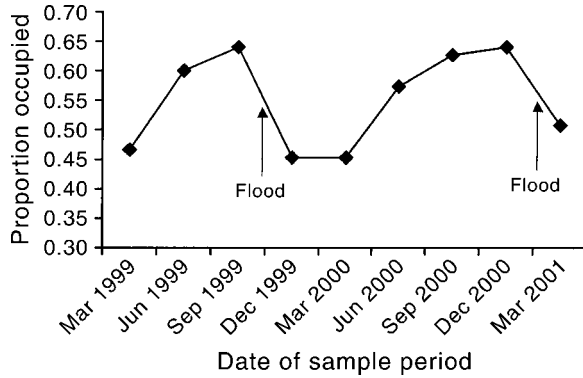
FIG. 1. Proportion of *Pleiostachya pruinosa* patches occupied by *Cephaloleia fenestrata* from March 1999 to March 2001.

signify the number of replicates), we can estimate the likelihood of $\mathbf{O}_t$ by taking the arithmetic mean of the above calculated transition probabilities:

$$P[\mathbf{O}_t | \boldsymbol{\Theta}] \approx \frac{1}{N} \sum_{u=1}^{N} P[\mathbf{O}_t | X_{t-1,u}, \boldsymbol{\Theta}]. \qquad (10)$$

This method, unlike the logistic regression method, accounts for spatial dependency in the occupancy pattern (Moilanen 1999). The Monte Carlo method is sensitive to any bias in the selection of occupancy patterns for $\mathbf{X}_{t-1}$. To avoid such bias, the simulations were initiated at randomly generated occupancy patterns and allowed to run for 1000 time steps before occupancy patterns were selected at 200 time step intervals for use as the $\mathbf{X}_{t-1}$ vectors.

SPATIAL AUTOCORRELATION

I probed for evidence of spatial autocorrelation in the observed occupancy statuses using a modification of Moran's *I* statistic (Smith and Gilpin 1997). For the Moran statistic, residuals, the difference between the incidence function and the occupancy status ($p_i = 0$ or 1), were calculated for each patch ($J_i - p_i$). The covariance of each possible pair of patches was calculated by multiplying their respective residuals. Each covariance was multiplied by a measure of connectivity of the two patches, in this case a power decay function of the Euclidean distance between the patches, thus, covariance between neighboring patches is more heavily weighted than between nonneighboring patches. The sum of each weighted covariance is divided by the sum of the square of the residuals, and is the *I* statistic:

$$I = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} d_{ij}^{-\alpha}(p_i - J_i)(p_j - J_j)}{\sum_{i=1}^{N} (p_i - J_i)^2} \qquad (11)$$

where $i \neq j$. When neighboring patches in empirical occupancy data are more likely to be in the same state than would be predicted from the *J* values, then em-

pirically generated *I* statistic is higher than the *I* statistic calculated from randomly generated occupancy patterns created probabilistically from the *J* values. Thus, if we assume that the model is representative of observed metapopulation dynamics, then a significant difference between *I* statistics is evidence for spatial autocorrelation in the empirical metapopulation pattern. The *I* statistics from empirical occupancy data were contrasted against a probability distribution of *I* statistics that were calculated from 1000 independently generated occupancy patterns from the incidence function values (*J*) for each of the four study sites (thus, the latter lack spatial autocorrelation).

RESULTS

The proportion of occupied patches in La Selva I ranged from 0.45–0.64 with a turnover rate of 24.25 per 6 mo (Fig. 1). The two observed decreases in the proportion of occupied patches coincided with two flood events, and were primarily caused by population extinctions in the flood zone (Fig. 2). The distribution of *P. pruinosa* patches at La Selva I is provided in Fig. 3A. The proportion of occupied patches at the other three sites was 0.59, 0.71, and 0.88 at La Selva II, Hacienda Baru, and Corcovado, respectively.

Of the eight IFMs with all permutations of the three possible effects on metapopulation dynamics, the model with flooding and patch-size-dependent emigration (FL + PDE) was the best fit to the model-development data based on the lowest AIC value (Table 1). When patch-size-dependent immigration was added to the model (FL + PDM), the fit was only slightly worse (ΔAIC = 1.02), thus, neither model was well supported over the other. Parameter estimates for all models are available in Appendix B. Adding flooding to the model improved the fits significantly (ΔAICs > 18), lending
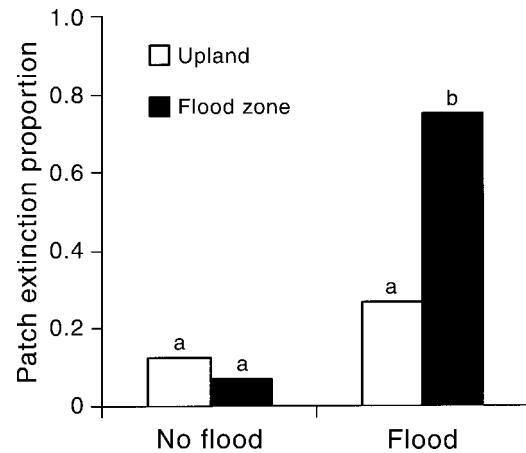

FIG. 2. Comparison of the proportion of patches going extinct over one time step in the flood zone and upland during time steps with and without a flood event (different letters above the bars indicate significantly different distributions according to pairwise contingency table analyses at the α = 0.05 significance level).
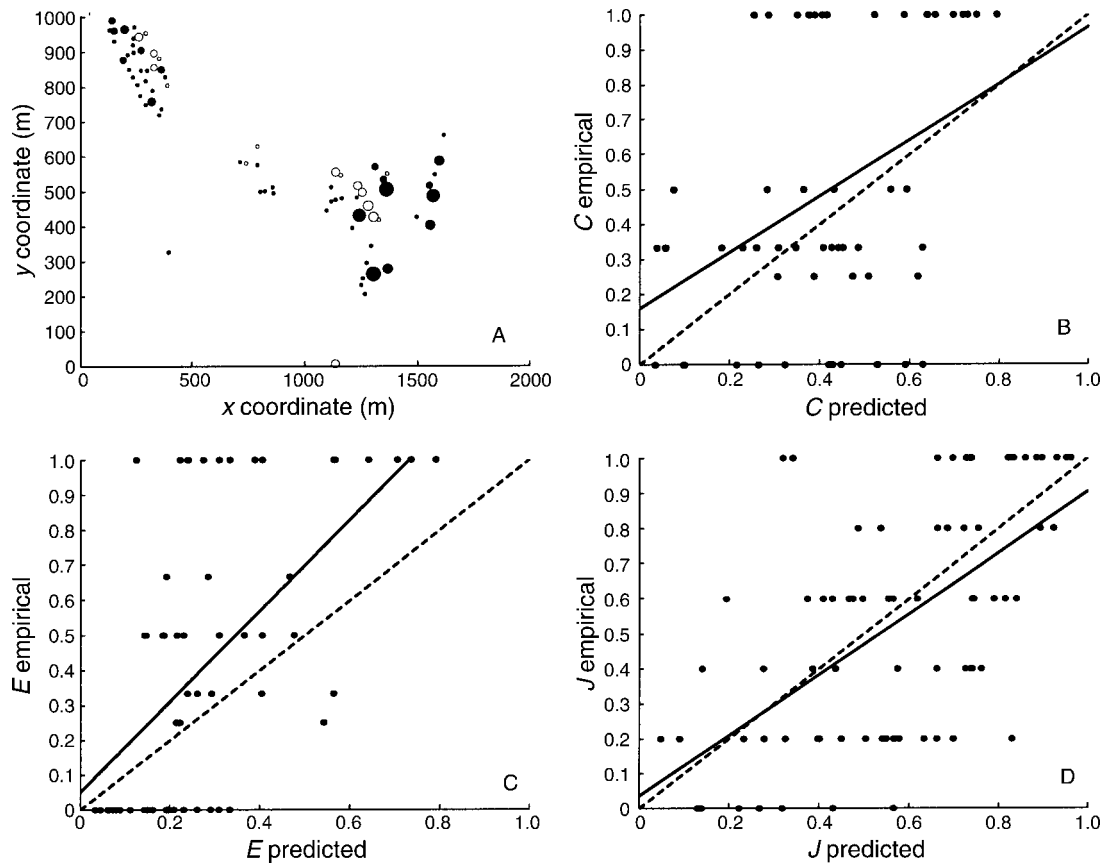
FIG. 3. (A) The distribution of *P. pruinosa* patches at La Selva I. The size of the circle is an indicator of the size of the patch (range 1–735 ramets). Open circles indicate the flood zone, and closed circles indicate upland habitat. (B–D) Plots of model-predicted (B) colonization probability, *C*; (C) extinction probability, *E*; and (D) incidence functions, *J,* on observed values from the five time steps of empirical data at La Selva I. The dashed line represents a hypothetical perfect relationship between predicted and observed values, while the solid line represents the observed relationship. All *y*-intercepts (b_0), slopes (b_1), and r^2 values were within 95% confidence limits generated from analyses of model-generated occupancy data (200 sets of data consisting of five time steps each). Empirical values are given below with model-generated 95% CI in brackets. (B) Colonization probability: $b_0 = 0.16$ [−0.11, 0.24], $b_1 = 0.81$ [0.66, 1.45], $r^2 = 0.17$ [0.11, 0.49]. (C) Extinction probability: $b_0 = 0.04$ [−0.08, 0.18], $b_1 = 1.30$ [0.57, 1.57], $r^2 = 0.34$ [0.08, 0.45]. (D) Incidence function: $b_0 = 0.03$ [−0.17, 0.16], $b_1 = 0.87$ [0.78, 1.19], $r^2 = 0.36$ [0.33, 0.64].

strong support. Adding patch-size-dependent emigration also improved the fits, lending strong support (ΔAICs > 7). Adding patch-size-dependent immigration had little effect on the model fits (ΔAICs < 2). The basic model was among the poorest fitting models. The predicted colonization probabilities, extinction probabilities, and incidence functions at La Selva I were reasonable fits to the observed data; the regression statistics (r^2, *y*-intercept, and slope) were all within the 95% CI generated from model simulations (Fig. 3B–D).

All of the modified models accurately predicted the proportion of occupied patches at La Selva I, La Selva II, and Hacienda Baru within less than 2 SD from the mean observed (Appendix C). However, all of the models significantly underestimated the proportion of occupied patches at Corcovado by 4 to 8 SD from the mean (Appendix C). In general, the models with patch-size-dependent migration and flooding modifications tended to predict a higher proportion of occupied patches than the basic model for all four sites (Appendix C). All of the models predicted the turnover rate at La Selva I by less than 1 SD from the mean observed (Appendix C).

Likelihood ratios were used to evaluate whether each model was among the best-fit models to independent data at each of the four sites. Each of four models (PDI, PDM, FL + PDI, and FL + PDM) was among the best fits at three of the four sites (Table 2). The FL and FL + PDE was among the best fits at two of the four sites, while the basic and PDE models were the worst predictive models, being among the best fits at none of the sites. In summary of these results, adding PDI and FL to the models improved their predictive ability, while PDE had no noticeable effect. Another method to test the fit of the model to the empirical data is to

TABLE 1. Akaike's information criteria (model fits) for the eight incidence function models.

Model	Free parameters	AIC	ΔAIC
Basic	3	170.47	26.32
PDE	3	162.69	18.54
PDI	3	171.46	27.31
PDM	3	163.73	19.58
FL	4	151.91	7.76
FL + PDE	4	144.15	0.00
FL + PDI	4	152.92	8.77
FL + PDM	4	145.17	1.02

Notes: Smaller values indicate better fits, and the ΔAIC indicates the difference between the particular model and the best-fit model. ΔAIC values <7 indicate that the model is not reliably distinguishable from the better fit model, while values >7 indicate that the model is a substantially poorer fit. Abbreviations: FL, flooding is explicit in the model; PDE, per capita patch-size-dependent emigration; PDI, per capita patch-size-dependent immigration; PDM, per capita patch-size-dependent migration (PDE + PDI). The "free parameters" column gives the number of parameters estimated in the estimation model (the three parameters refer to x, μ, and y; four parameters refers to ω in the flooding models). All other parameters were estimated independently of these analyses.

compare the predicted likelihood of the empirical data to a distribution of predicted likelihoods of simulated occupancy patterns. This method confirmed that the FL + PDM model was a good fit to the empirical data at all four sites (La Selva I, $P = 0.68$; La Selva II, $P = 0.97$; Hacienda Baru, $P = 0.93$; Corcovado, $P = 0.27$), as was the PDI model (all $P > 0.05$). Each of the remaining six models were good fits to the empirical data at three of the four sites (all excluding Corcovado).

Relationships between the fits from Monte Carlo and other evaluation methods

The Monte Carlo method is the only method used herein that estimates likelihoods and accounts for spatial autocorrelation due to endogenous effects; thus, I compare the predictive values of all other methods to the Monte Carlo method. The correlations between model fits to independent data (generated from the Monte Carlo method) and the fits to model development data were positive and significant at La Selva II ($r^2 = 0.67$, $P < 0.05$) and Hacienda Baru ($r^2 = 0.57$, $P < 0.05$), but was insignificant (all $P > 0.05$) at La Selva I and Corcovado ($r^2 = 0.01$ and $r^2 = 0.22$, respectively). There was a marginal positive relationship between a model's ability to predict the turnover rate (measured as the difference between the predicted and observed turnover rates divided by the observed SD at La Selva I) and the model fits generated from the Monte Carlo method ($r^2 = 0.43$, $P = 0.07$); however, all eight of the models satisfactorily predicted the observed turnover rate (Appendix C). The relationship between a model's ability to predict the mean proportion of occupied patches (measured as the number of standard deviations the predicted proportion diverged from the observed proportion of occupied patches) and fits generated from the Monte Carlo method were insignificant ($P > 0.05$) at all sites: La Selva I ($r^2 = 0.01$), La Selva II ($r^2 = 0.30$), Hacienda Baru ($r^2 = 0.33$), and Corcovado ($r^2 = 0.28$). There was a strong positive relationship between model fits using the likelihood based on the logistic regression method and the Monte Carlo method at Hacienda Baru ($r^2 = 0.98$, $P < 0.05$) and Corcovado ($r^2 = 0.96$, $P < 0.05$), a moderately strong significant relationship at La Selva II ($r^2 = 0.57$, $P < 0.05$), and a positive but marginally insignificant relationship at La Selva I ($r^2 = 0.48$, $P = 0.06$) (Fig. 4).

Spatial autocorrelation

Whether spatial correlation is detected in an occupancy pattern can obviously be dependent upon the site and on the model used to generate the J values. So for the purposes of this analysis, I focused on the FL + PDM model because this was the best predictor of occupancy patterns across the four sites based on the

TABLE 2. Model fits (−log likelihoods) to independent data, with likelihood ratios (R) in parentheses, using Monte Carlo methods at four sites.

Model	LS1	LS2	HB	CO	No. sites where model was accepted ($R < 6.64$)
Basic	49.97 (7.38)	18.19 (10.04)	23.12 (10.50)	74.03† (93.94)	0
PDE	51.51 (10.46)	16.79 (7.24)	24.29 (12.84)	35.83 (17.54)	0
PDI	46.28 (0.00)	15.43 (4.52)	19.23 (2.72)	62.08 (90.04)	3
PDM	47.69 (2.82)	15.34 (4.34)	19.09 (2.44)	38.71† (23.30)	3
FL	52.71 (12.86)	15.36 (4.38)	20.75 (5.76)	44.60† (35.08)	2
FL + PDE	53.07 (13.58)	15.63 (4.92)	21.74 (7.74)	27.06 (0.00)	2
FL + PDI	49.25 (5.94)	14.97 (3.60)	17.87 (0.00)	43.70† (33.28)	3
FL + PDM	50.04 (7.52)	13.17 (0.00)	18.24 (0.74)	29.27 (4.42)	3

Notes: Site abbreviations: LS1, La Selva I; LS2, La Selva II; HB, Hacienda Baru; CO, Corcovado. All model fits were within the 95% confidence interval calculated from simulated data with the exception of those from Corcovado that are indicated by daggers (critical $P = 0.05$). All likelihood ratios are pairwise calculations between −log likelihood of the given model (row) and that of the best-fit model at that particular site (column). Values of $R < 6.64$ indicate that the fits of the two models are not significantly different at a 99% confidence level. The last column is the number of sites for which the model was acceptable (insignificantly different from the best-fit model) based on likelihood ratios.
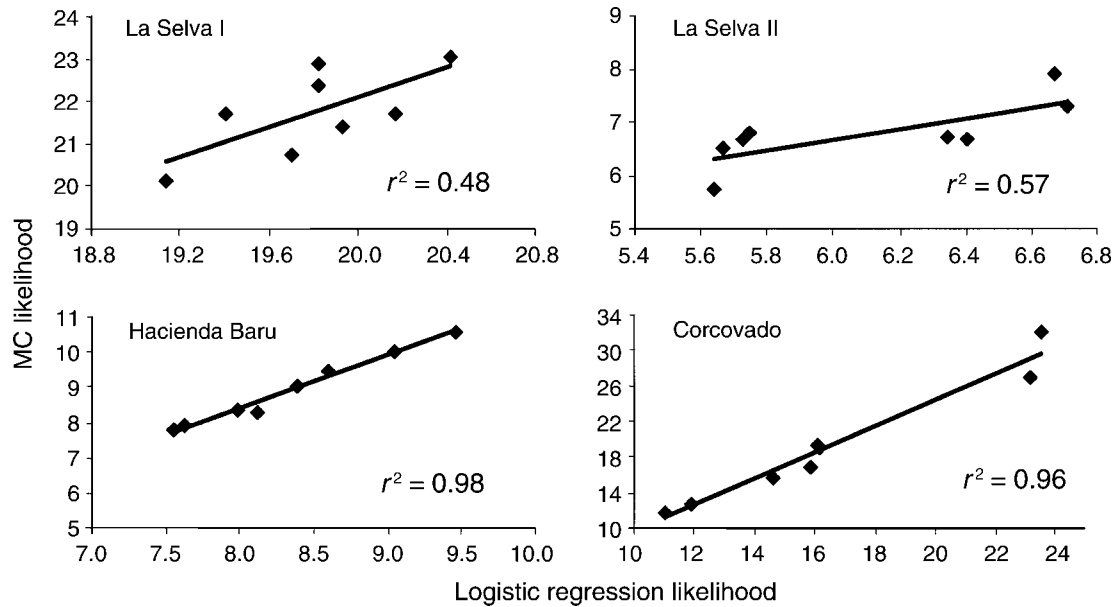
FIG. 4. Relationship between model fits based on logistic regression and Monte Carlo methods of measuring likelihoods (La Selva I, $F_{1,6} = 15.98$, $P = 0.007$; La Selva II, $F_{1,6} = 21.42$, $P = 0.004$; Hacienda Baru, $F_{1,6} = 27.90$, $P = 0.002$; Corcovado, $F_{1,6} = 104.48$, $P < 0.0001$; $N = 8$ for all comparisons).

Monte Carlo generated model fits (Table 2). Positive spatial autocorrelation was detected at Hacienda Baru ($P < 0.05$) and Corcovado ($P < 0.01$). For the other two sites, the probability values associated with positive spatial autocorrelation were suggestive, but insignificant (La Selva I, $P = 0.15$; La Selva II, $P = 0.16$). While these findings suggest that there is spatial autocorrelation in at least two of the occupancy patterns, this conclusion is dependent on the assumption that the model is a reasonable descriptor of the beetles metapopulation dynamics.

DISCUSSION

Spatial autocorrelation is ubiquitous in ecological data. For example, Smith and Gilpin (1997) found strong positive spatial autocorrelation in a metapopulation of the American pika where southern patches were disproportionately empty compared to northern patches. Smith and Gilpin (1997) hypothesized that the spatial autocorrelation was caused by two possible factors, either the "position effects," which, in short, comprise a set of exogenous factors (i.e., climate, predation, competition), or "spatial autocorrelation effects" which essentially are endogenous factors (i.e., dispersal limitation). Given the best-fit model, the patch occupancy pattern of *C. fenestrata* was positively spatially autocorrelated at two of the sites and positively, but insignificantly, spatially autocorrelated at the other sites. Results suggest the presence of exogenous spatial correlating factors because portions of two of the four sites were flooded during the study. In addition, endogenous effects (dispersal limitation) may also be a cause of a portion of the observed spatial autocorre-

lation in the observed patch occupancy patterns judging from dispersal limitation observed in a concurrent mark–recapture study (Johnson 2003).

Previous methods of evaluating patch occupancy models have used a variety of methods that are lacking in various ways. Using model development data to evaluate a model (Hanski 1994, Moilanen et al. 1998) lacks a rigorous test that requires independent data (Power 1993). Results from the present study indicate that fits to model development data are inconsistent indicators of the predictive value of a model. Metapopulation-level statistics such as the proportion of occupied patches (Wahlberg et al. 1996, McCarthy et al. 2000) and turnover rates (Hanski 1994) ignore possibly important patch-specific information. The present study indicates that the proportion of occupied patches is a poor indicator of the predictive power of a model. Turnover rate was only a fair predictor of the model fit, explaining 44% of the variation in the model fits estimated from the Monte Carlo method. Such broadstroke approaches may falsely suggest that a model fits the data, when in fact on a patch-by-patch basis the model is a poor fit.

Logistic regressions are commonly used tools in both parameterizing and evaluating patch occupancy models (Hanski 1994, Hanski et al. 1996, Wahlberg et al. 1996, ter Braak et al. 1998, Moilanen et al. 1998, McCarthy et al. 2001). When only one occupancy pattern is available, likelihoods produced by logistic regressions discount autocorrelation in the spatial occupancy pattern (instead assuming independence among data points), thus, are termed pseudo-likelihoods (ter Braak et al. 1998). In the present study, I compared the pseudo-

likelihoods from logistic regression to likelihoods derived from Monte Carlo simulation of *C. fenestrata* patch dynamics. At three of the four sites there were significant positive correlations between the likelihoods produced from the Monte Carlo and logistic regression methods, while the relationship at the fourth site was marginally insignificant. These results suggest that, even when there is spatial autocorrelation in occupancy data, the logistic regression is an acceptable measure of model fits to metapopulation data.

Concurrent studies on *C. fenestrata* indicated the following points: stochastic flood events cause great reductions of *C. fenestrata* populations in the flood zone (Johnson 2004*b*), immigration probability is positively correlated with patch size, and emigration probability is negatively correlated with patch size (Johnson 2003). In the present study, I used the IFM to evaluate whether these three aspects of *C. fenestrata* biology affect the beetle's regional population dynamics. Explicitly modeling regional extinction caused by flooding improved the fits of the models, suggesting that flooding is important to the regional dynamics of *C. fenestrata*. The traditional patch occupancy models such as the IFM assume that extinction is asynchronous among neighboring patches, and that synchrony in colonization events causes observed spatial correlation in occupancy patterns (Hanski 1994). Results from the present study indicate the presence of spatial synchrony in extinctions due to flooding events.

Patch-size-dependent migration has been demonstrated in a number of species (Raupp and Denno 1979, Kareiva 1985, Turchin 1986, Bach 1988, Hill et al. 1996, Hanski et al. 2000). In general, immigration probability is positively correlated with patch size while emigration probability is negatively correlated with patch size (Kareiva 1985, Turchin 1986, Hanski et al. 2000, Johnson 2003). These results are consistent with the resource concentration hypothesis which states that herbivores are more likely to find and remain in large stands of their host plants (Root 1973, Kareiva 1985). For *C. fenestrata*, adding patch-size-dependent emigration improved the fits to model development data, but patch-size-dependent immigration consistently improved the predictive power of the IFMs; thus suggesting that patch-size-dependent migration was important in shaping the regional dynamics of *C. fenestrata*.

In this study, I addressed two criticisms of the basic form of Hanski's IFM: that it ignores potentially important biotic and abiotic effects on regional population dynamics, and that a number of methods for model evaluation are suboptimal in various ways. I demonstrated that patch size-dependent migration and asynchronous extinctions significantly affected the regional dynamics of *C. fenestrata*. The flood effect can be particularly important to regional dynamics because such spatiotemporally correlated extinctions can significantly reduce persistence time of a metapopulation (Harrison and Quinn 1989). Finally, while the Monte Carlo method was developed for model parameterization (Moilanen 1999), the present study is the first to use the Monte Carlo method to test the predictive value of a patch occupancy model with independent data. This study suggests that the logistic regression method of model fitting is an acceptable substitute for the Monte Carlo method even when occupancy patterns are spatially autocorrelated.

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APPENDIX A

A discussion of selecting the appropriate basic incidence function model is available in ESA's Electronic Data Archive: *Ecological Archives* E086-169-A1.

APPENDIX B

A table showing parameter estimates for the eight incidence function models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-169-A2.

APPENDIX C

A table showing observed metapopulation statistics and model predictions is available in ESA's Electronic Data Archive: *Ecological Archives* E086-169-A3.