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Dispersal of annual plants in hierarchically structured landscapes

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The scale at which plants utilize spatially distributed resources may be determined by their ability to locate sites that can sustain population growth. We developed a spatially-explicit model of the dispersal of annual plants in landscapes which were hierarchically structured, i.e., the spatial pattern of suitable sites was nested and scale-dependent. Results show that colonizing ability and extinction probability are most sensitive to the mean dispersal distance of the species. Dispersal out of the parental site, but within the immediate neighborhood, was the most efficient means for popolation expansion. When landscape patterns change with scale then dispersal distances determine the spatial scales of habitat utilization. As a complicating factor, the type of statistical distribution of dispersal distances also influences the colonizing ability. However, the importance of dispersal distance mean and distribution decreased as the number and connectance of suitable sites increased. The results suggest that landscape models which consider the interaction between scale dependent changes in landscape pattern and species dispersal and establishment characteristics are relevant to many issues in community ecology, invasion biology, and conservation biology.

1. Introduction

One of the central problems in landscape ecology is determining the relationship between spatial pattern and ecological process (Risser ***et al.*** 1984, Forman and Godron 1986, Wiens ***et al.*** 1986). **A** combination of theoretical and empirical studies has shown that the spatial pattern of resources affects the persistence of organisms (O'Neill ***et al.*** 1988) and the potential for dispersal (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988b, Gardner ***et al.*** 1991, 1993). Because species respond to the environment at specific spatial and temporal scales, the same landscape may not be perceived in the same way by different organisms (Wiens 1985, Wiens ***et al.*** 1986, Addicott ***et al.*** 1987, Swihart ***et al.*** 1988, Milne ***et al.*** 1989, Wiens and Milne 1989).

The influence of landscape pattern on population processes needs to be examined in relation to the dispersal characteristics of the organisms. Mobile propagules provide sessile organisms with the ability to persist through escape from the immediate vicinity of their parents (Harper 1977, Motro 1982, Levin ***et al.*** 1984, Ellner 1985a, 1985b), and from locally unsuitable conditions (Platt 1975, 1976, Comins ***et al.*** 1980). Dispersal, however, involves many risks and may result in the loss of many propagules. If optimal rates of dispersal exist then the costs associated with the loss of propagules will be offset by the few that colonize more favorable

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sites (Gadgil **1971).** Theoretical results have shown the existence of Evolutionary Stable Strategies **(ESS,** Maynard-Smith **1976)** for the rate of dispersal (i.e., the fraction of propagules leaving the parental site) (Hamilton and May **1977,** Comins ***et al.*** **1980,** Olivieri and Gouyon **1985,** but see Cohen and Levin **1991).** Although dispersal is a spatial process, the majority of models have focussed on the rate of dispersal, rather than explicitly addressing the spatial dimensions of the problem (Fahrig and Paloheimo **1988a).** Those models which are 'spatially explicit' have represented the landscape heterogeneity in various ways (see Fahrig **1988** for a review). For instance, patch models such as metapopulation models (e.g., Levin **1974,** Olivieri and Gouyon **1985,** Horvitz and Schemske **1986),** and dispersal corridors models (Roff **1974a, 1974b,** Fahrig ***et al.*** **1983,** Fahrig and Merriam **1985,** Lefkovitch and Fahrig **1985),** use only a qualitative description of the spatial arrangement of patches while neighborhood and grid models (e.g. Pacala and Silander **1985,** Sawyer and Haynes **1985,** Crawley and May **1987,** Gardner ***et al.*** **1991)** explicitly account for the spatial positions of the populations or individuals. Fahrig **(1988)** proposed an intermediate method describing the arrangement of habitat patches by the pairwise distances between them.

In order to adequately address the question of the interaction between landscape structure and species dispersal characteristics, dispersal strategies need to be explicitly described through the distribution of the propagules around the parent. Although widely recognized as a primary factor relative to the dynamics of plant communities (e.g. Grubb **1977),** the effect of the seed shadow on colonization has been little studied (Kareiva and Andersen **1988).** Gardner ***et al.*** **(1991)** addressed this issue using a model of the dispersal of organisms across random maps used as neutral landscape models (see e.g. Gardner ***et al.*** **1987,** Turner ***et al.*** **1989).** Simulations of the spread of plant species characterized by the distribution of their seeds around the parental sites show that large differences in space utilization can result from small differences in species dispersal distance. The simulations also show that differences in the shape of the seed distribution function for a given mean dispersal distance will produce different patterns of population increase at landscape scales.

Simple random maps have been used as neutral models of landscape pattern (Gardner ***et al.*** **1987,** Gardner and O'Neill **1991),** but actual landscape maps have been found to be hierarchically structured (i.e., scale-dependent variability in the pattern of habitat suitability) (O'Neill, ***et al.*** **1991).** Therefore, generation of maps by random hierarchical procedures will provide an improved neutral model of landscape pattern (O'Neill ***et al.*** **1992,** Lavorel ***et al.*** **1993).** This paper uses a spatial model of the dispersal of annual plants in hierarchical random maps to extend the investigation of the interaction between landscape pattern and dispersal characteristics. We examine the following questions: **(1)** What is the role of species dispersal characteristics in their ability to colonize patchy landscapes? **(2)** How will the patterns of species spread be affected by landscape scale-dependent patterns of site suitability?

2. Methods

The model is a discrete-cell population model (Skellam **1951)** simulating the population dynamics of annual plants in landscapes with a hierarchical structure. Each landscape map consists in a grid of individual sites, over which plants of a monospecific annual population spread through seed dispersal. The probability of population extinction and the fraction habitat utilization once the population reaches a stable size are examined.

2.1 The landscapes

Randomly generated hierarchically structured maps were used to simulate nested scale-dependent changes in habitat heterogeneity. Suitability for plant establishment is assumed to be a discrete feature, with sites on the map labelled as **1** (a suitable or 'safe' site, ***sensu*** Harper **1977)** or 0, an unsuitable site. Suitability doesn't reflect site productivity, but describes whether plant establishment is possible. For example, locations covered by a rock would be labelled 0, while open soil would be labelled **1.** Site suitability is assumed to be a time-independent feature, so that the habitat map were fixed for the course of a simulation. Recursive algorithms derived from fractal geometry (Mandelbrot **1983,** Chayes et al. **1988,** see also O'Neill et *al.* **1992,** Lavorel et *al.* **1993)** were used to generate three level hierarchical maps by specifying: **(1)** the number of units, m_i ($i = 1,..3$), within each level, i, and (2) the fraction of suitable sites, p_i ($i = 1,..3$), for each level, i. In the following, the three nested scales will be referred to as macro-, meso-, and micro-scales respectively, and the suitable units at these levels will as macro-, meso-, and micro-units. Habitat maps were recursively generated by creating a matrix of $(m_1 \times m_1)$ macro-units and randomly setting the suitability of each site with a probability of p_1. Each macro-unit that was labelled as suitable (i.e., given the value of 1), was further subdivided into an $(m_2 \times m_2)$ matrix and suitable meso-units were selected randomly with probability of p_2. The process was repeated a third time by subdividing the suitable meso-units into an $(m_3 \times m_3)$ matrix and randomly labelling sites at this finest resolution with a probability of p_3. The total number of sites (or micro-units) in a three level hierarchical map will be $(m_1 \times m_2 \times m_3)^2$, the total fraction of suitable sites will be exactly $P = (p_1 \times p_2 \times p_3)$, and the total number of suitable habitat sites, *SS*, will be $(m_1 \times m_2 \times m_3)^2(p_1 \times p_2 \times p_3)$.

An interesting and desirable feature of hierarchical maps is that, unlike random maps for which the number, size, and shapes of clusters (i.e. groups of sites with at least one horizontal or vertical – but not diagonal – edge in common) are determined by **SS,** it is possible to generate in a controlled manner different spatial arrangements at fixed levels of *SS* (Table **1).** Hierarchical maps possess a scale-dependent structure, and the sizes (m_i) and fractions of site suitability (p_i) at each scale need to be known in order to predict spatial features (Lavorel et *al.* **1993).** In particular, maps with identical values for *SS* but different sets of parameters (m_i, p_i, $i = 1,..3$) display distinctly different patterns (Fig. 1, and see Lavorel et *al.* **1993).** While for an infinite random map, spatial properties shift rapidly around the value $P = 0.5928$ (Stauffer 1985), called the critical percolation threshold (p_c), for hierarchical maps, the spatial structure is sequentially determined by descending scales with critical thresholds observed at each hierarchical level (Lavorel et *al.* **1993).** Moreover, the small size of the submaps represented by each spatial unit make general percolation theory, which deals with infinite maps, irrelevant.

We used the above procedure to generate grids of 100 rows and columns with safe sites distributed at **3** different scales. The total number of sites on each map is **10,000** and the total number of suitable sites, *SS*, will be equal to $p_1 \times p_2 \times p_3 \times 10{,}000$. Each map was constructed of sixteen ($m_1 = 4$) statistically identical macro-units, with each macro-unit being subdivided into twenty-five ($m_2 = 5$) meso-units. The meso-units were, in turn, divided into twenty-five ($m_3 = 5$) micro-units. These grids may be thought of as **10** × 10 m plots with 10 × 10 cm sites representing the basal area that a herbaceous plant would cover. Macro-units of **2.5** × 2.5 m represent the area within which a herbaceous plant might be expected to deposit most of its seeds and meso-units of 50 × 50 cm were found to have homogeneous vegetation in Mediterranean old-fields (Lavorel et *al.* **1991).**

The suitability at macro-scale was held at $p_1 = 1.0$ for all simulations, i.e. each macro-unit will always contain some suitable sites, reflecting the potential of the habitats to carry a 100% vegetation cover. This way, habitat maps had exactly $p_2 \times p_3 \times 10{,}000$ suitable meso-units. A series of maps generated with all combinations of p_2 and p_3 drawn from **0.32, 0.6,** and 0.88 (Fig. **1)** were used for the dispersal simulations.

2.2 Population dynamics

Assuming that each pixel can support a single adult plant, individual-based algorithms were used to simulate demographical processes at each suitable map site (i.e., a matrix location set to 1) with a time step of one generation. Density-dependence of recruitment was included by allowing a single fertile adult each year at each suitable site containing one or more propagules. There is no year to year seed

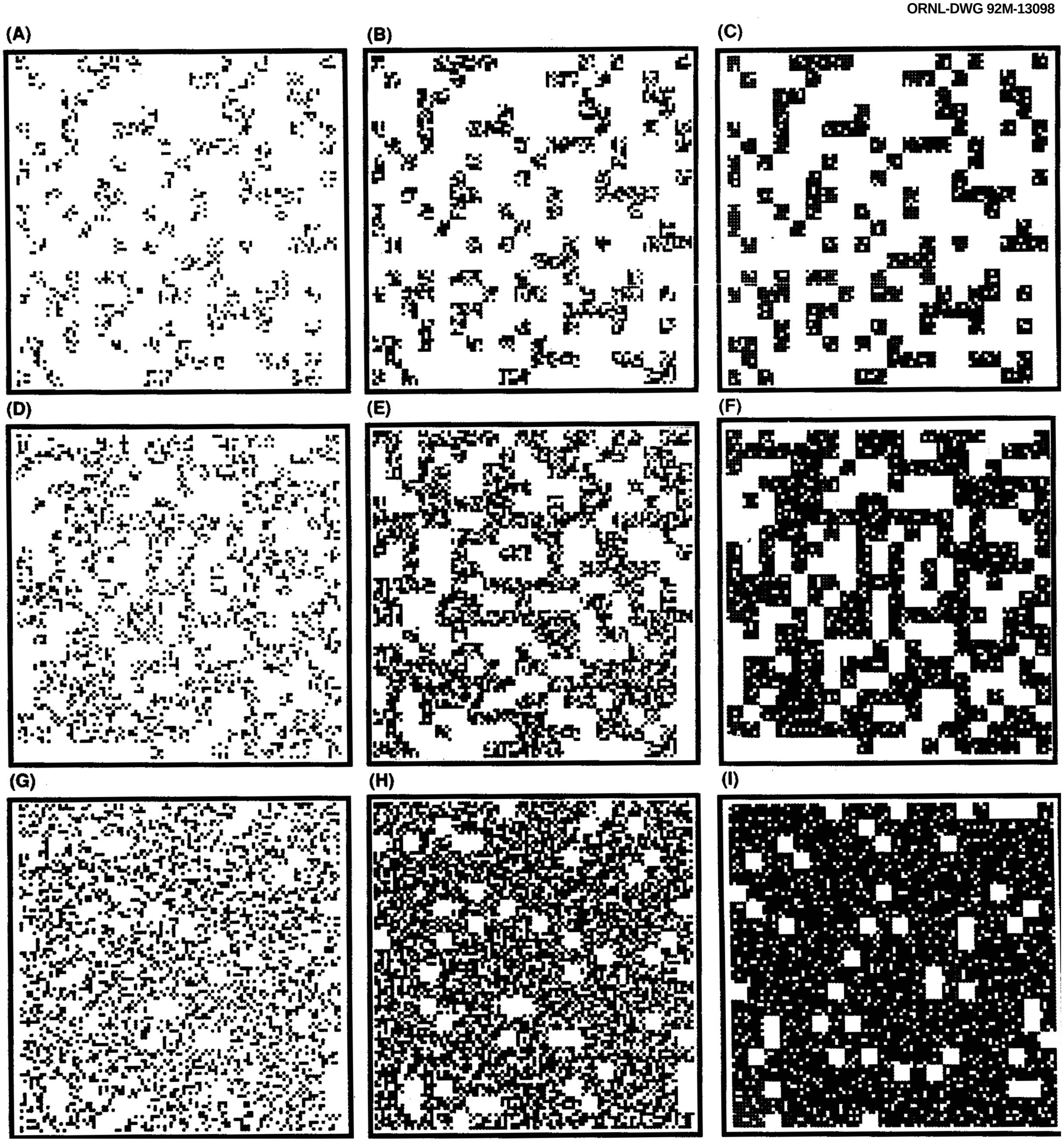

Fig. 1. Set of 9 maps with 3 hierarchical levels used to generated different landscape patterns. The dimensions of the hierarchical levels (m_1, m_2, m_3) were 4, 5, and 5, respectively. The maps differ in pattern due to differences in p_2 and p_3. The parameters (p_2, p_3) for each maptypeare: (a) 0.32, 0.32; (b) 0.32, 0.6; (c) 0.32, 0.88; (d) 0.6, 0.32; (e) 0.6, 0.6; (f) 0.6, 0.88; (g) 0.88, 0.32; (h) 0.88, 0.6; (i) 0.88, 0.88.

carry-over, and the seed content of all sites is reset to 0 after establishment. Species concerned could for example be a number of annual grasses (e.g. ***Avenasterilis, Bromus sp.pl. ,Lolium multiflorum)*** and forbs (in particular ***Asteraceae*** such as ***Crepis sp.pl., Sonchus sp.pl.*)** known as agricultural weeds. Because the species are assumed to be annuals, all individuals reproduce and then die at the end of each time step. The model allows fertility (the number of viable propagules per individual plant) to be

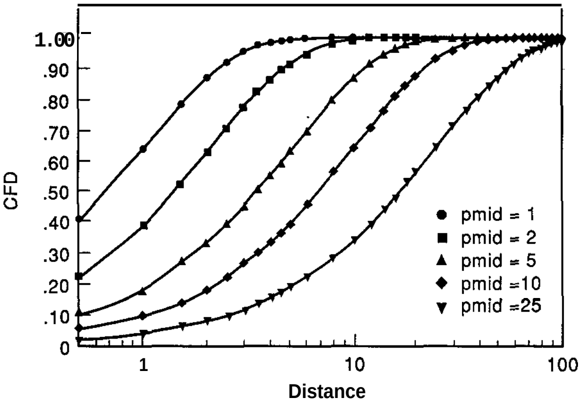

Fig. **2. Cumulative frequency distributions for exponential distributions with means (*pmid*) of** 1, 2, 5, **10 and 25.**

specified as a species characteristic. For these simulations, net fecundity of each plant was fixed at ten propagules per year. Net fecundity is the number of seeds per site which are successfully dispersed and, in the absence of competition, would produce a viable adult plant. Simulation of net fecundity, rather than total seed production, results in two or three orders of magnitude in computer efficiency.

Propagule dispersal is simulated as a stochastic isotropic process. Each propagule is independently dispersed according to one of the following species-specific strategies:

1. ***Bond dispersal:*** propagules are independently distributed within the parental site and to the four nearest neighbors (see Stauffer **1985** for a more complete discussion of bond and site percolation). Bond dispersal can in particular be used to represent vegetative spread, with 'propagules' being in that case buds on vegetative organs.

2. ***Continuous distributions:*** the location of each propagule is determined by selecting a random distance and a random angle between 0" and **360".** Different strategies of propagule dispersal were simulated by specifying dispersal distances (*pmid* = 1, **2,** 5, **10** or **25** sites) from the exponential, uniform, or normal distributions.

The effects of various dispersal agents on the shape and size of seed shadows have been investigated in the field and experimentally (e.g., Salisbury **1961,** Sheldon and Burrows **1973,** Rabinowitz **1978,** Rabinowitz and Rapp **1981).** Decreasing exponential and normal distributions centered on the parent plant are the most commonly used probability distributions to describe seed shadows (Kareiva and Andersen **1988).** The decreasing exponential distribution fits in particular wind dispersal (Sheldon and Burrows **1973,** Verkaar ***et al.*** **1983,** McEvoy and Cox **1987,** Klinkhamer ***et al.*** **1988).** Dispersal by rain wash (Van der Pijl **1972)** or echtozoochory (Bullock and Primack **1977)** can generate uniform seed deposits over a short distance. Animal dispersers, in particular those having nests such as ants (Culver and Beattie **1980)** or small mammals (Jensen 1985), explosive dispersal (Stamp and Lucas **1983)** and barochory (Rabinowitz and Rapp **1981)** tend to produce normal distributions. Other types of distributions such as erratic histograms could be valuable for describing the effects of endozoochory (by birds – Debussche and Isenmann **1994** – or earthworms – McRill and Sagar **1973)** or of microtopography (Tomback **1982).**

The boundaries of the map are assumed to be absorbing, i.e., the seeds landing beyond the limits of the grid are lost. Although this assumption results in a slight decrease in the population size, absorbing boundaries do not have severe effects when the map is large (Pacala and Silander **1985,** Crawley and May **1987).** After all propagules of all adults have been dispersed, safe sites will fall into two categories: those which received at least one seed and will support a plant at the next generation, and those that will remain empty.

2.3 Simulations

The simulations were initiated with a single plant at the center of the map and concluded after **100** generations. Most population sizes stabilized by **30** generations and all of them were stable after 50 generations (with a coefficient smaller than *5%* between genertions).

Mean distances of 1, **2,** 5, **10,** and **25** sites were chosen to investigate the relation between the scales of the map, as determined by m_i at each level ***i*,** and the mean dispersal distance. **A** comparison of the five cumulative frequency distributions of dispersal distances (Fig. **2)** generated from the exponential

Table 1. Summary of landscape structure for the 9 maps used with 3 hierarchical levels[a].

Landscape parameters		Spatial descriptors						
p_2	p_3	*SS*	N_{cl}	M_{cl}	*LC*	*Edg*	*me*	*%P*
0.32	0.32	1024	517	1.9	11	3052	2.98	0
0.32	0.6	1920	271	7.1	64	3847	2.00	0
0.32	0.88	2816	60	46.9	20	2812	1.00	0
0.6	0.32	1920	911	2.1	12	5602	2.92	0
0.6	0.6	3600	337	10.7	9	6702	1.86	0
0.6	0.88	5280	20	262	3428	4265	0.81	20
0.88	0.32	2816	259	224	16	8045	2.86	0
0.88	0.6	5280	296	17.8	1227	9118	1.73	80
0.88	0.88	7744	2.7	2868	7742	4772	0.62	100

[a] Each map is composed of 100 rows and columns (10,000 sites), with suitable sites distributed at 3 scales (*L* = 3). p_2 and p_3 are the probability of suitability for the meso and micro scale, respectively. See text for additional details on the generation of hierarchical maps. The results are means for **10** repetitions. *SS* is the number of suitable sites for the entire map, N_{cl} is the total number of clusters, M_{cl} is the mean cluster size (SS/N_{cl}), *LC* is the mean largest cluster size, *Edg* is the total number of edges, *me* is the mean number of edges per suitable site, and %P is percentage of maps that had a single cluster which connected opposite edges of the map.

distribution with pmid ranging from 1 to 25 shows the proportion of propagules that will remain within a unit radius of the parental site. When pmid = 1, over 95% of the seeds will remain on or immediately adjacent to the parental pixel; when pmid = 2, most seeds (over 95% for all distributions studied here) will be dispersed into the parental meso-unit when $m_3 = 5$, since an average distance of 2.5 is needed to move beyond its boundaries; when pmid ranges between 5 – 10, most propagules will fall beyond the parental meso-unit, but remain within the same macro-unit (with a probability greater than 0.95); and when pmid = 25, most propagules reach a macro-unit different than the parental unit.

Simulations using different cumulative frequency distributions (exponential, uniform, or normal distributions) were used to examine a range of seed shadow densities. In the case of normal distributions, two sets of simulations were made using (1) a standard deviation equal to that of an exponential distribution with the same mean, pmid, (i.e., σ = pmid) and (2) a standard deviation equal to that of a uniform distribution having the same mean (i.e., σ = pmid / $2\sqrt{3}$). Finally, model simulations using bond dispersal were also performed.

Since the pattern of the randomly generated maps is fairly stable once the m_i and p_i parameters are known (Lavorel *et al.* 1993), 10 simulations were run for each set of dispersal and landscape parameters. At each time step, the number of populated sites was measured. At the end of each simulation the fraction of suitable sites utilized at the stable population size (*%SS*) was calculated. The sensitivity of population extinction resulting from a combination of landscape pattern and dispersal strategy was assessed from the proportion of extinctions observed over the set of 10 simulations (populations go extinct when all propagules of a single generation land on unsuitable germination sites).

3. Results

Table 1 shows how the features of the habitat maps depend on the values of p, and p_3. The hierarchical maps show distinct patterns as a function of p_2 and p_3 with combinations of p_2 and p_3 resulting in the number of safe sites (*SS*) varying from 1024 (p_2 = p_3 = 0.32) to 7744 (p_2 = p_3 = 0.88). Because *SS* is determined by the product of p_2 and p_3, the order of these two terms does not affect the total number of safe sites. However, different combinations of p_2 and p, do affect the spatial arrangement of safe sites (Fig. 1), with large differences in the number of clusters (*Ncl*) and the size of the largest cluster (*LC*) for different combinations of p_2 and p_3. The effect of reversing the values of p_2 and p_3 on landscape pattern can be seen by contrasting Fig. 1c with 1g, Fig. 1b with 1d and Fig. 1f with 1h: the map with a lower p_2 has an aggregated pattern, while the map with a higher p_2 has a dispersed pattern. The percent percolation (*%Perc*; the proportion of map replicates for which there exists one cluster joining opposite edges of the map) for 10 iterations of each map type (Table 1) is directly related to the product of p_2 and p_3, with percolation for all iterations occurring only when $p_2 \times p_3$ is greater than **0.6.**

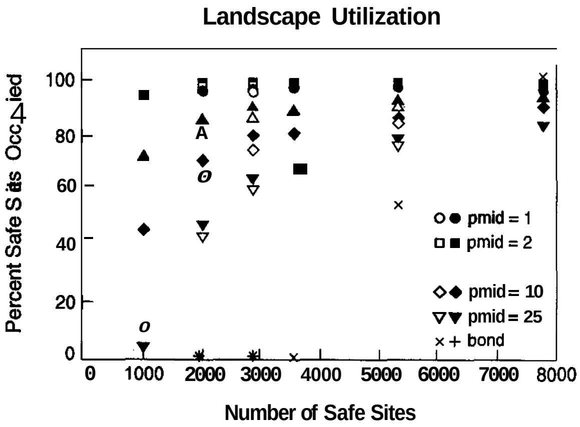

Fig. 3. Mean percent safe site utilization (*%SS*) as a function of the number of safe sites available (*SS*) for bond dispersal and exponential seed distributions with different mean dispersal distances ***(pmid)***. For suitability levels where two combinations of values for p_2 and p_3 were used, open (resp. filled) markers represent dispersed (resp. aggregated) map types.

Table 2. Number of extinctions over **10** repetitions ***(Next)*** as a function of map structure for bond and exponential dispersal with different dispersal distances. p_2 and p_3 are the probability of suitability at the meso- and micro-scale, respectively, and *SS* is the total number of suitable sites. ***pmid*** is the mean dispersal distance.

Partial probabilities			Number of extinctions					
			Exponential dispersal					Bond dispersal
p_2	p_3	*SS*	1	2	5	10	25	
0.32	**0.32**	**1024**	**0**	5	1	5	9	0
0.32	0.6	**1920**	1	3	2	1	1	0
0.6	**0.32**	**1920**	**0**	1	0	1	5	0
0.32	**0.88**	**2816**	**0**	1	1	0	0	0
0.88	**0.32**	**2816**	**0**	1	0	0	0	0
0.6	**0.6**	**3600**	*0*	*0*	*0*	*0*	*0*	0
0.6	**0.88**	**5280**	**0**	2	0	0	0	0
0.88	**0.6**	**5280**	**0**	0	0	0	0	0
0.88	**0.88**	**7744**	**0**	0	0	0	0	0

Table 3. Analysis of variance of the percent safe site utilization (*%SS*) for **9** hierarchically generated landscapes with dispersal generated from the exponential distribution.

Factor	F statistics	df	Significance
pmid	17.17	4	**0.0001**
p_2	13.17	2	**0.0005**
pmid.p_2	1.69	8	n.s.
p_3	17.47	2	**0.0001**
pmid.p_3	1.64	8	n.s.
p_2–p_3	3.6	4	**0.05**

The error sums of squares for the ANOVA was **1826.6** with **16** df. The model explained **92** percent of the variability of *%SS*.

The results of a series of simulations performed on each of these hierarchical maps is summarized in Fig. **3** and Tables **2** and **4.** For a given dispersal function, the percent of safe sites utilized (*%SS*) depends directly on the total number of available safe sites (*SS*, Fig. **3**). Bond dispersal resulted in a low proportion of sites (*%SS*) being utilized when sites are not well connected (p_2, $p_3 < 0.6$), but was more successful when connectance was high (p_2, p_3 = **0.88).** Because bond dispersal does not allow organisms to 'jump' across gaps, maps must be well connected for species with this dispersal strategy to be successful. Under these circumstances population growth will be constrained by the size of the cluster of safe sites around the initial plant. Species with longer-range dispersal are able to expand their range by dispersing across gaps and archieve a higher fraction of habitat utilization. The exponential distribution with a mean dispersal distance of **2** allowed the best performance (Fig. **3)** for all landscapes with *SS* greater than **1024.** However, the broader range of dispersal gained by the exponential distribution results in a correspondingly higher risk of extinction (Table **2).** The proportion of extinctions for bond dispersal is zero for all 9 landscapes, while the exponential distribution results in a high risk of extinction in landscapes with a low suitability at the micro-scale ($p_3 \le p_c$) (Table **2),** with risk of extinction increasing as *pmid* increases. Short distance exponential dispersal (pmid = 2) allows a profitable trade-off between this increase of risk and the benefit of being able to explore habitat patches that are disconnected from the parental micro-unit.

An analysis of variance was used to investigate the effects of mean dispersal distance (pmid) and landscape heterogeneity (p_2 and p_3) on the proportion of safe sites colonized (*%SS*) (Table **3).** The results show that *%SS* was primarily determined by the mean dispersal distances of the species, pmid,

Table 4. Mean percent safe site utilization depending on the mean dispersal distance and the frequency distribution[a].

Partial probabilities		pmid	Distribution function			
p_2	p_3		Exp	*Ne*	*unif*	*Nu*
0.32	0.32	1	11.1	0.2	8.4	3.2
		2	94.4	1.1	54.2	25.6
		5	72.9	1.5	55.9	15.2
		10	45.5	1.8	28.8	17.4
		25	4.6	1.0	2.7	1.9
0.32	0.6	1	91.5	1.3	8.3	6.3
		2	99.3	5.7	7.0	6.5
		5	86.4	4.8	74.5	56.8
		10	72.0	35.2	60.3	52.8
		25	48.0	25.5	39.2	27.8
0.32	0.88	1	98.0	8.7	25.1	13.9
		2	99.0	9.4	13.7	9.8
		5	90.9	8.0	81.7	56.6
		10	80.8	54.0	72.5	52.1
		25	64.9	48.1	57.6	49.3
0.6	0.32	1	96.1	0.3	29.6	0.53
		2	98.4	9.0	66.2	24.7
		5	81.3	39.6	67.9	40.4
		10	65.8	38.4	54.6	38.2
		25	43.6	28.7	35.1	27.6
0.6	0.6	1	98.2	37.8	91.9	53.4
		2	99.7	46.5	94.2	71.7
		5	90.4	65.7	84.4	66.0
		10	81.7	64.6	77.2	64.8
		25	68.7	58.3	65.7	58.1
0.6	0.88	1	98.7	59.1	91.7	88.6
		2	99.9	71.5	95.4	94.9
		5	93.5	75.5	88.7	95.3
		10	87.6	75.6	83.8	89.4
		25	79.0	70.4	75.6	83.6
0.88	0.32	1	97.0	9.2	79.0	1.49
		2	99.1	62.1	94.9	64.6
		5	97.2	70.2	77.4	58.3
		10	75.9	47.8	67.5	56.5
		25	60.6	38.8	53.8	47.3
0.88	0.6	1	98.4	61.1	95.5	68.5
		2	99.9	77.0	97.2	77.5
		5	92.3	77.3	87.8	77.2
		10	86.6	76.4	82.8	76.0
		25	78.1	71.1	75.1	70.6
0.88	0.88	1	99.9	79.6	96.9	93.3
		2	99.0	84.8	98.5	98.7
		5	95.0	84.5	92.3	98.2
		10	91.0	83.8	86.4	97.3
		25	84.9	79.9	82.7	93.3

[a] p_2 and p_3 are the probability suitability at the meso and micro scale, respectively. See text for additional details on the generation of hierarchical maps. The results are means of 10 interactions. pmid is the mean dispersal distance. Dispersal distances were generated from the exponential (Exp), normal with variance equal to exponential *(Ne)*, uniform *(unif)* and normal with variance equal to uniform *(Nu)*.

with the greatest value of *%SS* occurring when the mean dispersal distance is **2** and poorest when it is **25.** The spatial arrangement of sites (p_2, p_3, and the interaction term $p_2.p_3$) is also significant, indicating that for a given level of *SS* the pattern of plant colonization depended on the hierarchical patterns of the map (Fig. **3).** For maps with reversed values for p_2 and p_3, the habitat utilization by a given species was always greater for the more aggregated map (i.e., p_3 larger and p_2 smaller).

The shape of the statistical distribution of the seeds around the mother plant also influenced the efficiency in habitat colonization. For all mean dispersal distances, the exponential distribution allowed better performances than the uniform or any of the normal distributions (Table 4). **A** normal distribution was less efficient than an exponential or a uniform distribution having the same mean and variance. Normal distributions had opposite effects to exponential distributions, favoring long distance dispersal over short distance dispersal for poorly suitable landscapes **($SS \leq$ 3600).** Performances of different mean dispersal distances were comparable in more suitable habitats. The effect of uniform distributions was more complex, with unsuitable landscapes **($SS \leq$ 2816)** favoring long distance dispersal, while more suitable landscapes **($SS \geq$ 3600)** were better colonized by short range dispersers than long range dispersers. Differences between distribution functions tended to decline as the level of landscape suitability increases (Table 4).

4. Discussion

The development of a spatially explicit simulation model of the dynamics of annual plant populations in landscapes with nested scale-dependent structure allowed us to examine the population consequences of species dispersal in patterned landscapes. Natural landscapes tend to have continuous patterns rather than clear-cut habitat patches (McIntyre and Barrett **1992),** thus grid models appear quite relevant to the study of ecological processes in relation to landscape pattern. Gardner ***et al.*** **(1993)** showed that hierarchically structured landscape maps (O'Neill ***et al.*** **1992,** Lavorel ***et al.***

1993) provide a more realistic approximation to real landscapes than purely random maps.

The necessity of a trade-off between habitat utilization (Fig. 3) and the probability of extinction (Table 2) leads to suggest that a mean dispersal distance of 1 site would result in an optimal number of propagules leaving the locally crowded parental site, while still insuring that most of the remaining propagules will fall within the local neighborhood where other satisfactory sites are likely to be encountered. Because the hierarchically structured maps created a distribution of safe sites that were clumped at the meso-scale (Lavorel *et al.* 1993), a higher proportion of safe sites were usually near the parental plant. Hence, the probability of a site being suitable was greater next to an occupied site than for a randomly generated map. The aggregation of safe sites has been commonly observed in the field (e.g., Fowler 1988). A number of models (e.g., Levin 1974, Bullock 1976, Horvitz and Schemske 1986, Cohen and Levin 1991) have predicted selection for relatively short range of dispersal distances and evolutionary stable values have been shown to be even smaller than what may be otherwise regarded as optimum (Hamilton and May 1977, Comins *et al.* 1980, Olivieri and Gouyon 1985). Experimental measures of seed shadows indicate that mean dispersal distances tend indeed to be small (e.g., Sheldon and Burrows 1973, Levin and Kerster 1974, Rabinowitz and Rapp 1981, Verkaar *et al.* 1983). The arbitrary choice of a fixed net fecundity of 10 seeds per plant is likely to have bearing on the numerical values obtained for optimal dispersal distance because the level of fecundity determines both self-crowding around the parent plants and the risk of not reaching suitable sites for dispersed seeds. Higher fecundities would be expected to increase the optimal dispersal distance and conversely.

Our simulations did not include a further complicating factor: the existence of a seed bank. Seed banks would have two opposite effects which make simple predictions impossible: on one hand, they would provide species having longer dispersal distances with a better ability to persist in patches of favorable habitat once they are first reached; on the other hand, they would result in a reduced number of seeds dispersing each generation and thus favor short distance dispersal.

Differences in the performance, as measured by mean asymptotic population size and percent safe site utilization (Fig. 3), of different mean dispersal distances were affected by both the number and spatial arrangement of suitable sites. In the context of landscapes with habitat more aggregated than random, unsuitable landscapes ($SS \leq 1920$, Fig. 3) tended to strongly favor shorter dispersal distances, whereas more favorable and connected landscapes ($SS \geq 5280$, Fig. 3) discriminated less between different dispersal functions. When sites are connected (i.e., $P \geq 0.5280$), long-range dispersal is unnecessarily risky, and simple bond dispersal will insure full landscape occupation (Gardner *et al.* 1987, Von Niessen and Blumen 1988). One implication of this result is that in very connected habitats, risk and cost associated with seed reproduction are unnecessary because vegetative spread can insure adequate colonization. Using a patch simulation model, Levin *et al.* (1984) showed that the optimal dispersal rate out of the parental patch depends on the degree of habitat suitability, as it is an increasing function of the probability of landing into a suitable site. Cohen and Levin's (1991) further developments of this model showed that spatial heterogeneity (i.e., positive spatial autocorrelation in suitability) tends to decrease the optimum dispersal rate.

The structured maps used in our simulations show that the degree of site suitability, SS, is only an approximate predictor of habitat utilization (Fig. 3). The analyses on $\%SS$ indicated that the levels of suitability at meso- and micro-scales influenced colonization. Since these parameters determine landscape pattern (Lavorel *et al.* 1993), the results show that spatial structure determines the possibilities of spread, with more aggregated and more connected habitats favoring colonization. For landscapes with low connectance, colonization was constrained by the habitat pattern and plants could colonize space according to the balance between their capacities to saturate each habitat patch occupied and to reach isolated patches. As a result, species with shorter dispersal tended to be confined to larger patches which they could saturate progressively, while species with larger dispersal tended to jump between clusters without ever fully occupying them. Landscapes with higher connectivity allowed short range dispersal to progressively achieve full saturation. Long-range dispersers ($pmid \geq 10$) could still not fully saturate the available space due to their spatial instability.

Our results show that the efficient colonization of spatially distributed habitat by annual plants was determined by species dispersal characteristics. Recent work (e.g. Taylor 1986, Fahrig and Paloheimo 1988a, 1988b, Perry and Gonzalez-Andujar 1993) has emphasized the key role of dispersal distance in population dynamics in patchy habitats. The results of studies which have related spatial patterns with species dispersal characteristics are conflicting. Fahrig and Merriam (1985) and Gardner *et al.* (1991) found that the effects of the landscape pattern on habitat utilization and species persistence were important, while Vance (1984) concluded that for a large class of dispersal models, the details of the arrangement of habitat patches are unimportant. In a model with disjunct habitat patches and normal dispersal distributions, Fahrig and Paloheimo (1988a) showed that the importance of the spatial arrangement of habitat patches increased with decreasing mean dispersal distance.

Our results suggest that the relations between the dispersal pattern and the scales of heterogeneity of the habitat are in fact complex. Firstly, the degree of aggregation and connectance of sites at landscape scales both affect the degree of species colonization. Similarly, Doak *et al.* (1992) found, using a model of hierarchically clustered habitats, that the scale of clustering was the most important feature in determining the performance of animal dispersers. Secondly, unlike in simple random maps, where species having different distance probability distributions achieve the same habitat colonization (Gardner *et al.* 1991), the type of the dispersal function influenced the ability of the plants to colonize suitable sites in hierarchically structured landscapes. The dispersal distributions studied differed in the variance around the mean dispersal distance, the degree of clumping of the seeds around the mother plant, and the extent of the tail of the distribution. The existence of differences in performances between normal distribution and exponential or uniform distribution with the same mean and variance suggests that these two parameters are not sufficient predictors (Table 4). Risk-spreading strategies with dispersal by processes which couple clumping of the seeds near the parental site with exploring a wide range of distances will be most successful. This would in particular be the case of heteromorphy associating two distinct types of seeds with short and long dispersal (Venable 1985), for example ***Crepis sancta*** or some ***Medicago*** species. Green (1983) showed that long-tailed distributions are favored when safe sites are rare around the parent, whereas local abundance in safe sites favors distributions with a strong clumping around the parent. A literature review by Portnoy and Willson (1993) indicated that distribution tails were not specifically related to different dispersal modes, and that selection would tend to favor longer 'reach'. Our results emphasize the necessity to experimentally determine the extreme values of dispersal distance distributions and to examine the importance of the various portions of the seed dispersal curve (Portnoy and Willson 1993), that is resolve the relative importance of clumping around the parental site versus scattering of propagules.

5. Conclusion

This study suggests that neutral models ***(sensu*** Caswell 1976) using hierarchically structured landscapes to study the relations between patterns and ecological processes at the scales relevant to the biological characteristics of organisms (e.g., the neighborhood size), or to environmental factors (e.g., the homogeneous patch) will make it possible to identify when the scale of environmental change affects the organism of interest (Wiens ***et al.*** 1986, Addicott ***et al.*** 1987, Wiens and Milne 1989). Such neutral models can also be used to generate hypotheses on competition for space, successional patterns, invasion by exotic species, conservation design, and evolutionary consequences of habitat fragmentation. Our results in particular suggest that in spatially heterogeneous environments, uniformly suitable to different species (i.e., site suitability is not species-dependent), differences between species in colonizing capacities can arise simply based on small differences in dispersal characteristics.

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