

Patchy Reaction-Diffusion and Population Abundance: The Relative Importance of Habitat Amount and Arrangement

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ABSTRACT: A discrete reaction-diffusion model was used to estimate long-term equilibrium populations of a hypothetical species inhabiting patchy landscapes to examine the relative importance of habitat amount and arrangement in explaining population size. When examined over a broad range of habitat amounts and arrangements, population size was largely determined by a pure amount effect (proportion of habitat in the landscape accounted for >96% of the total variation compared to <1% for the arrangement main effect). However, population response deviated from a pure amount effect as coverage was reduced below 30%–50%. That deviation coincided with a persistence threshold as indicated by a rapid decline in the probability of landscapes supporting viable populations. When we partitioned experimental landscapes into sets of “above” and “below” persistence threshold, habitat arrangement became an important factor in explaining population size below threshold conditions. Regression analysis on below-threshold landscapes using explicit measures of landscape structure (after removing the covariation with habitat amount) indicated that arrangement variables accounted for 33%–39% of the variation in population size, compared to 27%–49% for habitat amount. Thus, habitat arrangement effects became important when species persistence became uncertain due to dispersal mortality.

Keywords: persistence threshold, spatially explicit population model, fragmentation, landscape ecology, structured landscapes, dispersal.

For much of the earth’s terrestrial land base, large expanses of pristine habitats are becoming reduced in size and fragmented (Ehrlich 1988; McIntyre and Barrett 1992; Law and Dickman 1998). Increasing human populations and attendant land-use intensification (e.g., cultivation, grazing, urban development) have resulted in the loss and

subdivision of native habitats (Saunders et al. 1991), elevated species extinction rates (Pimm et al. 1995), and lowered species diversity within managed ecosystems (Rapport et al. 1985). Because of the compelling implications for conservation science, these observations have motivated an expansion of research focused on how habitat fragmentation affects the distribution, abundance, and persistence of populations inhabiting patchy landscapes (Kareiva 1990; Opdam 1991; Kareiva and Wennergren 1995; Hanski 1999).

Habitat fragmentation has been described as the most serious threat to the maintenance of biological diversity (Wilcox and Murphy 1985). The degree to which one agrees with this claim depends on how “fragmentation” is defined. Fragmentation is a multidimensional issue that can simultaneously involve the loss of habitat, a shift in the patch-size distribution toward smaller patches, and an increase in the distances separating habitat patches (Wiens 1989). Although habitat loss is viewed unequivocally by ecologists as an important factor explaining declines in species populations (Simberloff 1988), the same cannot be said for those factors related to the arrangement of habitats. Because fragmentation occurs through a process of habitat destruction under most circumstances, the effects of habitat amount and habitat arrangement on populations are confounded (Fahrig 1997). Consequently, it can be difficult for observational studies conducted along a fragmentation gradient to partition the population response between habitat-loss and habitat-arrangement components. Although modeling studies have shown that spatial arrangement can influence the size and persistence of populations (Cantrell and Cosner 1991; Davis and Howe 1992; Doak et al. 1992; Adler and Nuernberger 1994; Boswell et al. 1998; Hill and Caswell 1999; Holyoak 2000), what continues to be debated (see Sih et al. 2000) is the relative importance of habitat amount versus habitat arrangement in explaining observed variation in populations inhabiting patchy landscapes.

Some studies have concluded that habitat arrangement is the key determinant of population response (Hiebeler 2000) and that habitat placement is a vitally important

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management consideration if conservationists are to compensate for the effects of habitat destruction on population persistence (Hill and Caswell 1999). Other investigators have found the antithesis, namely, that the effects of habitat amount far outweigh effects associated with habitat arrangement and that habitat placement can rarely mitigate extinction risks induced by habitat loss (Fahrig 1997, 1998). Further complicating the debate is the possibility that the relative influences of habitat amount and arrangement on a population may shift when some critical threshold (sensu Turner and Gardner 1991) in landscape structure is encountered (Andr  n 1996; Bascompte and Sol   1996).

Our goal in this article is to examine independently the effects of varying amounts and configurations of habitat at a landscape scale, with particular attention to critical persistence thresholds. In place of mathematical analysis, we numerically simulate population dynamics over randomly generated landscapes with specified levels of habitat quantity and spatial aggregation. A discrete reaction-diffusion model is used to estimate a long-term equilibrium population for each landscape. We systematically sample the habitat amount and arrangement to address three questions related to population response in spatially structured habitats. First, what is the relative importance of habitat quantity versus spatial arrangement in explaining variation in population size among landscapes? Second, do critical persistence thresholds exist, and do they affect our assessment of the relative importance of habitat quantity and arrangement in explaining variation in abundance? Finally, are there key attributes of landscape structure that can serve as predictors of population response? Furthermore, we compare our modeling approach and findings with those of others in an attempt to explain some of the differences in conclusions reported in the literature.

Methods

Patchy Reaction-Diffusion

At certain spatial and temporal scales, organism movement has been likened to molecular diffusion, an analogy that has spawned a long history in biodiffusion modeling (Turchin 1998). Under this approach, movement is formulated as a random walk (Fisher 1937) undertaken by dispersing organisms. When summed across the individuals composing a large population, a deterministic population-diffusion model results (see Okubo 1980). Because biodiffusion models often account for reproduction as well as movement, they are closely allied to biochemical reaction-diffusion models (Turing 1952), with reproduction and dispersal as the reaction and diffusion components, respectively (Segel and Jackson 1972). Although the move-

ment path of individual organisms may be more complicated than a simple diffusion process, stochastic simulations suggest that in the aggregate, population distribution and abundance patterns can be approximated well by biodiffusion models over large time scales (Johnson et al. 1992; Holmes 1993). Early reaction-diffusion models were directed at understanding the spread of invading organisms across homogeneous habitat (Skellam 1951; Holmes et al. 1994). Although these spatially unstructured models proved useful in explaining such phenomena as plankton blooms (Kierstead and Slobodkin 1953) or geographic range extensions (Lubina and Levin 1988; Hengeveld 1989; Okubo et al. 1989), their continuous-habitat assumptions (compelled by their single-patch focus) limited their suitability for studying heterogeneous systems.

Allen (1987), following Levin (1974), proposed a spatially discrete reaction-diffusion model for a complex of habitat patches. We have noted elsewhere that for species that establish and defend distinct breeding territories, territory size defines a convenient spatial scale over which reproduction and dispersal processes occur (Bever and Flather 1999b). Under these circumstances, it is useful to replace the Levin-Allen patch-based formulation with a network of appropriately sized grid cells that converts the habitat map into a lattice representation reflective of breeding territories. Furthermore, discretizing reaction-diffusion models with respect to time converts a cellular system of ordinary differential equations into a coupled map lattice (Kaneko 1993) consisting of an enlarged system of difference equations (Holmes et al. 1994). Formulating the model as discrete units of space and time allowed us to explore population responses to a very general set of habitat layouts (Bever and Flather 1999b).

In our discrete patchy reaction-diffusion formulation, population abundance over a landscape is modeled as

$$v_{it} = \min \{b_{it}, \sum_{j=1}^N [1 + r_j(v_{j,t-1})]v_{j,t-1}g_{ji}\} \quad \forall i, t, \quad (1)$$

where i and j each index all cells (i.e., potential breeding territories) in the landscape, v_{it} is the population in cell i at time t , b_{it} represents adult carrying capacity in cell i for time period t , $r_j(v_{j,t-1})$ is the net per capita rate of reproduction within cell j (not accounting for mortality associated with dispersal), and g_{ji} reflects the probability of an individual emigrating from breeding territory j to territory i a full breeding season later by any number of possible routes.

For simplicity, we make a number of assumptions related to the mechanisms of dispersal and reproduction. First, we assume that individuals disperse identically from the center of each habitat cell in uniform random direc-

tions. The probability that an individual disperses from one habitat cell to another declines with distance (x) according to the following Weibull distribution (Johnson and Kotz 1970):

$$f_x(x) = \frac{\varphi}{\mu} \left[\frac{(x - \delta)}{\mu} \right]^{\varphi-1} \exp \left\{ - \left[\frac{(x - \delta)}{\mu} \right]^{\varphi} \right\},$$

$$x > \delta, \mu > 0, \varphi > 0, \quad (2)$$

where μ defines a mean dispersal distance from the source cell, with a minimum dispersal distance of δ . As in Fahrig (1992), dispersal probabilities follow an exponential distribution when $\varphi = 1$. Varying the shape parameter (φ) away from 1 allows additional flexibility for approximating a broader range of dispersal distribution possibilities. Diffusion proportions (g_{ij}) for equation (1) were estimated using equation (2) by numerical integration over distances and angles defined by the boundaries of each destination cell (indexed by i) relative to the center of each cell that served as a source of dispersers (indexed by j). Thus, emigrants from any breeding territory move on a trajectory and over a distance that is independent of the neighborhood surrounding the territory. We have outlined elsewhere (Bever and Flather 1999b) how our formulation could be modified to capture habitat- or density-biased diffusion.

Second, we assume that the net per capita rates of reproduction and carrying capacity are constant across all habitat cells and across all time periods in the simulation. Cellular populations from equation (1) in excess of b_{ii} in each time period are treated as mortality resulting from dispersal into saturated territories. Dispersal-related mortality also occurs when an individual emigrates to a non-habitat cell or outside the boundary of the habitat complex. Thus, the landscape lattice on which our population model operated was spatially autonomous (no immigration of individuals from outside the complex) with absorbing boundaries (individuals that dispersed beyond the complex boundary died) as in Fagan et al. (1999). Although we assume a constant mean fecundity rate with a simple cap on adult breeders for each territory, nonlinear density-dependent population growth emerges as a property of population dynamics at the landscape scale through competition for space and elevated dispersal-related mortality (Bever and Flather 1999b).

Landscape Simulation

Past modeling efforts exploring the effects of patch structure on populations have often treated the arrangement of habitats in a highly stylized manner (e.g., simple random distributions or orderly geometric clustering; Doak et al.

1992). Such representations of habitat heterogeneity have been convenient simplifications to support analytical solutions (Lande 1987) and have been useful in the context of neutral landscape analyses (Gardner and O'Neill 1991). However, binary maps (landscapes with two states) derived from actual landscape scenes have been found to have much higher degrees of spatial aggregation than randomly generated landscapes (Schumaker 1996). Consequently, simple random maps offer little opportunity for systematically examining population responses along a gradient of habitat patchiness that is more typical of that observed in natural systems.

Approaches to generating landscapes that mimic the level of aggregation observed in actual landscape data are now common (see Gardner and O'Neill 1991; Gustafson and Parker 1992; Palmer 1992; Fahrig 1997; With et al. 1997; Hargis et al. 1998; Wiegand et al. 1999). We generated binary (habitat, nonhabitat) landscape maps using the midpoint displacement method (Saupe 1988) as coded within RULE (Gardner 1999). This algorithm has its basis in fractal geometry and was chosen since it has been found to generate landscapes that strongly resemble real landscapes (Keitt and Johnson 1995). Furthermore, this algorithm has the advantage of allowing one to vary the amount of habitat and the degree of habitat aggregation in simulated landscapes easily and independently (With and King 1997).

The midpoint displacement method generates a continuously varying set of real numbers on a two-dimensional lattice through an iterative process of successive division, interpolation, and random perturbation. The real number value (y) in any grid cell is defined as the mean of its four nearest neighbors and a random variate drawn from a Gaussian distribution with mean 0 and variance equal to $\sigma^2(1/2)^{nH}$, such that the probability density function is given by

$$f_y(y) = \frac{1}{\sqrt{2\pi\sigma}} e^{-y^2/2\sigma^2(1/2)^{nH}}. \quad (3)$$

For the purposes of our simulation experiments, we fixed σ^2 to 1 and varied H to reflect the degree of spatial autocorrelation. The dimension ($m \times m$) of the lattice is specified in the choice of n , where n represents the iteration of successive map divisions and is related to m , as $m = 2^n$. All of our simulated landscapes were generated with $n = 5$ (i.e., a 32×32 lattice). The surface of real numbers over the map lattice is translated into discrete landscape states by generating a relative cumulative frequency distribution. Under this translation, each cell is represented by a value z_i that varies over the interval 0–1. Users can specify a habitat proportion (p) such that cells are classified

as habitat if $z_i \leq p$. In this discrete landscape case, H values near 1 promote a contagious pattern of habitat occurrence (producing highly aggregated habitat layouts), and H values near 0 promote heterogeneity (producing highly disaggregated habitat layouts; fig. 1). Because H affects the spatial aggregation of habitat within a landscape, we treat H as an index of habitat arrangement.

Hypothetical Species (Reaction-Diffusion Parameter Choices)

We parameterized our reaction-diffusion model to reflect a generic forest-breeding passerine bird that prefers habitat interiors and therefore should be sensitive to habitat arrangement effects (Boulinier et al. 1998 and citations therein). Such species are often migratory and during the breeding season defend a ≈ 1 -ha territory (Temple and Cary 1988). Recall from equation (1) that $r_j(v_{j,t-1})$ is the net per capita reproduction within a territory not accounting for dispersal-related mortality. We derived an estimate of $r_j(v_{j,t-1})$ from clutch size, nest success, post-fledging survivorship, subadult survivorship, and adult survivorship data in the literature (table 1). This parameter set was used to bound an estimate of $r_j(v_{j,t-1})$. The lower bound was based on an estimate over the full annual cycle without partitioning out dispersal-related mortality (per capita $r_j(v_{j,t-1}) = [4(0.7)(0.69)(0.62) + 2(0.66)]/2 - 1 \approx 0.26$). The upper bound was based on assuming that all dispersal-related mortality occurred once fledglings attained independence and that no adult mortality occurred during the breeding season (per capita $r_j(v_{j,t-1}) = [4(0.7)(0.69) + 2]/2 - 1 \approx 0.97$). The estimate of net per capita reproduction used in the simulation experiments was simply the midpoint of those two values ($r_j[v_{j,t-1}] = 0.6$).

The availability of empirical estimates of dispersal distances is much sparser compared to demographic param-

eters. Villard et al. (1995 and citations therein) found that median breeding dispersal (the movement of adults between successive breeding sites) distances are usually < 350 m. For our hypothetical species that defends a 1-ha territory, that translates into three territory units from the center of the previous year's territory. Natal dispersal (the movement of individuals from their birth site to their first breeding territory) can be much further. Villard et al. (1995) speculated that natal dispersal distance could be an order of magnitude larger than breeding dispersal distances ($\approx 3,500$ m, or 35 territory units). Based on these data, we chose a mean dispersal distance of four territory units ($\mu = 4$) with a minimum distance of 0 ($\delta = 0$). Recognizing that our formulation does not distinguish breeding and natal dispersal (all individuals disperse identically), we chose to set the shape parameter to one-half ($\varphi = 0.5$) in order to draw the distribution closer to both axes (fig. 2). The resulting lower portion (small distances) of this distribution approximates breeding dispersal probabilities, while the upper tail (large distances) approximates natal dispersal probabilities (fig. 2). Under these parameter choices, 63% of dispersing individuals settle within three territories of their previous location, yet individual movements (with an admittedly small probability) can span the simulated landscapes. Our experiment was thus conducted on a globally coupled map lattice (sensu Kaneko 1993) interspersed with nonhabitat where species dispersal events were concentrated within a local neighborhood.

Simulation Experiment and Data Analysis

A series of simulation experiments were conducted to examine the effects of habitat amount (p), arrangement (H), and their interaction ($p \times H$) on equilibrium populations within our 32×32 -cell landscapes. We have scaled the landscapes for our experiment such that terri-

Habitat proportion = 0.3

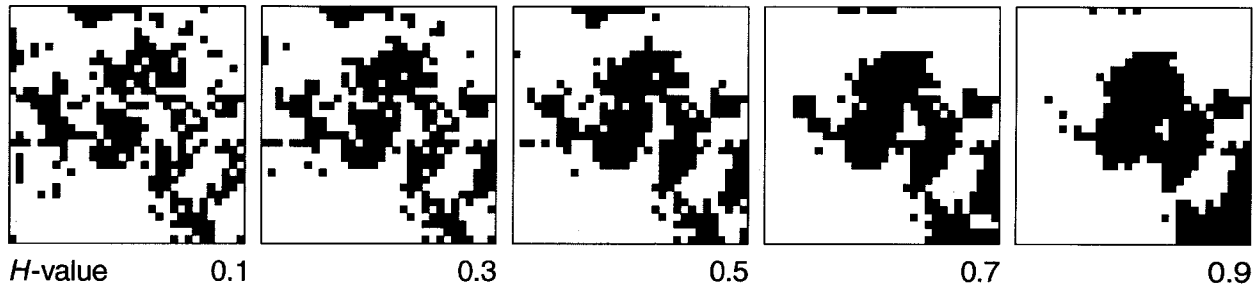


Figure 1: Sequence of landscapes showing the influence of H (aggregation index) on habitat arrangement; all landscapes have 30% habitat (dark)

tory size defined the grain and the length of rare long-distance dispersal defined the spatial extent. Habitat amount was altered by specifying the proportion of the landscape that was classified as suitable habitat. This proportion was varied from 0.1 to 0.9 in increments of 0.1. Habitat arrangement was specified by varying H in equation (3) from 0.1 to 0.9 in increments of 0.1. Each treatment combination was replicated 30 times. This resulted in a 9×9 , balanced, fixed-effects factorial design with 2,430 experimental units. We chose this design because we were interested in examining the effects of habitat amount, arrangement, and their interaction over a broad spectrum of treatment levels (see Cochran and Cox 1957). The response variable in these experiments was population size as determined by imposing our model (eq. [1]) on each landscape treatment. Initial populations within each landscape were set to fully saturated conditions (i.e., all habitat cells were populated with two breeding individuals). The model was run until the population either went extinct or reached a nonzero equilibrium level.

Our intent here is to explore landscape-scale population behavior of a hypothetical species whose defined vital rates and movement rules offer a high chance of detecting habitat arrangement effects (as in Fahrig 1997). Moreover, by modeling populations deterministically and introducing variation in population response through landscape structure replication, we have ensured that all variation in population response will be a function of either the amount or arrangement of habitat on the landscape or both. Failure to observe arrangement effects under these circumstances would be quite informative.

The data from this experiment formed the basis for answering the three questions we posed earlier. To address the relative importance of habitat quantity and spatial arrangement (first question), we used two-way ANOVA (GLM procedure; SAS 1989). Although our estimated equilibrium populations were neither normally distributed nor homoscedastic, inferences based on ANOVA appear to be robust to violation of these assumptions (Zar 1996)

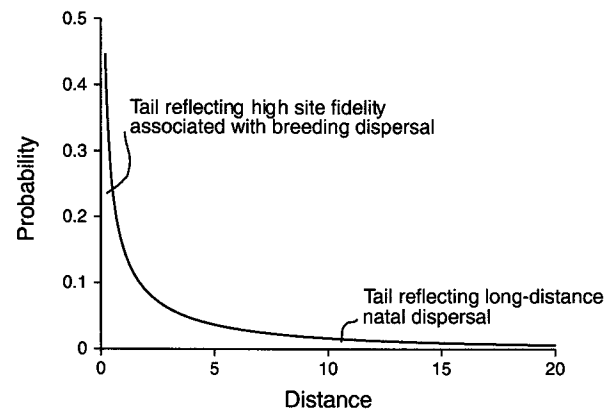


Figure 2: Probability density function (Weibull distribution: $\delta = 0$, $\mu = 4$, $\varphi = 0.5$) for dispersal distance used in the simulation experiments.

as long as the number of replicates for each treatment are nearly equal (Glass et al. 1972).

Addressing the question of whether the existence of a persistence threshold would affect the relative importance of habitat amount and spatial arrangement on equilibrium populations (second question) required that we first determine if our simulated landscapes exhibited a threshold associated with population persistence. A critical threshold has been defined as “the point at which there is an abrupt change in a quality, property, or phenomenon” (Turner and Gardner 1991, p. 7). Mathematical analysis of analytical population models has led to definitive determinations of persistence thresholds (see Lande 1987). However, the analytical models that produced these crisp thresholds are based on simplifying assumptions (e.g., random distribution of habitats that are equally accessible to all dispersers) that limit their relevance to truly heterogeneous environments. Under numerical simulation of populations inhabiting patchy landscapes when a mortality cost is associated with dispersal, it was not clear that a crisp and unambiguous persistence threshold would be observed.

To acknowledge this uncertainty, we used two methods to define a persistence threshold among our simulated landscapes. Both methods relied on the persistence probabilities associated with each landscape treatment to define the threshold. Persistence probabilities were estimated as the number of landscape replicates within a treatment that supported nonzero equilibrium populations divided by the total number of treatment replicates (30 in our case). For the first method, we looked for those levels of habitat amount and aggregation that first resulted in persistence probabilities <1.0 as in Fahrig (1997). In the remainder

Table 1: Parameter estimates and literature sources used to estimate of $r_j(v_{j,t-1})$

Parameter	Value	Source
Clutch size	4	Morse 1989 ^a
Nest success	.70	Ricklefs 1973 ^b
Postfledging survivorship	.69	Ricklefs 1973 ^c
Subadult survivorship	.62	Ricklefs 1973
Adult survivorship	.66	Morse 1989 ^d

^a Mode from frequency distribution of wood warblers.

^b Reports a range of 30%–80%.

^c Based on a mean from four species.

^d Average of seven Parulene warblers.

of the article, we refer to this method as “less than total persistence” (LTTP).

The second method was based on classification tree analysis (CTA; Breiman et al. 1984). The purpose of CTA is to develop a classification of observations into discrete sets. This analysis method is nonparametric and sorts observations into categories by developing a binary decision tree whose rules for assigning membership are based on a suite of explanatory variables (De'ath and Fabricius 2000). CTA assigns class membership in a way that minimizes the overall misclassification rate given the set of explanatory variables. Our objective in using CTA was to classify each landscape replicate as either persistent or extinct using habitat amount (p) and its degree of aggregation (H) as explanatory variables. An overall misclassification rate was estimated using cross-validation procedures (Breiman et al. 1984).

We used the persistence threshold defined by each method to partition the treatments into above-LTTP, below-LTTP, above-CTA, and below-CTA threshold sets. For each method, we then ran separate ANOVAs above and below the persistence threshold to see if the relative importance of habitat amount and arrangement in explaining variation in population size changed as we crossed the persistence threshold.

Our final question (are there key landscape structure attributes that predict population response?) was motivated to determine whether recommendations related to the placement of habitat on managed landscapes could be developed. Although the fractal-based algorithm for generating landscapes offered a convenient way to independently vary habitat quantity and its arrangement, the H parameter in equation (3) does not lend itself to intuitive interpretation leading to spatially explicit habitat recommendations for conservationists. Consequently, we characterized landscape structure according to a small subset of attributes that we felt captured important differences in the arrangement of habitat. By “landscape structure,” we mean those general factors that relate to the spatial distribution of habitat (see Keymer et al. 2000) and not the amount of habitat in the landscape.

Based on previous work (Bever and Flather 1999b; Trzcinski et al. 1999), we defined two broad sets of landscape structure attributes. One set was related to landscape-wide descriptors and included average habitat patch size, number of habitat patches, total length of habitat edge, and the mean nearest-neighbor distance among habitat patches. A second set was related to structural attributes specifically tied to the largest patch of habitat in the landscape and included the size of the largest patch, the total edge length of the largest patch and its converse, and the shape of the largest patch. Patch shape was measured as the perimeter of the largest patch normalized to a square

reference shape and quantified as $P_{LG}/4\sqrt{A_{LG}}$, where P_{LG} and A_{LG} are the perimeter and area of the largest patch, respectively (Austin 1984). Because these landscape structure attributes co-vary with habitat amount in predictable ways (e.g., the size of the largest patch is expected to increase with increasing habitat amount), we used regression analysis to statistically remove the empirical relationship of habitat amount from each landscape structure attribute using either linear (including n th-order polynomials) or nonlinear models, selecting that model resulting in the highest R^2 and a favorable distribution of residuals (i.e., symmetry about 0.0). In this manner, we transformed our measures of landscape structure into a set of residual arrangement variables that were now independent of the amount of habitat in the landscape.

The descriptors of landscape structure, along with the proportion of available habitat (p), were then subjected to a variable selection procedure to determine the simplest predictive model of population size that preserved the greatest explanatory power from among a set of candidate models suggested by Akaike's information criterion (AIC). Conceptually, AIC measures the loss of information $I(\tau, q)$ when model q is used to approximate truth τ . This can be written as the difference between two expectations (taken with respect to τ) as

$$I(\tau, q) = E_{\tau}\{\log_e[\tau(\omega)]\} - E_{\tau}\{\log_e[q(\omega | \Psi)]\},$$

where $q(\omega | \Psi)$ represents the approximating model q for data ω given the parameters Ψ . Low values of AIC indicate a low loss of information, and we seek that model that retains the greatest information content (see Burnham and Anderson 1998 for details). Habitat amount was forced into all candidate models to retain our ability to assess the relative importance of amount and arrangement. Our final model was selected based on a three-step process. First, we estimated all possible regressions (REG procedure; SAS 1989) and ranked all k -variable models (where k is the number of predictor variables) from low to high AIC. Candidate models for possible selection were defined as each k -variable model with the lowest AIC. Second, from this set of candidate models, we identified that model with the lowest AIC and labeled it “the best.” Finally, we chose the most parsimonious model (i.e., had the smallest k) that also preserved the explanatory power of the best model ($R_{\text{best}}^2 - R_{\text{simpler}}^2 \leq 0.01$) as our final model. A model was selected in this manner for each method of defining the persistence threshold.

Results

Habitat Amount versus Arrangement

When analyzed across the full complement of landscape treatments, both main effects (habitat amount and ar-

rangement) and their interaction had statistically significant effects on population size (table 2). However, habitat amount was by far the most important, accounting for nearly 97% of the total variation in population size. Arrangement and its interaction with habitat amount each accounted for <1% of the variation. These results suggest that the size of our simulated populations is largely driven by a pure habitat amount effect (*sensu* Andrén 1994, 1996), implying that the abundance-landscape relationship can be approximated by a simple linear function of habitat amount.

Since we imposed a population limit of two individuals in each habitat cell, the expected slope of the relationship between habitat amount and abundance under a pure habitat amount effect would be 2.0. A bivariate plot of population size and habitat proportion does not support a pure habitat effect across the full range of habitat amounts examined in the simulation experiment (fig. 3A). The average slope among population medians for each level of habitat amount was estimated as 2.5, and equilibrium populations show a pattern of increasing deviation from a pure habitat-loss effect once the habitat proportion within the landscapes was ≤ 0.5 . A three-dimensional plot of the treatment means further illustrates this deviation (fig. 3B). The slopes of the grid lines reflecting the relationship between population size and arrangement are essentially 0 for those landscapes with substantial amounts of habitat (≥ 0.7). Those slopes become increasingly negative as habitat amounts fall below 0.5, which reflects the impact of increasing dispersal-related mortality under more disaggregated landscape structures (low values of H). Consequently, there does appear to be a region in the experimental treatment space (fig. 3B) where landscape populations are influenced by the arrangement of habitat.

Persistence Thresholds and Their Effects

A plot of persistence probability against habitat amount and arrangement (fig. 4A) indicated that persistence decayed rapidly once habitat dropped below 50% for low degrees of aggregation ($H \leq 0.3$) and below 40% for high degrees of aggregation ($H \geq 0.7$). Moderate levels of habitat aggregation ($0.4 \leq H \leq 0.6$) showed moderate declines in persistence in the 40%–50% habitat range but declined rapidly below 40%. The abrupt change in persistence is indicative of a critical threshold, and it is generally coincident with the region in figure 3B where arrangement effects appear most to influence population size. The persistence threshold using the LTTP method was determined to be those landscape treatments where all landscape replicates were persistent (*upper dashed line*, fig. 4A). Any further reduction in habitat amount or aggregation resulted in persistence probabilities that were <1 (i.e., the

Table 2: ANOVA results examining the influence of habitat amount (p) and arrangement (H) on equilibrium population levels

Source of variation	df	Type III SS	Percentage of total SS	F	P
p	8	959,431,514	96.8	15,871	<.0001
H	8	7,517,621	.7	124	.0001
$p \times H$	64	6,430,890	.6	13	.0001
Error	2,349	17,749,595	1.8

Note: Results are from a 9×9 fixed-effects factorial simulation experiment. Population levels estimated by equation (1). SS = sums of squares.

population in at least one of the replicate landscapes went extinct). The decision rules (table 3) for defining the persistence threshold using the CTA method (*lower bold line*, fig. 4A) assigned experimental landscapes into mostly extinct and mostly persistent sets with an overall cross-validation accuracy estimate of 91.5%.

The two persistence thresholds were mapped onto the mean population size response surface (fig. 4B) and used to partition the experimental landscapes into above- and below-threshold sets. The ANOVA results were qualitatively similar for both methods of defining the persistence threshold (table 4). Above the persistence thresholds, habitat amount accounted for >96% of the total variability in population size, while arrangement and the interaction term each accounted for <1% of the variation.

The explanatory power of habitat amount was much reduced among those experimental landscapes defined to be below threshold (table 4). Under the LTTP-defined threshold, habitat amount accounted for about 52% of the variation in population size. Habitat amount accounted for only 30% of the population size variation under the CTA-defined threshold. A portion of the lost explanatory power attributed to habitat amount was redistributed to the arrangement main effect and the interaction term. Whereas arrangement effects accounted for <1% of the total sums of squares above threshold, they accounted for about 6%–10% below threshold (table 4). Similarly, the population size variation accounted for by the interaction term increased from <1% to >6% as landscapes passed from above- to below-threshold conditions. Another substantial change in the partition of population size variation was the increase in the error term when thresholds were encountered. The error variance increased from $\leq 2.5\%$ above threshold to 31% below the LTTP-defined threshold and 57% below the CTA-defined threshold (table 4).

One explanation for the increased error associated with explaining population size below persistence thresholds is that the aggregation index (H ; a measure of arrangement based on the spatial covariation in habitat occurrence) may not be sensitive to changes in habitat configuration that affect landscape population size. We explored this possi-

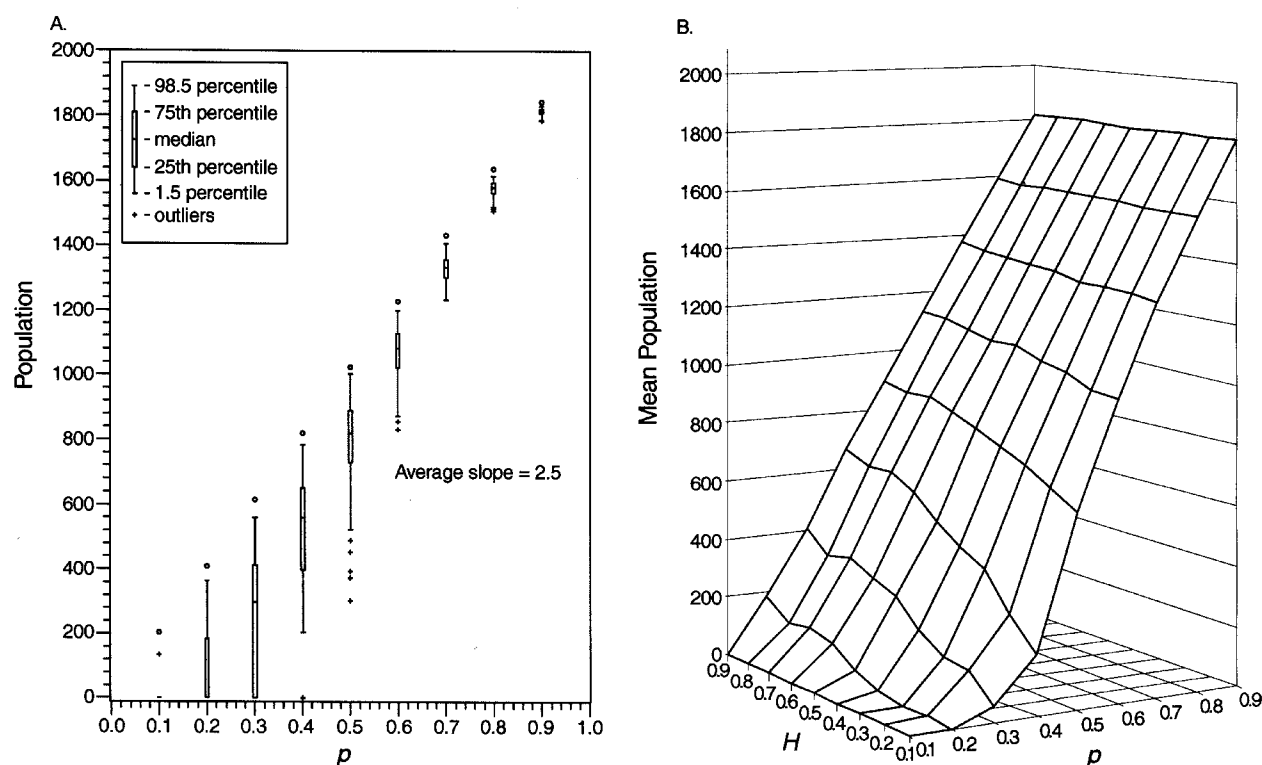


Figure 3: A, Bivariate plot of habitat amount proportion (p) and equilibrium population. Open circles represent the expected population size under a pure habitat effect. The box-and-whisker plots reflect the variability in population size within each habitat amount treatment level. The average slope for the medians was estimated after converting habitat proportion back to raw habitat amount estimates. B, Population treatment means for p and arrangement (H) effects.

bility by measuring specific landscape structure attributes (e.g., total edge, average patch size, etc.) and using them to explain variation in population size rather than relying on H . If the error term is reduced under this analysis, it has the additional benefit of providing more tangible attributes from which to propose landscape management recommendations that would otherwise be obscure if we had to base such recommendations on H alone.

Landscape Structure Predictors

The model selection problem for landscape structure predictors of population size focused solely on those landscapes classified as below a persistence threshold. The search for landscape structure predictors above a persistence threshold would be uninteresting since habitat amount accounted for so much of the variation in population size and the error variance was small (table 4). Our model selection procedure, when implemented on landscapes below the LTTP- and CTA-defined thresholds, identified two four-variable models as the most persi-

monious predictors of landscape population size (table 5). These two models substantially reduced the overall error variance associated with the ANOVA models below threshold. Using H as the sole measure of habitat arrangement resulted in the unexplained variance ranging from 31% to 57% under the two threshold definitions (table 4). By replacing H with specific measures of landscape structure, those error variances were reduced to 18%–34% (table 5).

The final models chosen did not appear to be greatly sensitive to the method used for defining the persistence threshold. Both models selected size of the largest patch and number of patches as important predictors of population size. The models did differ in the edge-related metrics chosen; the LTTP-derived threshold selected total edge length in the landscape, whereas the CTA-derived threshold selected the edge length associated with the largest patch, which suggests that shape as well as size of the largest patch becomes more important as persistence probability declines.

The models also differed with respect to the relative influence of p in predicting population size. Although hab-

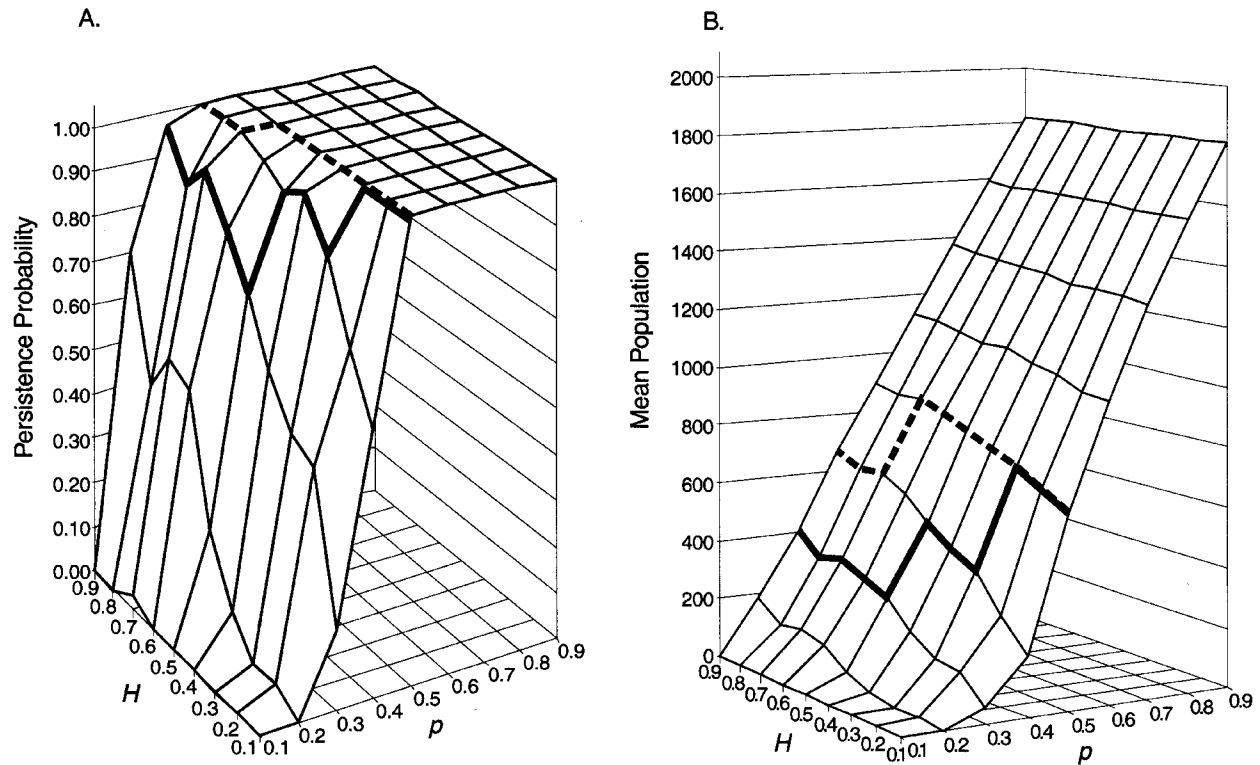


Figure 4: Relationship of (A) population persistence and (B) population treatment means with habitat amount (p) and arrangement (H). Persistence is estimated as the number of replicates within each treatment combination with nonzero equilibrium populations divided by the total number of replicates. Persistence thresholds are mapped using the less than total persistence (LTTP; upper dashed line) and classification tree analysis (CTA; lower bold line) methods.

itat amount remained an important predictor of population size under both threshold definitions, the percentage of variance explained that was attributable to habitat amount declined from 49% to 27% as we shifted from the LTTP- to the CTA-defined threshold (table 5). As the explanatory power of habitat amount was reduced, the percentage of variance explained by all landscape structure variables increased from 33% (LTTP method) to 39% (CTA method). Under the CTA method (i.e., with relatively less habitat), arrangement variables actually accounted for a greater amount of the population size variation than did habitat amount, as evidenced by partial R^2 . The standardized regression coefficients suggest that total length of habitat edge had the greatest effect on population size below the LTTP-defined threshold, while the size of the largest patch had the greatest effect below the CTA-threshold (table 5). Habitat amount had the second largest standardized coefficient under both threshold definitions.

Discussion

Thresholds and the Relative Importance of Habitat Amount and Arrangement

When analyzed over the full range of amount and arrangement treatment levels, our results support the view that habitat amount dominates as an explanation for population size variation in heterogeneous landscapes. More than 96% of the observed variation in population size was explained by the habitat amount main effect. However, we did observe a departure away from a pure amount effect as habitat coverage was reduced below 30%–50% of our total landscape (fig. 3). That departure generally coincided with a persistence threshold as indicated by a rapid decline in the probability of landscapes supporting viable populations (fig. 4). Based on an ANOVA (table 4), we found that habitat arrangement explained a greater proportion of the variation in population size below our persistence thresholds (6%–10%) than it did above those thresholds

Table 3: Decision rules estimated from classification tree analysis to classify 2,430 experimental units into “extinct” and “persistent” sets

Decision rule	Outcome	Number of experimental units	
		Extinct	Persistent
1. Is $p < .4$?			
Yes	Go to 2		
No	Go to 4		
2. Is $p < .3$?			
Yes	Classify as extinct	540	
No	Go to 3		
3. Is $H < .5$?			
Yes	Classify as extinct	120	
No	Classify as persistent		150
4. Is $p < .5$?			
Yes	Go to 5		
No	Classify as persistent		1,350
5. Is $H < .3$?			
Yes	Classify as extinct	60	
No	Classify as persistent		210
Σ		720	1,710

(<1%). Furthermore, when we replaced H with specific measures of landscape structure (after covariation with habitat amount was removed statistically) and regressed amount and structure variables on population size (table 5), we found that even more of the variation in population size was associated with landscape structure (33%–39%). In one case (below the CTA-defined threshold), landscape structure variables explained a greater amount of variation in population size than did habitat amount. These results suggest that both habitat amount and habitat geometry are important considerations in ensuring population persistence once landscapes pass through a persistence threshold, although when habitat amounts become too low, arrangement effects on survival time may be small (see table 1C in Fahrig 1997).

Our result has been anticipated by others and can be traced to the observation that landscape structure measures themselves exhibit abrupt shifts as the proportion of habitat in the landscape changes (Turner 1989; Gardner and O'Neill 1991; Green 1994; Bascompte and Solé 1996). These abrupt shifts in landscape structure are expected to affect other ecological processes such as organism movement and population dynamics. In one of the first empirical attempts to specifically link thresholds associated with structural attributes of landscapes to the distribution and abundance of organisms, Andrén (1994) hypothesized that critical thresholds in landscape structure should also result in a detectable shift in the relative importance of habitat amount and arrangement in explaining variation

in population size among different landscapes. Andrén's (1994) analysis of the literature indicated that for birds and mammals inhabiting archipelago systems, such a threshold may exist when 10%–30% of the original habitat remains. Theoretical work following Andrén (1994) did not support his empirical findings. Fahrig (1997) found little evidence that configuration measures became more important as habitat amounts were reduced. It was not until Fahrig (1998) varied certain life-history and landscape parameters that she observed a habitat-arrangement effect when $\leq 20\%$ of the landscape was covered with suitable breeding habitat.

Our results provide additional support for Andrén's (1994) predictions, although we observed habitat configuration effects with greater amounts of habitat coverage (30%–50% of the landscape). However, we caution against overinterpreting quantitative differences in observed habitat amount levels at threshold. The differences could simply be due to the use of relative measures (percentages of habitat amount on differently scaled landscapes). Our findings also make explicit a link between species persistence thresholds and the landscape where geometry has an important influence on equilibrium population size. This result may offer an explanation for why some empirical studies have failed to find strong evidence for habitat arrangement effects (e.g., McGarigal and McComb 1995; Meyer et al. 1998), namely, that arrangement effects may be difficult to detect when examined over a broad range of habitat amounts, particularly when complicated by additional noise associated with real-world observations.

This raises an important question. In a noisy world, will it be possible for conservationists to detect the threshold effects we report here? The few empirical studies that have specifically evaluated the relative importance of habitat amount and arrangement have found little evidence for threshold effects (Trzcinski et al. 1999; Villard et al. 1999), although our own investigations (C. H. Flather and M. Bevers, unpublished data) suggest that more research into empirical verification seems warranted.

Comparisons with Other Modeling Studies

As we noted previously, the theoretical literature related to the importance of habitat amount versus habitat arrangement is characterized by a considerable degree of ambiguity, with different investigations assigning what appear to be conflicting degrees of importance to each factor (cf. Andrén 1996; Fahrig 1997; Hill and Caswell 1999; Hiebeler 2000). The main finding from our simulation experiment (that habitat arrangement has an important, and perhaps prominent, influence on regional population size over a restricted range of landscape structure) is qual-

Table 4: ANOVA results from above- and below-threshold sets examining the influence of habitat amount (p) and arrangement (H) on equilibrium population levels

Source	Above threshold				Below threshold			
	df	Type III SS (%) ^a	<i>F</i>	<i>P</i>	df	Type III SS (%) ^a	<i>F</i>	<i>P</i>
LTTP-defined threshold:								
p	5	212,663,955 (97.1)	17,518.7	.0001	3	24,365,928 (52.3)	541.2	.0001
H	8	1,631,492 (.7)	84.8	.0001	8	4,859,440 (10.4)	40.5	.0001
$p \times H$	34	1,278,455 (.6)	15.5	.0001	21	3,009,438 (6.5)	9.6	.0001
Error	1,392	3,386,157 (1.5)			957	14,363,438 (30.8)		
CTA-defined threshold:								
p	6	379,144,249 (96.3)	10,497.2	.0001	3	4,111,247 (30.3)	122.3	.0001
H	8	2,687,381 (.7)	55.8	.0001	8	838,578 (6.2)	9.4	.0001
$p \times H$	42	2,096,702 (.5)	8.3	.0001	12	832,985 (6.1)	6.2	.0001
Error	1,653	9,950,720 (2.5)			696	7,798,876 (57.4)		

Note: Population levels estimated by equation (1). LTTP = less than total persistence; CTA = classification tree analysis; SS = sums of squares.

^a The percentage of total variation attributed to each source.

itatively consistent with Andrén (1994, 1996) and Fahrig (1998). Similar population behavior stemming from different models with different biological assumptions adds confidence that our observed population response to spatial heterogeneity is not an idiosyncratic artifact of our particular modeling approach. However, we must also note that our findings deviate fundamentally from the conclusions of others. For example, Hiebeler (2000) found the degree of habitat clustering largely to determine the populations on simulated landscapes, while habitat amount had little effect. This variability in outcome has been both a motivation for further research and a source of great frustration. As summarized by de Roos and Sabelis (1995), spatially explicit population models have produced a “bewildering variety of dynamical phenomena” (p. 347).

Explanations for the varying results regarding the relative importance of habitat amount and arrangement are likely related to the variety of formulations and assumptions in spatially explicit population models. Many investigators have used metapopulation patch occupancy models based on patch-level extinction and colonization rates (e.g., Andrén 1996; Bascompte and Solé 1996; Hill and Caswell 1999; Hiebeler 2000), while others have modeled population response at a territory level based on individual or aggregated birth-death-movement models (e.g., Fahrig 1997; With and King 1997; Boswell et al. 1998; this study). We note, however, that when patch occupancy models are implemented on a lattice and a habitat patch is defined as a cell in that lattice (rather than as a contiguous set of habitat cells), then patch occupancy models based on colonization-extinction processes (e.g., Hill and Caswell 1999) tend to behave much like formulations that model individual rates of reproduction and localized dispersal at the territory level; occupancy and abundance tend to become synonymous at the territory level for many species

(e.g., monogamous noncooperative breeders). Because we would ordinarily expect patch-level colonization and extinction rates to depend more on patch populations than on simple occupancy, it may in fact be more appropriate to interpret the results from these models at the territory scale. For this reason, we found it difficult to argue that this difference in formulation (patch occupancy vs. birth-death-movement models) was necessarily the source of the divergent conclusions on the relative importance of habitat amount and arrangement that are reported in the literature.

Another important difference among these models is the choice of population response variable. Patch occupancy models commonly use a normalized occupancy measure (i.e., the proportion of habitat in the landscape that is in fact occupied by individuals) as their response variable (e.g., Bascompte and Solé 1996; Hill and Caswell 1999; With and King 1999; Hiebeler 2000). Birth-death-movement models, however, tend to measure population response using absolute counts of individuals (e.g., abundance [this study], number of colonies [Boswell et al. 1998]) or binary events (e.g., extinct/not extinct [Fahrig 1997]). We can demonstrate the significance of these differences with our data by comparing plots of abundance and normalized patch occupancy response variables against habitat amount. Figure 5A shows a family of curves portraying our abundance response with respect to habitat amount at three different levels of habitat aggregation. These curves are qualitatively similar to Boswell et al.’s (1998; see fig. 2) plot of ant colony numbers as a function of habitat amount. Converting our abundance response variable to normalized patch occupancy (fig. 5B) results in a family of curves that are qualitatively similar to the proportional patch occupancy results reported by Hill and Caswell (1999; see fig. 5) and With and King (1999; see

Table 5: Regression models selected for predicting population size based on habitat amount (p) and landscape structure variables below the LTTP and CTA persistence thresholds with p forced into the models

Variable	LTTP-defined threshold					CTA-defined threshold				
	$\hat{\beta}$	SE	t^a	$\hat{\beta}'$	Partial R^2	$\hat{\beta}$	SE	t^a	$\hat{\beta}'$	Partial R^2
p	1,633.89	27.59	59.22	.82	.49	1,321.95	37.83	34.95	.92	.27
max_sz	1.00	.07	13.41	.26	.33 ^b	3.04	.13	24.11	1.08	.39 ^b
pat_no	8.68	.56	15.57	.54		1.64	.32	5.14	.17	
tot_edge	-1.85	.09	-21.49	-.83		
edg_lgpat		-2.00	.13	-15.05	-.49	
F	1,127.46					358.22				
P	<.0001					<.0001				
R^2	.82					.66				

Note: Residuals after removing the covariation with habitat amount. We report regression coefficients ($\hat{\beta}$), their SEs, the t statistic testing for a nonzero regression coefficient, the standardized regression coefficients ($\hat{\beta}'$), and partial R^2 estimates attributable to habitat amount and landscape structure variables. Landscape structure variables: size of largest patch (max_sz), number of patches (pat_no), total length of habitat edge (tot_edge), and length of habitat edge associated with the largest patch (edg_lgpat).

^a All regression coefficients are different from 0 ($P < .0001$).

^b The partial R^2 reported here has been summed across all selected landscape structure variables.

fig. 5). Even among studies that did not vary the degree of habitat aggregation (e.g., see fig. 4 in Andrén 1996 and fig. 6 in Bascompte and Solé 1996), we observe qualitative similarities (i.e., a strong convex pattern in the proportional occupancy response variable as habitat is reduced) with figure 5B. Because patch occupancy in these studies is measured as the fraction of available habitat that is occupied, habitat amount effects are dampened. For example, as habitat is reduced from 90% to 60% of the landscape in our model, abundance is reduced by $\approx 45\%$ (fig. 5A), yet proportional occupancy is reduced by $< 20\%$ (fig. 5B). Although we agree with Hill and Caswell (1999) that the proportion of suitable habitat that is occupied is of interest to conservationists, we also note that proportional occupancy can be difficult to interpret without also considering some measure of absolute population response.

Variation in response variable may also explain why our results differ from Fahrig (1997), who found using a birth-death-movement model that habitat amount effects always far outweighed the effects of arrangement. Response in Fahrig's experiments was measured using a binary (extinct/not extinct) variable analyzed with logistic regression (table 1A, 1B in Fahrig 1997). We repeated her logistic regression analysis with our data using a persistent/not persistent response variable and found results that were consistent with hers, namely, that habitat amount effects dominated even in landscapes with low amounts of habitat. Although we did observe increased relative contributions to classification accuracy from arrangement below threshold, the logistic regression coefficients for p and H when estimated across all of our experimental landscapes ($\hat{\beta}_p = 25.4$, $\hat{\beta}_H = 5.9$) were essentially unchanged when compared to those estimated for landscapes below our

LTTP-defined threshold ($\hat{\beta}_p = 24.3$, $\hat{\beta}_H = 5.7$). As noted earlier, our LTTP-defined threshold was analogous to the criteria used by Fahrig (1997) to see if arrangement effects became more important at low habitat amounts. We also observed similar results from landscapes below our CTA-defined threshold.

Response variable is not the only model attribute that varies among spatially explicit population models. These models also differ with respect to model structure (individual-stochastic, continuous-deterministic), landscape boundary conditions (reflecting, periodic, absorbing), dispersal process (passive, biased), and lattice coupling (local, global) to enumerate just a few (see Fahrig 2001 for a detailed comparison of models based on some of these attributes). Despite this myriad of differences, the fact that we were able qualitatively to mimic the results of others by simply changing our response variable implies that this model attribute may explain much of the inconsistency in the reported relative strengths of habitat amount and arrangement effects. This suggests the possibility that our results and Andrén's (1996) prediction might be fairly general, that is, that the influence of habitat arrangement on abundance would typically be small until habitat amounts drop below some threshold related to population persistence.

Conservation Implications

The existence of regions in the parameter space (as defined by landscape attributes in our case) where our population model exhibited fundamental shifts in behavior not only defines a threshold but may also serve to delimit domains of applicability for particular habitat management prescriptions. This would lead one to ask, do habitat-

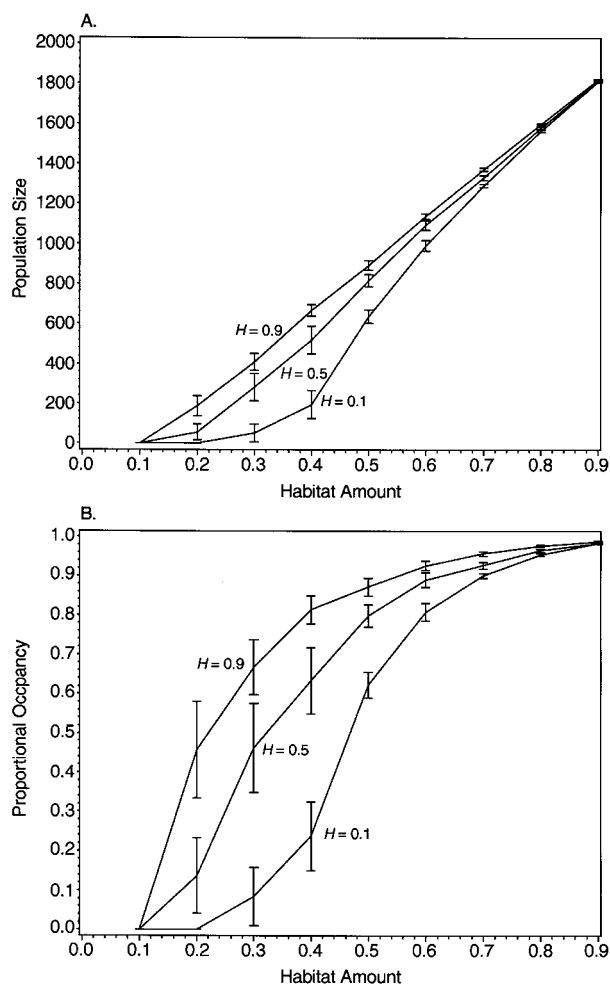


Figure 5: Equilibrium response to varying amounts of habitat at three levels of habitat aggregation ($H = 0.1$, 0.5 , and 0.9) as estimated from our reaction-diffusion model (eq. [1]). The error bars represent the 95% confidence intervals for (A) population size and (B) normalized patch occupancy response variables.

management considerations differ if the landscape is below or above threshold?

Our results suggest that conservation efforts for populations inhabiting landscapes below threshold conditions will be affected both by the amount and arrangement of habitat. Often, actual restoration efforts will involve the creation of habitat, and our results show that significant population gains are to be expected by simply adding habitat to the landscape. However, when there are choices of where to locate habitat, our findings also indicate that the size of the largest patch and its total perimeter are key landscape structure attributes (table 5). This outcome, along with those of a previous study (Bever and Flather 1999b), suggests that an efficient way for conservationists

to enhance the persistence of populations dispersing passively in patchy landscapes would be to focus on the largest patch in the complex with the goal of increasing its size (to augment population capacity) and reducing its total edge (to curtail exposure to dispersal-related mortality). This finding is consistent with other mathematical studies that have found that an entire habitat complex will persist if a single patch within the complex persists (DeAngelis et al. 1979) and that persistence is enhanced by clustering habitat (Adler and Nuernberger 1994), although any negative effects associated with spatially correlated population disturbances should also be considered (Goodman 1987; Hof and Flather 1996).

For populations inhabiting landscapes above threshold, habitat amount is the dominating consideration for population managers. Our experiment indicates that little can be gained by a search for some optimal arrangement, since the benefit to populations will not justify the increased management cost of dealing with spatial complexity. However, it does not necessarily follow that habitat arrangement can always be ignored for those ecological circumstances determined to be above threshold. Disregard for habitat arrangement considerations can only be justified if landscapes remain above a conservatively defined threshold.

Our results also imply that as landscapes pass through a persistence threshold, the opportunities for habitat management are likely to become more spatially constrained the further down the persistence surface (fig. 4A) landscapes slide (see also Bever and Flather 1999a). A comparison of the standardized regression coefficients under each threshold definition indicates that landscape-wide measures of habitat arrangement (total length of habitat edge and number of habitat patches) are more important when landscapes are high on the persistence surface (LTPP-defined threshold). Under the CTA-defined threshold (lower on the persistence surface), variables linked to characteristics of the largest patch (size of the largest patch and length of edge associated with the largest patch) become more important. There is more flexibility in manipulating habitat when dealing with landscape-wide measures of structure than when focusing on the most contiguous unit of habitat.

The implications we have derived are, of course, contingent on our choice of parameters and the assumptions underlying our formulation. An important aspect of our formulation not previously discussed is that the landscapes inhabited by our hypothetical species were treated as static mosaics (i.e., habitat patches were neither created nor destroyed over the period of the simulations). Consequently, our conservation implications may be relevant only to species whose generation time is much shorter than the dynamics associated with habitat change on the landscape. If species are found to be inhabiting highly dynamic land-

scapes, then the rate of habitat change will be important in understanding population dynamics in heterogeneous landscapes (Keymer et al. 2000) and may outweigh the influence of habitat arrangement (Fahrig 1992).

In addition, these conservation implications need to be tempered by two unanticipated results from our landscape structure regressions. First, the positive coefficient on patch number was counter to our expectation. Increasing the number of patches on landscapes while holding habitat amount constant would be expected to result in lower populations of species that prefer habitat interiors. However, positive patch number effects have been observed empirically with forest birds breeding in eastern North America. Trzcinski et al. (1999) found that two out of six species with a significant patch number effect (as evidenced by a principal component that was strongly loaded on patch number) had positive coefficients, while Villard et al. (1999) found that all six species with a significant effect were positively related to patch number.

Although these empirical results suggest that a positive patch number effect may be real, we suspect that a more likely explanation is related to ill-conditioning (Belsley et al. 1980) caused by correlation among the landscape structure predictor variables. In our study, as in Villard et al. (1999), we removed a source of collinearity by statistically controlling for the covariation between habitat amount and landscape structure variables. However, we also observed patterns of strong covariation among the landscape structure variables themselves. For example, the Pearson product-moment correlation between patch number and total length of edge was high for landscapes below the LTTP-threshold ($r = 0.82$, $P < .0001$). This relationship is not surprising if we consider that the number of patches in a landscape can be increased (if we hold habitat amount constant) only by breaking apart other patches, which will also increase the amount of edge in the landscape. Specific evidence of collinearity problems was observed when we examined sequentially more complex models built from our final models shown in table 5. Table 6 shows how the sign and magnitude of the patch number coefficient varied depending on the mix of variables in the model. Although these results indicate that interpretation of individual landscape structure coefficients should be done cautiously, collinearity among landscape structure variables should not affect our assessment of the relative importance of habitat amount and arrangement.

A second unanticipated result was the magnitude of the unexplained variation in population response that remained in our below-threshold regression models. Our reaction-diffusion model is deterministic, and the only factors that vary among experimental units are the amount and configuration of habitat on the landscape. One would predict that such a simple system would nearly be ex-

Table 6: Changes in the estimated regression coefficients for patch number for increasingly complex models built from the final models selected for landscapes below the LTTP- and CTA-defined thresholds

Model variables	$\hat{\beta}_{\text{pat_no}}$
LTTP-defined threshold:	
pat_no	-1.12
pat_no, p	-6.06
pat_no, p , max_sz	-1.62
pat_no, p , tot_edge	9.02
pat_no, p , max_sz, tot_edge	8.68
CTA-defined threshold:	
pat_no	-4.44
pat_no, p	-3.65
pat_no, p , edg_lgpat	-3.41
pat_no, p , max_sz	.16
pat_no, p , edg_lgpat, max_sz	1.64

Note: Landscape structure variables: number of patches (pat_no), proportion of habitat (p), total length of habitat edge (tot_edge), size of largest habitat patch (max_sz), and length of edge associated with the largest patch (edg_lgpat).

plained by some set of landscape predictor variables. The error remaining in the regression models could thus be caused by model underspecification. One source of the underspecification could be related to absence of variables that capture patch isolation effects. Because dispersal-related mortality in our model is affected by the neighborhood of surrounding habitats, one would have expected isolation effects to have been observed (Doak et al. 1992; Adler and Nuernberger 1994). Our measure of isolation (mean nearest-neighbor distance) may not be a particularly good indication of habitat isolation for a passive disperser because the distance associated with the nearest neighbor of some source patch of dispersers does not capture the availability of habitat within some dispersal neighborhood as well as measures of habitat proximity (Gustafson 1998).

Another source of underspecification could be our failure to consider landscape structure variables that quantify the proximity of habitat to the landscape boundary (see Cantrell and Cosner 1991). Because we assumed an absorbing boundary, proximity of the largest patch to the landscape boundary or some overall measure of mean habitat proximity to the boundary would capture variation in the number of individuals that "perished" due to emigration from the landscape.

Our below-threshold models may be underspecified and therefore underestimate habitat arrangement effects. However, it is unlikely that inclusion of a more comprehensive set of landscape structure variables would have altered our conclusion that habitat arrangement effects become important, if not prominent, from a species-conservation

perspective as persistence becomes more uncertain due to elevated dispersal mortality.

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