
Extinction Thresholds for Species in Fractal Landscapes

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Abstract: *Predicting species' responses to habitat loss and fragmentation is one of the greatest challenges facing conservation biologists, particularly if extinction is a threshold phenomenon. Extinction thresholds are abrupt declines in the patch occupancy of a metapopulation across a narrow range of habitat loss. Metapopulation-type models have been used to predict extinction thresholds for endangered populations. These models often make simplifying assumptions about the distribution of habitat (random) and the search for suitable habitat sites (random dispersal). We relaxed these two assumptions in a modeling approach that combines a metapopulation model with neutral landscape models of fractal habitat distributions. Dispersal success for suitable, unoccupied sites was higher on fractal landscapes for nearest-neighbor dispersers (moving through adjacent cells of the landscape) than for dispersers searching at random (random distance and direction between steps) on random landscapes. Consequently, species either did not suffer extinction thresholds or extinction thresholds occurred later, at lower levels of habitat abundance, than predicted previously. The exception is for species with limited demographic potential, owing to low reproductive output ($R'_o = 1.01$), in which extinction thresholds occurred sooner than on random landscapes in all but the most clumped fractal landscapes ($H = 1.0$). Furthermore, the threshold was more precipitous for these species. Many species of conservation concern have limited demographic potential, and these species may be at greater risk from habitat loss and fragmentation than previously suspected.*

Umbrales de Extinción para Especies en Paisajes Fraccionados

Resumen: *La predicción de las respuestas de especies a la pérdida del hábitat y su fragmentación es uno de los retos más grandes a los que se enfrentan los biólogos conservacionistas, particularmente si la extinción es un fenómeno de umbrales. Los umbrales de extinción son declinaciones abruptas en la ocupación de parche de una metapoblación a lo largo de un rango somero de pérdida de hábitat. Los modelos de tipo metapoblacional han sido usados para predecir umbrales de extinciones para poblaciones amenazadas. Estos modelos frecuentemente simplifican las suposiciones sobre la distribución del hábitat (al azar) y la búsqueda de sitios de hábitat apropiado (dispersión al azar). Relajamos estas dos suposiciones en un modelo que combina un modelo de metapoblación con modelos de paisaje neutral de distribuciones de hábitat fracturados. El éxito de dispersión para sitios disponibles y desocupados fue mayor en paisajes fracturados para dispersores del vecino más cercano (moviéndose a través de celdas en el paisaje), que para dispersores en búsquedas al azar en paisajes aleatorios (distancia al azar y dirección entre pasos). Consecuentemente, las especies no sufrieron umbrales de extinción o los umbrales ocurrieron más tarde, a niveles aún más bajos de abundancia del hábitat que los predecidos anteriormente. La excepción es para especies con potencial demográfico limitado, debido a un bajo rendimiento reproductivo ($R'_o = 1.01$), en las cuales los umbrales de extinción ocurren más temprano que en paisajes aleatorios, en todos los paisajes fraccionados excepto aquellos muy ramificados ($H = 1.0$). Más aún, los umbrales fueron más precipitados en estas especies. Muchas de las especies de importancia en conservación tienen un potencial geográfico limitado y podrían estar en un riesgo mayor al previamente supuesto, debido a la pérdida de hábitat y a la fragmentación.*

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Introduction

Critical thresholds in species' responses to habitat fragmentation have serious implications for the conservation of biodiversity. In this context, a critical threshold is an abrupt, nonlinear change that occurs in some parameter across a small range of habitat loss. Neutral landscape models, derived from percolation theory in the field of landscape ecology (Gardner & O'Neill 1991; With 1997; With & King 1997), characterize habitat fragmentation as a threshold phenomenon. Above the threshold, habitat destruction results in a simple loss of suitable habitat; the effect of habitat loss on landscape structure is a quantitative one, a reduction in the proportion of habitat (b) on the landscape (e.g., Andr en 1994; Bascompte & Sol e 1996). A qualitative change in landscape structure occurs at the threshold: a small additional loss of habitat at this point produces a fragmented landscape in which habitat is dissected into many small, isolated patches. Further habitat loss can lead to further fragmentation. The threshold at which landscapes become fragmented is defined by the presence or absence of a continuous cluster of habitat that spans the entire landscape (the *percolating cluster*). It is the disruption of the percolating cluster that produces a threshold in landscape connectivity (With 1997). The level of habitat loss at which this threshold in landscape connectivity occurs is determined by the pattern of habitat distribution and the dispersal capabilities of the species (With & Crist 1995; Pearson et al. 1996; With 1997; With et al. 1997).

If habitat loss leads to a critical threshold in landscape connectivity—fragmentation—then the ecological consequences of habitat fragmentation may also exhibit threshold behavior. Consider that an abrupt decline in landscape connectivity may interfere with dispersal success (Wiens et al. 1997; With & King, in press) such that formerly widespread populations may suddenly become fragmented into small, isolated patches (Andr en 1994; With & Crist 1995). This may in turn lead to an abrupt decline in patch occupancy and extinction of the population across the landscape (extinction thresholds; Lande 1987; Kareiva & Wennergren 1995; Bascompte & Sol e 1996; Ritchie 1997). Because habitat fragmentation can have nonlinear effects, it may be difficult to predict the consequences of land-use change or habitat destruction for biodiversity until the threshold is exceeded. Thus, critical threshold phenomena have been identified as “a major unsolved problem facing conservationists” (Pulliam & Dunning 1997).

It is desirable to understand under what conditions extinction thresholds occur as a result of habitat loss and fragmentation. Are extinction thresholds, for example, coincident with thresholds in landscape connectivity? One of the most useful applications of spatial models in conservation biology is to alert conservationists to the potential consequences of habitat fragmentation (Wen-

nergren et al. 1995). We present a synthesis of metapopulation theory and percolation theory in which we couple Lande's (1987) demographic model of extinction thresholds for territorial populations with neutral landscape models. This modeling synthesis enables us to investigate the relative effects of landscape pattern, habitat loss, and fragmentation on population persistence for species with different dispersal abilities and life-history traits. We show how relaxing assumptions in Lande's original model, concerning habitat distribution and the search behavior of individuals seeking suitable habitat, influences whether and under what conditions extinction thresholds occur.

Extinction Thresholds of Territorial Populations

Lande (1987) extended Levins's (1969) metapopulation model to quantify extinction thresholds—the minimum proportion of suitable habitat necessary for population persistence—for territorial species with different life-history characteristics and dispersal abilities. In this model a landscape is divided into discrete territories of equal size. A proportion b of these territories is designated as suitable for survival and reproduction, and territories are assumed to be distributed randomly across the landscape. The proportion of unsuitable territories is $u = 1 - b$. Each territory can be occupied by only one pair or reproductive female, and juveniles either inherit their natal territory with constant probability ϵ or disperse and search up to m territories for a suitable, unoccupied site. Assuming random encounter with potential territories, the probability that a juvenile successfully finds a suitable unoccupied territory is

$$1 - (1 - \epsilon)(u + ph)^m, \quad (1)$$

where p is the proportion of suitable territories already occupied by adult females. At demographic equilibrium, the proportion of suitable, occupied territories is given by the Euler-Lotka equation, which identifies the net lifetime reproductive output (female offspring per female, R'_o) with unity, or

$$[1 - (1 - \epsilon)(u + p^*h)^m]R'_o = 1, \quad (2)$$

where R'_o is the net lifetime production of female offspring per female, which depends on their finding a suitable territory. The proportion of suitable territories occupied by females at demographic equilibrium is then

$$p^* = 1 - (1 - k)/h \quad \text{if } h > 1 - k, \quad (3)$$

$$\text{or } p^* = 0 \quad \text{if } (h \leq 1 - k),$$

where

$$k = [(1 - 1/R'_o)/(1 - \epsilon)]^{1/m}. \quad (4)$$

Lande referred to the composite parameter k as the demographic potential of the population. It incorporates both reproductive output R'_o and dispersal ability m . The parameter k also gives the maximum occupancy of territories at equilibrium when the entire landscape is suitable ($b = 1.0$). The extinction threshold is at $b = 1 - k$, where $p^* = 0$ (Fig. 1). The population can persist only when the proportion of suitable habitat or territories is greater than $1 - k$. Lande's model also predicts that species will not occupy all available habitat, even when the entire landscape is suitable; a proportion $1 - k$ of the sites will remain unoccupied when $b = 1.0$ (Fig. 1).

The equilibrium occupancy of sites as a function of habitat loss is of conservation interest. For example, a species with low demographic potential (e.g., $k = 0.20$), either as a consequence of low reproductive capacity or limited dispersal ability or both, cannot persist if suitable habitat is reduced below 80% (Fig. 1). A species with greater demographic potential (e.g., $k = 0.80$), due to its higher reproductive output or better dispersal ability, will occupy a greater proportion of suitable territories (80% when $b = 1.0$) and will be able to persist at lower proportions of suitable habitat (Fig. 1). As habitat loss approaches the extinction threshold, however, a relatively small change in the amount of suitable habitat will result in a disproportionately large decline in p^* . For example, consider a species with $k = 0.9$. A change in suitable habitat from 90% to 80% would have relatively little impact on p^* , whereas a similar amount of habitat loss from 20% to 10% would result in extinction of the population (Fig. 1).

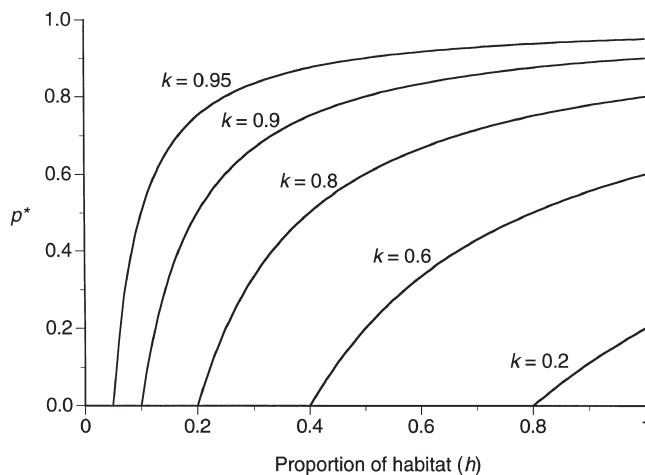


Figure 1. The proportion of territories occupied at demographic equilibrium for species with different demographic potentials (k) on random landscapes (after Lande 1987). Extinction thresholds are given by the value of h where $p^* = 0$. Different curves correspond to species with different demographic potentials.

Dispersal Success in Fractal Landscapes

Lande's model assumes that suitable territories are randomly distributed across the landscape. Random landscape structure is a practical null model for assessing the ecological consequences of habitat fragmentation (Gardner et al. 1987, 1993; With & King 1997), and Lande's model has been useful for predicting the effects of habitat destruction on endangered populations such as the Northern Spotted Owl (*Strix occidentalis caurina*; Lande 1988; Lamberson et al. 1992; Noon & McKelvey 1996). Habitats are often patchily distributed, however, and the assumption of random distribution may not be valid when the model is applied to natural landscapes. How does a clumped, nonrandom distribution of suitable habitat affect patch occupancy and extinction thresholds predicted by Lande's model?

Fractal algorithms are increasingly being used to generate complex spatial patterns for habitat and other resource distributions (Milne 1992; Palmer 1992; With et al. 1997). A fractal distribution of habitat results in landscapes that are statistically more clumped than a random landscape (With et al. 1997; Fig. 2). The clumping of habitat is determined by the fractal dimension D . To get a sense of this, consider fractal landscape maps generated by the midpoint displacement algorithm (Saupe 1988; Palmer 1992; With et al. 1997). Although this fractal algorithm generates a continuously varying surface of "elevation" or "topography," it is possible to divide the surface to produce either binary (two-state) landscapes (habitat versus nonhabitat) or heterogeneous landscapes comprised of more than one habitat type (With et al. 1997). In Fig. 2, the continuously varying surface has been truncated at a selected "elevation" to produce a binary landscape map with a proportion b of the landscape identified as habitat. Truncated landscapes generated from fractal surfaces with a high degree of spatial autocorrelation ($H = 1.0$) have extremely clumped habitat distributions. At the opposite extreme, habitat is distributed as small, isolated patches for truncated landscapes generated from fractal distributions with low spatial autocorrelation ($H = 0.0$; Fig. 2). Fractal landscapes provide a means of systematically controlling both the amount (b) and spatial contagion (H) of habitat. It is therefore possible to tease apart the effects of habitat loss per se from those of fragmentation (or changes in spatial distribution) on population persistence. The terms *habitat loss* and *fragmentation* are often used synonymously (e.g., Noon & McKelvey 1996). Habitat loss does not necessarily lead to fragmentation, however (Fahrig 1997). We adopted the definition of fragmentation as a disruption in landscape connectivity (a threshold phenomenon; Gardner et al. 1987, 1993; With 1997), as defined by percolation theory in the implementation of neutral landscape models. Fragmentation is thus a qualitative change in landscape structure apart from a quantitative change in loss of total habitat area (Andrén 1994; Bascompte & Solé 1996).

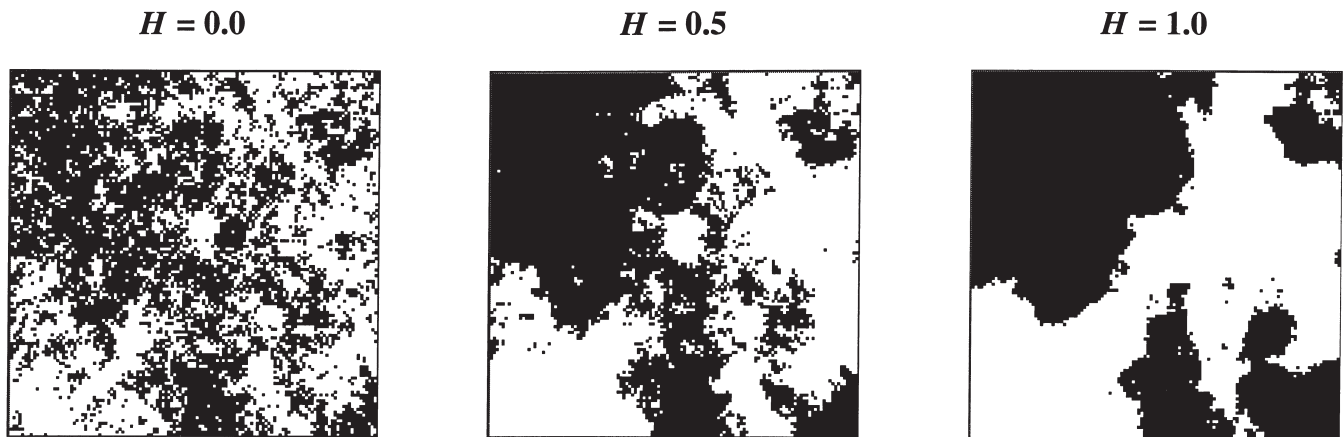


Figure 2. Fractal landscapes generated by midpoint displacement with different levels of spatial contagion or “clumping” (H). Habitat abundance (h) is 50% in all maps.

Lande’s model also assumes that dispersing juveniles randomly encounter potential territories. This can occur either when suitable territories are randomly distributed across the landscape or when dispersal is a random walk, random with respect to both direction and distance at each step. If juvenile dispersal is truly random and the dispersing individual can randomly sample the entire landscape, the assumption of random encounter with potential territories holds regardless of the spatial distribution of suitable habitat. Lande’s model thus applies to both random and clumped (fractal) landscapes. The distribution of habitat does not affect the ability of individuals to locate suitable habitat; only the abundance of habitat, h , affects dispersal success under the assumption of random dispersal or encounter with suitable habitat.

The assumption of random encounter is also a “good approximation when suitable territories are evenly (rather than randomly) distributed, if the root-mean-squared dispersal distance of individuals is much larger than the distance between suitable territories” (Lande 1987:625; emphasis ours). If, however, the scale at which juveniles search for suitable territories is fine relative to the scale of the landscape pattern, such as when the juvenile is constrained to search in the neighborhood of its natal territory, then the assumption of random encounter is neither valid nor a good approximation when suitable habitat is clumped rather than randomly distributed. In this circumstance a clumped distribution of habitat should increase dispersal success over that for a random distribution (e.g., Doak 1989; Doak et al. 1992; Adler & Nuerenberger 1994; Lamberson et al. 1994). We therefore relaxed Lande’s assumption regarding dispersal behavior (effectively an assumption of random dispersal). We constrained dispersers to search in the neighborhood of their natal territory and redefined the scale at which individuals interact with the patch structure of the landscape.

A challenge in developing this synthesis between metapopulation theory and neutral landscape models lies in defining dispersal success on a fractal landscape within the analytical framework of Lande’s model. In doing so we can investigate the consequences of our alternative assumptions about habitat distribution and dispersal behavior by direct comparison with the analytical results of Lande’s extinction threshold model. We have not been able to derive a closed-form solution for dispersal success (assuming fine-scale local dispersal) on a binary fractal landscape from a “first principle” consideration of the probability of encounter with suitable territories. A closed-form solution may not exist. Instead, we approximated the probability of dispersal success by first simulating dispersal success on fractal landscapes that vary in habitat abundance (h) and spatial contagion (H). We then fit a mathematical function to describe the relationship between dispersal success and landscape structure (h and H), which we can substitute for equation 1, the probability that a juvenile finds a suitable unoccupied territory. This was then substituted in equation 2, which we solved for p^* , the expected proportion of territories occupied at demographic equilibrium in a fractal landscape, to compare with the response curves generated by Lande’s model (Fig. 1).

Description of Simulation Model

We simulated dispersal on fractal landscape maps generated by the midpoint displacement algorithm, in which we varied habitat abundance, h , and spatial contagion (H ; Fig. 2). Each map was a square lattice of 128 rows and 128 columns. Cells were labeled as either suitable or unsuitable habitat; each cell represented a territory as in Lande’s model. We represented landscapes as binary habitat maps—suitable versus unsuitable habitat—to re-

main consistent with Lande's model, but it is possible to generate heterogeneous landscape maps with habitats of different quality or suitability (e.g., With et al. 1997). We generated fractal landscapes for 3 levels of contagion ($H = 0.0, 0.5, 1.0$; Fig. 2) and 9 levels of habitat abundance ($b = 0.1, 0.2, \dots, 0.9$). Because the probability of successfully finding a territory is also a function of p , the proportion of sites already occupied (equation 1), we included 10 levels of habitat occupancy ($p = 0.0, 0.1, \dots, 0.9$). Occupied cells were randomly distributed among suitable habitat cells; the proportion of suitable unoccupied sites is thus $(1 - p)b$. The simulations thus involved a factorial of 3 levels of H (landscape pattern), 9 levels of b (habitat abundance), and 10 levels of p (prior occupancy), or 270 ($3 \times 9 \times 10$) different landscape configurations.

Dispersal was initiated from a randomly selected natal (i.e., occupied) cell of suitable habitat. In these simulations we assumed that ϵ , the probability of inheriting the maternal cell, was zero, so all juveniles were forced to disperse (obligate juvenile dispersal). Dispersal was modeled as a nearest-neighbor random lattice walk, in which the disperser could move only into one of the four neighboring grid cells (vertically and horizontally adjacent) at each step; the direction of movement (the cell to which the disperser moved) was chosen randomly with equal (0.25) probability. Individuals were able to move through habitat as well as nonhabitat cells in their search for a suitable unoccupied territory. By constraining individuals to move only through adjacent cells, we tended to restrict dispersal to the neighborhood of the natal territory. We designated this dispersal behavior as nearest-neighbor dispersal (NND) to distinguish it from the effectively random or broader-scale dispersal of Lande's model, which we designated as random dispersal (RD). Nearest-neighbor dispersal effectively altered the scale of dispersal, such that the organism interacted with the spatial pattern of the landscape at a finer scale than in RD.

The edge of the landscape map was modeled as a reflective barrier. Edge effects (Haefner et al. 1991) were unlikely given the extremely large size of these landscape grids (16,384 cells), the large number ($n = 1000$) of individuals that were run independently on these maps, and the limited number of grid cells ($m = 50$) dispersers could search for a suitable unoccupied territory. Individuals were allowed to move until they encountered an unoccupied cell of suitable habitat and were scored as a success or until they had made a total of $m = 50$ steps without finding a territory and were scored as a failure and "died." No other cost to dispersal was assessed in this version of the model, to keep it general and consistent with Lande's original formulation (but for a treatment of continuous mortality during dispersal see Carroll & Lamberson 1993). Dispersal success was scored for a total of $n = 1000$ independent individuals for each landscape configuration ($n = 270$). The proba-

bility of successfully finding a suitable territory was the proportion of dispersal trials (individuals) scored as a success on each landscape.

Comparison of Dispersal Success on Random and Fractal Landscapes

Nearest-neighbor dispersers generally had greater success in finding suitable habitat on fractal landscapes than did random dispersers on random landscapes, especially when dispersal was limited and habitat was rare (Fig. 3). The poorest nearest-neighbor dispersers ($m = 1$) searching for rare habitat ($b = 0.1$) in even the most frag-

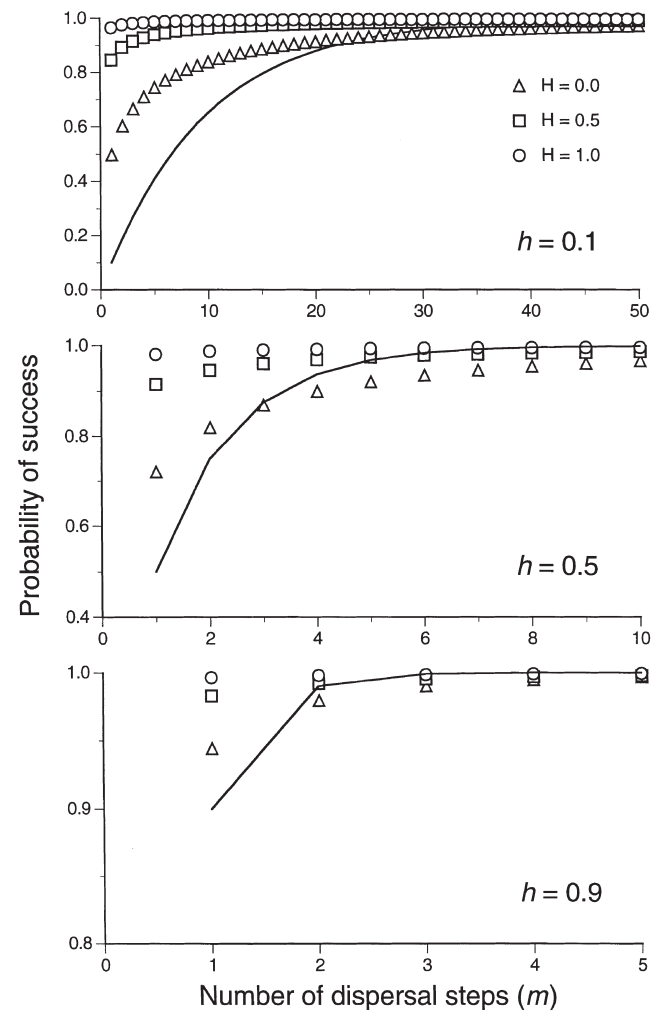


Figure 3. Probability of successfully finding a suitable, unoccupied territory for nearest-neighbor dispersal on different fractal landscapes with different proportions of habitat (h). Prior patch occupancy (p) is set to $p = 0$ in this example so that the effects of landscape structure (h and H) on dispersal success are apparent. Solid lines are the dispersal success for random dispersers on random landscapes derived from Lande's (1987) model (equation 1 in text).

mented fractal landscapes ($H = 0.0$) were able to find suitable habitat 50% of the time. By comparison, only 10% of poor dispersers searching at random on a random landscape were successful. Dispersal success increased for nearest-neighbor dispersers with increased clumping of suitable habitat. When suitable habitat was rare ($b = 0.1$), success rates increased to greater than 80% for NND in highly clumped landscapes ($0.5 \leq H \leq 1.0$; top panel, Fig. 3). The enhanced search success of NND diminished as dispersal range (m) or habitat abundance (b) increased, however. When most of the landscape was suitable ($b \geq 0.5$), NND was more successful than RD for only the poorest dispersers ($m < 5$). When habitat was abundant ($b = 0.9$), success in locating suitable habitat was 90% or more for even the poorest dispersers ($m = 1$) and was nearly absolute when $m \geq 2$, regardless of the underlying pattern of habitat distribution (Fig. 3).

Not surprisingly, the probability of successfully finding a suitable unoccupied territory increased with dispersal range (m) and decreased as degree of habitat occupancy p increased (Fig 4). There were, however, significant interactions between dispersal ability and prior occupancy, whereas the proportion of suitable habitat had a smaller effect. When suitable habitat was common ($b = 0.9$), poor dispersers ($m = 1$) on nearly saturated landscapes ($p = 0.9$) had only a 10% chance of finding a territory, compared to a 50% chance when the habitat was half occupied or 90% when only 10% occupied (Fig. 4 for $b = 0.9$). When habitat was rare ($b = 0.1$) or covered half the landscape ($b = 0.5$), the probability of success for poor dispersers decreased to less than 50% when half the suitable habitat was occupied ($p = 0.5$) and was 80% when only 10% was occupied ($p = 0.1$; Fig. 4). These differences were ameliorated by the dispersal range (m) of the species, however. When prior occupancy was low ($0.1 \leq p \leq 0.5$), the probability of successfully finding a territory was 100% when $m \geq 10$. Available territories were more difficult to find in heavily occupied landscapes ($p = 0.9$), as expected; success was not certain even for species with exceptional dispersal abilities ($m = 50$) unless habitat was abundant ($b = 0.9$; Fig. 4).

Extinction Thresholds on Fractal Landscapes

To incorporate dispersal success on fractal landscapes in Lande’s analytical framework, we fitted the simulation results (Figs. 3 & 4) with a mathematical function that could be substituted for equation 1 and applied in equation 2. Dispersal success for NND on fractal landscapes is described by the equation

$$\text{Pr}(\text{success}) = 1 - (1 - \epsilon)[(1 - h')^{m\beta_1} + (ph')^{m\beta_2}], \quad (5)$$

where ϵ , p , and m are as in equation 1; $b' = a + b$,

where b is the abundance of habitat and a and b are fitted parameters that vary with the spatial contagion H of the landscape. The parameters β_1 and β_2 are also fitted; β_1 varies with H , and β_2 varies with both H and b . The mathematical form of this function was selected for its relative simplicity and consistency with the analytical form of equation 1; this equation provided the best fit among several other functions we generated.

Properly calibrated or parameterized (by choice of a , b , β_1 , and β_2), equation 5 provided a good fit to the simulation data, as shown by the comparisons between simulated dispersal success for NND (symbols) on fractal landscapes and the curves generated by equation 5 (lines) in Fig. 4. We selected this particular example because it represents the poorest fit of the function to the

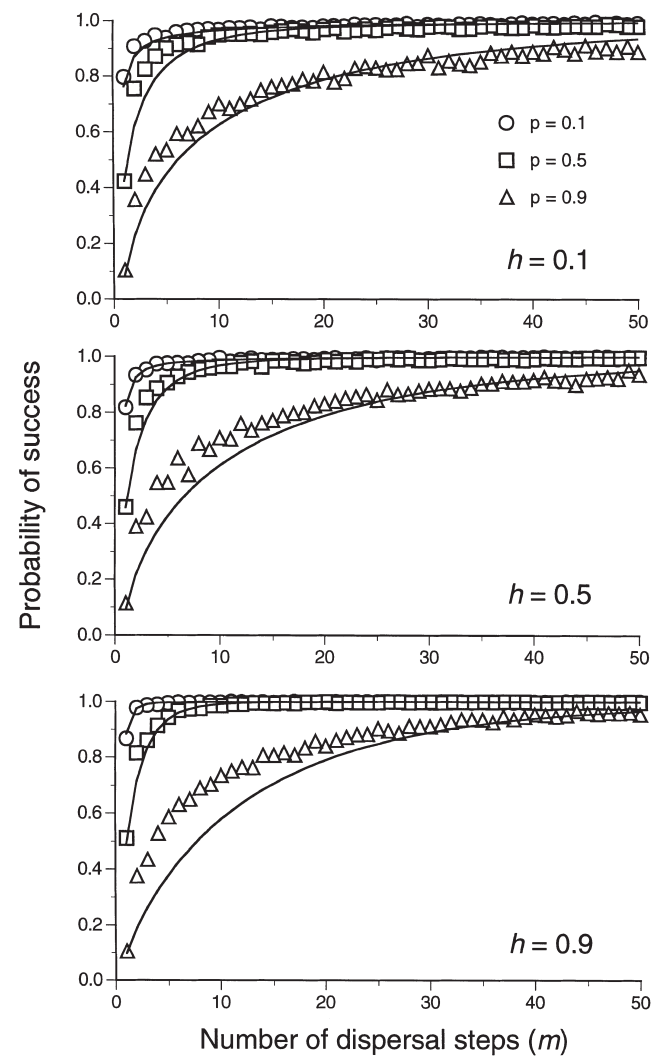


Figure 4. Comparison of dispersal success for nearest-neighbor dispersers (symbols) and the fit of the mathematical function (lines; equation 5 in text) at different levels of patch occupancy (p) on a fractal landscape ($H = 0.5$) with different proportions of habitat (h).

simulations (e.g., compare curves for $p = 0.9$ at $b = 0.9$). Even so, it aptly described the behavior of the simulation model. The fit improved at lower levels of p and b in this example (Fig. 4) and in all other landscape scenarios.

Substituting equation 5 for the Pr(success) term in equation 2, the proportion of suitable territories occupied at demographic equilibrium (p^*) is given by

$$p^* = [(k' - (1 - h')^{m_1})^{m_2}]^{1/\beta_2} / h, \quad (6)$$

where

$$k' = [(1 - 1/R'_o)/(1 - \epsilon)]. \quad (7)$$

Compare equation 6 with equation 3 and equation 7 with equation 4. Lande presents p^* as a function of b for different values of the composite parameter k (Fig. 1), which combines the life-history parameters R'_o , m , and ϵ in a measure of what Lande termed the “demographic potential” (equation 4). To compare our estimates of p^* from equation 6 with those of Lande’s model (equation 3), we decomposed his composite variable k and made comparisons for values of R'_o , m , and ϵ . If we assume that $\epsilon = 0.0$ (obligate juvenile dispersal), then we need only specify m (dispersal ability) and R'_o (reproductive potential).

Model Results

Populations were generally able to persist across a greater range of habitat loss on fractal landscapes for nearest-neighbor dispersers than was predicted by Lande’s model (Table 1; Figs. 5–7). Extinction thresholds did not occur at all for species exhibiting modest reproductive potentials ($R'_o \geq 1.10$) in maximally clumped fractal landscapes ($H = 1.0$; Figs. 6 & 7). These species persisted at or near maximum patch occupancy (k) across the entire range of habitat loss ($b = 0.1$ – 1.0). It was only when the reproductive potential was near replacement ($R'_o = 1.01$) that populations went extinct on these clumped landscapes, but even then they persisted longer than random dispersers on random landscapes (Fig. 5). At the other extreme

in extensively fragmented fractal landscapes ($H = 0.0$), extinction thresholds occurred sooner for nearest-neighbor dispersers with limited-to-moderate reproductive potentials ($1.01 \leq R'_o \leq 1.10$) than for random dispersers in random landscapes (Figs. 5 & 6). The only exception was for species that were good dispersers ($m = 20$) and had a moderate reproductive potential ($R'_o = 1.10$), in which the extinction threshold occurred later than predicted for random dispersers on random landscapes (Fig. 6). Once populations achieved a reproductive potential of $R'_o = 1.25$, thresholds either occurred later ($m = 1$ – 7) or not at all ($m = 10$ – 20) in even the most fragmented fractal landscapes ($H = 0.0$, Fig. 7).

Lande’s composite parameter, k , combines the life-history parameters R'_o and m into a single index of demographic potential (equation 4). The behavior of Lande’s model is controlled by the composite value of k . For example, a species with $k = 0.79$ will always have an extinction threshold at $b = 0.21$ in Lande’s model, regardless of the combination of R'_o and m that contributes to that particular k value. That is not the case for our model. For example, if a species has an extremely low reproductive output ($R'_o = 1.01$) but good dispersal abilities ($m = 20$), such that $k = 0.79$, populations on fractal landscapes are predicted to go extinct at 50% when $H = 0.0$ and at 32% habitat when $H = 0.5$ (Fig. 5). In contrast, populations with the same demographic potential ($k = 0.79$) but with a slightly higher reproductive output ($R'_o = 1.10$) and a correspondingly lower dispersal range ($m = 10$) are predicted to go extinct at $b = 0.28$ only in highly fragmented fractal landscapes ($H = 0.0$) and at $b < 0.1$ for less fragmented fractal landscapes ($H \geq 0.5$; Fig. 6). If reproductive output is increased to $R'_o = 1.25$ and m reduced to 7 to maintain $k = 0.79$ (Fig. 7), then persistence is greater for nearest-neighbor dispersers on fragmented fractal landscapes ($H = 0.0$) than for random dispersers on random ones ($H = 0.0$: $b = 0.11$; random: $b = 0.21$; Fig. 7).

In our model, the effects of reproductive output and dispersal ability on extinction thresholds were not equivalent. Reproductive output appeared to be more

Table 1. Summary of population responses to habitat loss in fractal landscapes that vary in spatial contagion (H) for species with different reproductive capacities (R'_o) and dispersal abilities (m).*

R'_o	$H = 1.0$	$H = 0.5$	$H = 0.0$
1.01	for all m : threshold occurs later (at lower values of b)	$m = 1$ – 2 : threshold occurs later $m = 5$ – 20 : threshold occurs sooner	$m = 1$: threshold occurs marginally later $m = 2$ – 20 : threshold occurs much sooner
1.10	for all m : thresholds not evident; population persists at or near maximum patch occupancy (k)	$m = 1$ – 2 : threshold occurs later $m = 5$ – 20 : thresholds not evident; population persists at or near maximum patch occupancy	$m = 1$: threshold occurs marginally later $m = 2$: threshold is the same $m = 5$ – 10 : threshold occurs sooner $m = 20$: threshold occurs later
1.25	for all m : thresholds not evident; population persists at or near maximum patch occupancy	for all m : thresholds not evident; population persists at or near maximum patch occupancy	$m = 1$ – 7 : threshold occurs later $m = 10$ – 20 : thresholds not evident; population persists at or near maximum patch occupancy

*Comparisons are made between extinction threshold values obtained by our model and those of Lande’s (1987) model in which the habitat distribution was assumed to be random.

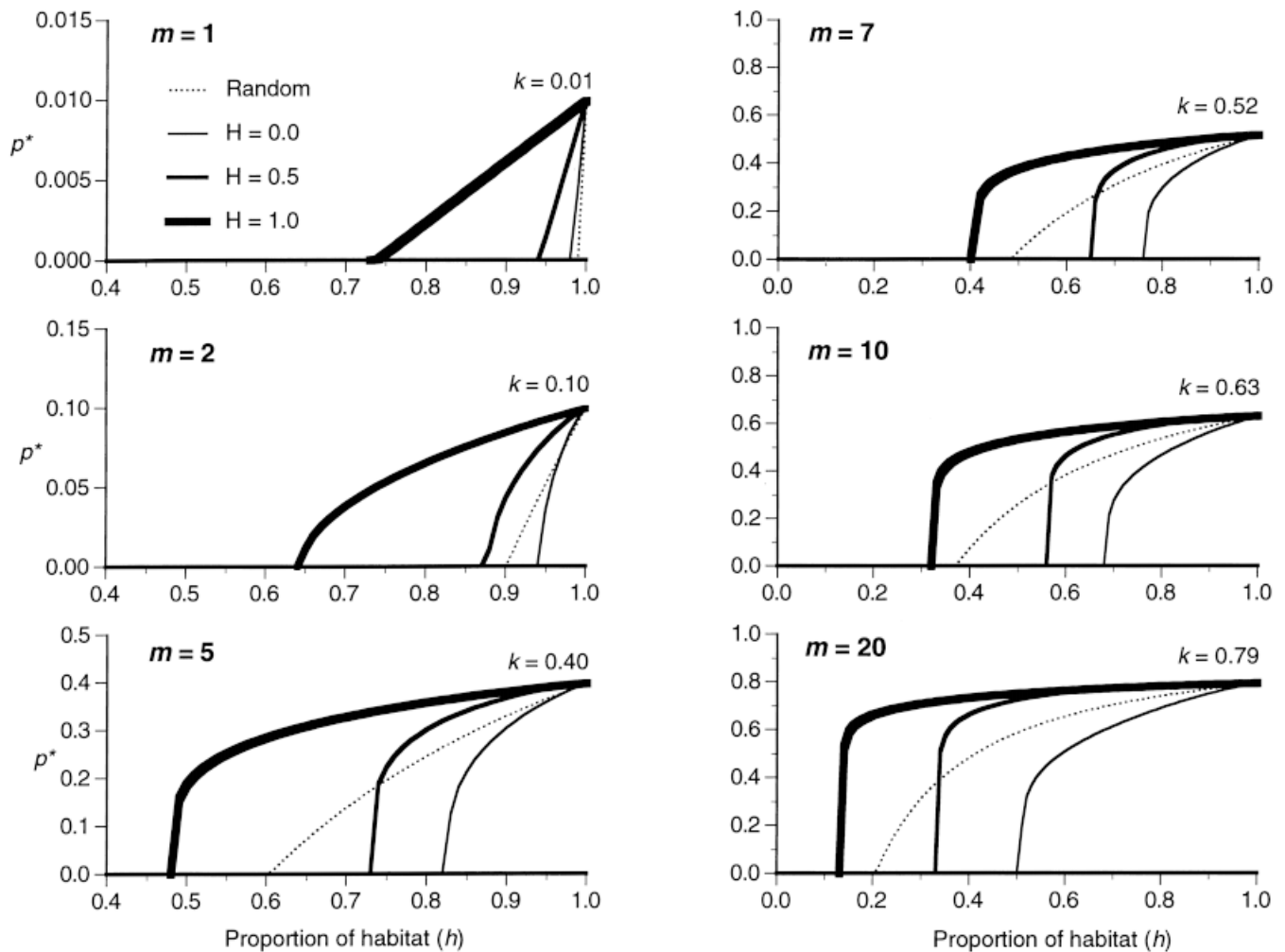


Figure 5. Equilibrium patch occupancy (p^*) for populations with a net lifetime reproductive output $R'_o = 1.01$ and different dispersal abilities (m). "Random" indicates random dispersal on random landscapes (i.e., Lande's model); nearest-neighbor dispersal is modeled on fractal landscapes with different levels of spatial contagion (H) (k , demographic potential).

important than dispersal ability in favoring population persistence. This is not true for Lande's model, at least for $R'_o < 2.00$. At $R'_o = 1.01$, extinction thresholds generated from Lande's model for random dispersers on random landscapes ranged from $b = 1.0$ to $b = 0.2$ as dispersal increased from $m = 1$ to $m = 20$ (Random, Fig. 8). As reproductive output increased from $R'_o = 1.01$ to $R'_o = 2.00$ (when $m = 1$), the thresholds ranged from $b = 1.0$ to only $b = 0.5$ (Random, Fig. 8). For populations on fragmented fractal landscapes ($H = 0.0$), extinction thresholds ranged from $b = 0.98$ to $b = 0.5$ (for $R'_o = 1.01$) as a function of increasing dispersal, but ranged from $b = 0.98$ to $b = 0.11$ (at $m = 1$) as reproductive output increased (Fig. 8). The relative effect of increased reproductive output on population persistence became even more pronounced in clumped fractal landscapes ($H = 0.5 - 1.0$). In these landscapes, populations were predicted to persist when $b \geq 0.1$ for all species except

those with the lowest reproductive potential (e.g., $R'_o = 1.01$). In fractal landscapes with intermediate clumping ($H = 0.5$), extinction thresholds ranged from $b = 0.94$ to $b = 0.33$ (for $R'_o = 1.01$) as dispersal increased (Fig. 8). Likewise, in clumped fractal landscapes ($H = 1.0$) extinction thresholds ranged from $b = 0.74$ to $b = 0.12$ (for $R'_o = 1.01$) with increasing dispersal, but even a small increase in R'_o beyond 1.01 pushed the extinction thresholds to $b < 0.10$; these species persisted at near maximum occupancy across a wide range of habitat abundance (Fig. 8).

Discussion

Predicting extinction risk for populations in the face of widespread habitat loss and fragmentation is one of the major challenges facing conservation biologists. The po-

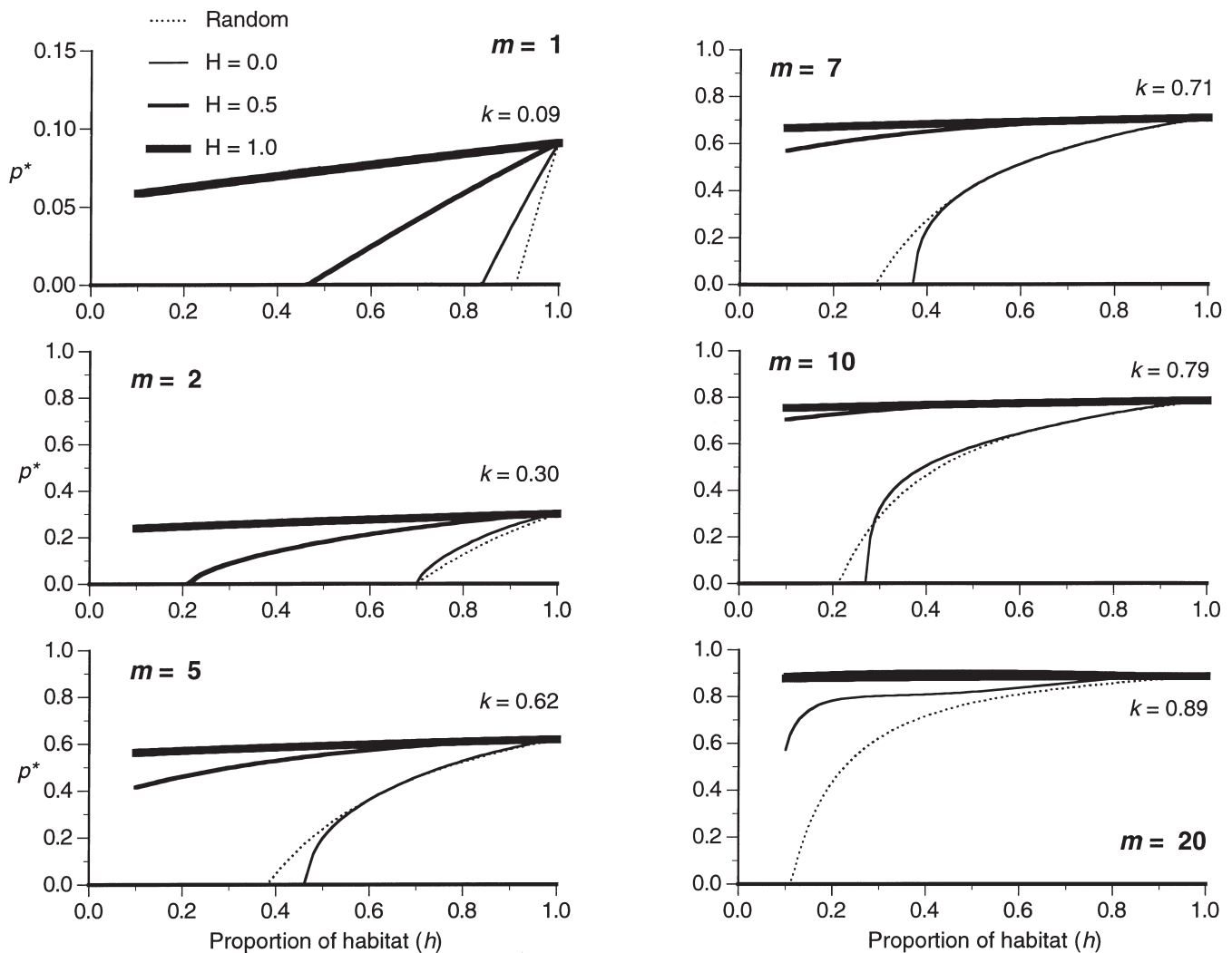


Figure 6. Equilibrium patch occupancy (p^*) for populations with a net lifetime reproductive output $R'_o = 1.10$ and different dispersal abilities (m). "Random" indicates random dispersal on random landscapes (i.e., Lande's model); nearest-neighbor dispersal is modeled on fractal landscapes with different levels of spatial contagion (H) (k , demographic potential).

tential for threshold responses, such as a precipitous decline in the regional persistence of a species owing to a small loss of habitat near the threshold, makes this task all the more urgent. The fear, however, is that it may be impossible to develop general predictions of how species respond to scenarios of land-use change leading to habitat loss and fragmentation. As our model results demonstrate, species are predicted to exhibit a diverse array of responses to habitat fragmentation depending upon the specific combination of life-history traits and dispersal capabilities. Nevertheless, some general patterns emerge.

Clumped habitat distributions enhance dispersal success for dispersers whose search is at finer scales than that of the overall landscape pattern (e.g., Doak et al. 1992; Adler & Nuernberger 1994; this study). The critical assumption that we modified in Lande's (1987) ex-

tinguished threshold model pertains to how individuals interact with landscape structure. This involved relaxing assumptions about both habitat distribution and dispersal behavior. We generated fractal landscape patterns, which are perhaps more representative of natural habitat distributions than the random distribution used in Lande's model (Mandelbrot 1983). Fractal landscapes contain fewer, larger habitat patches with less edge than random landscapes, and thus they maintain connectivity across a greater range of habitat destruction (With et al. 1997). In both models, juveniles initiate dispersal from their natal territories, which by definition are in suitable habitat. In our model, however, we constrained dispersers to move through adjacent cells in search of suitable habitat, rather than effectively searching at random throughout the landscape as in Lande's model. This

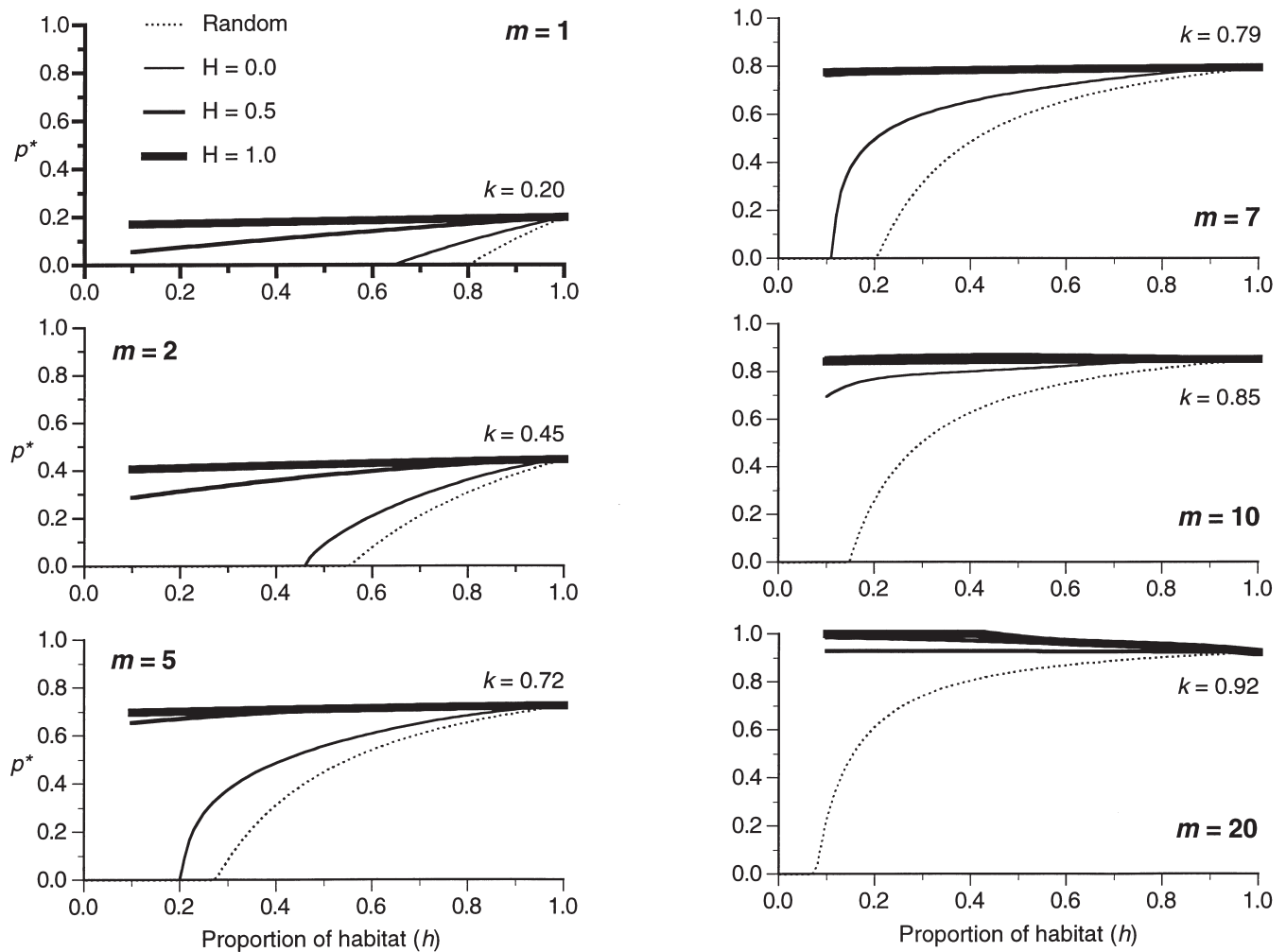


Figure 7. Equilibrium patch occupancy for populations with a net lifetime reproductive output $R'_o = 1.25$ and different dispersal abilities (m). "Random" indicates random dispersal on random landscapes (i.e., Lande's model); nearest-neighbor dispersal is modeled on fractal landscapes with different levels of spatial contagion (H) (k , demographic potential).

forced dispersers to interact with the patch structure of the landscape at a finer scale and tended to restrict dispersal to within patches of suitable habitat, especially when the habitat was maximally clumped. It also tended to minimize the tendency of dispersers to leave patches of suitable habitat that can occur when dispersal is on a broader scale or at random, especially when habitat is rare. Dispersal success was thus greater for dispersers in our model than in Lande's model.

Subsequently, most species were not predicted to suffer extinction thresholds. Or, if they did, the threshold generally occurred later than predicted by Lande's model. Most species were able to find suitable habitat even when habitat was scarce ($b = 0.1$) if the habitat was clumped ($H = 0.5$ or 1.0). They were also able to maintain near-maximum patch occupancy if the population was capable of even modest reproduction ($R'_o \geq$

1.1). These results suggest that some populations may be more resilient to the effects of habitat destruction than previously suspected.

Although some populations maintained near-maximum patch occupancy across a wide range of habitat loss, habitat fragmentation (the pattern of habitat loss) did affect patch occupancy and population persistence. Populations in highly clumped fractal landscapes ($H = 1.0$) were always more abundant (higher p^*) than populations in fragmented fractal landscapes ($H = 0.0$), except when reproductive output and dispersal ability were high (e.g., $R'_o = 1.25$ and $m = 20$; Figs. 5–7). Furthermore, extinction was more likely to occur and to occur sooner (at higher levels of b) on highly fragmented fractal landscapes than on clumped fractal landscapes. The fine-scale destruction of habitat ($H = 0.0$) produces many small gaps that disrupt landscape connectivity—and thus dis-

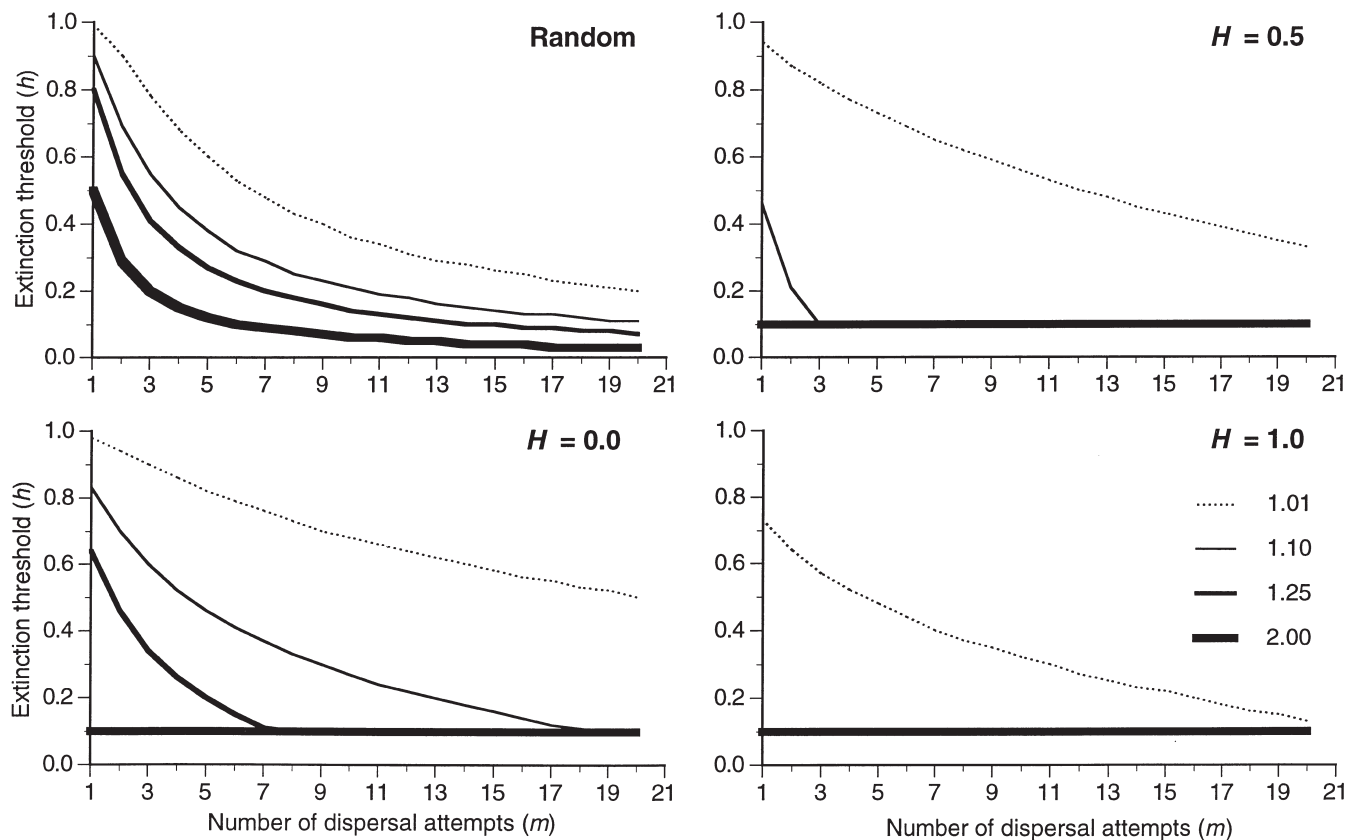


Figure 8. Extinction thresholds as a function of dispersal ability (m) for species that differ in net lifetime reproductive output ($R'_o = 1.01, 1.10, 1.25, \text{ and } 2.00$) in random and fractal landscapes. Fractal landscapes vary in spatial contagion (H), ranging from highly fragmented ($H = 0.0$) to highly clumped ($H = 1.0$). The extinction threshold is defined as the proportion of habitat on the landscape (h) at which equilibrium patch occupancy is zero ($p^* = 0$).

persal success and patch colonization—sooner than if habitat is destroyed at a coarser scale ($H = 1.0$) so as to leave large, continuous patches of habitat (Pearson et al. 1996). The impact of habitat loss and fragmentation must be assessed with respect to the scale of the habitat destruction (e.g., change in spatial pattern) and the scale at which the organisms of concern interact with that pattern.

Just because a species does not exhibit an extinction threshold, however, does not mean that it is not affected by habitat loss or fragmentation. A species that maintains a maximum patch occupancy of 80% across the full range of habitat destruction will still occur in fewer patches when habitat is scarce ($b = 0.1$) than when the landscape is totally suitable ($b = 1.0$); occupying 80% of habitat patches when the landscape is totally suitable is clearly preferable to occupying 80% of the patches when only 10% of the landscape is suitable. A reduction in the regional distribution of a species could render populations more susceptible to demographic and environmental stochastic events, produce Allee effects, reduce genetic variability, and lead to an overall decline in population viability. Furthermore, habitat destruction may produce effects that are not apparent until years later (“extinction debt,”

Tilman et al. 1994). Our assessment of population persistence is thus based on only one measure—patch occupancy—and these other effects should also be considered to render a full evaluation of population responses to habitat loss and fragmentation.

Nevertheless, species with limited reproductive potential ($R'_o = 1.01$) are predicted to go extinct sooner than predicted by Lande’s model (Fig. 5). Many species of management concern have limited reproductive potential, which limits their ability to respond to environmental disturbance such as anthropogenic habitat fragmentation. Moreover, the approach to the extinction threshold is often more precipitous for these species (Fig. 5). Thus, the effects of habitat fragmentation may actually be far worse than previously suspected for species with limited demographic potential, which are often the species of concern to conservation biologists.

In our model the dispersal and demographic components of the demographic potential (k) are not interchangeable as in Lande’s model. Because dispersal success is high for nearest-neighbor dispersers on fractal landscapes, dispersal ability had little effect on extinction thresholds (Fig. 8). Instead, reproductive capacity

(R'_0) was a more important determinant of population persistence. This suggests a reappraisal of applications based on Lande's (1987) model (e.g., Lande 1988; Noon & McKelvey 1996) in which dispersal ability has been shown to have a profound effect on patch occupancy and population persistence. Maintaining connectivity in landscapes with even minimal clumping (e.g., $H = 0.0$) by construction of corridors may not be as important, for even poor dispersers, as enhancing reproductive output by management of high-quality habitats, establishing additional nest sites, or supplementing food resources.

Implications for Conservation Biology

The coupling of metapopulation and neutral landscape models moves us closer to the "exciting scientific synthesis" between metapopulation theory and landscape ecology envisioned by Hanski and Gilpin (1991) by providing a generalized, spatially explicit framework for assessing species' responses to habitat loss and fragmentation (also see Wiens 1997). Analytical metapopulation models have the advantage of high generality and have provided the underlying theoretical framework for understanding population or community responses to fragmentation (e.g., Hanski & Simberloff 1997). Their shortcoming, however, is that they cannot be easily applied to a specific landscape to predict how land-use change or timber-harvest schedules will affect different species in that landscape (e.g., Hanski 1994). At the other end of the continuum are "spatially realistic" (Hanski & Simberloff 1997) or spatially explicit (Dunning et al. 1995) population models that couple population simulation models with specific landscape maps generated by geographic information systems (GIS) to predict the consequences of proposed or actual management scenarios on target species (e.g., Liu et al. 1995). These models are clearly important management tools, but they lack the generality and discrete solutions of spatially implicit metapopulation models. Furthermore, it will not be possible to develop spatially explicit models for every species and landscape. Such models are generally parameterized for only a single species in a given landscape and are not easily generalized even to other species in the same system (e.g., Liu et al. 1995).

Thus, general demographic models coupled with neutral landscape models offer the best features of both modeling approaches: generality and the potential for application in spatially complex landscapes. This type of modeling approach can provide a baseline for understanding how habitat loss and fragmentation are likely to affect species with different life-history characteristics and dispersal abilities. Furthermore, the grid structure of neutral landscapes integrates well with raster landscape maps generated by GIS, thereby facilitating comparisons between theoretical expectations and management applications in a given landscape.

The ultimate objective of a generalized, spatially explicit extinction model is to generate hypotheses about the persistence of species with different suites of life-history characteristics and dispersal abilities in landscapes subjected to varying degrees of habitat loss and fragmentation. Nevertheless, predictions regarding extinction thresholds must be interpreted carefully in the formulation of conservation policy. Predicted extinction thresholds may underestimate true thresholds if they fail to accommodate demographic or environmental stochasticity or immigration from outside the region (Lande 1988; Lamberson et al. 1992; Pagel & Payne 1996; Noon et al. 1997). Our concern, then, is the use of theoretical models as prescriptions for conservation without regard to the underlying assumptions. Theoretical models are useful as null models or for otherwise assessing how habitat fragmentation might affect population persistence, but they are only tools and should not be used uncritically to formulate blanket conservation policies. We have illustrated how changing model assumptions, such as the underlying habitat distribution and dispersal behavior, can fundamentally alter predictions of extinction thresholds, and this may have profound implications for the management of biodiversity. The best application of theory in conservation is thus to inform research, generate hypotheses, and identify unforeseen threats, while recognizing that theoretical generalizations should not be accepted as dogma or blindly implemented as policy (Doak & Mills 1994; Dunning et al. 1995).

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Literature Cited

- Adler, F., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45:41-75.
- Andr n, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355-366.
- Bascompte, J., and R. V. Sol . 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology* 65:465-473.

- Carroll, J. E., and R. H. Lamberson. 1993. A continuous model for the dispersal of territorial species. *SIAM. Journal of Applied Mathematics* **53**:205-218.
- Doak, D. F. 1989. Spotted Owls and old growth logging in the Pacific northwest. *Conservation Biology* **3**:389-396.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. *Ecology* **75**:615-626.
- Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* **41**:315-336.
- Dunning, J. B., Jr., D. J. Steward, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**:3-11.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603-610.
- Gardner, R. H., and R. V. O'Neill. 1991. Pattern, process, and predictability: the use of neutral landscape models for landscape analysis. Pages 289-307 in M. G. Turner and R. H. Gardner, editors. *Quantitative methods in landscape ecology*. Springer-Verlag, New York.
- Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* **1**:19-28.
- Gardner, R. H., R. V. O'Neill, and M. G. Turner. 1993. Ecological implications of landscape fragmentation. Pages 209-226 in S. T. A. Pickett, and M. G. McDonnell, editors. *Humans as components of ecosystems: subtle human effects and ecology of populated areas*. Springer-Verlag, New York.
- Haefner, J. W., G. C. Poole, P. V. Dunn, and R. T. Decker. 1991. Edge effects in computer models of spatial contagion. *Ecological Modelling* **56**:221-244.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151-162.
- Hanski, I., and M. E. Gilpin. 1991. Metapopulation dynamics: a brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3-16.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5-26 in I. A. Hanski, and M. E. Gilpin, editors. *Metapopulation biology*. Academic Press, San Diego.
- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* **373**:299-302.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. *Conservation Biology* **6**:505-512.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology* **8**:185-195.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**:624-635.
- Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis*). *Oecologia* **75**:601-607.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237-240.
- Liu, J. J. B. Dunning, Jr., and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's Sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. *Conservation Biology* **9**:62-75.
- Mandelbrot, B. B. 1983. *The fractal geometry of nature*. W. H. Freeman, New York.
- Milne, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. *American Naturalist* **139**:32-57.
- Noon, B. R., and K. S. McKelvey. 1996. A common framework for conservation planning: linking individual and metapopulation models. Pages 139-165 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C.
- Noon, B., K. McKelvey, and D. Murphy. 1997. Developing an analytical context for multispecies conservation planning. Pages 43-59 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. *The ecological basis of conservation*. Chapman and Hall, New York.
- Pagel, M., and R. J. H. Payne. 1996. How migration affects estimation of the extinction threshold. *Oikos* **76**:323-329.
- Palmer, M. W. 1992. The coexistence of species in fractal landscapes. *American Naturalist* **139**:375-397.
- Pearson, S. M., M. G. Turner, R. H. Gardner, and R. V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. Pages 77-95 in R. C. Szaro and D. W. Johnston, editors. *Biodiversity in managed landscapes*. Oxford University Press, New York.
- Pulliam, H. R., and J. B. Dunning. 1997. Demographic processes: population dynamics on heterogeneous landscapes. Pages 203-232 in G. K. Meffe, C. R. Carroll, and contributors. *Principles of conservation biology*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
- Ritchie, M. E. 1997. Populations in a landscape context: sources, sinks and metapopulations. Pages 160-184 in J. A. Bissonette, editor. *Wildlife and landscape ecology*. Springer-Verlag, New York.
- Saupe, D. 1988. Algorithms for random fractals. Pages 71-113 in H.-O. Petigen and D. Saupe, editors. *The science of fractal images*. Springer-Verlag, New York.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65-66.
- Wennergren, U., M. Ruckelshaus, and P. Kareiva. 1995. The promise and limitation of spatial models in conservation biology. *Oikos* **74**:349-356.
- Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 5-26 in I. Hanski and M. Gilpin, editors. *Metapopulation dynamics*. Academic Press, San Diego.
- Wiens, J. A., R. L. Schooley, and R. D. Weeks Jr. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* **78**:257-264.
- With, K. A. 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* **11**: 1069-1080.
- With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* **76**:2446-2459.
- With, K. A., and A. W. King. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* **79**:219-229.
- With, K. A., and A. W. King. In press. Dispersal success in fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology*.
- With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**:151-169.

