SIMULATION OF THE SCALE-DEPENDENT EFFECTS OF LANDSCAPE BOUNDARIES ON SPECIES PERSISTENCE AND DISPERSAL

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Abstract. The relationships between life history characteristics and broad-scale patterns of species abundance were investigated with a model that simulates the dispersal of populations through heterogeneous landscapes. Movement was simulated on randomly generated landscapes and on forested landscapes digitized from aerial photographs. Simulation results indicated that population abundances will change suddenly near the critical threshold in habitat connectivity as predicted from percolation theory. The existence of critical thresholds is important for many management and conservation issues, but these thresholds suggest that data are required at spatial scales that are specific to the dispersal characteristics of the simulated population.

Key words: landscape boundaries, species dispersal, habitat connectivity, life history effects, broad scale predictions.

INTRODUCTION

The problem of predicting the effects of extensive and rapid changes in land use patterns on the distribution and abundance of organisms continues to be an important ecological challenge (e.g., Burgess and Sharpe 1981, Forman and Godron 1981, Risser et al. 1984, Wiens et al. 1985*b*, Naiman et al. 1988). Many of the practical and theoretical problems associated with prediction might be resolved if the appropriate scales of interaction between pattern and process were understood (Wiens et al 1985*a*, Brown and Allen 1989, Carlile et al. 1989, Milne et al 1989). For example, measurements of landscape pattern depend on the scale at which the data are taken (e.g., Gardner et al. 1987, Meentemeyer and Box 1987, Urban et al. 1987, O'Neill et al. 1988). Theoretical studies based on fractal geometry (Mandelbrot 1967) show that measured boundary length changes as the scales of resolution change. Although simulation with a variety of spatial models (e.g., Gardner et al. 1987, Turner et al. 1989) can relate the number, size, and shape of landscape patches to the grain and extent of the map, this information is not sufficient to set the appropriate scales for predicting resource utilization by populations in heterogeneous environments.

Because species respond to environmental conditions at specific spatial and temporal scales (Swihart et al. 1988, Milne et al. 1989), it appears that an organism-centered view (sensu Wiens 1985) is essential for relating changes in landscape patterns to processes that affect the distribution and abundance of species. Previous applications of models based on percolation theory have shown that the spatial patterning of resources constrains the potential movement of populations across the landscape (O'Neill et al. 1988), with a sparse or patchy distribution of resources requiring organisms to operate at broader spatial scales.

This paper examines the proposition that the scale at which species are able to utilize landscape resources will be sensitive to the distance an organism (or propagule) must travel to colonize another site. The model we developed examines the effect of different combinations of population dispersal characteristics and the patterns of

habitat boundaries on the predicted patterns of population growth, abundance, and habitat utilization. The results suggest that the mean and shape of the dispersal function (i.e., the probability of long distance movement) are critical determinants of the scale at which both data and model are required to predict population utilization in a patchy environment.

METHODS

A heterogenous distribution of habitats and their boundaries can be created by methods derived from percolation theory (Gardner et al. 1987) by randomly generating a map of m by m sites, with the habitat type of the m^2 sites selected with a probability of p. For sufficiently large maps an average of pm^2 sites will be designated as suitable habitat (e.g., a forested site) while $(1 - p)m^2$ sites will be designated as other (e.g., nonforested) sites. When the length, l, of a single site is specified (e.g., 100m for a 1-ha resolution), then the total area of the map is equal to $(lm)^2$. The scale of the map is defined by these two parameters: l is the resolution or grain size and $(lm)^2$ is the area or extent of the map.

Percolation theory defines a patch as a group of similar sites with at least one common edge along the vertical or horizontal direction. The number, size, and shape of the random patches are similar from map to map but will change as a function of p. Rapid changes in the size and shape of patches occur near the critical probability, p_c, when the largest patch just manages to extend from one edge of the map to the other. The value of p_c for extremely large maps has been empirically determined to be 0.5928 (Stauffer 1985). The relationship between patch size and boundary shape is also affected by p (Stauffer 1985): boundaries are short and straight when $p < p_c$, but longer and more convoluted when $p \geq p_c$.

The movement of populations across a heterogenous landscape can be simulated by two types of "rules" derived from percolation theory: bond percolation "rules" simulate random, independent movement to individual nearest-neighbor sites; while site percolation "rules" simulate random, simultaneous movement to all nearest-neighbor sites (see von Niessen and Blumen 1988 for further description of bond and site percolation). When the probability of movement to new sites, i, is equal to 1.0, the movement patterns generated by bond or site percolation are equivalent and all sites within a patch will be colonized by the dispersing population. Differences between bond and site percolation become more apparent as the value of i decreases (see the Results section). Because habitat patches are highly fragmented when $p < p_c$, and because movement rules based on bond or site percolation only allow movement within a single patch, dispersal rules based on bond or site percolation methods will not allow the spread of a population across the map when $p < p_c$.

In addition to a model that simulates the spread of a population in a heterogenous landscape with dispersal rules based either on bond or site percolation methods, we have developed a model that simulates the spread of a population based on sets of functions which generate dispersal distances from continuous frequency distributions. The generation of dispersal distances from continuous frequency distributions relaxes the assumption of impermeable landscape boundaries and allows populations to colonize adjacent habitat patches. Continuous dispersal distances are generated by (1) selecting a random angle over the interval from 0^0 to 360^0; (2) selecting a random distance from some prespecified frequency distribution (uniform, triangular, or exponential); and (3) converting the angles and distances to appropriate map coordinates. The three types of continuous frequency distributions all produce circular patterns of dispersal but with different central tendencies. Although one might imagine that different dispersal functions can be used to represent different species characteristics (see Hanson, et al. 1989 for an example of this approach), the

results reported are limited to the determination of the sensitivity of broad-scale predictions to potential differences in species dispersal characteristics.

The choice of parameters for the continuous dispersal functions affects both the shape and the distance that the organisms move from the parent population. If the maximum possible dispersal distance is less than ½*l*, the population will not disperse beyond its current site. When the maximum possible dispersal distance equals *l*, the pattern of movement is similar to bond percolation. When the maximum possible dispersal distance is greater than *l*, then the habitat boundary is "permeable" and the population can disperse beyond the edge of the current habitat patch.

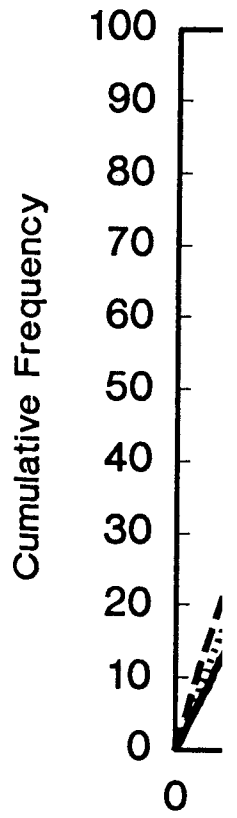
The model also considers other life history attributes, including the number of viable seeds, ***v***, per generation per site; the probability of local population extinction, ***e*** (expected residence time is 1/***e***); and the probability of site alteration, ***h***, after local extinction. The parameters selected for the simulations reported here are analogous to populations of annual plants with a mean life expectancy of 10 generations (***e*** = 0.1), whose seeds (***v*** = 10) disperse a mean distance from the parent site. Because the site is not damaged by the population (***h*** = 0.0), reinvasion after local extinction is possible. The parameters **v**, **h**, and **e** were held constant for all simulations.

Replicate simulations (N = 10) were performed on a series of random maps (***m*** = 100 and ***l*** = 1) with different values of ***p***. Landscape data on the distribution of forested sites in 9 counties in Georgia (Turner and Ruscher 1988) were used as input to the model to compare simulations with actual habitat patterns against simulations based on randomly generated maps. Aerial photographs for the 9 counties at 3 time periods were used to develop 27 different landscape maps. The nine counties included three from the piedmont, and two each in the mountains, upper coastal plain, and lower coastal plain. The photographically interpreted information was assembled into 100 X 100 grids (each cell = 1 ha) with forested sites considered as the habitat of interest (see Turner and Ruscher 1988 and Turner 1990 for additional details).

RESULTS

Figure 1 compares the dispersal distances generated from the three continuous frequency distributions when the mean distance for all three distributions is equal to 1.0. The dispersal distances for the uniform distribution range from a minimum of 0.0 to a maximum of 2.0; the triangular distribution results in a minimum and mode of 0.0 and a maximum of 3.0; and 10,000 samples drawn from the exponential distribution produce a maximum distance of 10.0. The differences in the shapes of the distributions (Fig. 1) result in median values for the triangular (0.9) and exponential distribution (0.7) that are less than the uniform (1.0). However, the upper percentiles of the triangular and exponential distributions are 11% and 14% greater, respectively, than the maximum of 2.0 for the uniform distribution. Although the expected values for all three distributions are identical, differences in the shapes of the dispersal function create a higher probability of the triangular and exponential distribution, respectively, generating distances that result in species crossing habitat boundaries.

Figure 2 compares population growth through time, as measured by the number of map sites successfully populated, for four different sets of dispersal characteristics. The simulations were performed on a random landscape with ***p*** = 0.5 (50% of the sites are suitable habitat). The results show that when species movement is restricted to nearest-neighbor sites (bond percolation), less than 1% of the available habitat was utilized. When dispersal characteristics allow habitat boundaries to be readily crossed, then the rate at which a species spreads across the landscape increases for the uniform, triangular, and exponential distributions, respectively.



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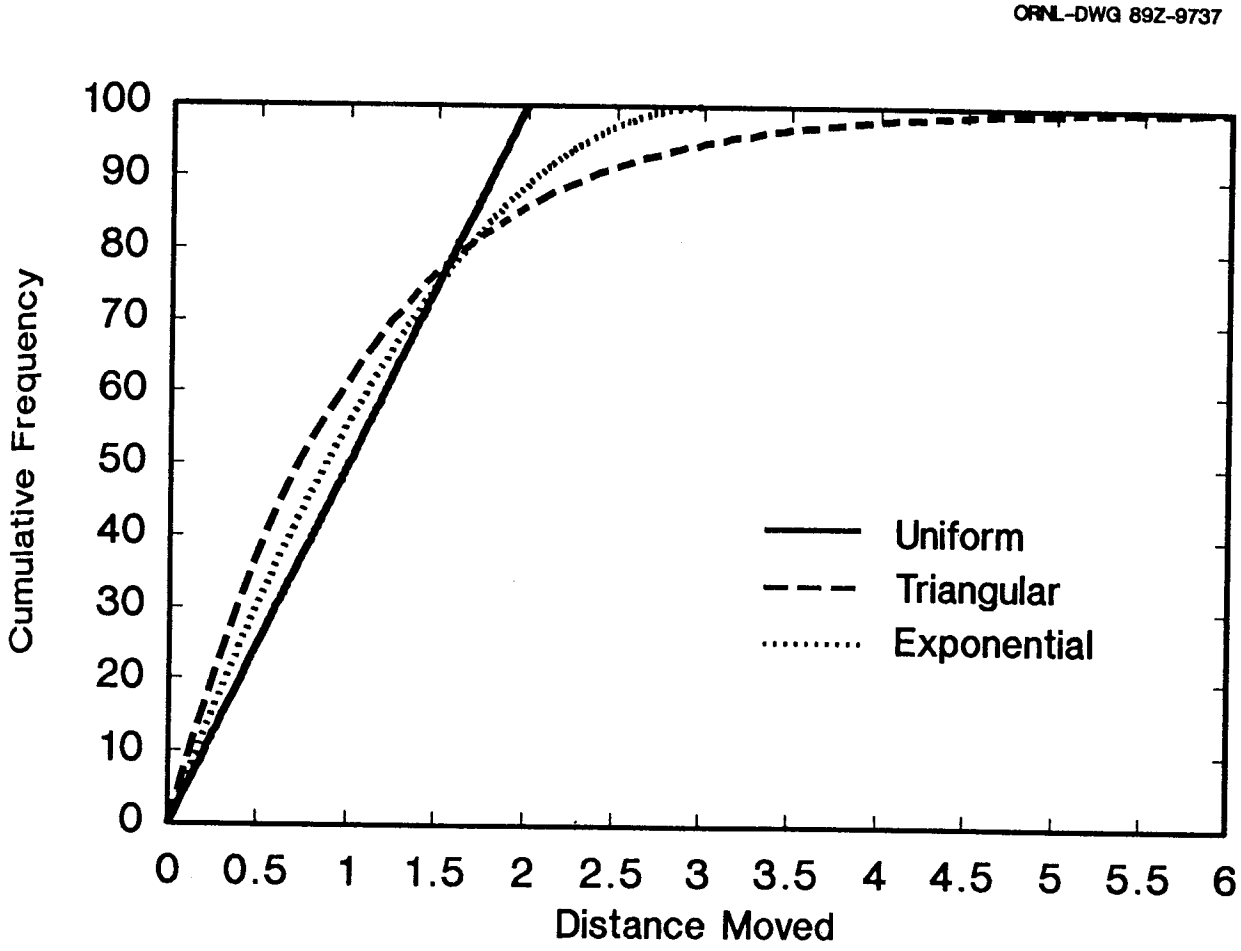

Figure 1. Cumulative frequency distributions for dispersal distances generated from the uniform, triangular, or exponential distributions. All three distributions have the same mean dispersal distance (mean = 1.0).

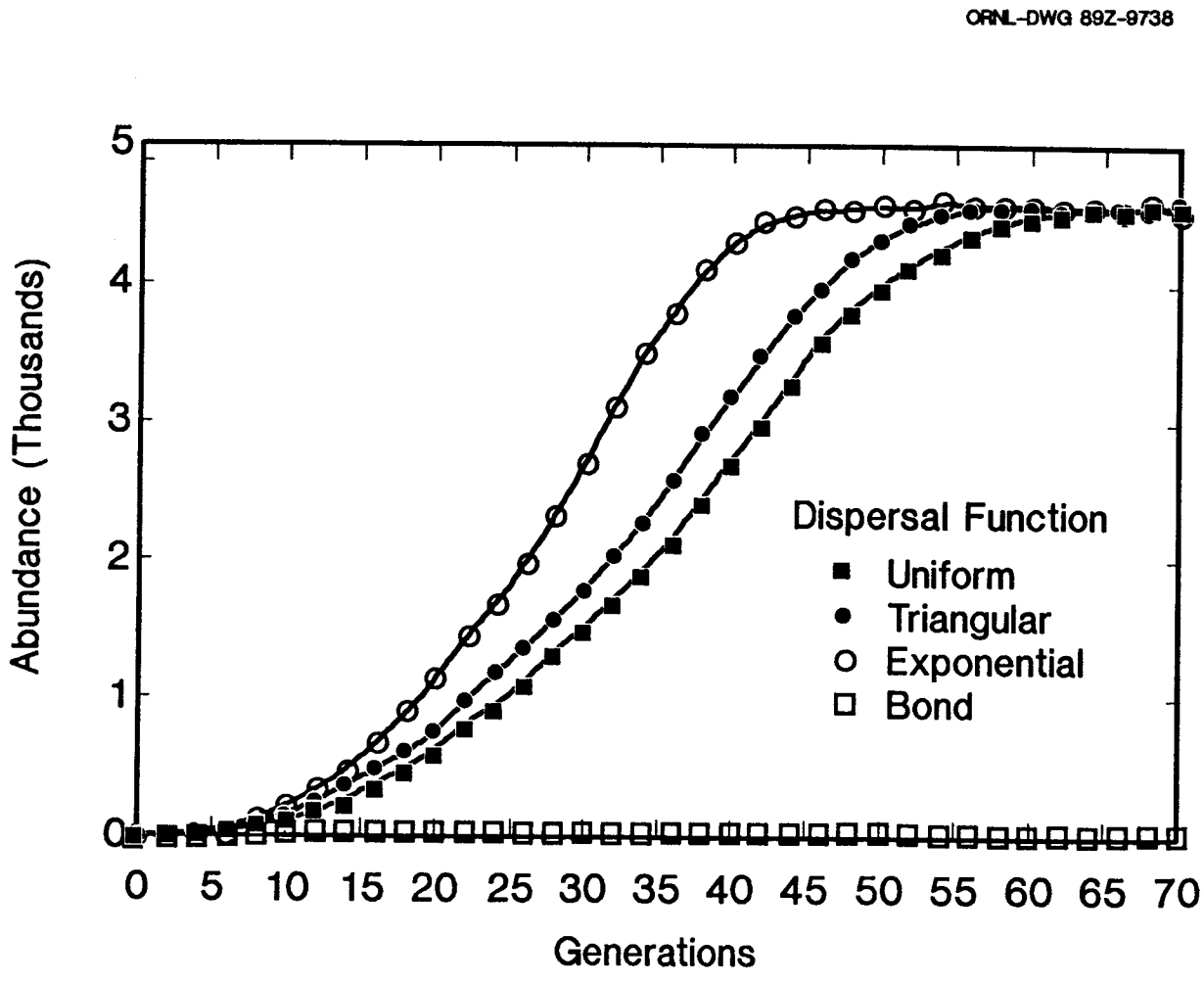

Figure 2. Comparison of the abundance through time of populations with different dispersal characteristics on a random landscape. Map dimensions are 100 rows by 100 columns with ***p***, the fraction of sites that are suitable habitat, equal to 0.5 (5,000 total suitable sites per map).

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If we assume that all available habitat sites can be reached by the simulated species, then the asymptotic population levels will be $pm^2(1.0 - e)$, where p is the fraction of suitable sites, m is the size of the grid, and e is the site-specific probability of population extinction. The asymptotic population level for the results illustrated in Fig. 2 is $0.5 \times 100^2 \times [1.0 - 0.1] = 4500$ populated map sites. Because of differences in the maximum possible dispersal distances, the asymptotic levels were achieved at generations 46, 56, and 62 for the exponential, triangular, and uniform distributions, respectively.

A percolating map is defined as any map with a single, continuous habitat patch that spans the map. Thus, a map that "percolates" will allow a population that is restricted to nearest-neighbor movement (bond or site percolation with $i = 1.0$) to successfully spread across the map. The percolation characteristics of the 27 maps of Georgia landscapes were examined, and the results are illustrated in Figure 3. Although random maps show a sudden shift from nonpercolation below p_c to percolation above p_c, the Georgia landscapes show a broader range of values ($p = 0.42$ to 0.7) at which percolation may or may not occur. The two forested landscapes that determine the range of percolation values are illustrated in Figure 4. The photographs of Walker County taken in 1938 illustrate the ridge and valley system of this northwestern Georgia county. Because forests dominate the ridge tops (Fig. 4a), a continuous forest spans the map from north to south at p (the fraction of the grid points on the map occupied by forest) of only 0.43. The Herd County landscape, photographed in 1978, is dominated by forest habitat ($p = 0.68$). However, 33% of this Piedmont landscape is farmland or abandoned land concentrated in the upper third of the map, effectively disconnecting the northern forested areas from the southern portion of the map. Although the effects of topography, climate, and land use can be expected to cause differences from the expected patterns produced by random maps, only 2 of the 27 landscapes demonstrated percolation characteristics different from random (Fig. 3).

The similarities and differences between random and real maps are also illustrated by comparing the amount of habitat edge and the number of habitat patches on random and actual landscape maps (Fig. 5). The amount of edge on randomly generated maps is extremely consistent, with the maximum number of edges occurring at $p = 0.5$ (Fig. 5a), while the 27 Georgia landscapes show much less edge, with no apparent peak values. Because it is theoretically possible to produce "structured" maps with more edge than can be randomly generated (see Franklin and Forman 1987), it is apparent that the abiotic, human, and historical factors which structure actual landscapes produce patches of forested land with less edge than expected (see also Krummel et al. 1987).

The comparison of the number of habitat patches on random maps with the 27 maps of Georgia forested landscapes is shown in Figure 5b. A striking feature of this figure reveals that the random and real landscape maps are quite similar at values of p above 0.6. Although it is a trivial observation that no difference will exist between a random and an actual map when $p = 1.0$, Figure 5b indicates that differences between actual and random landscape patterns are rather small for values of p above p_c.

The pattern of **habitat utilization** (i.e., the number of sites occupied by the species of interest) on random and real landscapes is illustrated in Figure 6. The effect of movement patterns restricted to habitat patches (impermeable boundaries simulated by bond percolation) prevents much of the habitat from being utilized in disconnected landscapes; hence a sharp change in abundance occurs at $p = p_c$ ($p_c = 0.5928$ on random landscapes). A greater fraction of the Georgia landscape can be utilized by populations that do not cross the forest habitat boundaries (bond percolation, Fig. 6a) because these landscapes tend to be

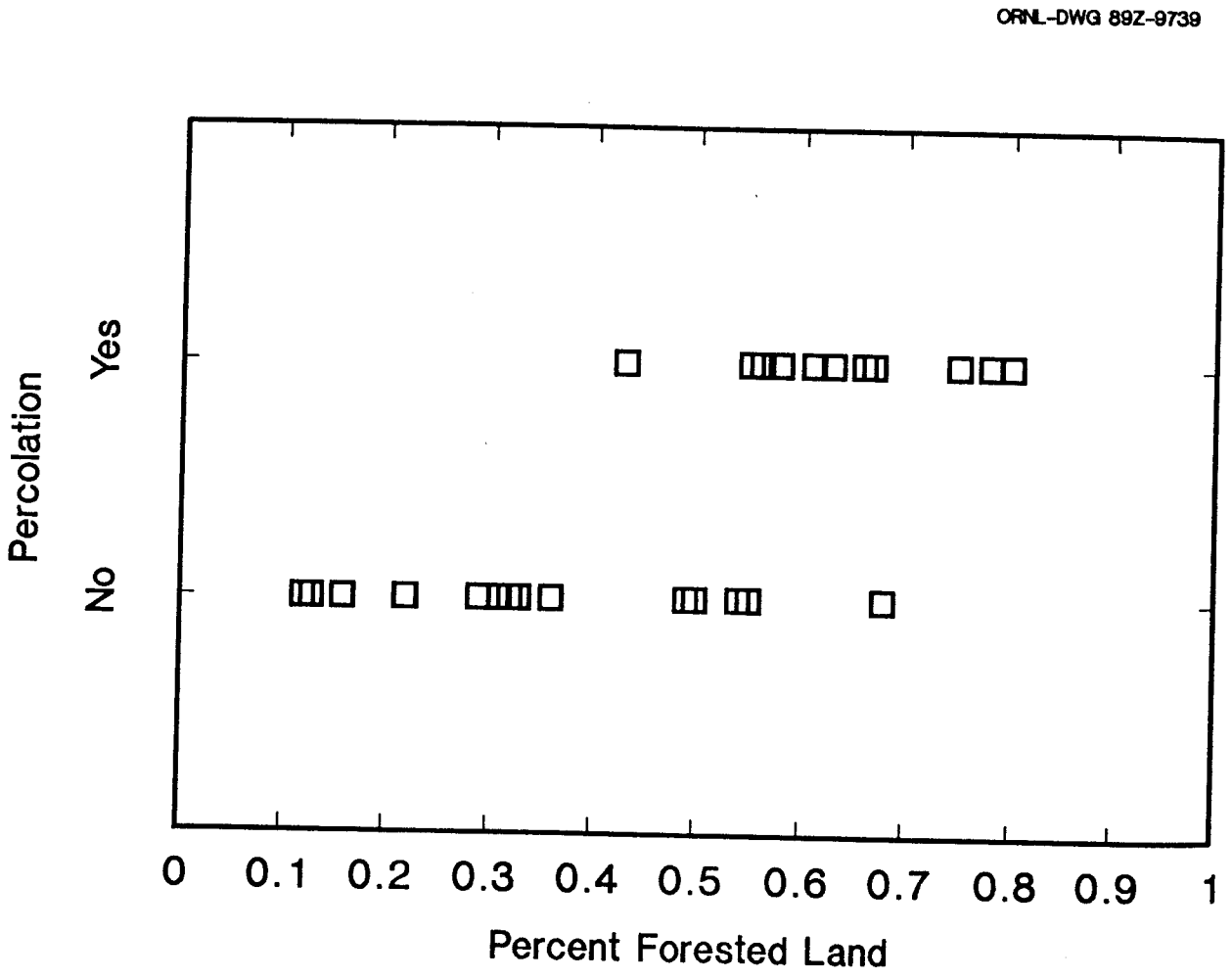

Figure 3. Percolation characteristics of forested areas taken from aerial photographs of nine counties in Georgia. A percolating map is one in which a single habitat patch spans the map.

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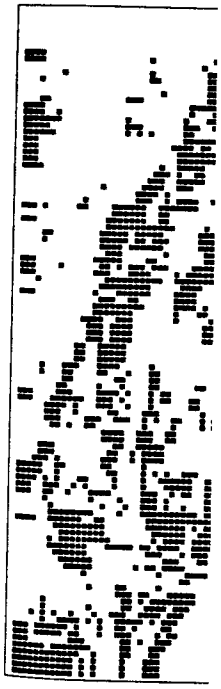

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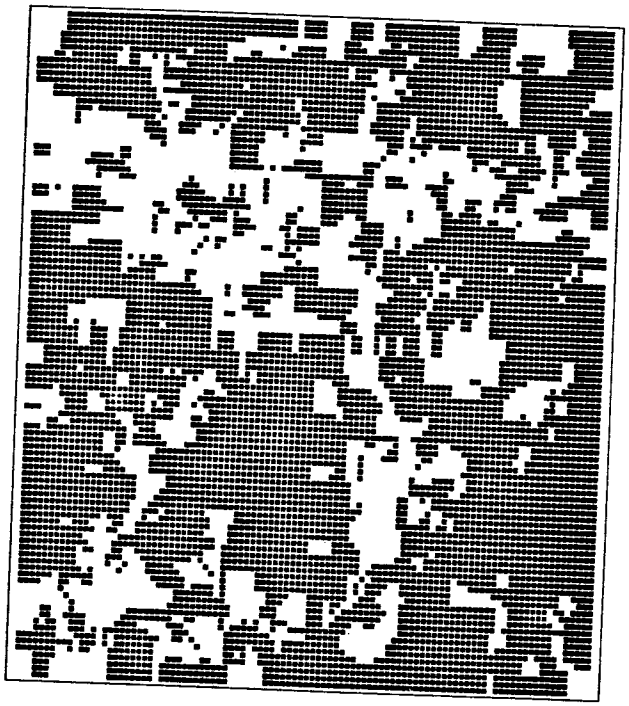
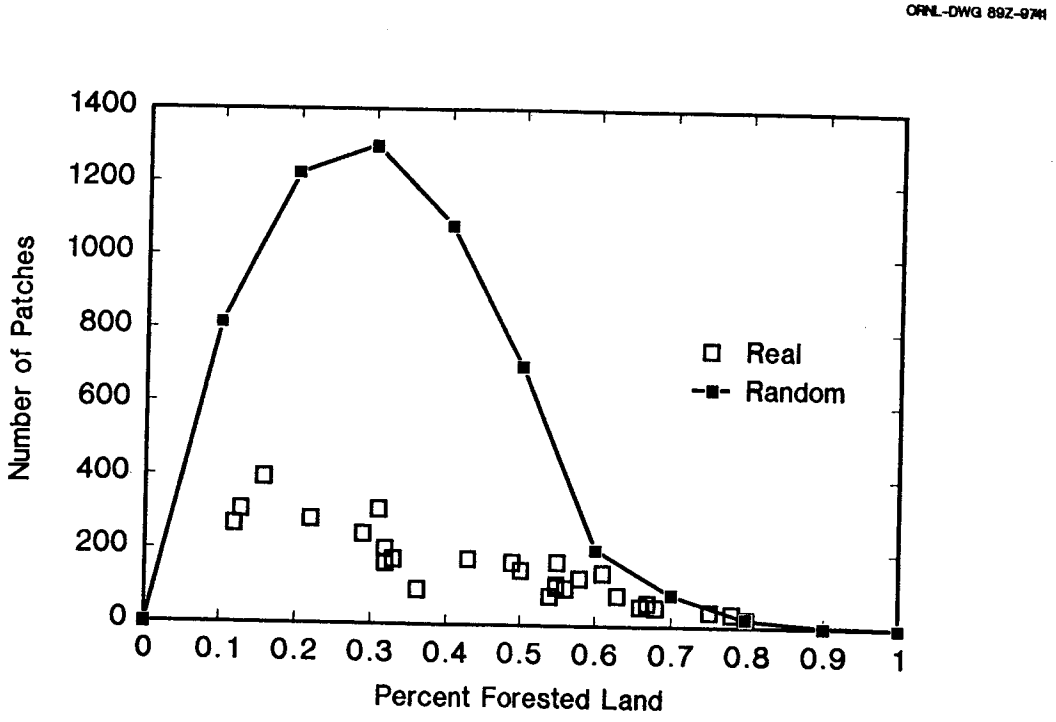


Figure 4. The dark areas represent forested regions of Herd County (Fig. 4a) and Walker County (Fig. 4b), Georgia. The data are based on aerial photos taken in 1978 for Herd County and 1938 for Walker County. Each grid point covers one hectare (see Turner and Ruscher 1988 and Turner 1990 for additional details). North is at the top of the figure.



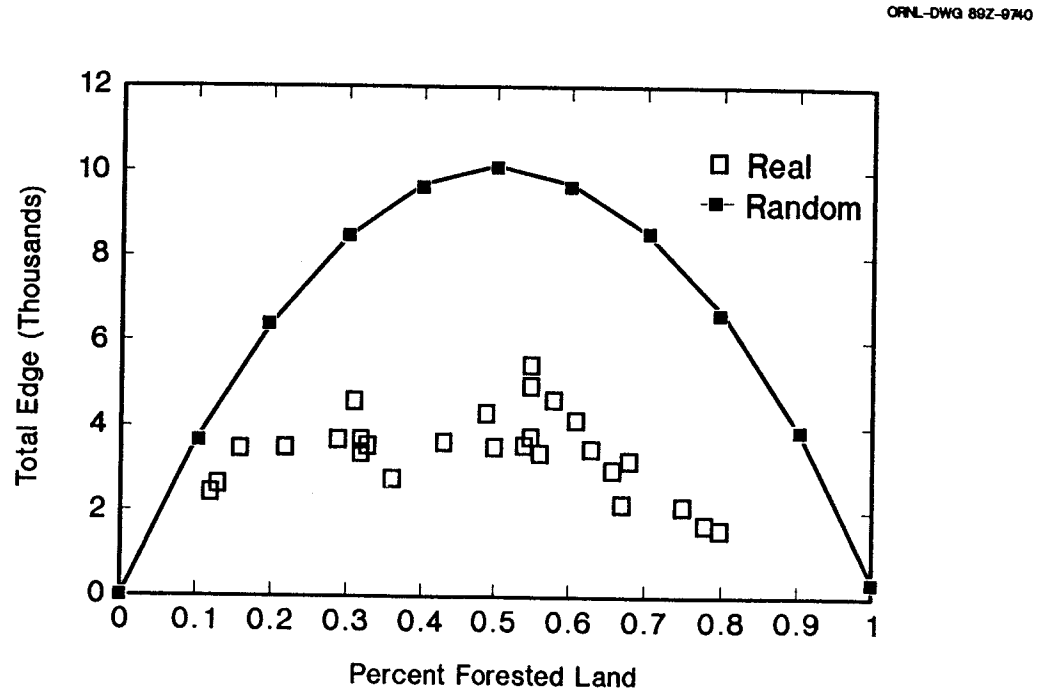


Figure 5. A comparison of habitat characteristics for randomly generated and actual landscape maps: a) Total habitat edge and b) Number of habitat patches.

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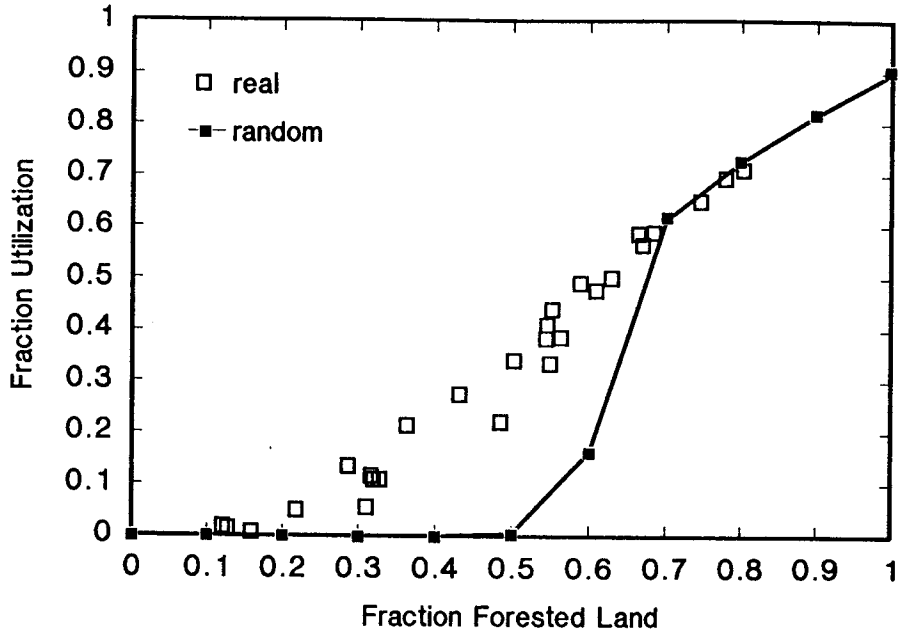

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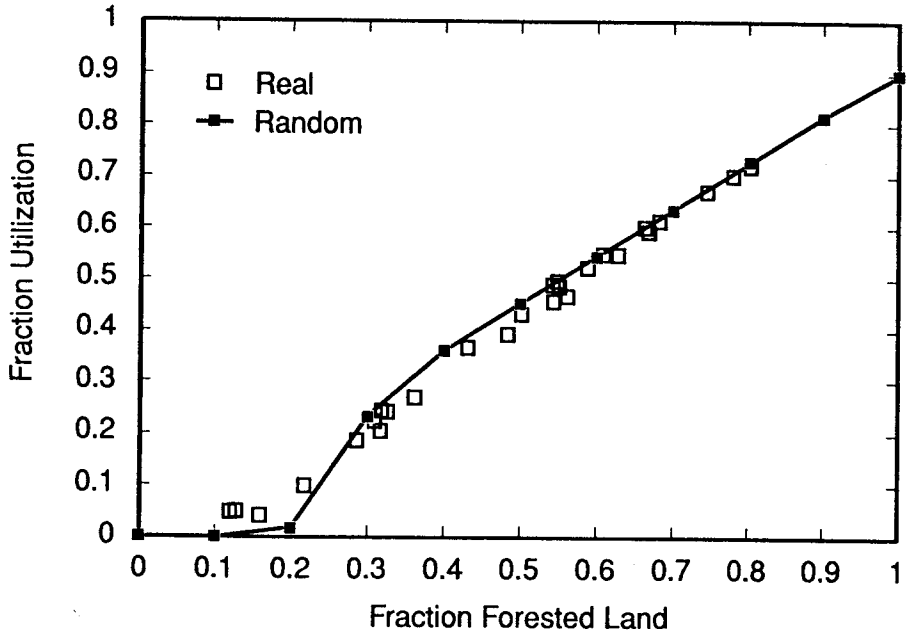

Figure 6. The fraction of habitat utilized on randomly generated and actual landscape maps for species dispersal characteristics which a) restrict dispersal to nearest-neighbor sites (bond percolation) or b) allow propagules to disperse a maximum of two-sites' distance from the parent population. Refer to the text for an explanation of algorithms used to generate dispersal distances.

connected over a broader range of values of p (Fig. 3) with fewer patches and fewer edges (Fig. 5). However, if the entire amount of available habitat were utilized, then a line through the points in Figure 5a could be drawn equal to $p * m^{2} * (1.0 - e)$, representing the asymptotic population levels which may be achieved under ideal conditions. The difference between any observation and this theoretical line is equal to the number of unpopulated but available habitat sites.

Movement by bond percolation (Fig. 6a) can be contrasted to movement patterns generated from the uniform distribution (Fig. 6b). Although the same maps and life history attributes were used for the two sets of simulations, Figure 6b shows that when dispersal distances are generated from a uniform distribution (minimum = 0.0, maximum = 2.0) the pattern of species abundance for random and real landscapes is essentially the same. Thus, when species movement patterns allow a small amount of permeability of the habitat edge, then the structure of the habitat (i.e., number and shape of suitable habitat patches) does not affect the fraction of the landscape that can be utilized.

CONCLUSIONS

The continuing loss of natural habitat and the associated decline in species abundance and diversity have made the design of natural reserves (i.e., the number, size, and spatial arrangement of critical habitat) an important conservation issue (Noss 1983, Noss and Harris 1986, Simberloff 1988). Arguments for many small isolated reserves are based on the observation that islands often have higher diversity per unit area than adjacent mainlands (Quinn and Hastings 1987). Studies of disturbance and recovery, however, argue for management policies that maintain habitat heterogeneity (Levin 1976a, Norse et al. 1986) and connectance between reserves (Fahrig and Merriam 1985). Other studies show that some species may be insensitive to both the size and arrangement of critical resources (Fahrig and Paloheimo 1988). These different views of the effect of landscape design on biodiversity might be resolved by considering the scale at which organisms perceive and utilize natural resources (Levin 1976b, O'Neill et al. 1988). Because the scale at which species can distribute their progeny is fixed by their life history attributes, it is unlikely that fixed landscape patterns will be optimal for all species.

The simulations reported here allow the effect of landscape pattern and species dispersal characteristics to be systematically evaluated. The comparison of random maps to actual forested regions of nine counties in Georgia shows that the number (Fig. 5b), size, shape, and arrangement of habitat patches and their boundaries (Fig. 5a) are similar when the fraction of the forested landscape is greater than 0.6. The fact that actual landscapes show patterns similar to those predicted by studies of critical thresholds in percolation theory (Stauffer 1985, Gardner et al. 1987) confirms the usefulness of these concepts for studying the effects of landscape pattern on species abundances. When the fraction of forested landscape is below 0.6, then the effect of factors which "organize" actual landscape patterns (e.g., topography, land use history, human development, disturbance, etc.) can be expected to show "unique" results that are pattern (i.e., landscape) specific.

Simulations of the spread of populations across heterogeneous landscapes when the fraction of available habitat is above 0.6 show that results are not sensitive to species-specific differences in dispersal characteristics (Fig. 6a). Above 0.6, all landscapes are well connected and, no matter how far each species can disperse per generation, all populations will be able to reach a large fraction of the available habitat. Below 0.6, patches are highly fragmented, and simulations show that large differences in species abundances and habitat utilization are produced by small changes in the maximum possible dispersal distance. Species capable of moving

greater distances are, therefore, not affected by landscape heterogeneity below the scale set by this dispersal parameter.

The landscape data necessary to identify critical thresholds for a variety of species--and thus produce an optimal design for the conservation of biodiversity--should not be gathered at fixed spatial scales. Rather, the spatial scales (i.e., the "grain" and extent of resources) should be determined for particular species and then the arrangement of critical resources evaluated at that scale. When the latter procedure is followed, it is possible to evaluate the effects of landscape pattern on the abundance and distribution of different species. Previous results have shown that above p_c habitat disturbance will increase the number of boundaries, but below p_c the effect will be to remove additional habitat and associated resources (Turner et al. 1989). Therefore, broad-scale differences in species abundance due to landscape structure are best studied on appropriately scaled maps with values of p ranging from 0.3 to 0.6.

Simulated population abundances of species which differ in dispersal characteristics show different rates of increase even though fecundity parameters are identical (Fig. 2). Because the converse is also true, that is, different landscape patterns result in different rates of increase for the same species, pattern and scale are critical in the management and design of natural resources. Further investigations will be needed to relate dormancy (Levin et al. 1984) and soil seed banks (Malanson 1984) to landscape patterns. Available field and experimental data lead us to expect that the presence of a seed bank will dramatically affect both the consequences of species dispersal characteristics and their response to disturbance.

Landscape studies of species abundance and diversity must be performed at scales appropriate to the species of interest. When this prerequisite is met, then new theory, methods, and empirical information can be used to relate pattern and process at broad spatial scales. The failure of many studies to first determine the appropriate scales for measurement and prediction may be responsible for the familiar complaint of lack of predictive theories in ecology (Pickett and White 1985).

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