



# Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter?

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Received 12 July 2000; received in revised form 20 April 2001; accepted 7 May 2001

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## Abstract

Dispersal is a fundamental component of many spatial population models. Concerns over the need to incorporate detailed information on dispersal behavior in spatially explicit population models (SEPMs) motivated us to undertake a simulation study in which we explored (1) the conditions under which landscape structure affects dispersal success and (2) the dependency of dispersal success on the choice of dispersal algorithm. We simulated individual dispersal as a random process (the mean-field approximation), a percolation process (PD) or a nearest-neighbor process (NND) on random and fractal neutral landscapes across gradients of habitat fragmentation and abundance (0.1–90%). Both landscape structure and dispersal behavior affected dispersal success in landscapes with < 30–40% habitat. Landscape structure, in the form of contagious habitat, was always important for predicting the success of weak dispersers constrained to move within a local neighborhood, unless habitat was abundant ( $\geq 80\%$ ). Dispersers generally attained highest success on landscapes in which habitat had high spatial contagion. Habitat clumping may thus mitigate the negative effects of habitat loss on dispersal success. Spatial pattern is generally not important for predicting dispersal success when habitat abundance exceeds 40% and the mean-field approximation (random dispersal) adequately describes dispersal success in these landscapes. Because species of conservation concern generally occur in landscapes with < 20% habitat, modeling dispersal as a random process may not be warranted for these species. In these cases, the required interaction between spatial structure and dispersal may be captured adequately by a simple local dispersal algorithm such that detailed movement rules may not be needed. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** Dispersal; Fractal landscapes; Neutral landscape models; Percolation; Spatially explicit population models

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## 1. Introduction

Dispersal success—the ability of organisms to locate suitable habitat on a landscape—is a fundamental property of most spatially structured population models. For metapopulation models,

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in which the extinction–colonization dynamics of populations occupying habitat patches are modeled, dispersal success is equivalent to, or determines, the patch colonization rate. Dispersal is thus modeled phenomenologically as the probability that a given patch will be colonized. In spatially implicit metapopulation models, this probability may be a function of the size or relative isolation of the patch (i.e. landscape structure; see Hanski, 1999 for a comprehensive treatment of metapopulation models). In contrast, spatially explicit population models (SEPMs), in which a population simulation model is coupled with a landscape map (Dunning et al., 1995), often simulate dispersal explicitly using an individual-based approach with movement rules describing how organisms interact with the spatial complexity of the landscape. The landscape is usually represented as a lattice of habitat cells, such as a raster-based map of a real landscape in a geographical information system (GIS) or as a hypothetical habitat distribution (neutral landscape models; Gardner et al., 1987; With, 1997; With and King, 1997). At a minimum, the dispersal modules of individual-based SEPMs include information on (1) the type of movement (e.g. random, correlated random walk, self-avoiding walk) and (2) either the dispersal distance or number of sites that can be searched by individuals (e.g. Doak et al., 1992; Lamberson et al., 1992, 1994; Lindenmayer and Possingham, 1996; With and King, 1999a) or a dispersal-distance function for the distribution of propagules in the case of plants (e.g. Lavorel et al., 1995). More elaborate dispersal modules may additionally include habitat-specific rates of movement or mortality, habitat-specific movement behaviors (such as more linear movement in habitat matrix) and density-dependent dispersal (e.g. Pulliam et al., 1992; Lamberson et al., 1994; Liu et al., 1995; Lindenmayer and Possingham, 1996). Dispersal success is calculated as the fraction of individuals that successfully locate and occupy new habitat (Doak et al., 1992; With and King, 1999b).

Because habitat destruction and fragmentation are cited as the major causes of species endangerment (e.g. Meffe and Carroll, 1997), SEPMs have become increasingly popular in conservation ap-

plications. One of the more immediate consequences of habitat loss and fragmentation should be a disruption of dispersal or movement between habitat patches, which may lower colonization success and lead to local extinction. Consequently, ecology and conservation biology has become preoccupied with space and modeling dispersal success (Dunning et al., 1995; Wennergren et al., 1995; Ruckelshaus et al., 1997; South, 1999a). Spatial structure may not always be important, however, for predicting dispersal success. Whether or not dispersal success is affected by landscape pattern depends upon the scale of movement relative to the scale of fragmentation (Doak et al., 1992; With and King, 1999b). In fact, definitions of landscape connectivity—whether a given landscape is perceived as fragmented by a particular species—are based on how organisms interact with spatial pattern (Taylor et al., 1993; Pearson et al., 1996; With, 1997; With et al., 1997). Detailed information on dispersal of real organisms is often lacking, however, particularly for parameters such as dispersal mortality and thus, it can be very difficult to parameterize the individual-based dispersal algorithms used in SEPMs (Wennergren et al., 1995). Incorrect estimates of dispersal distances and dispersal mortality resulted in the greatest prediction errors for dispersal success (Ruckelshaus et al., 1997). If these errors propagate in SEPMs, then estimates of population viability (patch occupancy and probability of persistence) may be so seriously biased as to be worthless (but see South, 1999a).

Because of these concerns and the central importance dispersal has in spatial population models, it is important to understand the conditions under which landscape structure affects dispersal success, as a means of identifying when a spatially explicit approach is necessary. Other investigators have used simple landscapes to investigate the effects of landscape structure on dispersal success (e.g. Doak et al., 1992; Ruckelshaus et al., 1997), but have not explored the full range of spatial complexity across a gradient of habitat abundance and fragmentation, as we do here using neutral landscape models. It is also important to understand how sensitive dispersal success is to different movement algorithms, particularly those

encountered in the lattice-based SEPMs that have become so popular. Many of these lattice-based approaches use simple movement rules, which may lack realism but which therefore do not require detailed empirical behavioral data to implement. If dispersal success is less sensitive to the way in which dispersal is modeled than to the effects of landscape structure, then concerns over the realism of movement rules become less critical and would be welcome news given the paucity of empirical data on dispersal. We therefore undertook a simulation study to address the relative effects of landscape structure and dispersal behavior on dispersal success.

## 2. Methods

### 2.1. Neutral landscape models

We used the program RULE (Gardner, 1999) to generate spatially structured landscapes (i.e. neutral landscape models). Binary landscapes were generated as either a random or fractal distribution of habitat and non-habitat on a two-dimensional square grid measuring  $128 \times 128$  cells (Fig. 1). Random landscapes were created by randomly assigning some fraction ( $h$ ) of the cells to be habitat. Fractal landscapes were generated using the mid-point displacement algorithm (Saupe, 1988) in which both the fraction ( $h$ ) and the contagion of habitat ( $H$ ) were varied to create complex landscape patterns across a gradient of habitat fragmentation (see With, 1997; With et al., 1997 for further details). Habitat abundance ( $h$ ) was simulated at 12 levels ( $h = 0.001, 0.01, 0.05,$

$0.10, 0.20, \dots, 0.90$ ) for random and fractal landscapes. For fractal landscapes, we also varied the contagion of habitat ( $H$ ) across three levels ( $H = 0.0, 0.5, 1.0$ ) for each level of  $h$ . This resulted in landscapes that varied in the degree of habitat fragmentation (Fig. 1) and also allowed us to tease apart the relative effects of habitat abundance ( $h$ ) and fragmentation ( $H$ ) on dispersal success. Ten replicate maps were generated for each landscape type (random: 12  $h$ -levels  $\times$  10 = 120 maps; fractal: 12  $h$ -levels  $\times$  3  $H$ -levels  $\times$  10 = 360 maps; total = 480 landscape maps). We then simulated individual dispersal and calculated dispersal success for different dispersal algorithms on these landscape maps.

### 2.2. Dispersal algorithms

We modeled dispersal as a random process, a nearest-neighbor process (NND) or as a percolation process (PD).

#### 2.2.1. Random dispersal

In random dispersal, the disperser moved with random direction and distance to any point (cell) on the landscape. If dispersal is modeled in this fashion, spatial structure does not matter and only the amount of habitat and the number of cells searched affect dispersal success:

$$P(\text{success}) = 1 - u^m \quad (1)$$

where  $u = 1 - h$  and  $m$  is the number of cells that can be searched (Lande, 1987; With and King, 1999a). This is equivalent to the mean-field approximation for the probability of dispersal success and serves as a baseline for assessing how

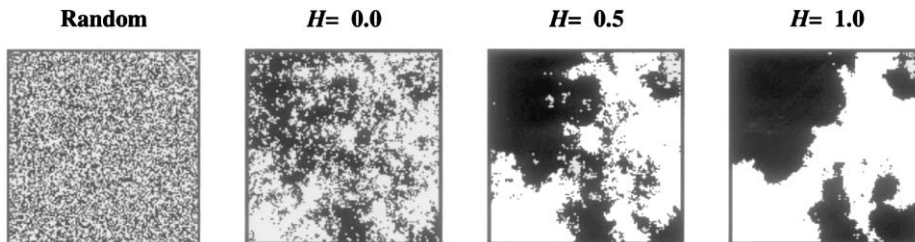


Fig. 1. Neutral landscape models. All four maps contain the same amount of habitat ( $h = 0.5$ , black cells). Fractal landscapes vary in the spatial contagion ( $H$ ) of habitat, which produces a gradient of fragmentation.

spatial structure and different dispersal behaviors affect dispersal success (Bascompte and Solé, 1998). Note that in this definition of random dispersal,  $m$  does not define a local neighborhood. It simply defines the number of cells across the entire landscape that can be visited in seeking habitat. The distance between visited cells and the distance from the cell of origin are random variables. Random movement of the type described by our random dispersal algorithm has been shown to be a reasonable estimate of dispersal in many insects.

### 2.2.2. Nearest-neighbor dispersal

In simulating nearest-neighbor dispersal (NND), individual dispersers ( $n = 1000$ ) were independently initialized at randomly chosen habitat cells on the landscape. At each time step, the dispersers were constrained to move with equal probability into one of the four neighboring cells (the ‘nearest neighbors’). The direction of movement was random, but the dispersal step length was limited to one cell. This is a non-self-avoiding random walk of fixed step-length and the ‘area-limited dispersal’ (ALD) of With and King (1999b). On average, this movement rule produces more localized dispersal than a random dispersal algorithm, in which both direction and step length are random. Dispersers were permitted to take up to  $m$  steps in their search for a suitable habitat cell ( $m = 1, 2, 5, 10, 20$  or  $50$  steps), and could move through non-habitat cells. Upon encountering a cell of suitable habitat, the disperser stopped and was scored as a success. The number of steps a disperser can take ( $m$ ) may be interpreted as either the innate dispersal ability of the species or as an indirect measure of matrix quality that affects dispersal for a given species in different landscape contexts (e.g. dispersal distances  $m$  may be reduced in landscapes with hostile matrix habitat, perhaps because dispersers are unwilling to cross such inhospitable habitat or suffer higher mortality if they do). While a theoretical abstraction, NND might approximate dispersal by larger mammals or birds willing to cross unsuitable habitat to find appropriate habitat in which to establish dens or nests. The edge of the grid was a reflective barrier, but edge effects were insignifi-

cant because of the large size of the grid (16,384 cells), the relatively limited number of grid cells dispersers could search ( $m < 50$ ) and the large number of independent dispersal events ( $n = 1000$ ) (With and King, 1999b).

### 2.2.3. Dispersal by percolation

Dispersal as a percolation process (PD) is similar to NND except individuals were constrained to move only through habitat cells. This is basically the With (1997) ‘Rule 1’ movement, which describes organisms that are unable or unwilling to cross unsuitable habitat (i.e. a species that lacks gap-crossing abilities; Dale et al., 1994). PD might approximate the dispersal of voles or other small animals unwilling to leave the cover of suitable habitat and risk predation or environmental stress. Dispersal by percolation (PD) is the most restrictive movement algorithm of the three we explored, and it has the potential to result in the most localized dispersal if habitat is not well connected and landscapes lie below the percolation threshold (i.e. the threshold amount of habitat,  $h_{crit}$ , at which a continuous cluster of habitat no longer occurs on the landscape; see With, 1997). As with NND, the map boundaries (edges of the grid) were reflective barriers.

## 2.3. Simulation design

Simulations were conducted in a factorial design, in which landscape pattern (random,  $H = 0.0$ ,  $H = 0.5$  and  $H = 1.0$ ), habitat abundance ( $h$ ) and dispersal ability ( $m$ ) were varied, resulting in 2880 simulation runs (480 landscape maps  $\times$  6  $m$ -levels). The probability of NND and PD dispersal success on a given landscape for a given level of  $m$  was calculated as the proportion of individuals ( $n = 1000$ ) that located a suitable habitat cell within  $m$  steps. We compared dispersal success for random dispersal and for NND and PD on both random and spatially structured landscapes. We also examined variability in dispersal success among replicate maps for a given landscape (With and King, 1999a calculated dispersal success on fractal landscapes for only a single map for each landscape combination of  $h$  and  $H$ ).

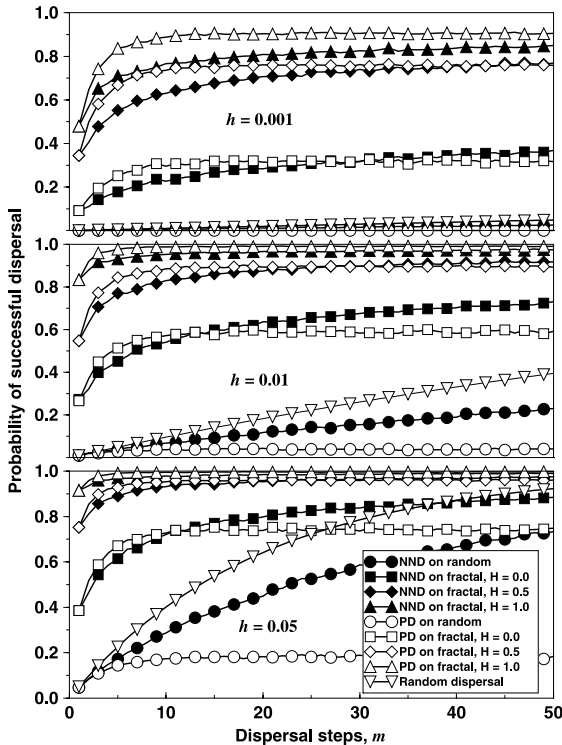


Fig. 2. Mean dispersal success ( $N = 10$  replicate landscapes) as a function of dispersal strength ( $m$ ) for different dispersers on random and fractal landscapes with 0.1, 1 or 5% habitat. NND, nearest-neighbor dispersal; PD, percolation.

### 3. Results

Dispersal success is an increasing function of dispersal strength ( $m$ ) for all landscape patterns and dispersal behaviors (Figs. 2–5). The relationship is typically non-linear, with a rapid increase in dispersal success at small  $m$  followed by an asymptotic approach to a maximum probability of dispersal success. The asymptote is achieved most rapidly in landscapes with abundant habitat (Fig. 5). When habitat is very rare, the rate of approach to that asymptote is very slow for both random dispersal and NND on random maps; PD on random maps asymptotes quickly to low levels of success (Fig. 2).

Dispersal success is also an increasing function of habitat abundance ( $h$ ) for all landscapes and dispersal behaviors (Figs. 6 and 7). The function is linear or approximately linear for PD and

NND on random landscapes and for random dispersal when dispersal ability is limited ( $m = 1, 2$ ) (Fig. 6). Dispersal success is non-linear and asymptotic for NND and PD on fractal landscapes (Figs. 6 and 7) and for greater dispersal strengths by random dispersers and NND and PD on random landscapes (Fig. 7). The function is generally monotonic, except for PD on random or highly fragmented fractal landscapes ( $H = 0.0$ ) (Figs. 6 and 7), but these exceptions are perhaps a consequence of stochasticity. Dispersal as a percolation process (PD) produces greater variability in dispersal success among replicate landscapes, particularly if the habitat is randomly distributed (Fig. 8). This is attributable to the greater variability in the clustering of habitat cells into contiguous patches among replicate random maps. Contiguous clustering greatly influences the success of PD since those dispersers cannot cross

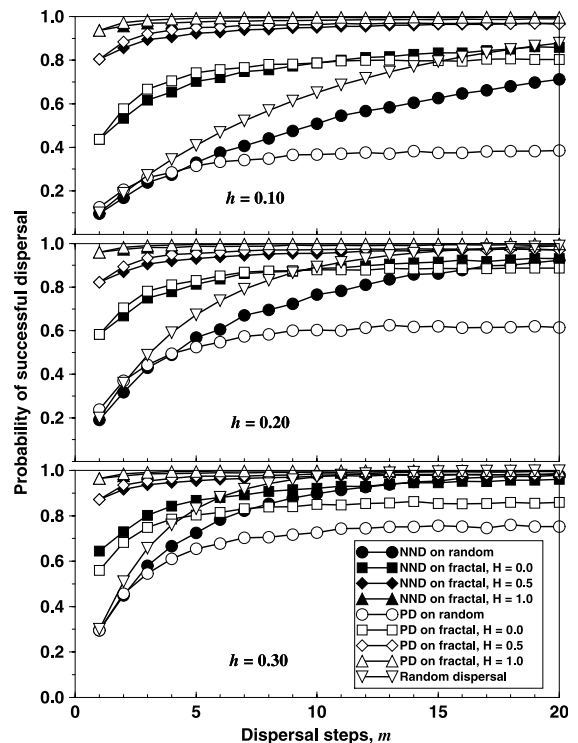


Fig. 3. Mean dispersal success ( $N = 10$  replicate landscapes) as a function of dispersal strength ( $m$ ) for different dispersers on random and fractal landscapes with 10, 20 or 30% habitat. NND, nearest-neighbor dispersal; PD, percolation.

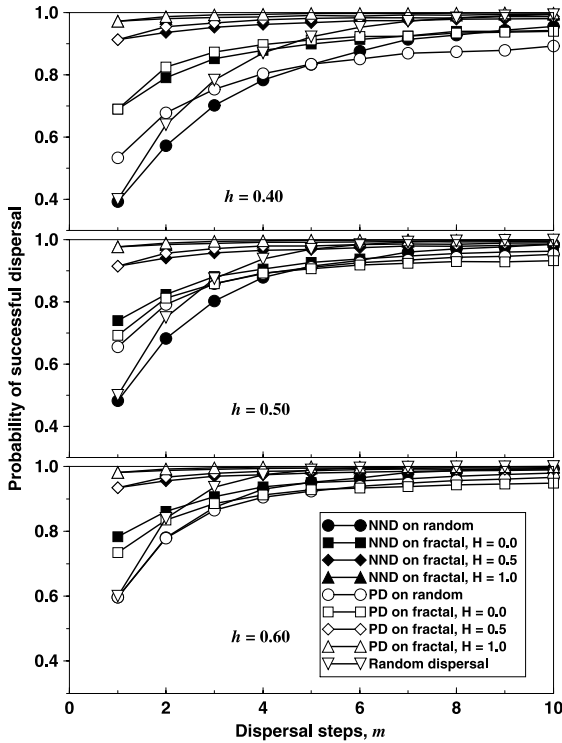


Fig. 4. Mean dispersal success ( $N = 10$  replicate landscapes) as a function of dispersal strength ( $m$ ) for different dispersers on random and fractal landscapes with 40, 50 or 60% habitat. NND, nearest-neighbor dispersal; PD, percolation.

non-habitat to find habitat. Hence, variability in clustering is reflected in variability in dispersal success.

When habitat is abundant (e.g.  $> 70\%$ ), the probability of success is high ( $> 70\%$ ) even for the most limited dispersers ( $m = 1$ ; Fig. 5) and success is virtually guaranteed ( $> 95\%$ ) within five dispersal steps regardless of dispersal behavior or landscape structure (Fig. 5). Dispersal success is not, however, independent of landscape structure and dispersal behavior at intermediate levels of habitat abundance. At intermediate levels of habitat abundance (40–60%), success is not generally guaranteed ( $> 95\%$ ) until dispersal strength approaches  $m = 10$  (Fig. 4). However, on clumped fractal landscapes ( $H = 0.5, 1.0$ ) of intermediate habitat abundance, dispersal success for NND and PD is still high even for weak dispersers ( $m \leq 5$ , Figs. 4 and 6). When habitat is rare to

uncommon (10–30%), success is not assured except when habitat is highly clumped ( $H = 1.0$ ) until  $m = 20$  (Fig. 3). Even then, at 10% habitat, dispersal success is  $< 90\%$  for random dispersal and for NND and PD dispersal on random and highly fragmented fractal landscapes ( $H = 0.0$ ; Fig. 3). When habitat is very rare ( $< 10\%$ ), levels of success as high as 90% may not be achieved until  $m \geq 50$ , except for NND and PD on clumped fractal landscapes ( $H = 0.5, 1.0$ ; Fig. 2). At 0.1% habitat, mean dispersal success rarely exceeds 90%, although it may exceed that for NND and PD on some clumped fractal landscapes (Fig. 2).

Thus, dispersal success tends to converge with increasing dispersal strength ( $m$ ) and habitat abundance ( $h$ ), but differences emerge among landscape patterns and dispersal behaviors when dispersal is limited (small  $m$ ) and habitat is scarce

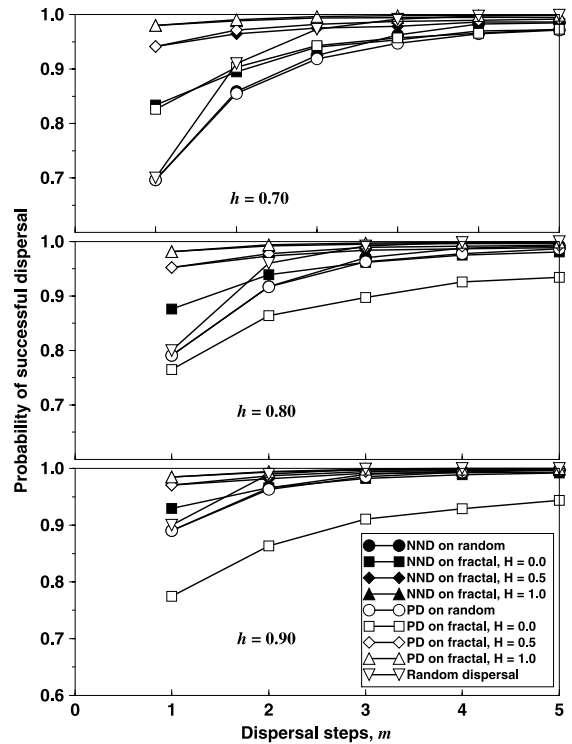


Fig. 5. Mean dispersal success ( $N = 10$  replicate landscapes) as a function of dispersal strength ( $m$ ) for different dispersers on random and fractal landscapes with 70, 80 or 90% habitat. NND, nearest-neighbor dispersal; PD, percolation.

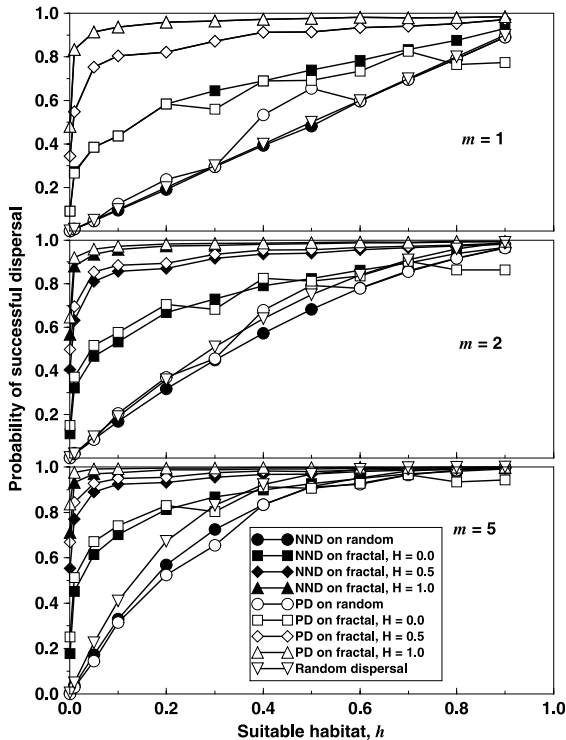


Fig. 6. Mean dispersal success ( $N = 10$  replicate landscapes) as a function of habitat abundance ( $h$ ) for different dispersers with limited dispersal strength ( $m = 1, 2$  or  $5$ ) on random and fractal landscapes. NND, nearest-neighbor dispersal; PD, percolation.

and fragmented. The probability of successful dispersal is thus often a consequence of interactions between dispersal behavior, habitat abundance and landscape structure. It is useful to try and separate these influences into landscape effects and behavioral effects.

### 3.1. Landscape effects: random versus fractal landscapes

Recall that dispersal success for random dispersers is independent of landscape pattern and depends only upon the amount of suitable habitat ( $h$ ) and the number of dispersal steps ( $m$ ) (Eq. (1)). In contrast, landscape pattern does affect dispersal success for NND and PD. Dispersal success is generally higher for both NND and PD on fractal landscapes than on random landscapes,

especially if dispersal strength is limited (Fig. 3) or habitat is scarce ( $h \leq 0.1$  for all fractal landscapes; Tables 1 and 2, Fig. 6). Because individuals begin their search from a habitat cell, even individuals constrained to move only to an adjacent cell ( $m = 1$ ) have a higher probability of encountering habitat in fractal landscapes with high spatial contagion than in landscapes where habitat is randomly distributed. This effect of contagious pattern is greatest when habitat is rare (low  $h$ ). Not unexpectedly, landscape pattern is unimportant if dispersal strength is high or if habitat is abundant (Fig. 7). Differences between random and fractal landscapes exist even for strong dispersers ( $m = 50$ ), however, when habitat is scarce. For NND, this occurred in landscapes with  $\leq 5\%$  habitat (Table 1, Figs. 2 and 7). For PD, strong dispersers had lower success in random than frag-

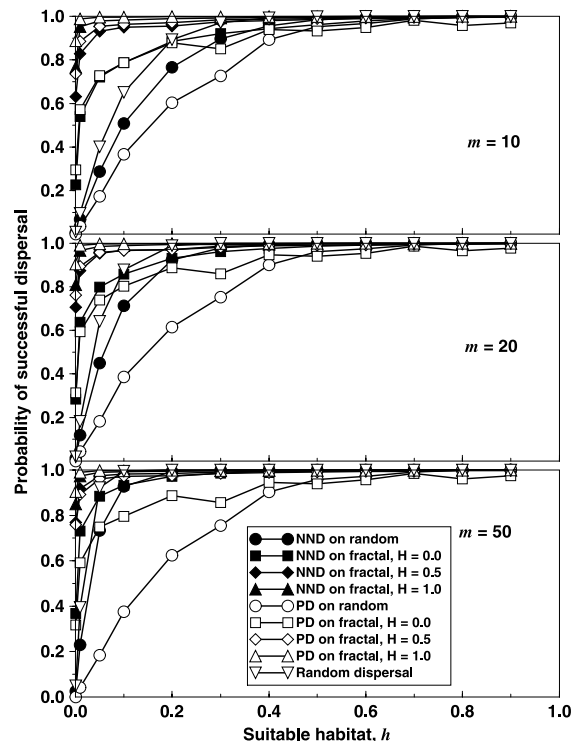


Fig. 7. Mean dispersal success ( $N = 10$  replicate landscapes) as a function of habitat abundance ( $h$ ) for different dispersers with moderate to high dispersal strength ( $m = 10, 20$  or  $50$ ) on random and fractal landscapes. NND, nearest-neighbor dispersal; PD, percolation.

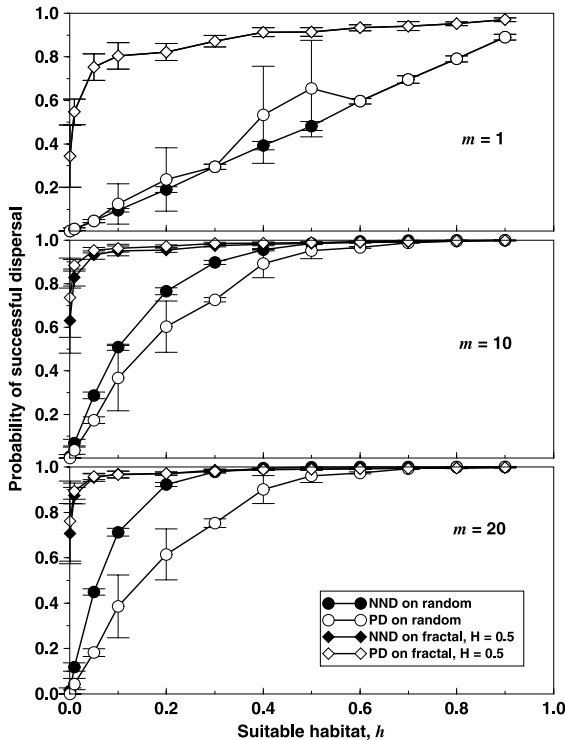


Fig. 8. Dispersal success (mean  $\pm$  S.D.,  $N = 10$  replicate landscapes) as a function of habitat abundance ( $h$ ) for dispersers with different dispersal strength ( $m = 1, 10$  or  $20$ ) on random and fractal landscapes of  $H = 0.5$ . NND, nearest-neighbor dispersal; PD, percolation. Note the greater variability among replicate maps for PD on random landscapes.

mented fractal landscapes ( $H = 0.0$ ) with  $< 30\%$  habitat (Table 2, Figs. 2, 3 and 7). Alternatively, for weak dispersers ( $m = 1, 2$ ), landscape pattern generally affected dispersal success even when habitat was abundant (Tables 1 and 2, Figs. 5 and 6). When habitat was abundant ( $\geq 80\%$ ) but highly fragmented ( $H = 0.0$ ), weak dispersers constrained to move through habitat (PD), generally had lower success than in random landscapes (Figs. 5 and 6), reversing the general trend of greater success on fractal landscapes. A similar exception apparently occurs for weak PD on highly fragmented landscapes ( $H = 0.0$ ) with  $50\%$  habitat. Dispersal success did not increase monotonically as a function of habitat abundance for PD with extremely localized dispersal ( $m \leq 2$ ); a difference in success between random and frac-

tal landscapes with minimum contagion ( $H = 0.0$ ) is not present at  $50\%$  habitat, but is present at  $40$  and  $60\%$  habitat (Fig. 6). This may be a stochastic result owing to high variability in dispersal success among maps for PD on random and highly fragmented fractal landscapes ( $H = 0.0$ ), or it may indicate a complex relationship between PD and spatial pattern. In general, however, dispersal success of both NND and PD tended to increase with increased spatial contagion of habitat.

The RULE-generated landscape metrics for the random and fractal landscapes used in this study are given in With and King (1999b). Theoretically, dispersal success for PD should be highly correlated with the RULE calculated correlation length (a measure of patch contagion). Correlation length is itself correlated with  $H$  (as  $H$  increases, correlation length increases) and that correlation is reflected in the greater dispersal success for PD with increasing  $H$  (Figs. 2–7). However, With and King (1999b) found that correlation length does not predict dispersal success for NND. Indeed, dispersal success was not related to any of the patch-based measures of landscape structure (including correlation length), but was correlated with lacunarity thresholds, a measure of gap structure or inter-patch distances (cf. Figs. 4 and 5 of With and King, 1999b).

### 3.2. Behavioral effects: comparison of dispersal algorithms

There is essentially no difference between PD and NND on fractal landscapes with  $H \geq 0.5$  (Figs. 2–7, Table 3). On highly fragmented fractal landscapes ( $H = 0.0$ ) with  $5$ – $20\%$  habitat, there is some tendency for NND to become more successful than PD as dispersal strength increases. This crossover occurs, for example, at  $m > 17$  for  $20\%$  fragmented fractal landscapes (Fig. 3) or at  $m > 25$  for  $5\%$  fragmented fractal landscapes (Fig. 2).

The comparison between PD and NND on random landscapes is more complicated. When habitat is extremely rare ( $0.1\%$ ) (Fig. 2) or dispersal is limited to a single neighboring cell ( $m = 1, 2$ ) (Fig. 6), there is no difference between PD and NND, although dispersal success is more variable for PD on random landscapes (Table 3). Simi-



larly, allowing for the greater variability in PD, there is no difference between PD and NND on random landscapes with  $\geq 40\%$  habitat (Table 3, Figs. 4, 5 and 8), although there is some tendency for PD to be more successful than NND when dispersal is limited (Figs. 4 and 8). Within the range of 1 and 30% habitat, however, differences in the success of these two types of dispersal depend upon dispersal strength. For example, dispersal success is higher for NND on random landscapes with 5% habitat for  $m > 6$  and continues to increase with increasing dispersal strength, whereas dispersal success plateaus for PD at  $\approx 18\%$  (Table 3, Fig. 2). For strong dispersers ( $m = 50$ ), this results in a difference in dispersal success of 57% on these 5% random landscapes (Fig. 7). Depending upon the dispersal strength, differences may occur between PD and NND at various points within or across the entire range of 1–40% habitat on random landscapes (Table 3, Figs. 6 and 7).

Random dispersal does not differ from NND or PD on random landscapes for weak dispersers

( $m = 1$ ) or when habitat is exceedingly rare (0.1%; Table 4). Again, the higher mean success of PD over random and NND dispersal at  $h = 0.4–0.5$  and  $m = 1$  (Fig. 6) may be a stochastic effect. Differences between random dispersal and NND on random landscapes emerge across particular ranges of habitat depending upon the dispersal strength (Table 4). For example, dispersal success is higher for random dispersers than NND on random landscapes with 5–60% habitat for individuals constrained to move up to five steps (Figs. 2–4, Table 4). There is no difference between random dispersers and NND above or below this habitat range on random landscapes. Similar complex interactions emerge at particular levels of habitat abundance on random landscapes, in which differences in dispersal success between random dispersal and NND occur within a particular range of dispersal strengths. For example, dispersal success is  $\approx 10\%$  greater for random dispersers that can move two to 14 steps on 30% random landscapes (Fig. 3). Below this habitat range, however, dispersal success is greater for

Table 1

Summary of simulation results comparing the difference in dispersal success (probability of encountering a suitable habitat cell) between random and fractal ( $H = 0.0, 0.5$  and  $1.0$ ) landscapes for nearest neighbor dispersers (NND). Is there a difference between random and each of the fractal landscapes for NND?

	$H = 0.0$	$H = 0.5$	$H = 1.0$
<i>Dispersal strength</i>			
$m = 1$	Yes, if $h < 0.9$	Yes	Yes
$m = 2$	Yes, if $h < 0.8$	Yes, if $h < 0.9$	Yes, if $h < 0.9$
$m = 5$	Yes, if $h < 0.5$	Yes, if $h < 0.6$	Yes, if $h < 0.7$
$m = 10$	Yes, if $h < 0.3$	Yes, if $h < 0.4$	Yes, if $h < 0.5$
$m = 20$	Yes, if $h < 0.2$	Yes, if $h < 0.2$	Yes, if $h < 0.3$
$m = 50$	Yes, if $h < 0.2$	Yes, if $h < 0.2$	Yes, if $h < 0.2$
<i>Habitat abundance</i>			
$h = 0.001$	Yes	Yes	Yes
$h = 0.01$	Yes	Yes	Yes
$h = 0.05$	Yes	Yes	Yes
$h = 0.10$	Yes	Yes	Yes
$h = 0.20$	Yes, for $m < 17$	Yes, for $m < 20$	Yes, at least for $m \leq 20$
$h = 0.30$	Yes, for $m < 9$	Yes, for $m < 11$	Yes, for $m < 15$
$h = 0.40$	Yes, for $m < 7$	Yes, for $m < 9$	Yes, at least for $m \leq 10$
$h = 0.50$	Yes, for $m < 4$	Yes, for $m < 7$	Yes, for $m < 8$
$h = 0.60$	No, except for $m \leq 3$	Yes, for $m < 6$	Yes, for $m < 8$
$h = 0.70$	No, except for $m \leq 2$	Yes, for $m < 4$	Yes, for $m < 5$
$h = 0.80$	No, except for $m \leq 2$	No, except for $m \leq 2$	No, except for $m \leq 3$
$h = 0.90$	No, except for $m \leq 2$	No, except for $m = 1$	No, except for $m = 1$

Table 2

Summary of simulation results comparing the difference in dispersal success (probability of encountering a suitable habitat cell) between random and fractal ( $H = 0.0, 0.5$  and  $1.0$ ) landscapes for dispersal as a percolation process (PD). Is there a difference between random and each of the fractal landscapes for PD?

	$H = 0.0$	$H = 0.5$	$H = 1.0$
<i>Dispersal strength</i>			
$m = 1$	Yes, for $h < 0.4$ and $h = 0.7$	Yes	Yes
$m = 2$	Yes, for $h < 0.5$ and $h = 0.7$	Yes, for $h < 0.9$	Yes, for $h < 0.9$
$m = 5$	Yes, for $h < 0.3$	Yes, for $h < 0.7$	Yes, for $h < 0.7$
$m = 10$	Yes, for $h < 0.3$	Yes, for $h < 0.5$	Yes, for $h < 0.5$
$m = 20$	Yes, for $h < 0.3$	Yes, for $h < 0.5$	Yes, for $h < 0.5$
$m = 50$	Yes, for $h < 0.3$	Yes, for $h < 0.5$	Yes, for $h < 0.5$
<i>Habitat abundance</i>			
$h = 0.001$	Yes	Yes	Yes
$h = 0.01$	Yes	Yes	Yes
$h = 0.05$	Yes	Yes	Yes
$h = 0.10$	Yes	Yes	Yes
$h = 0.20$	Yes	Yes	Yes
$h = 0.30$	No, except for $m \leq 3$	Yes	Yes
$h = 0.40$	No	Yes	Yes
$h = 0.50$	No	No, except for $m = 1$	No, except for $m \leq 3$
$h = 0.60$	No	No, except for $m < 10$	No, except for $m < 10$
$h = 0.70$	No, except for $m \leq 2$	No, except for $m < 5$	No, except for $m < 5$
$h = 0.80$	No	No, except for $m \leq 4$	No, except for $m < 4$
$h = 0.90$	No	No, except for $m \leq 2$	No, for $m \leq 2$

random dispersal on random landscapes with 1–20% habitat, once sufficient dispersal strength has been attained ( $m \geq 3$  for 20% random landscapes,  $m \geq 17$  for 1% landscapes; Table 4).

Dispersal success is generally higher for NND than random dispersal on fractal landscapes, particularly if habitat is rare ( $h \leq 0.05$ ) or dispersal is limited to the neighboring cell or two ( $m = 1, 2$ ) and habitat is sufficiently abundant ( $h > 0.6$ ; Table 4). Increasing dispersal strength mitigates any differences between NND and random dispersal on highly clumped fractal landscapes ( $H = 0.5, 1.0$ ), except when habitat is scarce. For example, dispersal success is 10–70% higher for nearest-neighbor dispersers that can move up to five steps on highly clumped ( $H = 1.0$ ) fractal landscapes with < 50% habitat (Fig. 6). For strong dispersers ( $m = 50$ ), however, the higher success of NND over random dispersal occurs only with 10% habitat on clumped fractal landscapes (Fig. 7). The relationship is more complex on highly fragmented ( $H = 0.0$ ) fractal landscapes. Differences between NND and random dispersal

generally occur at particular levels or ranges of habitat abundance once a limited amount of dispersal has been attained (e.g.  $m \geq 5$ ), although the general effect of convergence with increasing dispersal strength still holds (Table 4). Alternatively, for a given level of habitat abundance between 20 and 70% on fragmented fractal landscapes, convergence between NND and random dispersal may occur within or across a particular range of dispersal strengths (Table 4). The relationship is more straightforward on clumped fractal landscapes ( $H = 0.5, 1.0$ ), although a significant difference between NND and random dispersal persists even when the landscape is mostly habitat (90%) for individuals constrained to move only a single step ( $m = 1$ ; Figs. 5 and 6).

#### 4. Discussion

Because dispersal is featured in most spatial population models, it is important to understand (1) the conditions under which landscape struc-

ture affects dispersal success and (2) the dependency of dispersal success on the choice of dispersal algorithm (movement rule). We therefore undertook this simulation study to address the relative effects of landscape structure and dispersal behavior on dispersal success. The main results are summarized in Table 5. A comparison of local dispersal on spatially structured landscapes with the mean-field approximation (random dispersal) provides the most general evidence for the importance of landscape structure on dispersal success. Differences between random and fractal landscapes for local dispersal processes represent a finer distinction regarding the importance of spatial structure in predicting dispersal success.

When do spatial pattern (landscape structure) and dispersal behavior really matter? The mean-field approximation (random dispersal) was a poor predictor of dispersal success for local dispersal processes (NND or PD) on spatially structured landscapes when habitat abundance was

< 40% and when dispersal was limited. Landscape structure (as measured by  $H$ ) was always important for predicting the success of weak dispersers constrained to move within a local neighborhood ( $m = 1, 2$  for NND and PD) unless habitat was very abundant ( $\geq 80\%$ ). In general, dispersers attained highest success on landscapes in which habitat had a high degree of spatial contagion ( $H = 0.5, 1.0$ ). Habitat clumping may thus mitigate the negative effects of habitat loss on dispersal success, a result also reported from other studies (e.g. Doak et al., 1992; Lamberson et al., 1994; Wennergren et al., 1995; Ruckelshaus et al., 1997). In our study, for example, even weak dispersers ( $m = 1$ ) could achieve high levels of success ( $> 70\%$ ) in landscapes with as little as 1% habitat when it was clumped ( $H = 1.0$ ). The effect of habitat clumping is particularly notable for dispersers that are constrained to move only within a particular habitat type (PD). Such dispersers were very sensitive to habitat fragmentation, and even strong dispersers ( $m = 20, 50$ )

Table 3

Summary of simulation results comparing the difference in dispersal success (probability of encountering a suitable habitat cell) between nearest-neighbor dispersal (NND) and dispersal as a percolation process (PD) on random and fractal ( $H = 0.0, 0.5$  and  $1.0$ ) landscapes. Is there a difference between NND and PD in each of these landscapes?

	Random	$H = 0.0$	$H = 0.5$	$H = 1.0$
<i>Dispersal strength</i>				
$m = 1$	No, although PD more variable	No	No	No
$m = 2$	No	No	No	No
$m = 5$	No, except for $h = 0.3$	No	No	No
$m = 10$	No, except for $h = 0.05$ and $h = 0.2-0.3$	No	No	No
$m = 20$	Yes, for $0.01 \leq h \leq 0.4$	No	No	No
$m = 50$	Yes, for $0.01 \leq h \leq 0.4$	Yes, for $0.05 \leq h \leq 0.2$	No	No
<i>Habitat abundance</i>				
$h = 0.001$	No	No	No	No
$h = 0.01$	Yes, if $m \geq 16$	No	No	No
$h = 0.05$	Yes, if $m > 6$	Yes, if $m > 25$	No	No
$h = 0.10$	Yes, if $m > 10$	Yes, if $m \geq 19$	No	No
$h = 0.20$	Yes, if $m > 9$	Yes, if $m > 17$	No	No
$h = 0.30$	Yes, if $m > 3$	No, PD success becomes more variable	No	No
$h = 0.40$	No	No	No	No
$h = 0.50$	No	No	No	No
$h = 0.60$	No	No	No	No
$h = 0.70$	No	No	No	No
$h = 0.80$	No	No	No	No
$h = 0.90$	No	No	No	No

Table 4

Summary of simulation results comparing the difference in dispersal success (probability of encountering a suitable habitat cell) between random dispersal and nearest-neighbor dispersal (NND) on random and fractal ( $H = 0.0, 0.5$  and  $1.0$ ) landscapes. Is there a difference between random dispersal and NND?

	Random	$H = 0.0$	$H = 0.5$	$H = 1.0$
<i>Dispersal strength</i>				
$m = 1$	No	Yes, if $h < 0.9$	Yes	Yes
$m = 2$	Yes, if $0.3 \leq h \leq 0.8$	Yes, if $h < 0.6$	Yes, if $h < 0.8$	Yes, if $h < 0.9$
$m = 5$	Yes, if $0.05 \leq h < 0.6$	Yes, except for $h = 0.3-0.4$ and $h > 0.6$	Yes, if $h < 0.4$	Yes, if $h < 0.5$
$m = 10$	Yes, if $0.05 \leq h < 0.4$	Yes, except for $h = 0.2$ and $h > 0.4$	Yes, if $h < 0.3$	Yes, if $h < 0.3$
$m = 20$	Yes, if $0.05 \leq h < 0.3$	Yes, except for $h = 0.1$ and $h \geq 0.3$	Yes, if $h < 0.2$	Yes, if $h < 0.2$
$m = 50$	Yes, if $0.05 \leq h < 0.2$	Yes, except for $h = 0.05$ and $h \geq 0.2$	No, except for $h \leq 0.05$	No, except for $h \leq 0.1$
<i>Habitat abundance</i>				
$h = 0.001$	No	Yes	Yes	Yes
$h = 0.01$	Yes, if $m \geq 17$	Yes	Yes	Yes
$h = 0.05$	Yes, if $m \geq 5$	Yes	Yes	Yes
$h = 0.10$	Yes, if $m \geq 4$	Yes, if $m \leq 15$	Yes	Yes
$h = 0.20$	Yes, if $m \geq 3$	Yes, except if $8 \leq m \leq 14$	Yes, if $m < 11$	Yes, if $m < 15$
$h = 0.30$	Yes, if $2 \leq m \leq 14$	Yes, except if $m = 5-9$ and $m \geq 13$	Yes, if $m < 7$	Yes, if $m < 9$
$h = 0.40$	Yes, if $2 \leq m \leq 10$	Yes, except if $m = 4-5$ and $m \geq 10$	Yes, if $m < 6$	Yes, if $m < 7$
$h = 0.50$	Yes, if $2 \leq m \leq 7$	No, except for $m = 1-2$ and $m = 5-6$	Yes, if $m < 4$	Yes, if $m < 5$
$h = 0.60$	No, except for $m = 2-4$	No, except for $m = 1$ and $4$	No, except if $m < 3$	No, except if $m < 4$
$h = 0.70$	No, except for $m = 2-4$	No, except for $m = 1$ and $m = 3-4$	No, except if $m < 3$	No, except if $m < 4$
$H = 0.80$	No, except for $m = 2-3$	No, except if $m \leq 3$	No, except for $m \leq 2$	No, except if $m \leq 2$
$h = 0.90$	No, except if $m = 2$	No, except for $m = 1$	No, except for $m = 1$	No, except for $m = 1$

experienced low success on random and fragmented fractal landscapes ( $H = 0.0$ ) that lay below the percolation threshold ( $h_{\text{crit}}$ ) where habitat connectivity had been disrupted ( $h_{\text{crit}} = 0.59$  for random landscapes,  $h_{\text{crit}} = 0.54$  for fractal  $H = 0.0$  landscapes; With and King, 1999b).

How sensitive is dispersal success to different dispersal algorithms, especially in terms of whether movement is modeled as a percolation process (restricted to move only within habitat) versus localized dispersal in which dispersers also move through non-habitat (NND)? PD and NND were very similar, especially in fractal landscapes because of the higher relative spatial contagion of habitat (measured by  $H$ ) and the high probability that adjacent cells would be habitat (Fig. 1). Divergence between these two localized dispersal processes occurred primarily in random landscapes, with 1–30% habitat, for which sufficient

dispersal strength had been attained (Table 5). Thus, the main difference is between local dispersal and random dispersal (the mean-field approximation). The difference between these algorithms is in step length relative to the spatial grain and extent of the landscape pattern. To what extent, then, can dispersal success be modeled as a random process that ignores localized interactions with spatial structure? Random dispersal is generally a good approximation in landscapes with  $> 40\%$  habitat unless dispersal strength is limited ( $m < 5$ ).

Many dispersal models are not based on the movement of individuals (representing the spread of populations instead), or are not spatially explicit, or if they are, do not consider heterogeneous or non-random spatial patterns (e.g. Wilder et al., 1995; Blackwell, 1997; Johst and Brandl, 1997; Torres-Sorando and Rodriguez, 1997; Mc-

Table 5  
Summary of the effects of landscape structure and choice of dispersal algorithm on dispersal success<sup>1</sup>

	0.001	0.01	0.05	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90
Is landscape structure important in predicting dispersal success?	Yes	Yes	Yes	Yes	Yes, unless $m > 20$ for NND	Yes, unless $m > 15$ for NND	Yes, unless $m > 10$	Yes, unless $m > 7$	No, unless $m < 5$	No, unless $m < 4$	No, unless $m < 3$	No, unless $m < 2$
Is dispersal success affected by choice of dispersal algorithm?	Yes, unless random landscape	Yes, unless random landscape and $m < 10$	Usually	Usually	Usually	No, except if $m < 8$ for PD with $m > 5$	No, except if $m < 5$	No, except if $m < 3$	No, except if $m < 3$	No, except if $m < 2$	No, except for $m = 1$	No, except for $m = 1$
Is landscape structure important in predicting dispersal success?	$m = 1$ Yes, unless $h \geq 0.9$	2 Yes, unless $h > 0.7$	5 Yes, unless $h > 0.4$	10 No, except when $h \leq 0.3$	20 No, except when $h < 0.3$	50 No, except if $h < 0.3$						
Is dispersal success affected by choice of dispersal algorithm?	Yes, unless $h \geq 0.9$	Yes, unless $h \geq 0.8$	No, unless $h < 0.4$	No, unless $h < 0.4$	No, unless $h < 0.4$	No, unless $h < 0.4$						

<sup>1</sup> To address the effect of landscape structure, comparisons are made between landscape types (random versus fractal) for a given type of dispersal algorithm and particularly against the mean-field approximation (random dispersal) which is unaffected by landscape structure. To assess the importance of the choice of dispersal algorithm on dispersal success, comparisons are made among dispersal algorithms for a particular landscape type and with the mean-field approximation of random dispersal.

Carthy, 1999; South, 1999b). Consequently, these models are not appropriate dispersal submodels for the individual-based SEPMS we are concerned with here. Other models describe the dispersal of plant seeds as algebraic or exponential decay functions of distance (e.g. Malanson and Armstrong, 1996; Latore et al., 1994), while our dispersal algorithms address animal movement and behavior. Moreover, few analyses of dispersal success systematically vary both spatial pattern and dispersal behavior as we have done here. Direct comparisons of our results with earlier results are thus difficult. Nevertheless, a variety of modeling studies have shown dispersal success to be influenced by landscape pattern or animal behavior. For example, Byers (1996) found that relatively few simulated bark beetles with very low flight speeds found suitable host trees when the trees were widely distributed, a situation comparable to our relatively weak dispersers ( $m < 5$ ) on random landscapes of rare habitat ( $h < 0.30$ ). Gustafson and Gardner (1996) found that most of the variability in the dispersal success of a self-avoiding random walker (similar to our NND, although our NND is not self-avoiding) was accounted for by differences in the size and isolation of patches. They also found that dispersal success was very similar on random and homogeneous landscapes, but significantly reduced on 'curdled' maps exhibiting patch contagion or aggregation (Gustafson and Gardner, 1996). In a simulation of forest beetles, Tischendorf et al. (1998) found that the proportion of individuals arriving at a sink patch varied with the length and width of modeled hedgerows. Other modeling studies, while not explicitly quantifying dispersal success, have shown that migration rates, species diversity, resource consumption, patterns of species distribution consumption and the survival of individuals, populations and metapopulations are all influenced by spatial heterogeneity (Dyer, 1995; Anderson, 1996; Baker, 1996; Malanson and Armstrong, 1996; Swart and Lawes, 1996; With and Crist, 1996; Blaine and DeAngelis, 1997; Fahrig, 1998; Carter and Finn, 1999; With and King, 1999b). That influence arises, at least in part, from the impacts of spatial pattern and movement behavior on dispersal success. These

results, combined with arguments for the critical importance of movement rules in individual-based SEPMS (Railsback et al., 1999), argue the need for a fundamental understanding of when and how spatial structure interacts with dispersal behavior to affect dispersal success.

Although the relationship between landscape structure and dispersal success may not be a simple matter to resolve (Doak et al., 1992), our simulation results indicate that both dispersal behavior and the explicit arrangement of habitat (landscape structure) are predicted to affect dispersal success in landscapes with  $< 30$ – $40\%$  habitat. Given that the amount of suitable habitat available to species of conservation concern may generally fall within this range (e.g. Ruckelshaus et al., 1997), details of how organisms interact with spatial pattern may be essential to the selection or development of dispersal modules in SEPMS implemented on landscapes with  $< 40\%$  habitat (Fig. 9). In other words, representations of dispersal based on mean-field approximations will not suffice under these circumstances and may provide biased estimates of dispersal success. Furthermore, errors in estimating dispersal parameters may be most severe in landscapes with a limited amount of habitat (Wennergren et al., 1995; Ruckelshaus et al., 1997). For example, Wennergren et al. (1995) found that 'modest' errors in estimating attributes of dispersal behavior propagated into huge errors in predicting dispersal success for a variety of habitat configurations in landscapes with  $2$ – $25\%$  habitat. If the per-step mortality rate during dispersal is overestimated by  $16$ – $24\%$ , the prediction error may be as high as  $90\%$  (Ruckelshaus et al., 1997). Prediction errors resulting from errors in estimating dispersal distances tended to be less than those associated with dispersal mortality, however, and were generally  $< 10\%$  in landscapes with  $> 16\%$  habitat (Ruckelshaus et al., 1997). Thus, it is landscapes in which habitat has been drastically reduced (e.g. to  $10\%$ ) in which all these sources of error have the greatest potential to be compounded and where details on dispersal behavior may be most critical for predicting dispersal success.

As has been pointed out recently by South (1999a), however, such concerns over accurate predictions of dispersal success may be misplaced. These concerns emanate from two assumptions: (1) errors in predicting dispersal success propagate into similar errors in estimates of population viability within SEPMS, and (2) dispersal success is important for predicting population viability in the first place. Although dispersal figures prominently in SEPMS, dispersal may not be the key to population persistence, contrary to conventional wisdom (e.g. Opdam, 1990). Studies are emerging that demonstrate demographic factors may, in some circumstances, be more important than dispersal for population persistence in fragmented landscapes (Pulliam et al., 1992; Liu et al., 1995; With and King, 1999a; South, 1999a). South

(1999a) found, for example, that if the intrinsic population growth rate ( $\lambda$ ) was sufficiently high (e.g.  $\lambda > 1.12$ ), populations persisted in the majority of cases irrespective of dispersal success. If dispersal is generally less important than demographic factors for population persistence, then SEPMS may not require detailed dispersal modules. Fairly simple movement rules, such as those featured in our study, or even patch incidence functions (With and King, 2001) may suffice to capture the essential properties of how organisms redistribute in space. The choice of movement rule should not be made, however, without consideration of the influence of spatial pattern on dispersal success. As we have shown here, modeling dispersal as a random process (the mean field approximation) is not likely to be sufficient when habitat is rare and fragmented (i.e. for species and landscapes of conservation concern). Localized dispersal algorithms, such as NND and PD with their coarse distinctions in movement behavior, may adequately capture the interaction between spatial structure and dispersal success such that more detailed movement rules, with their concomitant data requirements, may not be needed in many applications.

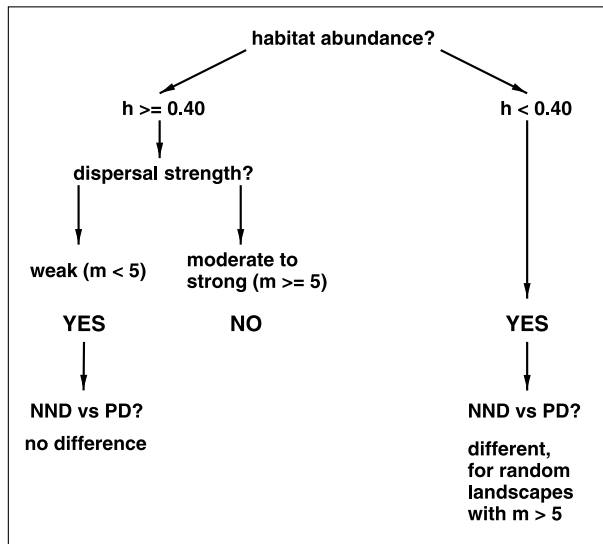


Fig. 9. An example of a screening process to determine when choice of a dispersal algorithm other than the mean-field approximation of random dispersal is appropriate. YES means selection of a localized dispersal algorithm is indicated (NND or PD in our examples) because dispersal success is affected by choice of dispersal and interactions with landscape pattern (Table 5); NO means the mean field approximation (random dispersal) is sufficient. On random landscapes with  $< 40\%$  habitat, the difference in dispersal success of NND or PD for moderate to strong dispersers ( $m > 5$ ) suggests that attention should be given to selecting between these alternative behaviors (right of figure). When habitat is abundant, these differences are unimportant in determining dispersal success (left of figure).

## Acknowledgements

This research was supported by a grant awarded by the National Science Foundation to KAW (DEB-9532079). AWK received support from the Strategic Environmental Research and Development Program through military interagency purchase requisition no. W74RDV53549127 and the Office of Health and Environmental Research of the US Department of Energy under contract DE-AC05-96OR22464 with Lockheed Martin Energy Research Corporation.

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