Nordic Society Oikos

Landscape Connectivity and Population Distributions in Heterogeneous Environments
Author(s): Kimberly A. With, Robert H. Gardner, Monica G. Turner
Source: *Oikos*, Vol. 78, No. 1 (Feb., 1997), pp. 151-169
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3545811
Accessed: 06/08/2011 01:11

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Blackwell Publishing and *Nordic Society Oikos* are collaborating with JSTOR to digitize, preserve and extend access to *Oikos.*

http://www.jstor.org

OIKOS 78: 151–169. Copenhagen 1997

Landscape connectivity and population distributions in heterogeneous environments

Kimberly A. With, Robert H. Gardner and Monica G. Turner

With, K. A., Gardner, R. H. and Turner, M. G. 1997. Landscape connectivity and population distributions in heterogeneous environments. – Oikos 78: 151–169.

Landscape connectivity refers to the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure. Heterogeneous landscapes provide a particular challenge for modelling population-level responses to habitat fragmentation, because individuals may be utilizing multiple habitats to varying degrees across the landscape. We apply neutral landscape models to understand how species' habitat affinities interacted with landscape structure (i.e., habitat abundance, distribution, and quality as measured by carrying capacity) to affect the redistribution of individuals. Two types of neutral models are presented: random maps, in which the distribution of habitat is spatially independent, and fractal maps, in which habitat exhibits an intermediate level of spatial dependence. The neutral landscapes comprised varying proportions of three habitat types, for which species exhibited a preference gradient (high, medium, low). We performed a series of simulation experiments as a factorial design of parameter states to tease apart the underlying factors responsible for population distributional patterns (random vs clumped) in spatially complex mosaics.

Landscape connectivity is a threshold phenomenon, in which even a minimal loss of habitat near the critical threshold (p_c) is likely to disconnect the landscape, and which may have consequences for population distributions. The exact value of p_c depends upon the spatial arrangement of habitat; fractal landscapes exhibited connectivity across a greater range of habitat abundance (p) than random maps (fractal p_c = 0.29–0.50, random $p_c = 0.59$). Although the spatial arrangement of habitat (random vs fractal) was the most important determinant of population distributional patterns, different landscape factors were important in structuring populations in the two types of maps. The relative abundance of habitat had the greatest effect on populations in random landscapes, whereas scale-dependent patterns were evident in fractal landscapes. At fine scales, population dispersion was determined by habitat abundance in both random and fractal maps, although populations were more aggregated (as measured by Morisita's Index, I_m) at this scale in random landscapes. But at coarse scales on fractal maps, population distribution was primarily influenced by species' habitat affinities. Assessment of the independent effects of habitat affinity and habitat carrying capacity on population distributions revealed that the differential interaction of species with landscape structure (i.e., different residence probabilities in each habitat type) was the primary determinant of distributional patterns. Neutral landscape models thus provide a useful tool for determining the relative importance of various components of landscape structure that affect population distributions.

K. A. With, R. H. Gardner and M. G. Turner, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6038, USA (present addresses: KAW: Dept of Biological Sciences, Bowling Green State Univ., Bowling Green, OH 43403, USA. – RHG: Appalachian Environmental Laboratory, Univ. of Maryland, Gunter Hall, Frostburg, MD 21532, USA. – MGT: Dept of Zoology, Birge Hall, 430 Lincoln Drive, Univ. of Wisconsin, Madison, WI 53706, USA).

Accepted 28 May 1996

Copyright © OIKOS 1997
ISSN 0030-1299
Printed in Ireland – all rights reserved

Spatially explicit models of landscapes depict environmental heterogeneity in a structurally complex fashion, and thus have great utility for exploring the relationships between landscape structure and population dynamics (e.g., Dunning et al. 1995). Patch-based models have a rich tradition in theoretical ecology (e.g., Pickett and White 1985, Stephens and Krebs 1986, Shorrocks and Swingland 1990, Gilpin and Hanski 1991), but such models are usually simplistic in their portrayal of landscapes as resource or habitat patches imbedded within an inhospitable matrix, a holdover from island biogeography theory. While this island analogy is an apt description of some systems (e.g., *Daphnia* in rock pools or fritillary butterflies in dry meadows; Hanski and Ranta 1983, Hanski et al. 1995), landscapes generally are not binary mosaics, but are comprised of a variety of habitat types that may be used for different functions (reproduction vs foraging) or to different degrees, perhaps based on habitat quality, by a particular species (e.g., Andrén 1990, Cummings and Vessey 1994).

Description and modelling of environmental complexity is complicated further by difficulties in defining how species perceive patch structure within landscapes (Wiens 1989, With 1994a). Species probably do not have binary perceptions of landscapes (presence/absence of resources), but instead respond to a gradient of resource quality. Species' perceptions of landscape structure are complicated further by the different spatial scales at which species interact with resource distributions, even within the same landscape, because of differences in vagility or in types of resources utilized (Kotliar and Wiens 1990, With 1994a, Wiens et al. 1995).

What is required, then, is the ability to link species' interactions with complex spatial patterns in a realistic fashion. The key to understanding how landscape patterns impact populations is to adopt an organism-centered view of landscape structure (Wiens 1989, With 1994a). Species' perceptions of landscape structure are determined by individual responses to spatial heterogeneity in terms of movement behavior (rate and tortuosity of movement in different habitats, response to edges, dispersal range), habitat affinities, assessment of habitat quality, and ultimately, the consequences of such habitat relationships for fitness (e.g., differential mortality or reproduction in habitats). Inasmuch as the individual organism can be considered the basic unit of ecology (Wiens et al. 1993), the aggregative responses of individuals result in higher-order phenomena such as population dynamics (Turchin 1989, 1991), which are generally of concern when considering the ecological consequences of habitat fragmentation.

Landscape structure is defined in terms of resource distributions – the number, size and shape of patches and the distances among them (e.g., Dunning et al. 1992). The key issue, however, is *connectivity* (Taylor et al. 1993). Landscape connectivity refers to the functional linkage among habitat patches, either because habitat is physically adjacent or because the dispersal abilities of the organism effectively connect patches across the landscape (O'Neill et al. 1988, Gardner et al. 1993, With and Crist 1995, Pearson et al. 1996). Thus, whether or not a landscape is fragmented depends upon how species are able to utilize and move through elements of the landscape. The development of generalized, spatially explicit models of how species interact with landscape structure would enhance our ability to predict when habitat fragmentation – a disruption in landscape connectivity – is likely to impact species with different life-history responses and dispersal capabilities in a given landscape.

In this paper, we explore how environmental heterogeneity affects the redistribution of individuals using neutral landscape models, which are grid-based, null models of environmental complexity (Gardner et al. 1987, Gardner and O'Neill 1991, O'Neill et al. 1992). Our emphasis is on species with different habitat affinities (degree of habitat association) and our objective is to determine what patterns of population dispersion are expected to emerge on landscapes that have variable habitat abundance and quality (carrying capacity), and differ in the spatial arrangement of habitat. We use methods from fractal geometry to generate neutral models with habitat distributions that are more similar to actual landscapes than simple random maps. Our modelling approach tackles the spatial complexity of heterogeneous (>1 habitat) landscapes and provides a means of adjusting spatial contagion and other attributes of landscape structure (e.g., patch size, shape, area and amount of edge) in a systematic fashion by adjusting p, the proportion of habitat(s) and the specific algorithm used to generate the neutral landscape (see below). Furthermore, since the scaling of landscape patterns may affect species' responses to habitat fragmentation (e.g., Biondini and Grygiel 1994, Pearson et al. 1996), we performed a multiscale analysis of the resulting population distributions to characterize the patch structure of populations and to identify what landscape features were important in determining population distributions at different scales. We demonstrate that connectivity in heterogeneous landscapes, and thus whether a species is likely to be affected by habitat fragmentation, can be determined by the interaction of individual movement responses with landscape structure.

Methods

Model description

Neutral landscape models

Neutral landscape models have provided an important theoretical tool for understanding ecological processes

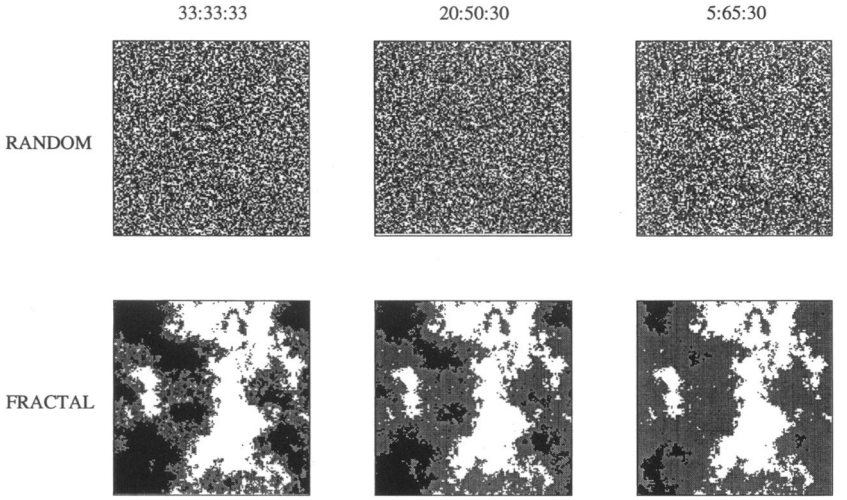

Fig. 1. Neutral landscapes used in simulation experiments. Maps were generated as either a simple random or fractal distribution of three habitat types. The relative proportions of habitat were varied for each set of maps.

in heterogeneous environments by providing generalized models of habitat distribution (Gardner et al. 1987, 1989, 1992, O'Neill et al. 1988, Gardner and O'Neill 1991, Milne 1992). As such, these neutral landscapes serve as null models for assessing the effects of spatial heterogeneity on ecological patterns. Simple random maps are generated as grids of size m by m, in which a proportion, p, of the m^2 sites are occupied at random (e.g., habitat is randomly assigned to pm^2 cells of the grid; Fig. 1). Although such landscapes are produced from a random distribution of habitat, random maps become connected when $p > 0.5928$, if connectance is defined by adjacency of neighboring habitat cells (see Plotnick and Gardner 1993). Above the critical threshold, the habitat is likely to form a continuous cluster that spans the map (Fig. 2). An organism located on this "percolating cluster" will be able to traverse or "percolate" across the landscape (see O'Neill et al. 1988, With and Crist 1995, Pearson et al. 1996).

Other types of neutral landscape models have been created to consider aspects beyond those of random connectance between adjacent sites. For example, hierarchically structured maps produce scale-dependent changes in pattern (i.e., the value of p, the proportion of habitat, changes with the level of resolution; O'Neill et al. 1992, Gardner et al. 1993, Lavorel et al. 1993). Random hierarchical maps provide a useful model of scale-dependent changes in resource distributions, which is a feature of natural landscapes (Urban et al. 1987, Kotliar and Wiens 1990). Simple random maps and hierarchically structured maps are usually created by the arrangement of a single habitat type, however, and therefore do not reproduce patch shapes, sizes and boundaries that result from the co-occurrence of multiple habitat types.

Fractal landscapes (Palmer 1992) have been used to represent landscape patterns (Petigen and Saupe 1988), and provide a simple method for controlling the relative abundances of multiple habitat types and the degree of habitat fragmentation. The midpoint displacement algorithm (MidPointFM2D, Saupe 1988: 101) can be used to produce a 2-dimensional landscape with multiple habitat types (Fig. 1). The variance associated with the displacement of points, σ^2, and H, the parameter that specifies the dependence between adjacent points, are the only two parameters required by this algorithm. The process of successive displacement of points results in an expected difference between any two points that is equal to $E[X_1 - (X_1 - d)] \propto d^H$ (Plotnick and Prestegaard 1993). When $H = 0.5$, the difference between any two points is proportional to the square of the distance, d and the correlation between any points separated by distance d is equal to $C(d) = 2^{2H-1} - 1$ (Mandelbrot 1983, Feder 1988). Adjustment of the value of H between 0.0 and 1.0 results in maps that range from extremely fragmented to highly aggregated. The fractal dimension, D, of maps generated by the midpoint displacement method is equal to $D = 3.0 - H$ (Saupe 1988). Because our interest was in generating neutral landscapes with clumped habitat distributions that were distinctly different from simple random maps (see Results, Analysis of landscape maps), we set $H = 0.5$, and thus $D = 2.5$ for all of the fractal landscapes portrayed in this paper.

Fractal landscapes produce edge effects created by the map boundary, and were therefore "wrapped" such that the habitat along opposite edges matched. This was done by fixing the right column and bottom row of the map to be equal, respectively, to the left column and top row. The midpoint displacement algorithm was then implemented as described above. Although the midpoint displacement algorithm produces a continuously varying surface of real numbers, we wanted to generate heterogeneous landscapes that portrayed discrete habitat types representing a gradient in habitat

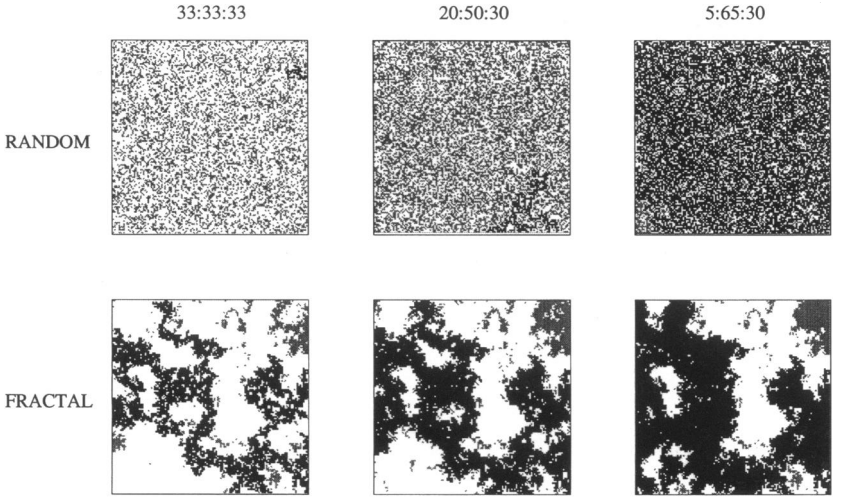

Fig. 2. Same neutral landscapes as in Fig. 1, but with the largest cluster highlighted in black. The largest cluster is associated with the most abundant habitat type (2) in the landscape. Habitat 2 percolates in all of these fractal landscapes, but only percolates on random maps when p, the proportion of habitat, exceeds the critical threshold ($p_c > 0.59$).

quality (differences in carrying capacity). We therefore rank-ordered these numbers from lowest to highest value and assigned integer habitat based on this ranking. If N is the number of habitat types, M is the total number of sites on the map, and c is a vector specifying the cumulative proportions of the map occupied by each habitat type, then the fraction of the map occupied by habitat type i will correspond to the sites whose rank-ordered values fall on the interval $c_{i-1}M$ to c_iM. Because we require only this ranking to produce the desired habitat map from the set of real numbers generated by the midpoint displacement method, the value of σ^2 is arbitrary and was set to 1.0 for all simulations.

Our objective was to examine how landscape structure influences patterns of population dispersion. Landscape structure is a function of the number of habitat types, their relative abundances and the method used to generate spatial patterning. We compared simple random maps of three habitat types with fractal landscapes, which enabled us to evaluate the effect of habitat clumping on population distributions. Three different proportions of the three habitat types were produced for both the fractal and random maps ($m = 128$, $m^2 = 16\,384$ cells). One series contained equal proportions of habitat ($p_1 = p_2 = p_3 = 0.33$); a second series had $p_1 = 0.2$, $p_2 = 0.5$, and $p_3 = 0.3$; and the final series set $p_1 = 0.05$, $p_2 = 0.65$, and $p_3 = 0.30$ (Fig. 1). The proportion of one habitat type (p_3) was similar in all landscapes, whereas that of a second habitat type (p_2) was increased beyond the theoretical critical threshold value expected for simple random maps [$(p_2 > p_c) = (0.65 > 0.59)$ in the final set of maps; Fig. 1].

Analysis of landscape maps

Metrics that are useful descriptors of landscape pattern include the number of clusters (patches), total amount of edge, largest cluster size, amount of edge around the largest cluster, area-weighted patch size, correlation length, and percolation frequency (Gardner et al. 1987, 1993, Turner et al. 1989, Lavorel et al. 1993). All of these metrics provide some measure of the extent of habitat fragmentation in a landscape. Patch area-to-edge relationships are depicted in the number, size, and shape of clusters and the corresponding amount of edge habitat. Determination of cluster size, and thus the number of clusters, is based on the neighborhood rule used to define what constitutes a cluster (e.g., Plotnick and Gardner 1993). Only nearest neighbors were considered in this analysis; that is, habitat cells must be adjacent along one of the four edges, excluding diagonals, to be considered members of the same cluster. Because the frequency distribution of patch sizes may be highly skewed, the area-weighted patch size gives a better estimate of average patch size. The amount of edge is the total number of dissimilar habitat cells adjacent to each site of a particular habitat type. The amount of edge increases to some extent with patch area, but is also affected by patch geometry. The correlation length is the average distance between two sites belonging to the same cluster, and provides a measure of connectivity of the entire map (Gardner et al. 1993). Percolation frequency is the proportion of maps for a given simulated landscape in which the opposite ends of the landscape are connected by a particular habitat type, and is a useful metric for assessing the ability of organisms to move across the landscape (O'Neill et al. 1988, Gardner et al. 1991).

Habitat quality

Apart from the abundance and spatial patterning of habitat, resource abundance within habitat types can be manipulated. We modified resource abundance indirectly by specifying the carrying capacity of each habitat type. Carrying capacity is the number of organisms that the habitat can support (number of individuals/cell

of a particular habitat type) and is assumed to reflect resource productivity within the various habitats. Levels of carrying capacity were set to low ($K = 5$ individuals/cell), medium ($K = 10$) and high ($K = 20$). It should be noted that carrying capacity did not influence whether or not individuals entered a particular cell type, but was subsequently applied to cull excess individuals when cell density exceeded carrying capacity for that cell type. The carrying capacity of the entire landscape ($M = 128 \times 128 = 16\,384$ cells) is thus a combination of the relative proportions of the three habitat types and their respective carrying capacities; theoretically, this ranged from 189 235 when proportions of habitat were equal (but each habitat had either a low, medium or high carrying capacity) to 266 240 when one habitat type dominated the landscape ($p = 0.65$) and had the highest carrying capacity ($K = 20$). Because populations were initialized as a random distribution around a cell density that was below maximum K (see Methods, Simulation experiments) and no birth or immigration processes were incorporated in this modelling exercise, the carrying capacity of the landscape was never attained by the simulated populations. We recognize that carrying capacity may be a poor indicator of habitat quality in some landscapes for habitats that are population sinks (Van Horne 1983, Pulliam 1988), but we will equate carrying capacity with habitat quality for the sake of discussion in this modelling exercise. Six different combinations of carrying capacity for the three habitat types were specified (Table 1). The combination of landscape type (random vs fractal), habitat proportion (3 sets), and carrying capacity (6 combinations) produces 36 maps ($2 \times 3 \times 6$) that we used to examine the effects of landscape structure on the spatial distribution of populations.

Species' responses to landscape structure

Movement is one mechanism by which animals interact with landscape structure (e.g., O'Neill et al. 1988, Johnson et al. 1992, With 1994a, b). In our simulations, individuals could move up to 10 cells according to an inverse squared distance function, although average dispersal was ≤ 2 cells. Individuals moved with random directionality. Individuals were allowed to "wrap" around map edges to eliminate boundary effects. The probability that an individual would remain within a given habitat site during each time step of the simulation was based on habitat-specific residence probabilities (P_r). An individual had either a high ($P_r = 0.9$), intermediate ($P_r = 0.5$), or low ($P_r = 0.1$) probability of remaining within each of the three habitat types in the landscape. Notice that $1 - P_r$ gives the transition probability, the probability that an individual will leave a given habitat site. Thus, a species with a high residence probability in a given habitat presumably has a preference for that habitat and would be unlikely to leave. There are six different possible combinations of habitat affinities (Table 1).

Table 1. Combinations of species' habitat affinities (residence probability, P_r) and habitat carrying capacities used independently in simulations.

	Residence probability			Carrying capacity		
	1	2	3	1	2	3
A	0.9	0.5	0.1	20	10	5
B	0.9	0.1	0.5	20	5	10
C	0.5	0.9	0.1	10	20	5
D	0.5	0.1	0.9	10	5	20
E	0.1	0.9	0.5	5	20	10
F	0.1	0.5	0.9	5	10	20

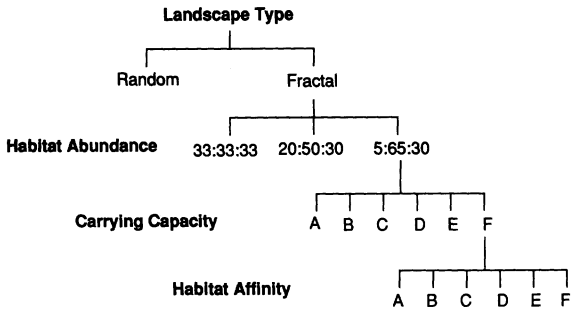

Fig. 3. Hierarchical design of simulation experiments.

Simulation experiments

We conducted a series of simulation experiments to assess how species' habitat affinities affected population distributions in different landscape mosaics.

Factorial design of all parameter states

In each experiment, we simultaneously varied aspects of landscape structure such as the map type (random vs fractal), habitat abundance and quality (carrying capacity of habitat), in conjunction with the species' habitat affinities. The simulations were organized into a hierarchical design that produced 216 different scenarios (Fig. 3). Only a single run was performed for each scenario because results were consistent among replicates (unpubl.). Populations were initialized as a random distribution around an initial cell density (10 individuals/cell); that is, each cell was randomly assigned a density of between 1 and 10 individuals. Simulations ran for 21 time steps, at which point the pattern of population distribution had stabilized and showed little change (ca 1%) for at least two time steps.

Independent effects

Because carrying capacity and residence probability are expected to interact, we ran two other series of simulations to assess directly the relative effects of these two parameters on population distributions: 1) Carrying capacity was fixed at the same level for all habitats across the landscape (at either high, medium or low levels), resulting in 108 scenarios (6 landscape maps × 3 levels of carrying capacity × 6 combinations of residence probabilities). In this series of experiments, the carrying capacity of the entire landscape was between 81920 when $K = 5$ ($M = 16\,384 \times 5 = 81\,920$) and 327 680 when $K = 20$; and, 2) Residence probability was fixed at the same level for all habitats (at either high, medium or low probabilities), which also resulted in 108 different scenarios (6 landscape maps × 3 levels of residence probability × 6 combinations of carrying capacity).

Analysis of effects on population distributions

Pattern of distribution

To describe the spatial pattern of the population, we used Morisita's Index (I_m), which provides a measure of the degree to which the population is aggregated. Morisita's Index measures how many more times likely it is that two individuals, drawn at random, came from the same cell than if the population were distributed at random (Hurlbert 1990). Values for I_m range from 0 for an even distribution, to 1 for a random distribution, to >1 for aggregated distributions. Thus, two individuals selected at random from a population with $I_m = 2.0$ are twice as likely to be found in the same cell than a population with randomly distributed individuals. Because I_m is affected by box size – the unit at which individuals are sampled – for nonrandom distributions (Elliott 1977), we calculated I_m at different scales by doubling box size at each level (levels = 7 for $m = 128$; minimum box size = 1 × 1, maximum box size = 64 × 64 cells). By considering how I_m changes as a function of scale, we may be able to determine the scale of patchiness at which the population occurs across the landscape. While it is possible for populations with different densities to possess the same I_m, population size is not analyzed in this simulation exercise because populations were initialized around an arbitrary density (10 individuals/cell), and no birth, death, immigration, or emigration processes were incorporated into the model that would have influenced population size. Instead, the resulting pattern of distribution is a more relevant response in the present analysis because we can determine how the spatial patterns of the population mirror that of the landscape.

Statistical analysis

The degree of patchiness of the population, as indexed by I_m, may be correlated across scales, producing domains of scale in which the patch structure remains constant. Abrupt shifts in I_m as a function of scale presumably reflect changes in the pattern of clumping for the population (Elliott 1977). We therefore performed a factor analysis to identify how the pattern of population dispersion varied across scales. We used principal components to identify the initial factors. The number of factors retained for interpretation and further analysis was then determined by the number of principal components with an eigenvalue > 0.9 (but see Jackson 1993). The varimax rotation method was used to facilitate the interpretation of factor loadings (Afifi and Clark 1984), and the loadings of the rotated factors on the initial 7 variables (I_m values calculated at 7 scales) were examined.

ANOVA was used to assess how landscape structure affected population distributional patterns across scales. The statistical model used in this analysis contained the factors previously extracted from factor analysis as the dependent variables (1–2 factors; see Results), and landscape type, habitat abundance and habitat quality as the independent variables. We also included species' habitat affinities as an independent variable in the model, to determine how species' attributes interact with landscape structure and affect population distributional patterns. The ANOVA model contained all two-way interactions among the independent variables.

Results

Analysis of landscape maps

Fractal maps contain fewer, larger patches with less edge habitat than do simple random landscapes (Table 2). Random maps contain 13–19 times more discrete patches of habitat 1; 2–11 times more individual patches of habitat 2; and about 17 times more patches of habitat 3 than the corresponding fractal maps. Fractal landscapes also possess a high degree of connectivity because habitat types are assigned along a gradient. In a three-habitat map, habitats 1 and 3 are separated by habitat 2. Consequently, habitat 2 spans the map, even well below the percolation threshold for simple random maps (Table 1, Figs 2 and 4). In random maps, habitat 2 percolates only when its abundance exceeds $p_c = 0.59$ (Table 1, Figs 2 and 4). Although random and fractal maps are both connected when $p_2 = 0.65$, random maps contain more individual clusters of habitat, and the percolating cluster (habitat 2) contains 4 times more edge habitat than the percolating cluster on a fractal landscape.

Effects on population distributional patterns

Factorial design of all parameter states

Factor analysis produced two factors that explained 94.4% of the variance in the data set. Factor 1 ex-

Table 2. Metrics ($\bar{x} \pm$ SD) describing habitat clusters within random and fractal landscapes generated with different proportions of three habitat types ($n = 10$ for each of six landscapes, see Fig. 1).

	33:33:33		20:50:30		5:65:30	
Metric	Random	Fractal	Random	Fractal	Random	Fractal
Habitat 1						
Total clusters	2038 (41.6)	125 (33.9)	1993 (23.6)	104 (19.6)	733 (22.5)	58 (22.1)
Total edge	14591 (95.6)	2496 (384.5)	10458 (113.6)	1848 (253.6)	3091 (83.7)	861 (270.1)
Largest cluster size	37 (8.2)	3715 (985.6)	14 (1.6)	2192 (541.2)	4 (0.82)	365 (211.1)
Largest cluster edge	67 (14.8)	926 (289.2)	28 (3.9)	744 (288.7)	10 (1.6)	219 (70.3)
Area-weighted average	7 (0.6)	5462 (49.1)	3 (0.1)	1676 (548.9)	1.2 (0.04)	271 (229.2)
Correlation length	3 (0.2)	30 (5.1)	2 (0.1)	23 (4.9)	1 (0.1)	10 (2.7)
Percolation frequency	0.0	0.0	0.0	0.0	0.0	0.0
Habitat 2						
Total clusters	2025 (22.0)	180 (29.7)	1109 (25.7)	150 (24.7)	255 (11.6)	107 (16.7)
Total edge	14620 (179.0)	4830 (763.4)	16502 (88.5)	4216 (552.3)	15109 (109.7)	3403 (521.2)
Largest cluster size	34 (4.5)	4446 (610.9)	267 (84.1)	7513 (289.8)	9826 (345.2)	10232 (262.5)
Largest cluster edge	61 (8.5)	3189 (584.4)	444 (133.5)	3007 (445.7)	13179 (452.6)	2617 (456.1)
Area-weighted average	6 (0.3)	3722 (909.3)	54 (9.3)	6894 (515.2)	9088 (582.2)	9824 (469.5)
Correlation length	2.7 (0.11)	44 (3.9)	9 (1.5)	47 (2.4)	52 (0.9)	49 (1.9)
Percolation frequency	0.0	0.8 (0.42)	0.0	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Habitat 3						
Total clusters	2034 (55.6)	131 (40.5)	2109 (50.8)	126 (38.4)	2109 (50.8)	126 (38.4)
Total edge	14575 (119.4)	2579 (582.1)	13789 (109.4)	2451 (557.6)	13789 (109.4)	2451 (557.6)
Largest cluster size	39 (8.2)	3352 (1098.6)	31 (6.4)	2797 (714.0)	31 (6.4)	2797 (714.0)
Largest cluster edge	70 (14.0)	896 (376.9)	58 (9.1)	750 (325.8)	58 (9.1)	750 (325.8)
Area-weighted average	7 (0.5)	2614 (1172.2)	5 (0.4)	2040 (709.6)	5 (0.4)	2040 (709.6)
Correlation length	3 (0.2)	30 (8.6)	2 (0.1)	26 (6.6)	2 (0.1)	26 (6.6)
Percolation frequency	0.0	0.2 (0.42)	0.0	0.1 (0.32)	0.0	0.1 (0.3)

plained 76.8% of the variance and described the spatial structure of the population from scales 2–7 (box sizes 2–64; factor loadings = 0.852–0.996). Factor 2 explained an additional 17.6% of the variance and consisted of the first scale (factor loading = 0.979). Landscape type had an overwhelming effect on the resulting pattern of distribution at both scales (Factor 1, coarse scale: $F = 1565.27$, df = 1, 100, $P = 0.0001$, Model $R^2 = 0.961$; Factor 2, fine scale: $F = 288.84$, df = 1, 100, $P = 0.0001$, Model $R^2 = 0.961$). At the finest scale, populations attained greater levels of aggregation within random than in fractal landscapes (Fig. 5). Aggregation occurs because cells of a given habitat type are more isolated on random maps, enabling individuals to aggregate up to carrying capacity within preferred habitat cells. At coarser scales, however, populations were patchier on fractal maps than random ones. Given the disparity in distributional patterns

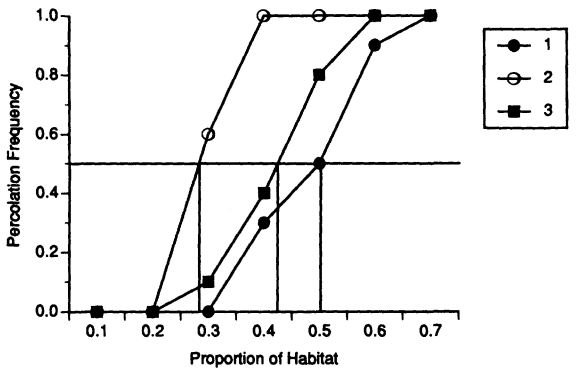

Fig. 4. Critical thresholds for each of three habitat types across a range of habitat abundance in heterogeneous fractal maps. The critical threshold is assessed as the proportion of habitat at which that particular habitat formed a percolating cluster (a habitat patch that spanned the entire landscape) on ≥50% of the maps ($n = 10$).

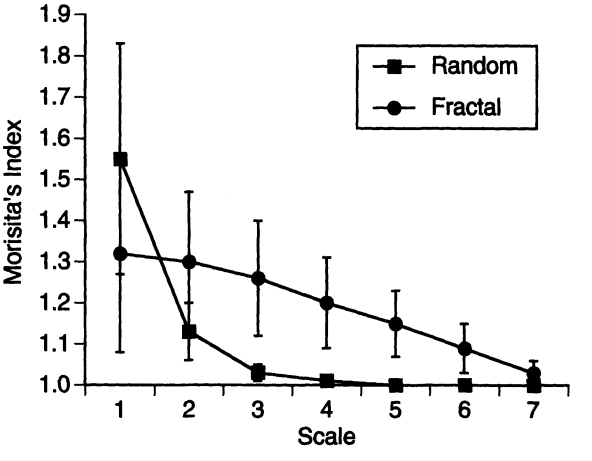

Fig. 5. Distributional pattern of populations on random and fractal landscape maps (each $n = 108$) as a function of scale. Morisita's Index, a measure of aggregation, was calculated at 7 different scales by doubling the box size at which the index was calculated at each level. Error bars are 1 SD of the mean.

Table 3. Summary of ANOVA results of effects on patterns of population distribution (as indexed by Morisita's Index, I_m) in artificially generated random and fractal landscapes. The dependent variables are the factors derived from a factor analysis of I_m calculated at different scales.

Source of variation	DF	MS	F	P
Random maps				
Factor 1				
Habitat abundance	2	6.36	52.93	0.0001
Habitat affinity	5	2.71	22.50	0.0001
Carrying capacity	5	1.33	11.02	0.0001
Habitat abundance × habitat affinity	10	1.50	12.48	0.0001
Habitat abundance × carrying capacity	10	0.27	2.25	0.03
Habitat affinity × carrying capacity	25	2.02	16.76	0.0001
error	50	0.12		
Fractal maps				
Factor 1 (Fine Scales)				
Habitat abundance	2	2.28	19.82	0.0001
Habitat affinity	5	1.16	10.11	0.0001
Carrying capacity	5	0.92	7.96	0.0001
Habitat abundance × habitat affinity	10	0.43	3.74	0.001
Habitat abundance × carrying capacity	10	0.33	2.84	0.01
Habitat affinity × carrying capacity	25	3.15	27.40	0.0001
error	50	0.12		
Fractal maps				
Factor 2 (Broad Scales)				
Habitat abundance	2	0.03	0.14	ns
Habitat affinity	5	5.95	26.98	0.0001
Carrying capacity	5	3.92	17.80	0.0001
Habitat abundance × habitat affinity	10	0.14	0.65	ns
Habitat abundance × carrying capacity	10	0.83	3.78	0.001
Habitat affinity × carrying capacity	25	1.47	6.68	0.0001
error	50	0.12		

between random and fractal landscapes, we conducted a separate analysis for these two map types to determine which factors were most important in determining population distributions on each landscape type.

Random maps. Populations quickly approached a random distribution as the scale of resolution increased; the pattern remained unchanged beyond the fourth scale (box size = 8; Fig. 5). Factor analysis thus generated a single factor composed of only the first four scales which explained 88.6% of the total variance (factor loadings = 0.810–0.983). Although all terms in the statistical model had a significant effect on distributional patterns, habitat abundance, habitat affinity and the interaction between habitat affinity and carrying capacity had the greatest influence on distributions (Table 3). Populations were less aggregated in random landscapes where one habitat dominated (5:65:30, Fig. 6). Population distribution exhibited a threshold effect as p_2 decreased in relative abundance ($5{:}65{:}30^{A} = 20{:}50{:}30^{A} > 33{:}33{:}33^{B}$; $n = 36$ maps each, Tukey test of factor scores, Fig. 7). Populations also attained the highest aggregation when the affinity for habitat 2 was low ($P_{r2} = 0.1$, B and D in Fig. 6). Conversely, species with high affinities for this habitat ($P_{r2} = 0.9$) had less-patchy distributions (C and E in Fig. 6). In two-thirds of the landscape maps, habitat 2 was the most abundant type in the landscape. Species with a corresponding affinity for the uncommon or rarer habitat types thus had patchy distributions in these landscapes ($D^{A} \geq B^{B} \geq F^{BC} \geq A^{CD} \geq C^{CD} \geq E^{D}$, $n = 18$ maps each, Tukey test of factor scores, Fig. 7).

Carrying capacity interacted with species' habitat affinities and enhanced the level of aggregation attained by the population (Random maps, Fig. 8). Populations were most aggregated in landscapes in which carrying capacity was lowest for habitat 2 ($K_2 = 5$, B and D in Fig. 6). The highest level of aggregation, however, was attained by species with a high affinity for habitat 1 (A or B), an uncommon or rare habitat type in two-thirds of the maps, in scenarios where habitat 1 had the highest carrying capacity (A or B; Fig. 8). Alternatively, clumping was enhanced in maps for which habitat 3 had the highest carrying capacity (D or F) and was the most preferred habitat by the species (D or F; Fig. 8). Again, clumped distributions are expected when a species has an affinity for a typically rare (habitat 1) or uncommon (habitat 3) habitat.

Fractal maps. Factor analysis generated two factors that explained 97.2% of the variance in distributional patterns on fractal maps. The first factor explained 84% of the variance and loaded on scales 1–6 (factor loadings = 0.680–0.975), while the second factor explained

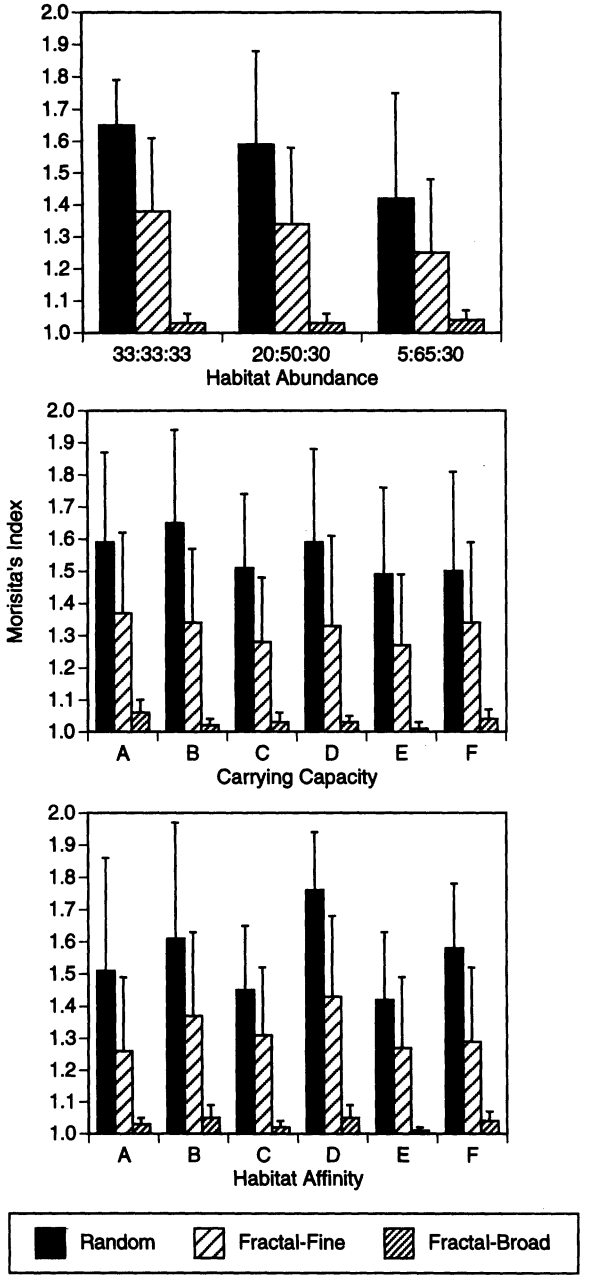

Fig. 6. Effect of habitat abundance, carrying capacity and habitat affinity on population distributions in different landscapes. Patterns assessed at the finest scale (scale 1) are presented for random maps. Populations on fractal landscapes exhibited two scales of patchiness (Fine and Broad), and thus patterns assessed at scales 1 and 7 are presented in this figure. Levels of carrying capacity and residence probability (A–F) are given in Table 1. Sample sizes: habitat abundance = 36 maps at each level for a total of 108 maps each for random and fractal landscapes; carrying capacity = 18 maps at each level; habitat affinity = 18 maps at each level.

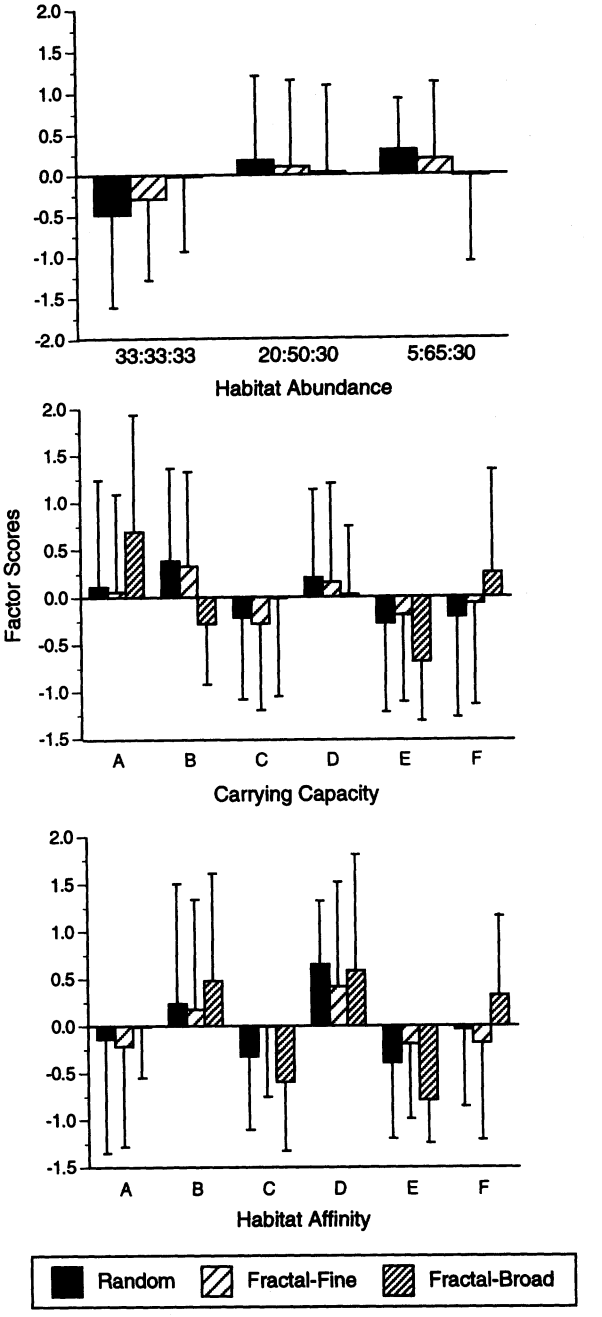

Fig. 7. Factor analysis of the effects of habitat abundance, carrying capacity, and habitat affinity on population distributions in different landscapes. Two factors were obtained for fractal landscapes (Fractal-Fine and Fractal-Broad). Levels of habitat affinity and carrying capacity (A–F) are given in Table 1. Sample sizes are the same as in Fig. 6.

an additional 13.3% of the variance and consisted of scales 5–7 (factor loadings = 0.614–0.970). Although there is some overlap between the two factors, the factor variables can be interpreted as describing spatial patterns at generally fine scales (Factor 1) and coarse scales (Factor 2). The lack of a sharp transition in spatial pattern as a function of scale is responsible for the overlap in the two factor variables (Fig. 5). There is

a near monotonic decrease in I_m with increasing scale for populations in fractal landscapes.

At finer scales, the interaction between species' habitat affinity and carrying capacity had the greatest impact on population distributions (Table 3). As in random maps, populations attained higher levels of aggregation when habitat 2, a generally common habitat, was the least preferred (e.g., B and D, Fractal-Fine in Fig. 6; $D^A \geq B^{AB} \geq C^{BC} \geq F^C = E^C = A^C$, $n = 18$ maps each, Tukey test of factor scores, Fig. 7). Similarly, the highest degree of clumping was observed in landscapes for which the carrying capacity was lowest in what is generally the most abundant habitat (p_2; B and D, Fractal-Fine in Fig. 6; $B^A \geq D^{AB} \geq A^{ABC} \geq F^{CD} = E^{CD} \geq C^D$, $n = 18$ maps each, Tukey test of factor scores, Fig. 7). The interaction between these two factors produced the same results as in random maps; populations were most aggregated in landscapes in which the most preferred habitat (A and B) was generally rare and had the highest carrying capacity (A and B) or in which the most preferred habitat was typically uncommon (p_3) but had the highest carrying capacity (D × D and D × F, Fractal-Fine Scales in Fig. 8).

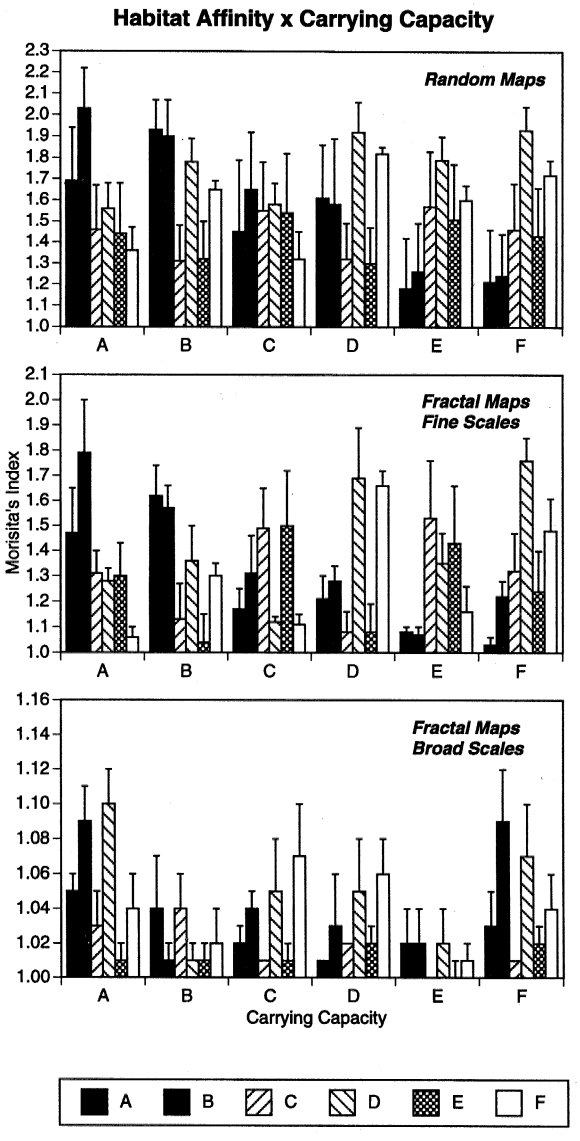

Fig. 8. Interaction between habitat affinity and carrying capacity for different landscapes. Patterns assessed at the first scale are presented for random maps. Two scales of patchiness emerged on fractal landscapes (Fine vs Broad Scales), and thus patterns assessed at scale 1 and 7 are presented in this figure. Sample sizes are 3 maps at each level of affinity × carrying capacity. Levels of habitat affinity and carrying capacity (A–F) are given in Table 1.

Habitat abundance also affected the spatial pattern of populations at fine scales (Table 3). A threshold effect is apparent even for fractal maps. There is a significant decrease in I_m for landscapes dominated by one habitat type (Fig. 6; $5{:}65{:}30^A = 20{:}50{:}30^A > 33{:}33{:}33^B$, $n = 36$ maps each, Tukey test of factor scores, Fig. 7). The relative abundance of habitat had no effect on the distributional patterns at coarser scales for populations in fractal landscapes, however (Factor 2, Table 3; Fractal-Broad in Fig. 6).

At coarser scales, the main effects of habitat affinity and carrying capacity of habitats were the most important determinants of population distributions (Factor 2, Table 3). Species' habitat affinities produced the same types of patterns as reported previously for random maps and at fine scales for fractal maps, with one exception: the degree of aggregation was also enhanced to some extent when a generally uncommon habitat (p_3) was preferred and the species exhibited a neutral preference for habitat 2 (F in Fractal-Broad in Fig. 7; $D^A = B^A \geq F^{AB} \geq A^B > C^C = E^C$, $n = 18$ maps each, Tukey test of factor scores). The effect of carrying capacity likewise mirrored the distributional patterns produced on other landscapes ($A^A \geq F^{AB} \geq D^{BC} = C^{BC} \geq B^{DC} \geq E^D$, $n = 18$ maps each, Tukey test of factor scores, Fig. 7). The main differences were that high carrying capacities in both habitats 1 and 2 (generally the rarest and most abundant habitats, respectively) resulted in populations with higher I_m values (A in Fig. 7), whereas a high carrying capacity in habitat 1 alone reduced I_m (B in Fig. 7). These differences were very subtle, however, because the spatial structure of populations in fractal maps was essentially random when considered at very broad scales (Figs 6 and 8).

Independent effects of carrying capacity and residence probability

(1) Fixed carrying capacity. Factor analysis produced two factors that explained 90.2% of the variance. The first factor loaded most heavily on scales 2–7 (scores = 0.731–0.978), and thus described patterns at coarse scales, whereas the second factor loaded on the first

scale (score = 0.912) and described fine-scale patterns. Landscape patterning again had an overwhelming effect on the resulting pattern of population distributions at both scales (Factor 1, coarse scales: $F = 746.71$, df = 1, 64, $P = 0.0001$, Model $R^2 = 0.949$; Factor 2, fine scales: $F = 151.88$, df = 1, 64, $P = 0.0001$, Model $R^2 = 0.945$, model df = 43, error df = 64). Populations were always more clumped on random landscapes (Fig. 9).

Because landscape geometry had the biggest influence on population distributions, we again performed separate analyses for random and fractal maps. Patterns on random map were scale invariant, and thus we analyzed the population distribution as measured at scale 1 (box size = 1). Habitat abundance had the greatest effect on distributional patterns (Model $R^2 = 0.990$, model df = 33, error df = 20; Table 4). Populations were significantly more aggregated in landscapes below the expected critical threshold ($33{:}33{:}33^A > 20{:}50{:}30^B > 5{:}65{:}30^C$, $n = 18$ maps each; Tukey test; Random maps in Fig. 9). Residence probability and carrying capacity also affected population distributions (Table 4). Aggregation was enhanced when the habitat that occupied a third of all landscapes (p_3) was the most preferred, or the most-abundant habitat type was the least preferred ($D^A > F^B > B^C > C^D = A^D = E^D$, $n = 9$ maps each; Tukey test). As before, levels of aggregation were highest when carrying capacity was high in all habitats ($20^A > 10^B > 5^C$, $n = 18$ maps each; Tukey test; Fig. 9).

In contrast, factor analysis revealed two scales of patchiness on fractal landscapes. Factor 1 (68.4%) loaded most heavily on scales 3–7 (scores: 0.693–0.950) and thus described population distributions at broad scales, whereas Factor 2 (23.1%) loaded on scales 1–3 (scores: 0.710–0.966) and described fine-scale patterns. At broad scales, carrying capacity was the single most important factor affecting population distributions (Model $R^2 = 0.90$, model df = 33, error df = 20; Table 4). Interestingly, populations were most clumped when carrying capacity was low across the landscape, although the effect was subtle given that distributions were essentially random at this scale ($5^A > 10^B = 20^B$, $n = 18$ maps each, Tukey test; Fractal-Broad in Fig. 9). At fine scales (Factor 2), relative habitat abundance, carrying capacity and residence probability were all significant determinants of population distributional patterns (Table 4). Populations were most aggregated on landscapes below the critical threshold ($33{:}33{:}33^A > 20{:}50{:}30^B > 5{:}65{:}30^C$, $n = 18$ maps each, Tukey test; Fractal-Fine in Fig. 9) and with high carrying capacity ($20^A > 10^B = 5^B$, $n = 18$ maps each; Tukey test). The effect of residence probability was more obscure; highest levels of aggregation were attained when affinity was highest for the most abundant habitat type ($C^A > E^{AB} > D^B > B^C = F^C > A^D$, $n = 9$ maps each; Tukey test).

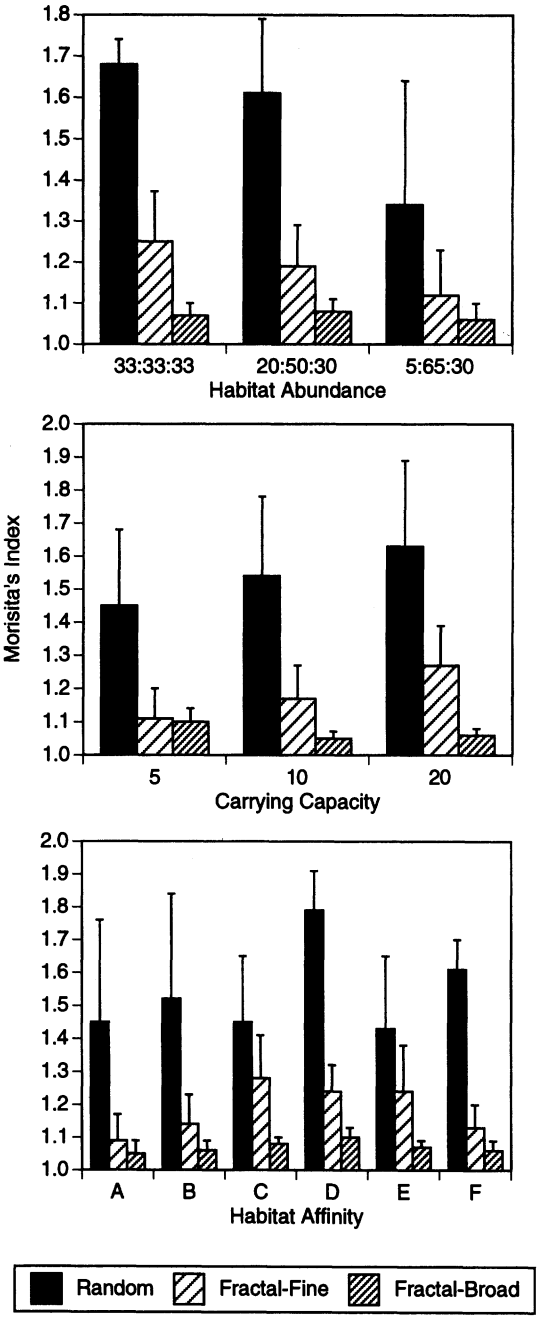

Fig. 9. The effects of habitat abundance, carrying capacity, and habitat affinity on population distributions in landscapes when carrying capacity is fixed at the same level across all habitat types. Two scales of patchiness were identified for populations on fractal landscapes (Fractal-Fine and Fractal-Broad). Levels of habitat affinity (A–F) are given in Table 1. Sample sizes: habitat abundance = 18 maps at each level for a total of 54 scenarios in each landscape type (random vs fractal); carrying capacity = 18 maps; habitat affinity = 9 maps.

Holding carrying capacity constant across the landscape thus did not produce fundamental changes in the resulting patterns of distribution that emerged on these

Table 4. ANOVA summary of parameters that affected population distributions in heterogeneous landscapes when carrying capacity was fixed at either high ($K = 20$ individuals/cell), medium ($K = 10$), or low ($K = 5$) levels in all habitats. Analyses on random maps were conducted on levels of aggregation (Morisita's Index, I_m) assessed at the first scale (box size = 1) because patterns were consistent across scales. Factors describing patterns at coarse and fine scales (factors 1 and 2, respectively) were used as dependent variables for the analysis of population distributions on fractal landscapes.

Source of variation	DF	MS	F	P
Random maps				
Habitat abundance	2	0.57	337.20	0.0001
Carrying capacity	2	0.14	85.18	0.0001
Habitat affinity	5	0.17	100.83	0.0001
Habitat abundance × carrying capacity	4	0.003	1.86	ns
Habitat abundance × habitat affinity	10	0.102	60.41	0.0001
Carrying capacity × habitat affinity	10	0.001	0.62	ns
error	20	0.002		
Fractal maps				
Factor 1 (Broad Scales)				
Habitat abundance	2	0.25	0.94	ns
Carrying capacity	2	14.37	54.93	0.0001
Habitat affinity	5	1.60	6.13	0.001
Habitat abundance × carrying capacity	4	0.10	0.38	ns
Habitat abundance × habitat affinity	10	0.90	3.44	0.009
Carrying capacity × habitat affinity	10	0.11	0.43	ns
error	20	0.26		
Factor 2 (Fine Scales)				
Habitat abundance	2	5.31	189.15	0.0001
Carrying capacity	2	4.66	166.25	0.0001
Habitat affinity	5	4.61	164.31	0.0001
Habitat abundance × carrying capacity	4	0.02	0.89	ns
Habitat abundance × habitat affinity	10	0.89	31.63	0.0001
Carrying capacity × habitat affinity	10	0.05	1.74	ns
error	20	0.03		

different landscapes; results were generally consistent with those produced in the full-factorial simulation experiment. Carrying capacity affected the degree of aggregation that could be attained by the population, but not whether it was generally clumped or randomly distributed.

(2) Fixed residence probabilities. When residence probabilities were the same in all habitats, the pattern of population distribution did not change as a function of scale. Factor analysis produced a single factor that was a composite of all scales (scores 0.891–0.993) and explained 92.7% of the variation in the data. Once again, landscape geometry was the biggest determinant of the resulting distributional pattern ($F = 539.43$, df = 1, 64, $P = 0.0001$; model $R^2 = 0.918$), with populations achieving greater clumping in fractal landscapes (Fig. 10) and we therefore performed separate analyses on the two map types.

In random landscapes, distributional patterns did not change as a function of scale and thus we performed separate analyses on distributions assessed at the first scale. Residence probability and carrying capacity each had a significant influence on population distributions (Table 5). Interestingly, populations were slightly more aggregated when random maps had either low or high residence probability ($0.1^A = 0.9^A > 0.5^B$, $n = 18$ maps each; Tukey test) and when carrying capacity was highest ($K = 20$) in the habitat that is generally the most abundant (p_2; $E^A = C^A \geq F^{AB} \geq A^{ABC} \geq D^{BC} \geq B^C$, $n = 9$ maps each; Tukey test). Nevertheless, all populations essentially retained their initial random distributions ($I_m = 1.0$; Fig. 10).

In fractal landscapes, patterns of population distribution also did not vary across scales, and residence probability, carrying capacity, habitat abundance and the interaction between habitat abundance and carrying capacity all affected the distributional patterns that emerged at the first scale (Table 5). Again, the effects were subtle. Populations attained slightly higher levels of aggregation when species had low residence probabilities ($0.1^A > 0.5^B > 0.9^C$, $n = 18$ maps each; Tukey test). Populations were generally more clumped in landscapes in which carrying capacity was lowest ($K = 5$) in the habitat type occupying a third of the landscape (p_3; $A^A = C^A = F^A > D^{AB} > E^{BC} > B^C$, $n = 9$ maps each; Tukey test). Populations also tended to be a bit more aggregated below the critical threshold ($33{:}33{:}33^A = 20{:}50{:}30^A > 5{:}65{:}30^B$, $n = 18$ maps each; Tukey test). Finally, the highest level of aggregation was attained in maps in which habitat abundances were equal and there was a low carrying capacity in habitat 2 ($I_m = 1.12 \pm 0.05$, $n = 3$ maps); habitat 2 is always connected in the fractal maps used in these simulations (Fig. 4).

These effects are weak when compared to the fixed effects of carrying capacity, when residence probability

was varied among habitat types, but the patterns are fundamentally different than those observed in the previous two simulation experiments. Populations are barely able to aggregate beyond their initial random distribution, and then only on fractal landscapes which have a more patchy distribution of habitat than random maps. Thus, differential movement among habitat types may be primarily responsible for the observed patterns of distribution that emerge on these different landscapes.

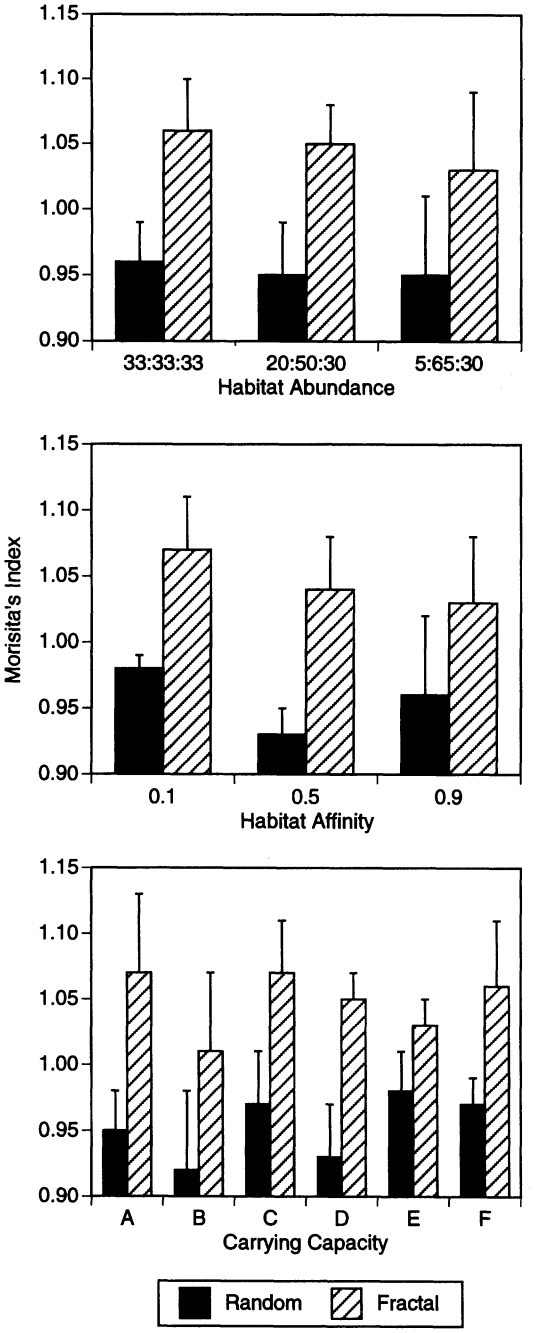

Fig. 10. The effects of habitat abundance, carrying capacity, and habitat affinity on population distributions in landscapes when level of habitat affinity is the same across all habitat types. Levels of carrying capacity (A–F) are given in Table 1. Sample sizes: habitat abundance = 18 maps at each level for a total of 54 scenarios in each landscape type (random vs fractal); habitat affinity = 18 maps; carrying capacity = 9 maps.

Density effects

While our focus has been on relating population distributional patterns to landscape pattern in this paper, it might also be useful to understand how densities within habitat patches are influenced by landscape structure and the parameters in our model, as an aid to interpreting relative levels of aggregation. Morisita's Index is not sensitive to differences in population densities, and thus different densities could give rise to the same levels of aggregation. Landscape geometry had a large effect on cell density only when assessed across all habitats; habitat cells within fractal maps supported larger populations on average than in random landscapes (Fractal: 5.1 ± 1.53; Random: 4.3 ± 2.20, $n = 108$ maps each; Landscape in Table 6). As might be expected, habitat affinity and carrying capacity primarily influenced densities within individual habitat types, with densities being highest when the habitat had either the highest carrying capacity or was the most preferred (Table 6, Fig. 11). Note that population densities remain constant when averaged across all habitat types at the landscape-level, however (Fig. 11). Thus, population size remains fairly constant in all of our simulation experiments, but patterns of distribution shift in different landscape scenarios owing to the aggregation of individuals within specific habitat types that are preferred, have a high carrying capacity or both. For example, individuals of a species with a high affinity for habitat 1 (A or B) in a landscape in which this habitat had the highest carrying capacity (A or B), would tend to aggregate within cells of this habitat (up to the carrying capacity of the individual cells). Morisita's Index measures the level of aggregation assayed at some scale in the landscape; thus, if these individuals are aggregating in a rare habitat type, higher levels of I_m are attained than if the habitat happens to be common (individuals are retained in fewer cells in the landscape, but populations reach carrying capacity within cells).

Discussion

Whether habitat fragmentation will impact the spatial distribution of populations depends upon how species perceive or respond to landscape connectivity. Landscape connectivity is a function not only of the spatial contagion of habitat, but also the habitat affinities of species and their ability to move across the landscape

Table 5. ANOVA summary of parameters affecting population distributional patterns in heterogeneous landscapes when residence probabilities (P_r, habitat affinity) are fixed at either high ($P_r = 0.9$), medium ($P_r = 0.5$) or low ($P_r = 0.1$) rates in all three habitats.

Source of variation	DF	MS	F	P
Random maps				
Habitat abundance	2	0.001	0.94	ns
Habitat affinity	2	0.012	18.77	0.0001
Carrying capacity	5	0.004	7.18	0.0005
Habitat abundance × habitat affinity	4	0.001	1.40	ns
Habitat abundance × carrying capacity	10	0.002	2.56	0.04
Carrying capacity × habitat affinity	10	0.002	2.69	0.03
error	20	0.001		
Fractal maps				
Habitat abundance	2	0.006	18.94	0.0001
Habitat affinity	2	0.01	32.26	0.0001
Carrying capacity	5	0.004	14.84	0.0001
Habitat abundance × habitat affinity	4	0.0003	0.97	ns
Habitat abundance × carrying capacity	10	0.004	14.13	0.0001
Carrying capacity × habitat affinity	10	0.001	3.70	0.006
error	20	0.0003		

and effectively utilize spatially distributed resources (O'Neill et al. 1988, Gardner et al. 1993, With and Crist 1995, Pearson et al. 1996). The application of neutral landscape models in ecology has provided a means for determining when landscapes become "disconnected" and thus when habitat fragmentation is likely to prove consequential to population-level processes.

Landscape connectivity is a threshold phenomenon, as demonstrated by percolation models. It is important to realize that the oft-reported $p_c = 0.5928$, as an indicator of potential threshold effects on landscapes, pertains only to certain types of maps (random distribution of a single habitat) in which organisms are constrained to move only among adjacent habitat cells (i.e., the four nearest neighbors, Plotnick and Gardner 1993). Increasing the "neighborhood size" – the number of cells over which an organism is able to move with each time step – lowers p_c because habitat cells are considered connected across a greater range. A species could then cross "gaps" where habitat cells were not immediately adjacent (Dale et al. 1994). For example, Pearson et al. (1996) documented a shift in p_c from 0.6 to 0.25 for a hypothetical species that was able to move across cell gaps on simple random maps. Such a species would thus be able to move across the landscape even when suitable habitat comprised only 25% of the landscape. Landscapes should be perceived as functionally connected across a greater range of fragmentation severity for good dispersers or highly vagile species.

Maps generated by different algorithms, such as the fractal maps in this paper, will have a different p_c owing to differences in the spatial patterning of habitat. For example, hierarchically structured random maps, in which the proportion of habitat changes at different scales, display a variable global p_c depending upon the scale at which habitat is most available, although habitat percolates at $p_c = 0.5928$ within each level (Lavorel et al. 1993). The scale of habitat fragmentation, coupled with the scale at which the organism is able to perceive resource distribution, can dramatically alter p_c. Simulated species perceived all hierarchically structured landscapes as connected when fragmentation occurred at the largest scale, producing big "clearcuts" in an otherwise continuous swatch of habitat (Pearson et al. 1996). But, even species with good gap-crossing abilities were unlikely to perceive the landscape as connected when extensive fragmentation covering two-thirds of the landscape occurred at the finest scale. On random maps, such species were able to percolate across the landscape when only 25% was covered with suitable habitat. Thus, fine-scale fragmentation poses the greatest risk to landscape connectivity, and from a management standpoint, it would be prudent to preserve large tracts of habitat rather than produce small, isolated clearcuts which disrupt landscape connectivity and enhance edge effects (Franklin and Forman 1987, Pearson et al. 1996).

On heterogeneous landscapes comprised of more than one habitat type, the issue of landscape connectivity is more complex. On random maps, landscape connectivity is determined by the dominance of a single habitat type. Each habitat percolates at the expected $p_c = 0.59$, but whether or not a species perceives the landscape as connected depends upon its vagility and habitat preferences. With and Crist (1995) demonstrated how simulated species that varied in habitat specificity and dispersal range viewed landscape connectivity on heterogeneous random maps. For habitat specialists with a minimal range of dispersal (at least 3% of landscape traversed), landscape connectivity was less important than absolute abundance of required habitat. For habitat generalists, however, p_c varied according to degree of habitat association and dispersal range. Heterogeneous neutral landscapes thus provide a new plat-

Table 6. Average cell density (individuals/cell) within habitats and across the entire landscape for populations on artificially generated landscapes ($n = 216$ landscape scenarios).

Source of variation	DF	MS	F	P
HABITAT 1				
Landscape type	1	33.61	40.92	0.0001
Habitat abundance	2	0.59	0.72	ns
Habitat affinity	5	527.72	642.35	0.0001
Carrying capacity	5	118.49	144.23	0.0001
Landscape type × habitat abundance	2	0.24	0.29	ns
Landscape type × habitat affinity	5	32.63	39.72	0.0001
Landscape type × carrying capacity	5	3.95	4.80	0.0004
Habitat abundance × habitat affinity	10	2.68	3.26	0.0008
Habitat abundance × carrying capacity	10	0.44	0.53	ns
Habitat affinity × carrying capacity	25	38.76	47.18	0.0001
error	145	0.82		
HABITAT 2				
Landscape type	1	32.39	51.77	0.0001
Habitat abundance	2	4.19	6.70	0.002
Habitat affinity	5	389.75	622.96	0.0001
Carrying capacity	5	112.24	179.40	0.0001
Landscape type × habitat abundance	2	0.20	0.32	ns
Landscape type × habitat affinity	5	8.11	12.96	0.0001
Landscape type × carrying capacity	5	1.48	2.37	0.04
Habitat abundance × habitat affinity	10	7.18	11.48	0.0001
Habitat abundance × carrying capacity	10	0.79	1.26	ns
Habitat affinity × carrying capacity	25	31.02	49.59	0.0001
error	145	0.63		
HABITAT 3				
Landscape type	1	25.17	38.84	0.0001
Habitat abundance	2	3.50	5.41	0.005
Habitat affinity	5	450.93	695.92	0.0001
Carrying capacity	5	125.27	193.32	0.0001
Landscape type × habitat abundance	2	0.75	1.16	ns
Landscape type × habitat affinity	5	19.58	30.21	0.0001
Landscape type × carrying capacity	5	1.97	3.04	0.01
Habitat abundance × habitat affinity	10	2.45	3.78	0.0002
Habitat abundance × carrying capacity	10	0.97	1.50	ns
Habitat affinity × carrying capacity	25	34.72	53.59	0.0001
error	145	0.65		
LANDSCAPE				
Landscape type	1	31.68	55.01	0.0001
Habitat abundance	2	3.15	5.47	0.005
Habitat affinity	5	5.62	9.75	0.0001
Carrying capacity	5	14.93	25.92	0.0001
Landscape type × habitat abundance	2	0.05	0.09	ns
Landscape type × habitat affinity	5	1.33	2.31	0.05
Landscape type × carrying capacity	5	0.58	1.00	ns
Habitat abundance × habitat affinity	10	2.22	3.86	0.0001
Habitat abundance × carrying capacity	10	5.07	8.81	0.0001
Habitat affinity × carrying capacity	25	19.70	34.20	0.0001
error	145	0.58		

form for exploring the impact of multiple resource use, variations in habitat quality, or the occurrence of source and sink habitats on population dynamics.

Fractal landscapes, in particular, offer a sophisticated way to model heterogeneous landscapes. Unlike random maps, p_c differs among individual habitat types on fractal landscapes (Fig. 4). This is a function of categorizing habitat types along a numerical gradient, but the resulting pattern can be viewed as vegetational changes along an elevational gradient or ecotones which occur in real landscapes (Palmer 1992). The threshold for habitat types at the extremes of this gradient (Habitats 1 and 3) is 0.43–0.50, whereas that for the intermediate habitat type (2) is 0.29. Habitat on fractal maps percolates at a lower threshold than on random maps because habitat is distributed with greater contagion on fractal maps, and thus fractal maps possessed fewer, larger patches with less edge habitat than random ones. It is difficult to imagine a landscape in which habitat is completely random in distribution, and thus fractal maps may provide more useful models of landscapes (Milne 1992, Palmer 1992). Connected landscapes of these two map types remain structurally distinct, however, because random maps

generate a greater amount of edge habitat owing to small, isolated patches that lie outside the percolating cluster (Fig. 2).

Are connected landscapes functionally equivalent from an ecological standpoint? If connectivity is the most important attribute of landscape structure, then do the finer details of habitat distribution or patch structure really matter to dispersing organisms? Based on the results of our modelling exercise, we can answer "probably not" and "it depends on scale" in response to these two questions. The spatial arrangement of habitat (random vs fractal) was shown to have the largest effect on population dispersion in our simulations. Populations on random maps exhibited a greater degree of aggregation at the finest scale of resolution (box size = 1), whereas populations were more aggregated at coarser scales on fractal maps. In fact, the patch structure of populations perfectly reflected the spatial scaling of the landscape. Populations in fractal landscapes exhibit a monotonic, nearly linear decrease in I_m as a function of scale (Fig. 5), owing to the self-similarity of landscape pattern across scales (Plotnick et al. 1993: 207). Thus, if individuals are able to redistribute themselves freely across the landscape according to their habitat affinities, then population dispersion can be adequately predicted by landscape patterns. This was further illustrated in the series of simulations where habitat affinity was held constant across the landscape; populations were generally unable to aggregate beyond their initial random distributions, although fractal maps generally had more clumped distributions (Fig. 10, Table 7). The response of populations to landscape structure, in terms of the distribution (random vs fractal), abundance and relative quality (K) of habitat types, was extremely weak in this series of simulations, suggesting that it is the differential interaction of individuals with landscape structure that gives rise to species distributions.

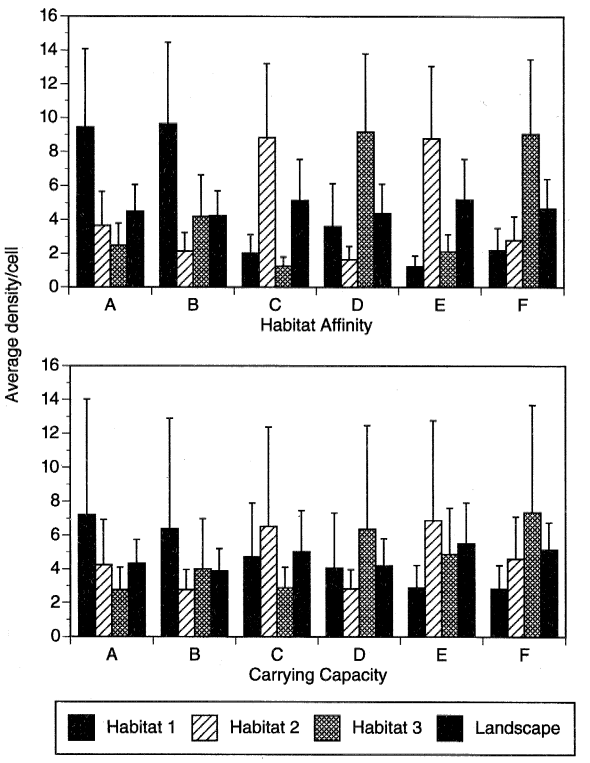

Fig. 11. Effects of habitat affinity and carrying capacity on the average population density within each habitat type, and across the entire landscape ($n = 36$ at each level for each habitat type and overall landscape). Levels for habitat affinity and carrying capacity are given in Table 1.

Given a particular habitat distribution (random vs fractal), however, different factors were important in structuring populations (Table 7). Despite the sharp transition in pattern between fine (box size = 1) and coarse scales for random maps (Fig. 4), one factor variable described almost all the variation in distributional patterns among scales. The relative abundance of habitat exerted a large effect on population dispersion, reflecting the threshold phenomenon of percolating networks (Figs 2 and 7, Table 7). Connectivity of landscape beyond p_c enhances movement across the landscape and effectively homogenizes it, resulting in randomly distributed populations. Predictably, species with affinities for typically rare (habitat 1) or uncommon (habitat 3) habitats occupied patchy distributions. Populations also became aggregated when a generally rare or uncommon habitat type possessed the highest carrying capacity and was preferred by the species (Table 7).

Scale-dependent effects on population dispersion were apparent on fractal maps (Table 7). At fine scales, the redistribution of individuals was affected by the same factors as on random landscapes; patchy distributions occurred when species preferred a rare or uncommon habitat type, which also had the highest carrying capacity across the landscape. Interestingly, a threshold effect was evident (Fig. 7), despite the fact that one habitat (2) percolates in all of these landscapes. This may result from an enhancement effect as the percolating cluster increases in area and dominates the landscape, providing even more area for individuals to move across. At coarse scales, species' habitat affinity was the most important determinant of population distributions, with habitat quality (carrying capacity) also affecting dispersion (Table 7). Although independent effects of these factors are similar to that observed on the other landscapes, some complex relationships emerged (e.g., high carrying capacities in the rare and abundant habitats boosts I_m, but a high K in the rare habitat alone decreased I_m; Fig. 7). Random and fractal maps thus behave similarly when viewed at fine scales. Species operating at this scale presumably would not be affected by differences in spatial patterning. It is

Table 7. Factors promoting aggregation in populations, in order of importance, for the different simulation experiments. Text in italics indicates the conditions which produced the greatest degree of aggregation among comparisons (ANOVA; see text for details).

Factorial design of all parameters	Carrying capacity fixed	Habitat affinity fixed
Total landscape maps		
Landscape type Fine scales *Random maps* Broad scales *Fractal maps*	Landscape type Fine scales *Random maps* Broad scales *Fractal maps*	Landscape type *Fractal maps*
Random maps		
Habitat abundance *Maps with habitat below critical threshold*	Habitat abundance *Maps with habitat below critical threshold*	Habitat affinity *Low* or *high habitat affinity*
Habitat affinity *Species with low affinity for most-abundant habitat type*	Habitat affinity *Species with low affinity for most-abundant habitat type* or *high affinity for habitat occupying a third of the landscape* (p_3)	Carrrying capacity *High carrying capacity in most-abundant habitat type*
Habitat affinity × carrying capacity *High affinity for a rare or uncommon habitat type* and *a high carrying capacity in that habitat*	Carrying capacity *High carrying capacity across landscape*	
Fractal maps		
Fine scales	Fine scales	
Habitat affinity × carrying capacity *High affinity for a rare or uncommon habitat type* and *a high carrying capacity in that habitat*	Habitat abundance *Habitat below the critical threshold*	Habitat affinity *Low habitat affinity across entire lanscape*
Habitat abundance *Maps with habitat above critical threshold*	Carrying capacity *High carrying capacity across landscape*	Carrying capacity *Low carrying capacity in habitat occupying a third of the landscape* (p_3)
	Habitat affinity *Affinity for most-abundant habitat type*	Habitat abundance *Habitat below critical threshold*
		Habitat abundance × carrying capacity *Low carrying capacity in habitat 2 when all habitats occupy equal proportions of the landscape* ($p_2 = 0.33$)
Broad scales	Broad scales	
Habitat affinity *High affinity for rare or uncommon habitat type*; *Uncommon habitat preferred* and *a neutral preference for most-abundant habitat*	Carrying capacity *Low carrying capacity across landscape*	
Carrying capacity *Rare* and *abundant habitats have highest carrying capacity*; *Uncommon habitat preferred* and *neutral preference for most-abundant habitat*		

at coarser scales that the patch structure of fractal maps manifests itself and affects ecological processes such as the redistribution of animals across the landscape.

Beyond neutral landscapes, what are the implications of landscape connectivity for ecological processes in real systems? Species' perceptions of landscape connec-

tivity were demonstrated for two grasshopper species (Orthoptera: Acrididae) in the shortgrass prairie of Colorado, in which individual movement was modelled as a percolation process to see if distributional patterns could be predicted in this grassland mosaic (With and Crist 1995). A large species, *Xanthippus corallipes*, exhibited fastest transit through habitat comprising 65% of the landscape, and correspondingly had increased residence time within the remaining third of the landscape. Enhanced residence time was equated with habitat preference. The rate of movement for a smaller species, *Psoloessa delicatula*, was basically unaffected by heterogeneity. Because the landscape was dominated (65%) by a single habitat type, it behaved like a percolating map of the neutral landscapes. Given that the largest species was able to traverse rapidly a proportion of landscape exceeding the hypothetical p_c for random maps, it should be able to locate and aggregate within the remaining third of the landscape, producing a clumped distribution. The smallest species was fairly sedentary, with a rate of movement about 6 times less than that of *X. corallipes* (With 1994a). Its low vagility, coupled with the rarity of its preferred habitat (8%), precluded an aggregated distribution for this species. The actual distributions of the two species supported the prediction of redistribution of individuals as a percolation process: *X. corallipes* was patchily distributed in this landscape, whereas *P. delicatula* was randomly distributed in the same mosaic. Thus, the large grasshopper was able to respond to the coarse-grained patchiness of the landscape, whereas the smaller species was not capable of interacting with patch structure at this scale. Connectivity of habitats or patches is not just a function of the landscape pattern, but also the ability of the organism to access those patterns. Different organisms may thus have disparate perceptions as to whether a particular landscape is connected or not.

Critical thresholds in landscape connectivity illustrate that fragmentation is not a linear function of habitat loss. Above the threshold, the primary consequence of habitat removal is a reduction in area of this habitat. Below the threshold, however, the landscape is effectively disconnected or fragmented, owing to the prevalence of small, isolated patches of habitat. In a review of the literature on avian and mammalian responses to habitat fragmentation, Andrén (1994) applied this concept of thresholds in landscape connectivity to dissect species' responses to habitat loss from critical responses to habitat fragmentation. Species richness within communities, population sizes of particular species, and persistence of populations were variously used to illustrate ecological responses to habitat fragmentation. His survey suggests that overall habitat abundance may be of greater importance than the actual spatial patterning of habitat in most landscapes; that is, disruption of connectivity does not occur until only 10–30% of the original habitat remains. The fact that this potential threshold differs from the expectations of percolating networks may indicate the greater complexity of ecological interactions on heterogeneous landscapes where species are able to use multiple habitat types and the high vagility of the species represented in the studies of this survey (e.g., bird species). This type of correlative approach nevertheless underscores the importance of identifying threshold effects in landscape connectivity as a means of pinpointing when critical responses to habitat fragmentation are likely to occur. The application of neutral landscape models in this context may thus provide an important tool for predicting species' responses to land-use change.

Acknowledgements – K. A. With received support from an Alexander Hollaender Distinguished Postdoctoral Fellowship, administered by the US Dept of Energy, Office of Health and Environmental Research, and managed by the Oak Ridge Inst. for Science and Education. We thank Michael Palmer and Henrik Andrén for their comments on this manuscript. This is publication number 4545 of the Environmental Sciences Division, Oak Ridge National Laboratory, TN, USA.

References

Afifi, A. A. and Clark, V. 1984. Computer-aided multivariate analysis. – Lifetime Learning Publ., Belmont, CA.

Andrén, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius* L. – Ecology 71: 1796–1803.

– 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

Biondini, M. E. and Grygiel, C. E. 1994. Landscape distribution and the scaling of soil resources. – Am. Nat. 143: 1026–1054.

Cummings, J. R. and Vessey, S. H. 1994. Agricultural influences on movement patterns of white-footed mice (*Peromyscus leucopus*). – Am. Mid. Nat. 132: 209–218.

Dale, V. H., Pearson, S. M., Offerman, H. L. and O'Neill, R. V. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. – Conserv. Biol. 8: 1027–1036.

Dunning, J. B., Jr., Danielson, J. B. and Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. – Oikos 65: 169–175.

– , Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H. and Stevens, E. E. 1995. Spatially explicit population models: current forms and future uses. – Ecol. Appl. 5: 3–11.

Elliott, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. – Freshwater Biological Association Scientific Publication No. 25.

Feder, J. 1988. Fractals. – Plenum Press, New York.

Franklin, J. R. and Forman, R. T. T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. – Landscape Ecol. 1: 5–18.

Gardner, R. H. and O'Neill, R. V. 1991. Pattern, process, and predictability: the use of neutral models for landscape analysis. – In: Turner, M. G. and Gardner, R. H. (eds), Quantitative methods in landscape ecology. Springer-Verlag, New York, pp. 289–307.

– , Milne, B. T., Turner, M. G. and O'Neill, R. V. 1987. Neutral models for the analysis of broad-scale landscape pattern. – Landscape Ecol. 1: 19–28.

– , O'Neill, R. V., Turner, M. G. and Dale, V. H. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. – Landscape Ecol. 3: 217–227.
– , Turner, M. G., O'Neill, R. V. and Lavorel, S. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. – In: Holland, M. M., Risser, P. G. and Naiman, R. J. (eds), The role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York, pp. 76–89.
– , Turner, M. G., Dale, V. H. and O'Neill, R. V. 1992. A percolation model of ecological flows. – In: Hansen, A. J. and di Castri, F. (eds), Landscape boundaries: consequences for biodiversity and ecological flows. Springer-Verlag, New York, pp. 259–269.
– , O'Neill, R. V. and Turner, M. G. 1993. Ecological implications of landscape fragmentation. – In: Pickett, S. T. A. and McDonnell, M. G. (eds), Humans as components of ecosystems: subtle human effects and ecology of populated areas. Springer-Verlag, New York, pp. 208–226.
Gilpin, M. E. and Hanski, I. 1991. Metapopulation dynamics. – Academic Press, New York.
Hanski, I. and Ranta, E. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. – J. Anim. Ecol. 52: 263–279.
– , Pakkala, T., Duussaari, M. and Guangchun, L. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. – Oikos 72: 21–28.
Hurlbert, S. H. 1990. Spatial distribution of the montane unicorn. – Oikos 58: 257–271.
Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. – Ecology 74: 2204–2214.
Johnson, A. R., Wiens, J. A., Milne, B. T. and Crist, T. O. 1992. Animal movements and population dynamics in heterogeneous landscapes. – Landscape Ecol. 7: 63–75.
Kotliar, N. B. and Wiens, J. A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. – Oikos 59: 253–260.
Lavorel, S., Gardner, R. H. and O'Neill, R. V. 1993. Analysis of patterns in hierarchically structured landscapes. – Oikos 67: 521–528.
Mandelbrot, B. 1983. The fractal geometry of nature. – Freeman, San Francisco, CA.
Milne, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. – Am. Nat. 139: 32–57.
O'Neill, R. V., Milne, B. T., Turner, M. G. and Gardner, R. H. 1988. Resource utilization scales and landscape pattern. – Landscape Ecol. 2: 63–69.
– , Gardner, R. H. and Turner, M. G.. 1992. A hierarchical neutral model for landscape analysis. – Landscape Ecol.: 7: 55–61.
Palmer, M. W. 1992. The coexistence of species in fractal landscapes. – Am. Nat. 139: 375–397.
Pearson, S. M., Turner, M. G., Gardner, R. H. and O'Neill, R. V. 1996. An organism-based perspective of habitat fragmentation. – In: Szaro, R. C. and Johnston, D. W. (eds), Biodiversity in managed landscapes: theory and practice. Oxford Univ. Press, Oxford, pp. 77–95.
Petigen, H.-O. and Saupe, D. (eds) 1988. The science of fractal images. – Springer, New York.
Pickett, S. T. A. and White, P. S. (eds) 1985. The ecology of natural disturbance and patch dynamics. – Academic Press, New York.
Plotnick, R. E. and Gardner, R. H. 1993. Lattices and landscapes. – In: Gardner, R. H. (ed.), Lectures on mathematics in the life sciences: predicting spatial effects in ecological systems, vol. 23. Am. Mathematical Society, Providence, RI, pp. 129–157.
– and Prestegaard, K. L. 1993. Fractal analysis of geologic time series. – In: Lam, N. and DeCola, L. (eds), Fractals in geography. Prentice-Hall, Englewood Cliffs, NJ, pp. 207–224.
– , Gardner, R. H. and O'Neill, R. V. 1993. Lacunarity indices as measures of landscape texture. – Landscape Ecol. 8: 201–211.
Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.
Saupe, D. 1988. Algorithms for random fractals. – In: Petigen, H.-O. and Saupe, D. (eds), The science of fractal images. – Springer, New York, pp. 71–136.
Shorrocks, B. and Swingland, I. R. (eds) 1990. Living in a patchy environment. – Oxford Univ. Press, Oxford.
Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton Univ. Press, Princeton, NJ.
Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. – Oikos 68: 571–573.
Turchin, P. 1989. Population consequences of aggregative movement. – J. Anim. Ecol. 58: 75–100.
– 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. – Ecology 72: 1253–1266.
Turner, M. G., O'Neill, R. V., Dale, V. H. and Milne, B. T. 1989. Effects of changing spatial scale on the analysis of landscape pattern. – Landscape Ecol. 3: 153–162.
Urban, D. L., O'Neill, R. V. and Shugart, H. H. 1987. Landscape ecology. – BioScience 37: 119–127.
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. – J. Wild. Manage. 47: 893–901.
Wiens, J. A. 1989. Spatial scaling in ecology. – Funct. Ecol. 3: 385–397.
– , Stenseth, N. C., Van Horne, B. and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. – Oikos 66: 369–380.
– , Crist, T. O., With, K. A. and Milne, B. T. 1995. Fractal patterns of insect movement in microlandscape mosaics. – Ecology 76: 663–666.
With, K. A. 1994a. Using fractal analysis to assess how species perceive landscape structure. – Landscape Ecol. 9: 25–36.
– 1994b. Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. – Funct. Ecol. 8: 477–485.
– and Crist, T. O. 1995. Critical thresholds in species' responses to landscape structure. – Ecology 76: 2446–2459.