

CRITICAL THRESHOLDS IN SPECIES' RESPONSES TO LANDSCAPE STRUCTURE¹

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Abstract. Critical thresholds are transition ranges across which small changes in spatial pattern produce abrupt shifts in ecological responses. Habitat fragmentation provides a familiar example of a critical threshold. As the landscape becomes dissected into smaller parcels of habitat, landscape connectivity—the functional linkage among habitat patches—may suddenly become disrupted, which may have important consequences for the distribution and persistence of populations. Landscape connectivity depends not only on the abundance and spatial patterning of habitat, but also on the habitat specificity and dispersal abilities of species. Habitat specialists with limited dispersal capabilities presumably have a much lower threshold to habitat fragmentation than highly vagile species, which may perceive the landscape as functionally connected across a greater range of fragmentation severity.

To determine where threshold effects in species' responses to landscape structure are likely to occur, we developed a simulation model modified from percolation theory. Our simulations predicted the distributional patterns of populations in different landscape mosaics, which we tested empirically using two grasshopper species (Orthoptera: Acrididae) that occur in the shortgrass prairie of north-central Colorado: increasing degree of habitat specialization and dispersal range of a species enhanced the level of aggregation—the degree of clumping exhibited by the population—in our simulations. The landscape threshold at which populations became aggregated was affected by dispersal range for habitat generalists, but not for habitat specialists. Habitat specialists exhibited aggregated populations when preferred habitat occupied <40% of the landscape. Habitat generalists with good dispersal abilities occurred as aggregated populations when <35% of the landscape contained suitable habitat; habitat generalists with limited dispersal only formed patchy distributions when the preferred habitat was a minor (20%) proportion of the habitat. In field tests, a large species of grasshopper (*Xanthippus corallipes* Haldeman) exhibited reduced rates of travel in two microhabitats that together comprised 35% of a grassland mosaic; a smaller species (*Psoloessa delicatula* Scudder) had the highest residence time in a rare microhabitat that occurred in only 8% of the landscape. On the basis of our simulation results, we predicted that the large species would be patchily distributed because the abundance of its associated habitat is at the critical threshold. The small species should be unable to aggregate, given the rarity of habitat for which it has an affinity, and thus should be randomly distributed across the landscape. The distribution of these two species in this grassland mosaic matched the predictions from our simulations. By providing quantitative predictions of threshold effects, this modelling approach may prove useful in the formulation of conservation strategies and assessment of land-use changes on species' distributional patterns and persistence.

Key words: critical thresholds; habitat fragmentation; landscape ecology; neutral models; percolation theory; population distributions; simulation modelling.

INTRODUCTION

Small changes in the spatial patterning of resources can produce abrupt, sometimes dramatic ecological responses; such transition ranges are deemed *critical thresholds* (Turner and Gardner 1991). Critical thresh-

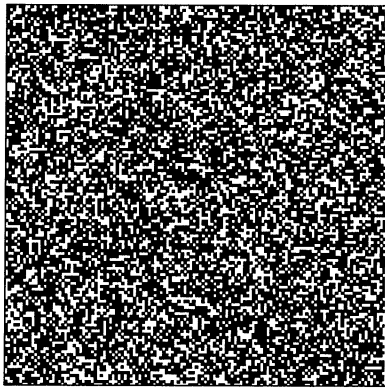
olds occur particularly where the phenomenon of interest exhibits a nonlinear relationship with spatial scale, owing to shifts in the underlying process(es) at different scales or because new constraints govern the process at different scales (O'Neill et al. 1986, Kotliar and Wiens 1990). Landscapes may exhibit critical thresholds in connectivity, often with serious ecological consequences (Gardner et al. 1987, Krummel et al. 1987, O'Neill et al. 1988b). A familiar example of this is habitat fragmentation. As the landscape becomes dissected into smaller and smaller parcels, *landscape connectivity*—the spatial contagion of habitat—may

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*Simple Random
Landscape*



Percolating Cluster

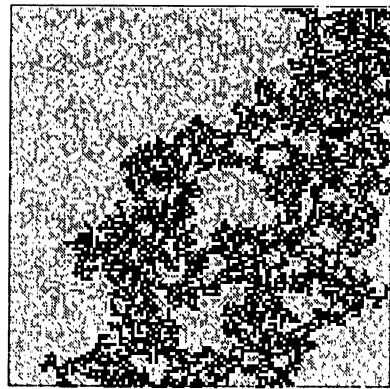


FIG. 1. Left: the neutral landscape, generated as a random distribution of habitat (black cells) across a grid (128×128 cells). Habitat occupies 65% of this simple random landscape. Right: same neutral landscape, with the percolating cluster highlighted (black) from the rest of the habitat (gray), which occurs as small, finite clusters in this landscape.

abruptly become disrupted. But at what point does habitat fragmentation disrupt landscape connectivity? Percolation theory (Orbach 1986, Stauffer and Aharony 1991) has recently been used as a neutral model to predict where these critical thresholds occur and thus how landscape structure might affect ecological processes (e.g., Gardner et al. 1987, 1989, 1992, O'Neill et al. 1988*b*). A neutral landscape map is produced from a random distribution of habitat(s) and is used as a null model to explore how ecological processes operate in heterogeneous environments in the absence of specific landscape patterns. Neutral landscapes thus serve as a baseline for statistical comparisons with patterns on real landscapes (Gardner et al. 1987, Gardner and O'Neill 1991).

To illustrate, consider a landscape to be a two-dimensional grid in which the grid cells are classified according to the landscape element of interest (e.g., habitat type). Percolation theory predicts that a random distribution of a single cell type that comprises at least 0.5928 of the landscape has a very high probability of spanning the map (Gardner et al. 1987). As the critical threshold (p_c) is reached, isolated patches of habitat become connected to form one continuous cluster. Each habitat cell of the percolating cluster is joined with a neighboring habitat cell along at least one horizontal or vertical edge (Fig. 1). Any organism capable of using the habitat should be able to traverse or "percolate" across this landscape, because it has a high degree of connectivity. Below this critical threshold ($p_c < 0.5928$), suitable habitat occurs as smaller, isolated patches. The landscape becomes disconnected when the "backbone" of the percolating cluster is broken by removing critical habitat cells along the spine and separating the cluster into two separate habitat patches. This results in the abrupt transition characteristic of percolating networks (Fig. 2). The disruption in land-

scape connectivity may limit movement of organisms, resulting in disjunct populations. Small changes in the composition of the landscape near the critical threshold are thus likely to have discernable effects on the distribution and persistence of populations (Turner and Gardner 1991).

The spatial mosaic of a landscape determines how a foraging animal responds to the distribution of resources (e.g., Senft et al. 1987). Spatial heterogeneity also influences the dispersal and distribution of animals

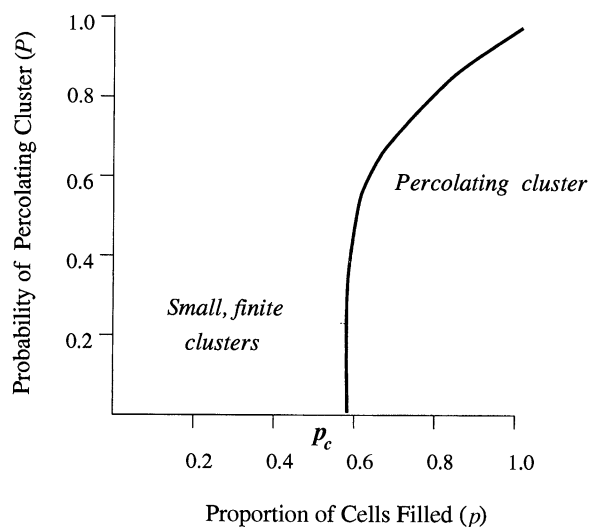


FIG. 2. Probability (P) that a percolating cluster will form on a random landscape map as a function of habitat abundance, the proportion of habitat cells (p) that occur on the grid. The abrupt transition between isolated patches of habitat and a percolating cluster that spans the map (see Fig. 1) is termed the percolation threshold, p_c . This critical phenomenon has been theoretically derived or empirically determined from Monte Carlo simulations (Plotnick and Gardner 1993). Modified from Zallen (1983).

across a landscape (Turchin 1991, Johnson et al. 1992), which in turn may have important consequences for the stability and persistence of populations (Wiens 1976, den Boer 1981, Fahrig and Merriam 1985, Kareiva 1990, Gilpin and Hanski 1991). Understanding how landscape structure affects the distribution of species may afford new insights into the organization of communities or species' responses to habitat fragmentation (e.g., Pearson et al., *in press*).

Our objective in this paper is to identify the critical threshold at which populations become disjunct as a function of increasing habitat fragmentation. The critical threshold is defined as the proportion of the landscape at which populations shift from random to clumped distributions. Toward this end, we assessed how species' dispersal capabilities and degree of habitat specialization interact with landscape structure to affect patterns of distribution. We suggest that the critical threshold is not an inherent property of a landscape, but emerges from the interplay of species' interactions with landscape structure. While habitat fragmentation refers to the connectivity of habitat types within a landscape, connectivity ultimately depends upon a species' ability to move across the landscape (O'Neill et al. 1988b, Pearson et al., *in press*). Species differ in the scales at which they interact with the environment (Morse et al. 1985, Swihart et al. 1988, Milne et al. 1992, With 1994). Even a scarce resource that has a patchy distribution is not necessarily fragmented if a species is able to operate at a broad enough spatial scale to use the resource effectively. Increasing habitat fragmentation may thus have little effect on species distributions until some critical level of connectivity is disrupted. It is not clear a priori where the critical threshold lies for species with different dispersal capabilities or habitat preferences (e.g., Plotnick and Gardner 1993). We provide an empirical example (grasshopper distributions in a shortgrass prairie) to illustrate how percolation theory can be applied to predict patterns of distribution for different species across a landscape.

As a caveat, it should be noted that percolation theory is strictly concerned with the movement behavior of a particle on a binary landscape; in ecological parlance, the organism is constrained to move only within suitable habitat and is not able to access the matrix. The dichotomy of suitable habitat vs. an inhospitable matrix is an extreme scenario adopted from island biogeography theory, but which may nevertheless apply to some species in certain landscapes (e.g., forest-interior bird species). More typically, landscapes are a mosaic of different habitat types, which differ in their suitability for a particular species (e.g., Cummings and Vessey 1994). Individuals may use these habitats for different activities (e.g., foraging vs. reproduction) or avoid certain habitats altogether; habitats may differ in quality (e.g., resource abundance), or in their structural complexity (thus affecting the permeability of the hab-

itat to dispersing individuals). Whatever the association, individuals will exhibit faster rates of transit through some elements of the landscape and increased residence times within others. Matrix habitat thus need not be viewed as "ecologically neutral" (Wiens et al. 1993), and marginal habitats may have profound effects on population dynamics (e.g., Pulliam and Danielson 1991). In this paper, we will generate neutral landscapes composed of multiple habitat types. Because the landscape maps are created as random associations of habitat, percolation theory is still the basis for understanding how movement behavior interacts with landscape structure to produce patterns of population distribution.

METHODS

Simulation model development

Landscape structure.—We generated artificial gridded landscapes (25×25 cells = 625 cells total) comprised of random associations of three habitat types. We created these neutral landscapes specifically with three habitat types to facilitate comparison of our model results with data on grasshopper populations in the shortgrass prairie. We previously identified three microhabitat types that characterized heterogeneity in the shortgrass prairie (With 1994; K. A. With and T. O. Crist, *unpublished manuscript*) and that differed in the abundance of forage for grasshoppers (see *Comparison with an ecological system: grasshopper distributions within bird territories*). Different landscape maps were generated by varying the proportion, p , of one habitat type (Habitat 1, p_1) from 0.1 to 0.8 of the total landscape; the other two habitat types comprised equal proportions of the remainder (Fig. 3). Thus, if $p_1 = 0.7$, then $p_2 = p_3 = 0.15$. This simulation exercise was conducted as an experiment in that we varied the proportion of one habitat independently of the others to determine how habitat fragmentation affected the spatial distribution of populations. Simultaneously varying two or more habitats was not illuminating in the present context (K. A. With and T. O. Crist, *unpublished data*).

Animal movement.—The simulated population ($n = 1000$ individuals) of a single species was initialized as a random dispersion pattern using a Poisson distribution. We simulated animal movement as the probability that an individual will move out of a given habitat cell during each iteration of the simulation run. This *probability of transition*, P_T , was calculated on the basis of the maximum dispersal range of a species in a given time period, as this indicates the degree to which individuals are able to interact with landscape structure. Although we will ultimately compare the theoretical expectations derived from this modelling exercise to a real system, the simulation experiments are designed to explore the model state space and be broadly applicable to a variety of organisms; parameter values are not based specifically on grasshoppers, therefore. An

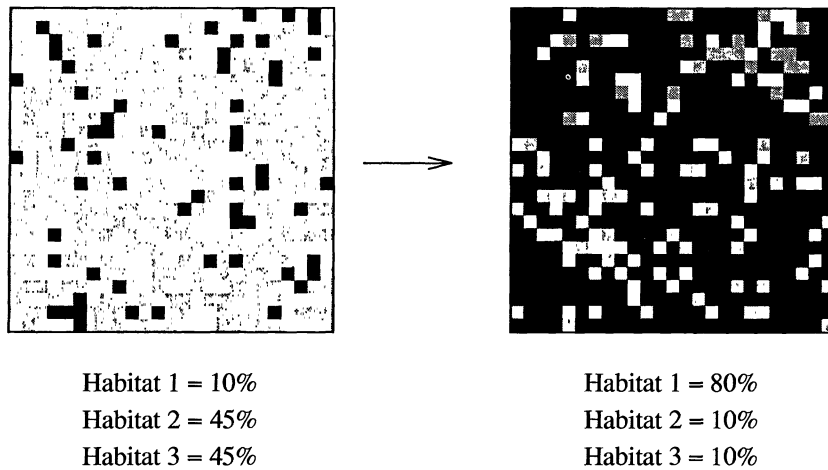


FIG. 3. Example of landscape maps used in simulation experiments. Maps (25×25 cells) are generated as random assemblages of three habitat types in which one habitat type (Habitat 1, black) is varied by increments (10%) to encompass from 10% (left) to 80% (right) of the total landscape. The other two habitat types (Habitat 2, gray; Habitat 3, white) comprise equal proportions of the remainder.

example of how P_T is calculated may nevertheless be of interest. If a hypothetical species is able to traverse 5% of a landscape during an 8-wk period, then an individual could make a maximum of 31.3 cell changes in our artificial landscape during the course of a model run (number of cell changes = 625 total cells in lattice $\times 5\% = 31.3$). If we simulate an 8-wk period of movement, with a 1-d time step (8 wk $\times 7$ d/wk = 56 d or iterations per run), then P_T for this species would be 0.558 (number of cell changes/iterations = $31.3/56 = 0.558$). This is the maximum rate of movement a species with a 5% dispersal range could maintain across the landscape. The transition probability was further adjusted by habitat type to simulate the increased residence time that presumably occurs in preferred habitat (i.e., an individual has a low probability of moving out of favorable habitat once it is encountered). Thus, a habitat specialist may have a 500 times greater affinity for this habitat relative to other habitat types that occur in the landscape mosaic. The calculation of P_T in preferred habitat for a habitat specialist with a 5% dispersal range would thus be $0.558/500 = 0.001$. The affinity factor, x , refers to the increased residence time (i.e., reduced transition probability, P_T) exhibited by the species in preferred habitat. In the present example, $x = 500$ and the species therefore has a 500 times greater affinity ($1/500 P_T$) for this habitat relative to the matrix. We will use the term "matrix" to refer to the other habitat type(s) in the landscape for which the species has a correspondingly higher transition probability (i.e., a high probability of leaving the cell).

The habitat-specific P_T was applied independently to the individuals occupying each grid cell; that is, the entire cell population did not move as a "cohort." If an individual did leave a cell, it was only able to move a distance of one cell into one of the four adjacent cells surrounding its present location (i.e., diagonal cells

were not accessible; "movement rule 1," Plotnick and Gardner 1993). The direction of movement (which one of the four cells) was random. Because movement was controlled by habitat-specific transition rates that relate to the propensity of individuals to leave a given cell type, individuals did not possess information on adjacent habitat types that might have differentially affected their probability of movement into a particular cell. This assumption is practical for organisms whose range of movement is small relative to the size of the grid cells and that do not exhibit directional biases in movement toward preferred habitat across distances > 1 cell. Our simulated landscapes were modelled as closed systems, such that individuals were not permitted to move outside the lattice. We did not observe "boundary effects" (e.g., accumulation of individuals around the edges of the grid), and we assume that the bounded landscape was not markedly different from an unbounded one (see Haefner et al. 1991).

Simulation experiments

Response to landscape structure.—Our objective was to pinpoint the critical threshold of habitat fragmentation at which the simulated population shifted from an initial random pattern of dispersion to an aggregated distribution in which most individuals were located in a small proportion of the landscape. The critical threshold was assessed as the proportion of habitat at which the population first exhibited a patchy distribution. We used Morisita's Index (I_m) as a measure of the degree of aggregation attained by the population. Morisita's Index measures the likelihood that two individuals, selected at random, were drawn from the same cell (Hurlbert 1990). For a population with a random distribution, the value of I_m is 1.0 (Fig. 4). For a population with $I_m = 7.0$, it is thus 7 times more likely that any two individuals, selected at random, occupy

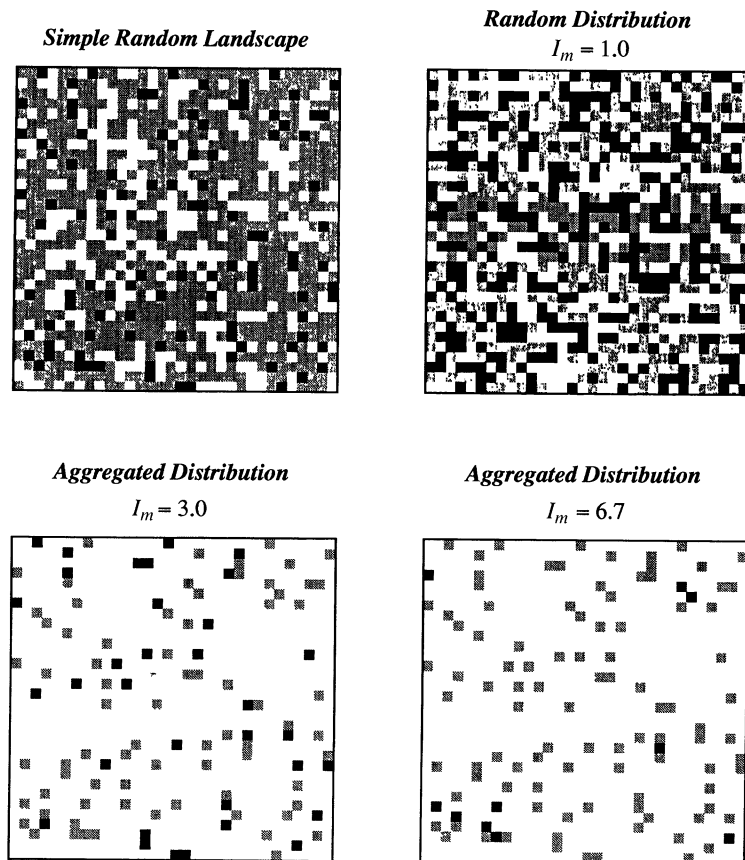


FIG. 4. Values for Morisita's Index (I_m), a measure of aggregation, for different computer-generated species' distributions. Top left: the neutral landscape used to generate patterns of species' distributions in this figure. The landscape comprises 10% Habitat 1 (black), 60% Habitat 2 (gray), and 30% Habitat 3 (white). Top right: a species that is randomly distributed across this landscape possesses an index value of 1.0. Shading corresponds to different categories of species' abundance within cells (black = highest density, white = lowest density). Bottom left: a habitat specialist, with an affinity for the rare habitat type (Habitat 1). Note that the species is aggregating in areas corresponding to the distribution of Habitat 1 (top left). Most individuals are contained within 5% of the landscape. An index value of 3.0 indicates that this population is 3 times more aggregated than that of a random distribution. Bottom right: a population exhibiting an extremely high level of aggregation, in which the population is primarily contained within $\approx 2\%$ of the landscape.

the same cell than if the population was distributed at random. This index is also robust to differences in sample size (e.g., comparison of populations of different densities; Hurlbert 1990). Natural populations of grasshoppers that were patchily distributed had values of $I_m > 2.5$ (K. A. With and T. O. Crist, *unpublished manuscript*). We therefore selected $I_m = 2.5$ to represent the transition point between random and aggregated populations in our simulation experiments to facilitate comparison of model results with empirical grasshopper distributions. Because the selection of a "cut-off value" for the response variable obviously affects the determination of the critical threshold (e.g., compare results of Figs. 6–9 for other values of I_m), care must be exercised in the selection of this transition value. This will depend upon the metric or spatial analysis used to assess species' responses to landscape structure (e.g., autocorrelation or semivariance analysis, Turner et al. 1991), as well as the objective of the modelling

exercise. Our cut-off value of I_m will suffice for the illustrative purposes of this modelling application and is consistent with the levels of aggregation observed in natural grasshopper distributions.

We performed four sets of simulation experiments (5 runs/experiment) to assess how species' interactions with landscape structure affected the occurrence of a critical threshold.

1. *Effect of habitat specialization.*—Habitat specialization was simulated as an increased residence time within the preferred habitat by decreasing the P_T in this habitat (Habitat 1) relative to the other two habitat types in the landscape (Habitats 2 and 3). We examined the effect that degree of habitat specialization had on the critical threshold by varying the species' affinity for Habitat 1 from 10 to 500 times that of the other two habitats (i.e., from 1/10 to 1/500 of the calculated value for P_T). Species were able to move across a maximum of 5% of the landscape in this series of

TABLE 1. Summary of simulation experiments to assess the effect of species' dispersal ranges and habitat preferences on critical thresholds in landscape structure.

Simulation experiment	Maximum dispersal range* (%)	Habitat affinity factor†	Preferred habitat
Effect of habitat specialization	5	10–500	1
Effect of dispersal range			
Habitat generalist	3–20	20	1
Habitat specialist	3–20	100	1
Effect of combined habitat preferences	5	20	1 + 2 1 + 3 2 + 3
Effect of partial habitat preferences	5	10 10–100	2 3

* Maximum dispersal range is calculated as the maximum percentage of the landscape with which the individual is able to interact during the simulation (see *Methods: Simulation model development: animal movement*).

† Habitat affinity was modelled as increased residence time within the preferred habitat(s). This was done by dividing the calculated probability of transition, P_T , by a given factor ($x = 10, 20, 50, 100, 500$) to simulate reduced rates of movement out of preferred cells of the landscape lattice. For combined habitat preferences, habitat affinities are 20 times greater ($1/20 P_T$) for each of two habitat types. For partial habitat preferences, the calculated value for P_T was applied to Habitat 1, but residence times were 10 times greater in Habitat 2 and up to 100 times greater in Habitat 3 (i.e., Habitat 2 = $P_T/10$, Habitat 3 = $P_T/100$).

simulations (Table 1). Note that the “attractiveness” of the preferred habitat is enhanced by increasing residence time within these preferred cells, but that the rate of movement across the remainder of the landscape remains unchanged subject to the constraints of the maximum range of dispersal.

The critical threshold was assessed as the proportion of preferred habitat at which the initial random distribution becomes aggregated ($I_m > 2.5$). In the binary landscapes of percolation theory, an individual can traverse the landscape when the proportion of suitable habitat exceeds $p_c = 0.59$. Note that in multihabitat landscapes, p_c corresponds to the proportion of habitat(s) across which the species has the highest rate of transit (high P_T), as in the habitat types comprising the matrix. Species should first form patchy distributions when the proportion of their preferred habitat comprises $\approx 40\%$ of the landscape (or, alternatively, when the matrix $\geq 60\%$; Fig. 5). By altering the affinities species have for habitat(s) within the landscape mosaic, we are able to detect how the degree of habitat association is likely to affect a species' perception of whether the landscape is fragmented and how this affects the distribution of individuals in space.

2. *Effect of dispersal range.*—We varied the extent to which species moved across the landscape to determine the critical threshold at which population aggregation occurred for species with different dispersal ranges (Table 1). The species exhibited a preference for one habitat (Habitat 1), which we simulated as a reduced probability of movement out of this habitat. Because we were interested in how species' characteristics interacted to affect the occurrence of critical thresholds, we modelled the response of a *habitat generalist*, where the affinity for the preferred habitat (Habitat 1) was 20 times greater ($1/20 P_T$) than that for the other two habitat types (the matrix), and for a *hab-*

itat specialist that had a 100 times greater ($1/100 P_T$) affinity for the preferred habitat (Habitat 1). This experiment assessed how the effective connectedness of the preferred habitat (via dispersal) affects the distribution of individuals.

The threshold at which aggregation occurs should depend on the relative vagility or dispersal capabilities of the species. The range of dispersal was varied to encompass 3%, 5%, 10%, and 20% of the total landscape (Table 1). Actual distance travelled by simulated individuals is certainly much less, because direction-

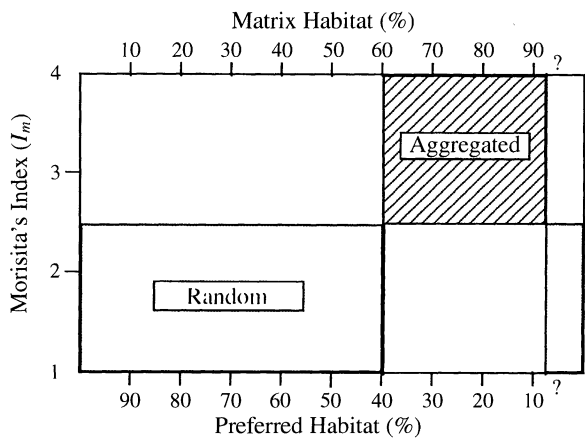


FIG. 5. The critical threshold at which populations are predicted to shift from a random to an aggregated distribution. Preferred habitat is modelled as an increased residence time within a particular habitat relative to other accessible habitats (matrix) in the landscape. Morisita's Index (I_m) measures the degree of aggregation of the population; we use $I_m \geq 2.5$ to represent the shift from a random to an aggregated distribution. Percolation theory predicts that this shift will occur when the matrix occupies $\geq 60\%$ of the landscape, or conversely, when the preferred habitat comprises $\leq 40\%$ of the landscape.

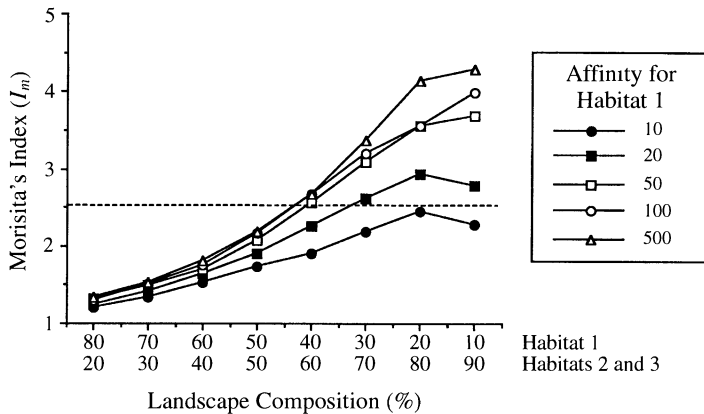


FIG. 6. Effect of habitat specialization on the critical threshold at which species exhibit aggregated distributions ($I_m > 2.5$; dashed line). Habitat specialization was modelled as an increased affinity for one habitat (Habitat 1) by reducing the transition probability (P_T) in this preferred habitat relative to the other two habitats in the landscape. In this series of simulations, the species was able to interact with a maximum of 5% of the landscape. Error bars (± 1 SD) are smaller than the size of the symbols.

ality of movement is random and because movement rarely occurs out of preferred habitat cells. The expected mean squared displacement for a diffusing particle on a percolating cluster was $\approx 70\%$ less than that on a homogeneous plane (Milne 1991). Thus, the effect of increasing the range of dispersal is to increase the degree of movement activity (number of cell changes) during the course of the simulation. Increased dispersal should increase the likelihood that preferred habitat is encountered. Species with greater vagility should encounter preferred habitat at a faster rate than less vagile species, and thus exhibit greater aggregation as individuals collect within preferred habitat cells.

3. *Effect of combined habitat preferences.*—Aggregation should occur at the point where reduced movement in the two preferred habitats combined ($p_1 + p_2 \leq 0.4$) produces a threshold effect in population distribution. We simulated a 20 times greater preference for each of two habitats (e.g., preferred habitat = $1/20 P_T$), with the assumption that individuals were capable of a maximum dispersal across 5% of the landscape (Table 1). If Habitats 2 and 3 are preferred, aggregated distributions should occur when the landscape comprises $< 40\%$ of these two habitat types (i.e., $p_2 = p_3 \leq 0.2$).

4. *Effect of partial habitat preferences.*—What if a species has partial preferences for different habitat types within the landscape? That is, the species responds to a gradient of habitat quality, such that habitats could be rank ordered in terms of preference or at least the amount of time spent in each. To assess the effect of partial habitat preferences on the critical threshold, we assigned a low transition probability ($1/10 P_T$) to one habitat (Habitat 2), while varying that for the other habitat type (Habitat 3) preferred by the species ($1/10 P_T$ – $1/100 P_T$). The P_T in the third habitat (Habitat 1) remained constant, permitting a maximum range of dispersal of 5% across the landscape (Table 1).

RESULTS

Simulation experiments

Effect of habitat specialization.—The degree of habitat specialization affected the landscape threshold at

which populations became patchily distributed. Habitat specialists, which have 100–500 times greater affinity for preferred habitat, occurred as aggregated populations even when the preferred habitat comprised nearly half (45%) of the landscape (Fig. 6). Because specialists were closely associated with a particular habitat, they were unlikely to leave once the patch was encountered. Interestingly, habitat generalists ($1/10 P_T$) formed aggregations when the “preferred” habitat was an *uncommon* (20%) element of the landscape. The rarity of a slightly more profitable habitat may enhance aggregation of individuals in these patches, up until the point where habitat is too scarce for species with such a nominal habitat preference and fairly limited vagility (5%) to locate (note that there is a decrease in the level of aggregation attained by the population beyond the critical threshold for species with a 10–20 times greater affinity for Habitat 1; Fig. 6).

Effect of dispersal range.—Increasing dispersal range enhanced the level of aggregation attained by the population because individuals were able to locate even scarce patches of preferred habitat (Fig. 7). Dispersal capabilities interacted with habitat affinity to affect the threshold at which patchy distributions formed on the landscape. Dispersal range had little effect on the threshold when species had a high affinity ($1/100 P_T$) for the preferred habitat (Habitat 1; Fig. 7). Species with dispersal ranges encompassing 3–20% of the landscape shifted from a random to an aggregated distribution when their preferred habitat occupied $\leq 40\%$ of the landscape. For habitat specialists, therefore, dispersal capabilities had less of an impact on patterns of species distribution than did abundance of required habitat.

For habitat generalists ($1/20 P_T$), dispersal range had a marked effect on the point at which populations became aggregated (Fig. 7). A threshold occurred when the preferred habitat comprised $\approx 35\%$ of the landscape for species with dispersal ranges varying from 5 to 20%. A shift in the threshold occurred at reduced dispersal ranges (3–5%). If a species was able to interact with 3% of the landscape, then populations became

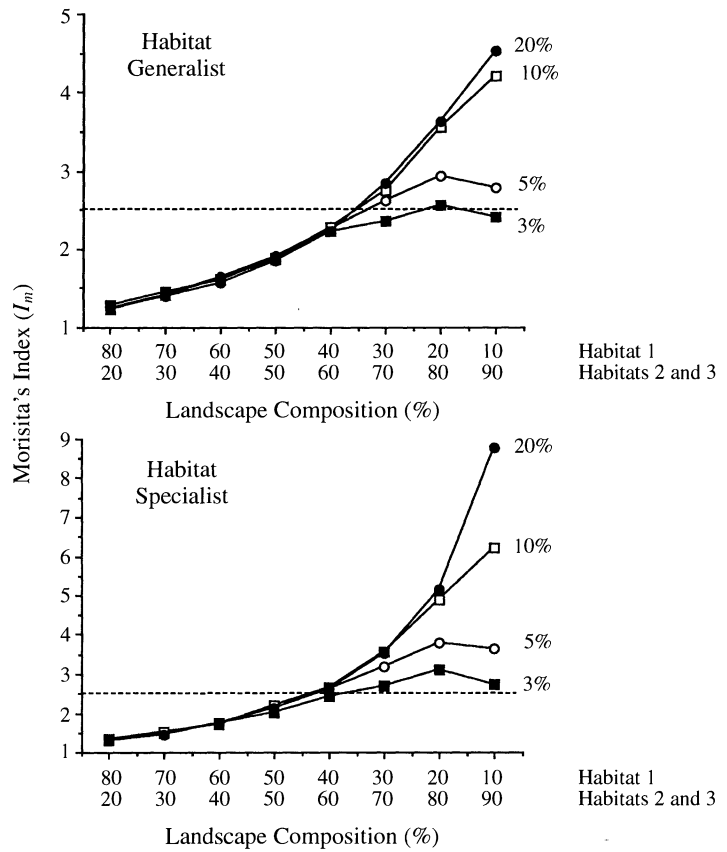


FIG. 7. Effect of dispersal range on the critical threshold at which species' distributions exhibit aggregation ($I_m > 2.5$; dashed line) in response to landscape structure. Dispersal range is the maximum percentage of the landscape with which the species can interact. Top: habitat generalist. The species' affinity for Habitat 1 is 20 times greater than for the other two habitats. Bottom: habitat specialist. Affinity for Habitat 1 is 100 times greater than for the other two habitats. Error bars (± 1 SD) are smaller than the size of the symbols for both panels.

aggregated when the preferred habitat occupied $\approx 25\%$ of the landscape. Small changes in dispersal capabilities thus produced large changes in the threshold at which populations of habitat generalists formed patchy distributions.

Effect of combined habitat preferences.—If a species had a slight preference ($1/20 P_7$) for more than one habitat type, then the threshold at which the population became aggregated was the combined abundance of the two preferred habitats; this occurred at $\approx 35\%$ in our simulated landscape if the species exploited Habitats

2 and 3, when each of these habitats occupied $\leq 17.5\%$ of the landscape (Fig. 8). Given this landscape configuration (p_1 varied while $p_2 = p_3$ of the remainder), any preference for Habitat 1 precluded an aggregated population because there are no landscape configurations for which a threshold effect is predicted (i.e., no combination of $p_1 + p_2$ or $p_1 + p_3 \leq 0.35$).

Effect of partial habitat preferences.—When the species had a slight affinity ($1/10 P_7$) for Habitats 2 and 3, populations only became aggregated when the preferred habitats comprised 20% of the landscape (Fig.

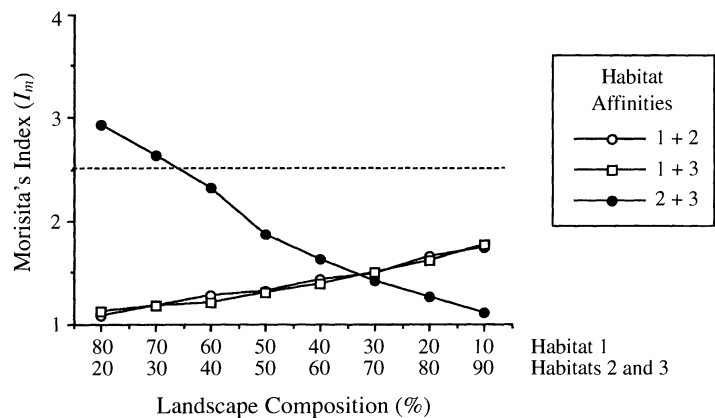


FIG. 8. Effect of combined habitat preferences on the critical threshold at which species are predicted to occur as aggregated distributions ($I_m > 2.5$; dashed line). Species are able to interact with a maximum of 5% of the landscape. Habitat preference is modelled as a 20 times greater affinity for each of two habitats relative to the third. Error bars (± 1 SD) are smaller than the size of the symbols.

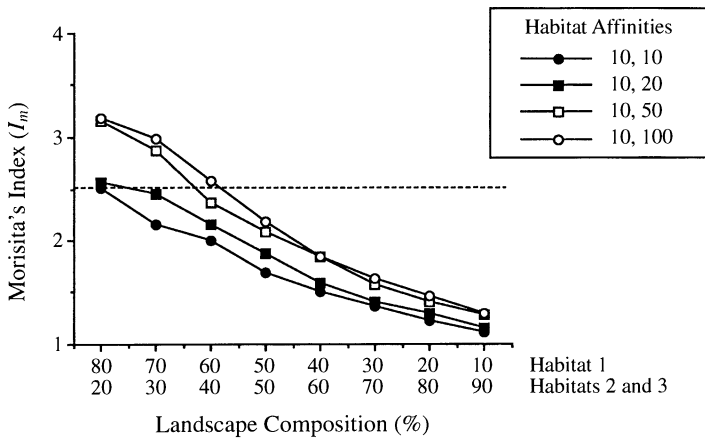


FIG. 9. Effect of partial preferences on the critical threshold at which species are likely to occur as aggregated distributions ($I_m > 2.5$; dashed line) in response to landscape structure. The transition probability, P_T , in one habitat (Habitat 1) is set to correspond to a maximum dispersal of 5% of the landscape and is maintained throughout this series of simulations. A nominal affinity for Habitat 2 (affinity factor $[x] = 10$) is modelled as an increased residence time within this habitat ($1/10 P_T$). The degree of preference for the third habitat is varied from $1/10 P_T$ to $1/100 P_T$. Affinity factors for Habitats 2 and 3, respectively, are shown in the key. Error bars (± 1 SD) are smaller than the size of the symbols.

9). Doubling the degree of affinity for one of these habitats ($1/20 P_T$ in Habitat 3) relative to the other preferred habitat (2) resulted in a shift in the threshold to 35%. A further 2.5 increase in affinity in this same habitat ($1/50 P_T$ in Habitat 3) resulted in another shift to $\approx 40\%$. Beyond this, however, subsequent increases in the affinity for one of the preferred habitats did not substantially change the critical threshold. Instead, populations attained higher levels of aggregation as individuals rapidly accumulated in the preferred areas of the landscape (e.g., Habitat 3 cells).

*Comparison with an ecological system:
grasshopper distributions within
bird territories*

To assess the utility of our model in predicting spatial patterns of populations in different landscapes, we examined the distribution of grasshopper populations (Orthoptera: Acrididae) in the shortgrass prairie of north-central Colorado. The shortgrass prairie of the Central Plains Experimental Range (50 km northeast of Fort Collins, Weld County; elevation = 1650 m), a Long-Term Ecological Research site, consists of a matrix of perennial grass species (blue grama, *Bouteloua gracilis*, and buffalo grass, *Buchloe dactyloides*), interspersed with cactus (primarily *Opuntia polyacantha*), shrubs (*Chrysothamnus nauseosus*, *Gutierrezia sarothrae*), midgrasses (e.g., *Aristida longiseta*, *Stipa comata*), forbs, and areas of bare ground. Grasshoppers are an abundant insect herbivore in this grassland system (Welch et al. 1991), and we expected that habitat, especially the abundance and distribution of their preferred forage, *B. gracilis*, would affect the distribution of grasshoppers.

As part of a larger study involving the spatial dynamics of prey and predator foraging patterns, bird territories were viewed as "microlandscapes" comprising a mosaic of different microhabitat types. Bird territories (size = 1 ha) were represented as gridded maps, in which grid cells ($6.25 \text{ m} \times 6.25 \text{ m}$) were classified by degree of heterogeneity (three microhab-

itat types). Heterogeneity was measured as the extent to which the shortgrass matrix, the main forage for grasshoppers, was disrupted by other types of vegetation. At the extremes, homogeneous (H) cells contained nearly continuous coverage of shortgrass, whereas very heterogeneous (VH) cells contained little shortgrass cover, which was extensively disrupted by other types of vegetation (see With 1994 for additional quantification of cell types).

Two of the most abundant early-season (April–June) grasshopper species in this system are *Xanthippus corallipes* (Haldeman), a large (35–65 mm) acridid (subfamily Oedipodinae), and *Psoloessa delicatula* (Scudder), which is a smaller (16–27 mm) species (subfamily Gomphocerinae). Previous research on the movement responses of these two species documented their differential responses to heterogeneity (With 1994). Habitat-specific P_T were calculated by extrapolating the average rate of movement within each cell type to the expected transition rates out of these cells per iteration of the simulation run (K.A. With and T.O. Crist, unpublished manuscript). The equation for this relationship was derived as $P_T = r_m t_a t_i / d$, where r_m is the average rate of movement (centimetres per hour) in the microlandscape, t_a is the average length of time per day that individuals are active (hours per day; ≈ 5.5 h/d for these grasshopper species, which is the average number of hours during which temperatures were 20–30°C), t_i is the time interval represented by each iteration (in days; set to 0.02 d to correspond to the 30-min observation period upon which individual movement rates were obtained), and d is the linear dimension of the cell (in centimetres; 625 cm). *Psoloessa delicatula* had reduced movement in H cells, whereas *X. corallipes* exhibited reduced movement in H and VH cells (Fig. 10). Because reduced rates of movement enhance residence time within a particular habitat, we will equate these movement responses with "habitat affinities." We recognize that different ecological mechanisms may be responsible for reduced movement in a particular habitat. Profitable habitats may increase foraging times

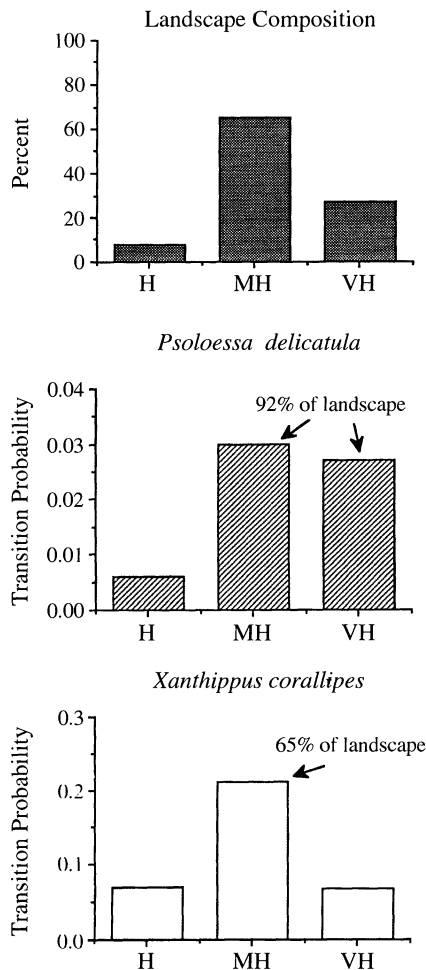


FIG. 10. Species' responses to landscape structure. Top: relative proportions of three microhabitat types (H = homogeneous, MH = moderately heterogeneous, and VH = very heterogeneous) across a representative bird territory (1 ha) in the shortgrass prairie of north-central Colorado. Heterogeneity is a measure of the degree to which the shortgrass matrix (the primary forage for grasshoppers) was disrupted by other types of vegetation. Middle: response of a small grasshopper (Orthoptera: Acrididae), *Psoloessa delicatula*, to the structure of this landscape. This species was retained in only a small portion of the landscape (as assessed by calculated transition probabilities; see *Results: Comparison with an ecological system: Grasshopper distributions . . .* for details). Bottom: response of the larger *Xanthippus corallipes* in this same landscape. This species exhibited increased residence times in one-third of the landscape.

through area-restricted search, or the habitat may offer some other positive attribute such as shade or cover from predators that would enhance residence time. Alternatively, the structural complexity of the habitat may form physical barriers that impede movement and increase residence time in a particular area for this reason. In the present context, we are only modelling the movement responses and not the specific mechanisms or the fitness consequences of such responses. Can the

pattern of distribution of these two species be predicted based upon their responses to landscape structure?

The landscape structure of the bird territory bears a striking resemblance to percolation maps (Fig. 10, Table 2). The landscape was dominated by a single habitat type (moderately heterogeneous, MH) that comprised 65% of the total area. Percolation theory predicts that even a random distribution of habitat should span the map when $p_{\text{habitat}} > p_c = 0.59$. The bird territory thus possesses a high degree of landscape connectance, as illustrated by the contagion index, D_2 , which measures the overall extent of habitat aggregation across the landscape (O'Neill et al. 1988b, Li and Reynolds 1993). The value of D_2 is similar for the territory and a totally random assemblage of the three habitat types (<10% difference, Table 2). The other habitat types (H and VH) are slightly more clumped than expected for a random distribution, however. Nearest neighbor probabilities are the likelihood that a particular cell type i is adjacent to a like cell type i (Turner et al. 1989). For example, H cells are 2.5 times more aggregated than if randomly distributed (compare q_{33} for territory and random maps, Table 2). Nevertheless, this habitat type is a rare component of the landscape (8% cover) and thus there is a low probability that homogeneous cells are adjacent ($q_{33} = 0.20$, Table 2). The two habitat types, H and VH, occur as small patches or isolated cells scattered across the landscape.

Psoloessa delicatula showed reduced movement in H cells, a rare (<10%) cover type on this landscape (Fig. 10). Consequently, individuals of this species were moving faster through >90% of the bird's territory. In contrast, *X. corallipes* exhibited reduced movement in H and VH cells, which comprise 35% of this landscape. Assume that both species initially emerged as a random distribution across the bird territory, and that the species are capable of only a very limited range of dispersal. Several grasshopper species were shown to disperse an average of 60–80 m during a 7-wk period (Joern 1983), the approximate season length for our two species in this system. An 80-m dispersal range would cover $\approx 5\%$ of the bird's territory (80 m/6.25 m linear dimension of grid cells \times 286 cells/territory = 4.5%). The results of our simulation experiments predict that a species such as *P. delicatula*, which has an affinity for a rare habitat, should not be able to aggregate beyond its initial random distribution (Fig. 5) because a species with relatively low vagility will have a low probability of locating and aggregating within scarce habitat. A species such as *X. corallipes*, which has a combined affinity for two habitats that comprise <40% of the landscape, should have an aggregated distribution.

How do these expectations from our simulations match the actual distributions of the two grasshopper species in a real landscape? *X. corallipes* is patchily distributed with a high degree of aggregation ($I_m = 4.1$), in which the population occupies 22% of the land-

TABLE 2. Measures of habitat adjacency and landscape contagion for the bird territory in which grasshopper distributions were assessed. Nearest neighbor probability is the probability that a particular cell type i is adjacent to a like cell type i : q_{11} = probability that very heterogeneous (VH) cells are adjacent, q_{22} = probability that moderately heterogeneous (MH) cells are adjacent, and q_{33} = probability that homogeneous (H) cells are adjacent. The contagion index, D_2 , provides a measure of landscape connectivity by evaluating the overall extent to which habitats are aggregated. These indices of spatial pattern are compared to simple random landscapes comprised of the same proportion of habitat types as in the bird territory.

Landscape type	Proportion of cell types			Nearest neighbor probabilities*			
	VH	MH	H	q_{11}	q_{22}	q_{33}	D_2
Territory	0.27	0.65	0.08	0.42	0.72	0.20	0.765
Random	0.27	0.65	0.08	0.28 ± 0.028	0.66 ± 0.013	0.08 ± 0.034	0.834 ± 0.072

* Values for random landscapes are the mean \pm 1 SD for 10 maps.

scape; most individuals (>10 individuals/cell) are in 2% of the territory (Fig. 11). The smaller *P. delicatula* possesses a random distribution ($I_m = 1.9$) and can be found in two-thirds (67%) of the landscape, although most individuals are concentrated in one-third (30%) of the territory (Fig. 11). The distributional patterns found for populations of these two grasshopper species match the predictions from our simulations, given the respective movement responses of each species to landscape structure. This is not to say that other processes, such as competition or predation, do not also play a role in dictating the distributional patterns of a species, only that our null model provides a good first approximation at predicting the pattern of distribution expected to emerge on a given landscape mosaic given information on species' dispersal ranges and habitat affinities.

DISCUSSION

Critical thresholds in landscape structure are not just a property of landscapes, but one that emerges from species' interactions with landscape structure. The exact value of the critical threshold, and thus whether a landscape is perceived as connected by the species, depends on the scale at which a species interacts with spatial heterogeneity (O'Neill et al. 1988b, Plotnick

and Gardner 1993, Pearson et al., *in press*). How an organism will be affected by habitat fragmentation is determined by its vagility, its habitat requirements, and relative rates of movement through various habitats comprising the landscape mosaic. Our simulations showed that good dispersers, which can move $\geq 5\%$ of the landscape, are likely to form patchy distributions when their preferred habitat comprises a minor proportion ($<35\text{--}40\%$) of the landscape. This threshold of aggregation is modified by habitat specificity, however. The relative abundance of preferred habitat in the landscape may be the primary determinant of distributional patterns for habitat specialists and may even override the importance of the species' dispersal capabilities, provided the species has a dispersal range encompassing $\geq 3\%$ of the landscape. Because the occurrence of the critical threshold is a function of whether or not a particular species perceives the landscape as connected, it is unlikely that a single threshold value can adequately describe the response of all species in a community to changes in landscape pattern. This necessitates a species-centered definition of landscapes (With 1994, Pearson et al., *in press*), which is a necessary vista if we are to adopt meaningful and effective conservation strategies (Hansen and Urban 1992).

Besides determining the effect of land-use changes

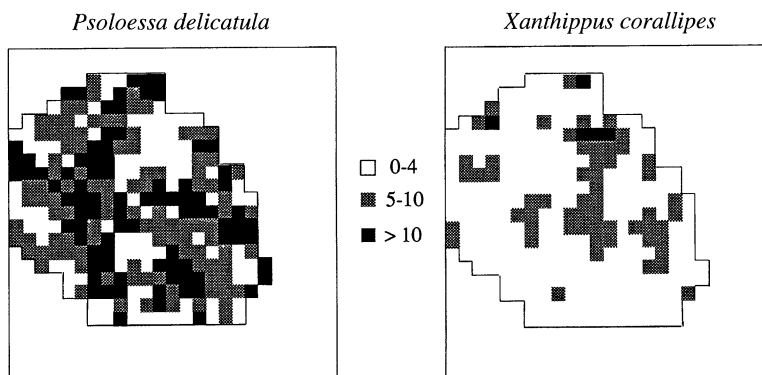


FIG. 11. Distribution of two acridid grasshoppers (Orthoptera) within a bird territory (1 ha) in the shortgrass prairie of north-central Colorado. Each cell is 6.25×6.25 m (39.1 m²). *Psoloessa delicatula* is a small species (16–27 mm) and occurs as a random distribution in this landscape, as indicated by the measure of aggregation ($I_m = 1.9$). *Xanthippus corallipes* is a larger species (35–65 mm) and occurs as a patchy distribution exhibiting a high level of aggregation ($I_m = 4.1$) in this same landscape.

on patterns of species distributions, conservation biologists are also concerned with achieving long-term persistence of species populations in the face of landscape fragmentation. Population dynamics for species in landscape mosaics involve two components: the dispersal of individuals among habitats and habitat-specific demographic rates (e.g., Pulliam 1988, Pulliam and Danielson 1991, Wiens et al. 1993). We have focused on dispersal in our modelling efforts, but the model could be enhanced to include habitat-specific mortality and/or reproductive rates that would generate source and sink habitats (sensu Pulliam 1988). This would certainly add an interesting dimension to this modelling framework by producing complex interactions between species' life-history attributes underlying habitat selection and landscape patterns. Not all habitats utilized by the species are necessarily valuable from a reproductive standpoint, and it is possible that preferred habitat may pose as "ecological traps" in which individuals aggregate but suffer lower reproduction or higher mortality than in other habitat types (e.g., Pulliam and Danielson 1991).

Lande (1987) developed a general metapopulation model for species that were postulated to occupy territories on binary landscapes in which suitable habitat was randomly distributed across the landscape. Although not a percolation model, Lande's metapopulation model established the existence of an "extinction threshold," defined as the minimum proportion of suitable habitat necessary for population persistence. The ability of a population to persist in a fragmented landscape may be suddenly compromised once a certain threshold is reached, depending upon the "demographic potential" of the species (k , the maximum occupancy of territories possible at equilibrium for a given dispersal range and suite of life-history traits of the species). Species with a high demographic potential (e.g., large dispersal range, high fecundity, high survivorship), persist even in the most extensively fragmented systems; the extinction threshold for such species is roughly 0.25–0.50 (Fig. 1 in Lande 1987). Thus, such species would be able to persist even when only 25–50% of the landscape comprised suitable habitat. Conversely, a species with a low demographic potential could not persist even when suitable habitat occupied 80% of the landscape. The potential utility of such models illustrating threshold effects was demonstrated by the application of Lande's model to predict the persistence of populations of Northern Spotted Owls (*Strix occidentalis caurina*) in old-growth forests subjected to various intensities of habitat fragmentation (Lande 1988, Lamberson et al. 1992). The population was predicted to go extinct if the proportion of old-growth forest was reduced to <20% of the landscape.

These types of modelling exercises, as depicted by our percolation model and Lande's metapopulation model, illustrate what Kareiva (1990) has called the "recurring theme of critical rates, critical scales, and

critical geometries" in mathematical modelling. Environmental heterogeneity, such as that caused at the broad scale by habitat fragmentation, will have important consequences for population dynamics depending upon the dispersal rates of individuals and the spatial scale at which the process is considered. The notion of critical thresholds implies that certain ecological responses may be difficult to predict without recourse to this type of modelling exercise and may go undetected until a critical threshold is reached.

What evidence exists for the occurrence of critical thresholds in real systems? Most ecological research has not been interpreted in this context, and thus the occurrence of critical thresholds has not been tested empirically, or at least not directly. Yet examples of potential threshold effects abound in the ecological literature. Andr n (1994) reviewed the literature on responses of birds and mammals to habitat fragmentation and proposed that a critical threshold of 10–30% might exist. Interestingly, the actual threshold may be lower than that predicted by percolation theory, possibly because habitat occupies a clumped rather than random distribution in real landscapes. Above this threshold, the primary effect of habitat fragmentation is loss of habitat with a concomitant decrease in species richness or population size. Below the threshold, habitat fragmentation increases isolation of habitat patches, thereby reducing landscape connectance. Biodiversity may in fact present two threshold effects: low diversity in homogeneous, well-connected landscapes comprised of "interior species," shifting to highest diversity at some point when the landscape becomes sufficiently fragmented to afford a mixture of interior and "edge" species, and a corresponding decrease in diversity once again as the landscape becomes increasingly dissected into small, isolated fragments that support primarily edge species (e.g., hedgerow networks; Burel 1992). Other examples of critical thresholds in ecology may occur at finer spatial scales than that of landscapes. Foraging animals shift search strategies in response to the distribution of resources; the shift from area-restricted search (aggregated behavior) to random search is a predictable behavioral response that is linked to spatial heterogeneity and is modified by the size of the organism, its vagility, its sensory capabilities, and other traits that modify the scale at which the organism interacts with the environment (e.g., Smith 1974, Swihart et al. 1988, Johnson et al. 1992). The economic defensibility of maintaining a territory, as opposed to foraging in groups, appears to be based on similar principals related to foraging energetics and the spatial patterning and abundance of resources, although much of this area of research remains theoretical in nature (e.g., Davies and Houston 1984, Carpenter 1987). Thus, while the general notion of thresholds is apparently not a new one in ecology, research programs are needed to address explicitly the occurrence of critical threshold effects in ecological phenomena.

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