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Assessment of climatic warming using a model of forest species migration

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Abstract

Significant shifts in plant species ranges are anticipated next century if climate warms due to greenhouse gas emissions. The magnitude of the projected warming is considerable; the rate at which it is predicted to occur is unprecedented. There is genuine reason for concern that the extent of the range shifts will exceed the dispersal abilities of many plant species, especially in the context of extensive habitat fragmentation. This study attempts to assess explicitly the influence of two factors – mechanism of dispersal and land use configuration – on the ability of plant species to migrate in response to climatic warming. Computer models were developed to simulate dispersal at the time interval of a generation for wind-dispersed and bird-dispersed tree species. These models were applied to three study areas in the eastern United States, each consisting of two 1:250 000 USGS land use land cover quadrangles, which had been reclassified according to probabilities of successful colonization. The study areas reflected the continuum of human impact on the landscape, from areas in intensive agriculture to heavily forested areas. The fastest modeled migration rate observed was 81 m/yr for the wind-dispersed species and 136 m/yr for the bird-dispersed species. Average migration rates were significantly lower. The wind-dispersed species was especially sensitive to habitat isolation and fragmentation. Significant variations in average bird-dispersed migration rates occurred with modest differences in the land use pattern within a landscape; no single predictor of bird-dispersed migration success emerged. Model results indicate that many species may be unable to migrate as range limits shift with a climatic warming, resulting in long-term climatic disequilibrium.

Keywords: Climate; Forest ecosystems; Migration

1. Introduction

A climate warming, driven by the release of greenhouse gases into the atmosphere, is projected to occur in the next century. This warming could result in the highest global temperatures in the past 100 000 years, and the most rapid warming since the last ice age (Schneider, 1989; Webb, 1992). If substantial warming occurs, range limits

of many plant species will shift significantly (e.g., Overpeck et al., 1991; Davis and Zabinski, 1992). Although wholesale shifts in species distributions have occurred during Earth's history, no direct analog exists in the geologic record to assess the potential impact of a rapid climate change on vegetation.

Although previous work has addressed the potential rate and magnitude of range adjustments

in response to future warming, no study explicitly has sought to simulate tree species migration through actual landscapes. The objective of this study was to develop models of migration for two common means of dispersal (wind and bird) in order to assess the potential impact of land use patterns and means of dispersal on migration success in present-day landscapes of the eastern United States.

The two classes of dispersal selected for this study, anemochory (wind dispersal) and ornithochory (bird dispersal), encompass the strategies of a large number of terrestrial plants. In addition,

they offer notable contrasts in terms of dispersal distances, the stochasticity of dispersal events, and the ecological roles of plants possessing the different strategies. Pine (*Pinus*) species were used to specify the parameters of the wind-dispersed model, and oak (*Quercus*) species represented the bird-dispersed tree. These representative taxa were selected on the basis of their ecological and economical importance.

The models of dispersal presented operate on different spatial and temporal scales than other models. Most models of wind dispersal include specific micrometeorological and seed density

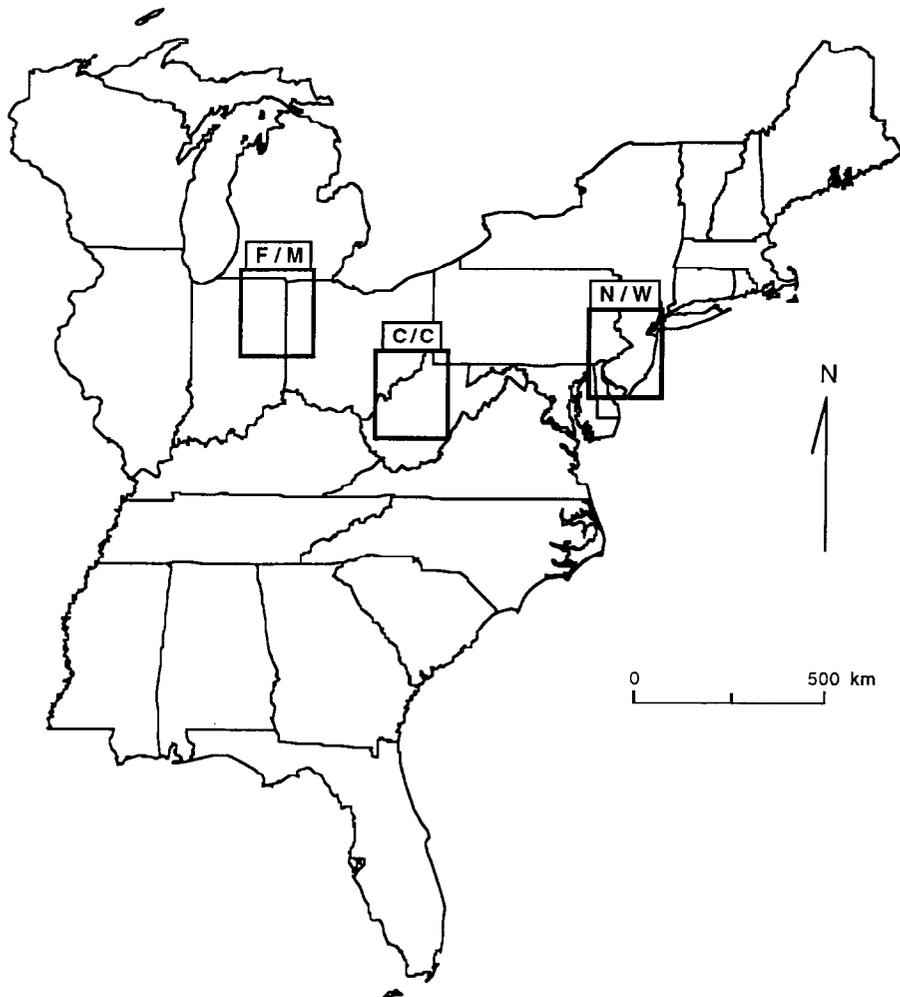


Fig. 1. Location of study areas. F/M = Fort Wayne/Muncie, C/C = Clarksburg/Charleston, N/W = Newark/Wilmington.

components (Johnson et al., 1981; McClanahan, 1986; Greene and Johnson, 1989). Previous animal-dispersal models require knowledge of seed densities, as well as the density of the dispersing animals and their behavioral characteristics (Johnson et al., 1981). The complexities of such dispersal models necessitate that applications be restricted to dispersal from individual plants. Although other workers have incorporated seed supply and dispersal into forest stand simulation models (Hanson et al., 1990), this requires an explicit assessment of tree densities, life-history characteristics, site conditions, and interspecific competition.

The models developed for this research are fundamentally different in scale and approach. Rather than describing individual dispersal events from a single source, they examine the cumulative effect of thousands of dispersal events over many years. Since the goal is to study range expansion, only presence/absence is modeled; density effects are excluded. Using this more general approach, the models are able to examine migration over extensive geographical areas. Additionally, since the models are coupled with a geographic information system (IDRISI), explicit spatial relationships are maintained, and visual inspection of the simulations are possible.

Although this modeling approach provides certain advantages, it is not without its limitations. For instance, the models at present do not include seasonal variations in temperature and precipitation which can influence the size and viability of a seed crop, the timing of seed release, and the loss of seeds to pests (Jemison and Korstian, 1944; Fowells, 1965). Wind speed and direction at the time of release will affect seed dispersal (Johnson et al., 1981); these factors were excluded from the models because they vary widely interannually (Fowells, 1965), and because of the difficulty in predicting their influence under a modified climate. In its present form the model also excludes certain life-history characteristics of the participant tree species, as well as specific landscape effects which would influence dispersal and establishment. For example, the role of soils and disturbance are not modeled; these factors may play a pivotal role in migration success (Pen-

nington, 1986; Pastor and Post, 1988; Overpeck et al., 1990; Perry et al., 1990). Additional factors pertinent to species dispersal and migration will be incorporated into future modeling efforts; however, scale constraints obviate a strict process-oriented approach. It is believed that the models in their present form summarize descriptive patterns of landscape effects based on broad propensities given a potential climate change.

2. Methods

2.1. Study areas

Three study areas representing a range from primarily forested land to primarily cropland were selected from the eastern United States (Fig. 1). Each measured 2° of latitude by 2° of longitude (approximately 220 km by 180 km). The first study area consists of the Clarksburg and Charleston 1:250 000 quadrangles. This area is primarily woodland and forest with some cropland and pasture, and represents one of the largest regions in the eastern U.S. with minimal fragmentation of the forest cover (although much of the forest cover is second growth). The second study area consists of the Fort Wayne and Muncie quadrangles and is mostly cropland; only scattered woodlots and strands of riparian forest remain. The third study area, composed of the Newark and Wilmington quadrangles, was selected for its diversity of land use and land cover. This area has large expanses of forest and wetland, as well as some of the most heavily urbanized areas on the eastern seaboard.

2.2. Data

Land Use and Land Cover (LULC) digital data were obtained for the study areas from the U.S. Geological Survey. The LULC data were in composite theme grid (raster) cell format, in which the map area is divided into 4-ha cells (200 m × 200 m). Cells are assigned the value of the level II category of the Land Use and Land Cover Classification System (Anderson et al., 1976) located at the center of that cell.

To simplify migration modeling, the LULC categories were reclassified according to the likelihood of their successful colonization by tree species. Cells were designated as: (1) impermeable, with a very low probability of successful establishment by migrating species, (2) semipermeable, with an intermediate probability of successful establishment, or (3) permeable, with a very high probability of successful colonization. Table 1 describes the assignment of level II LULC categories to these groups.

3. Landscape scale analysis

3.1. The models

The initial modeling of migration, hereafter referred to as the landscape scale of analysis, was performed on contiguous square grids of 50×50 cells (total area = $10 \text{ km} \times 10 \text{ km}$) extracted from the three study areas. For each grid, percent cover of the three permeability classes was computed. In addition, three measures relating to permeable land use perimeter, or permeable "edge" within each grid were determined: total

permeable edge, mean centroid of permeable edge cells within the grid, and standard radius, which is a measure of dispersion about the permeable edge centroid within the grid and is analogous to a standard deviation. (A permeable edge cell is defined as a permeable land use cell which borders a cell of a different land use category. As discussed below, edge cells are the "target" cells for bird dispersal.) Finally, for each grid Moran's I coefficient also was derived. Moran's I is an index of spatial autocorrelation that is based upon the covariation of juxtaposed cell values. As with a classical correlation coefficient, Moran's I approaches 1 when cells with similar values cluster, and approaches -1 as cells with dissimilar values become juxtaposed (Griffith, 1987).

The goal of the models was to determine the number of generations required for a tree species to migrate south-to-north through a 50×50 -cell grid. A generation is considered to be the average time required for an established seedling to reach reproductive maturity. Through-migration was said to occur when at least one of the cells in the top row of the grid was colonized. An initial condition was established wherein the entire bottom row of the grid was assigned a presence of

Table 1
USGS level II land use and land cover categories classified according to probability of successful colonization

Permeable (high probability)

Forest: Deciduous (41), Evergreen (42), Mixed (43)
Wetland: Forested Wetland (61)

Semipermeable (intermediate probability)

Urban or Built-up: Residential (11), Transportation, Communications, and Utilities (14),
Industrial and Commercial Complexes (15), Mixed Urban or Built-up (16),
Other Urban or Built-up (17)
Agriculture: Other Agricultural Land (24)
Rangeland: Herbaceous Rangeland (31), Shrub and Brush Rangeland (32),
Mixed Rangeland (33)

Impermeable (low probability)

Urban: Commercial and Services (12), Industrial (13)
Agriculture: Cropland and Pasture (21), Orchards, Groves, Vineyards, Nurseries,
and Ornamental Horticultural Areas (22), Confined Feeding Operations (23)
Water: All Categories (51–54)
Wetland: Nonforested Wetland (62)
Barren Land: All Categories (71–77)

Table 2
Model outline for wind-dispersed migration

Dispersal type	Dispersal distance	Recipient cells	Potential cell type	Colonization success
Local	200 m	all contiguous cells	Impermeable	No
			Semipermeable	Conditional ^a
			Permeable	Yes
Random long distance	200 m–2.5 km	single cell	Impermeable	No
			Semipermeable	No
			Permeable	Yes

Each generation, both types of dispersal occur from the current range. Program is terminated when through-migration occurs, or when the maximum number of iterations is reached.

^a Semipermeable cells are colonized only if at least two conterminous cells are already colonized, or if one side and all four diagonal cells are already colonized. This condition is not possible with random long distance dispersal.

the migrating tree (i.e., the bottom row represented the initial range limit). Due to the stochastic nature of long-distance dispersal in the models, three iterations of both the wind-dispersed and bird-dispersed models were performed on the grids. For each grid, the number of successful migrations and the average number of genera-

tions required for through migration were computed for each model.

Wind-dispersed migration model

The general principles of the wind-dispersed migration model are outlined in Table 2. For each generation, dispersal from the current range

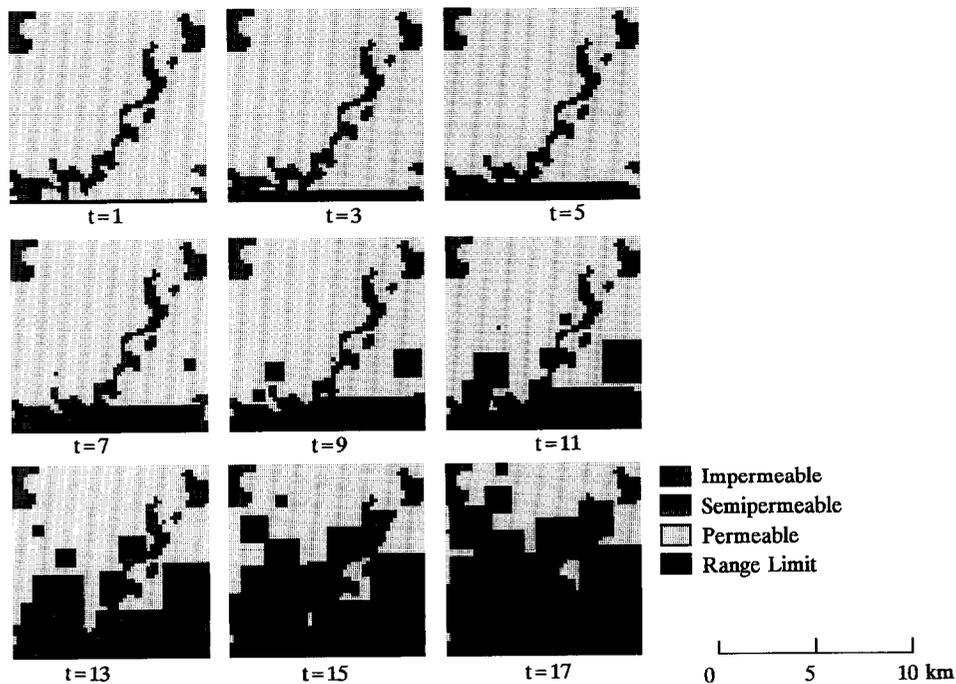


Fig. 2. Sample run for the wind-dispersal model in a forested landscape. Migration is uniform away from the contiguous range limit, and from more distant cells colonized by random long-distance events. Through-migration occurs after 17 generations.

extended 200 m to any adjoining cell, including diagonally-linked cells. This limit is in accord with average dispersal distances reported for primarily wind-dispersed pine species (Burns and Honkala, 1990). Successful establishment occurred if the propagule landed in a permeable cell. A semipermeable cell would present a more difficult colonization environment, and a minimum perimeter requirement was designed to reflect this. An inoculated semipermeable cell became colonized when at least two cells alongside of it already were colonized, or when one side and all four adjoining diagonal cells already were colonized. Impermeable cells were never colonized.

In addition to this local dispersal, one random long-distance dispersal event to a single cell occurred each generation. Although long-distance events are not common with wind-dispersed pines (Ridley, 1930), such dispersal events could play a critical role in range expansion. An apparent dispersal distance of 4 km has been reported for

loblolly pine (Reynolds, 1933, cited in Fowells, 1965), typical dispersal distances are much less, however; establishment of pines beyond a couple hundred meters from parent trees is usually erratic and uncertain (McQuilken, 1940). Since few reliable estimates of long-distance dispersal for pines was uncovered in the literature, values for random dispersal distance were set between 200 m (the local dispersal distance) and 2.5 km from the current range. This upper limit represents a compromise between “typical” dispersal distances, and the unusual long-distance event reported above.

The model run was terminated when colonization of the top row of the grid occurred, or when the maximum number of generations had been reached (set to $t = 50$, the time required for migration through the grid at the minimum dispersal rate of one row per generation). Figs. 2 and 3 show sample model runs of the wind-dispersal model, for a forested landscape and a fragmented landscape, respectively.

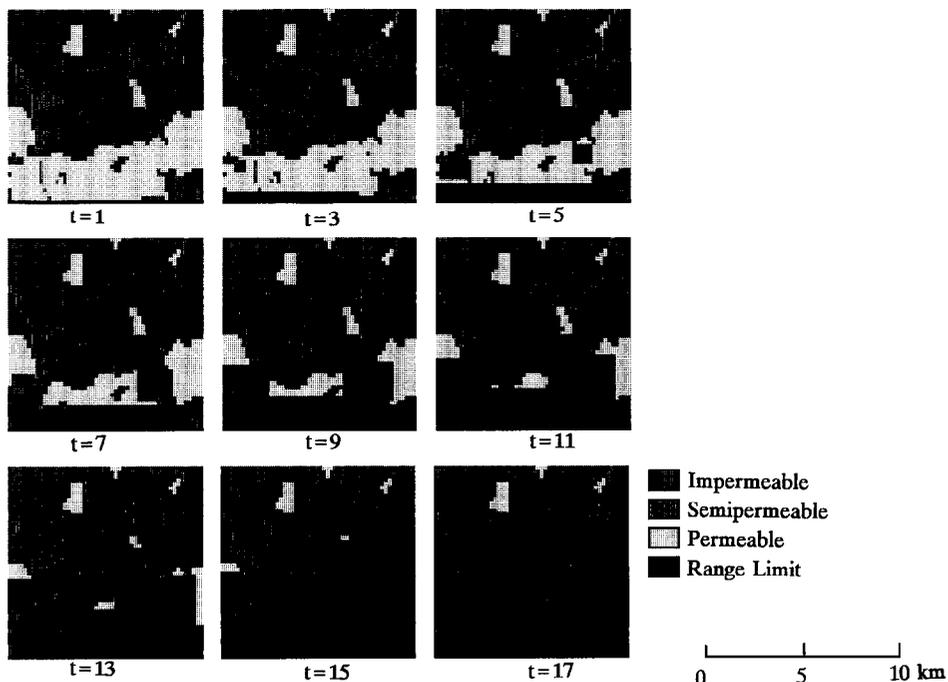


Fig. 3. Sample run for the wind-dispersal model in a fragmented landscape. A random long-distance dispersal event results in the colonization of an isolated habitat island ($t = 13$), but after 17 generations an impenetrable barrier is encountered and migration halted.

Bird-dispersed migration model

Although numerous animals include acorns in their diet (Martin et al., 1951), the blue jay (*Cyanocitta cristata* L.) is the principal agent of long-distance dispersal for the oaks. As evidence, Darley-Hill and Johnson (1981) report on the transport of an estimated 150 000 acorns in 28 days by 50 blue jays in suburban Virginia, USA, with dispersal distances ranging from 100 m to 1.9 km; maximum distances of at least 4 km were reported in rural Wisconsin (Johnson and Adkisson, 1985). In addition to transporting acorns considerable distance, behavioral traits possessed by jays enhance the probability of successful oak colonization. Jays transport only sound nuts from the source tree, and engage in scatterhoarding at caching sites (Darley-Hill and Johnson, 1981). Jays tend to select caching sites near conspicuous elements in the terrain, presumably to aid in subsequent recovery of hidden items. Jays prefer “edges” or transitions between vegetation types for caching sites, where they bury acorns or cover them with litter (Bossema, 1979; Johnson and Adkisson, 1986). Such locations are generally suitable for oak colonization. As Johnson and Webb (1989, p. 562) acknowledge:

“the blue jay appears to be the only animal in the eastern deciduous forest that routinely dis-

perses nuts much more than several hundred metres and caches them in the ground where they can germinate and successfully establish.”

The general principles of the bird-dispersed migration model are outlined in Table 3. Two types of dispersal occurred each generation for this model: local and long-distance. The former would be accomplished by gravity and especially by small rodents such as squirrels. Long-distance dispersal would be performed by birds, notably blue jays. A uniform density of blue jays is assumed throughout the study areas since there is no good alternative to this assumption aside from actual censuses; dispersal distances also do not vary geographically.

Local dispersal distance in this model is identical to that of the wind-dispersed model: propagules were dispersed 200 m from the current range to any adjoining cell, since squirrels and mice generally do not travel great distances from a source to cache acorns. In order for the receptive cell to have been colonized successfully, it must have been either permeable, or semipermeable with sufficient perimeter already adjacent to colonized cells.

Dispersal by blue jays occurred up to 1.1 km from the current range, which represents an average dispersal distance reported in the literature

Table 3
Model outline for bird-dispersed migration

Dispersal type	Dispersal distance	Recipient cells	Potential cell type	Colonization success
Local	200 m	all contiguous cells	Impermeable Semipermeable Permeable	No Conditional ^a Yes
Long distance	≤ 1.1 km	all permeable edge cells	Permeable	Yes
Random long distance	1.1 km–5.0 km	single permeable edge cell	Permeable	Yes
Random patch ^b	≤ 1.1 km	single permeable cell	Permeable	Yes

Each generation, all types of dispersal occur from the current range. Program is terminated when through-migration occurs.

^a Semipermeable cells are colonized only if at least two conterminous cells are already colonized, or if one side and all four diagonal cells are already colonized.

^b Random patch dispersal occurs only when no suitable edge cells exist to perform random long distance dispersal.

(Darley-Hill and Johnson, 1981). Only “edge” cells were considered receptive to jay dispersal; all permeable edge cells within dispersal range were successfully colonized. Although these target edge cells represent boundaries between “receptivity” classes and thus mask landscape edges which occur at a finer resolution, it is felt that broad landscape patterns of dispersal are maintained. Once edge cells were colonized, infilling of the interior of uniform blocks of cells was accomplished by local dispersal.

Since jays are known to fly longer distances than the average 1.1 km to cache acorns, one random long-distance dispersal event occurred each generation as well. Longest verified dispersal flights by jays are about 5 km; therefore it was assumed that each generation an acorn would be transported to one permeable edge cell 1.1–5.0 km from the current range. With the bird-dispersed model, an appropriate target cell always will be inoculated and colonized by a random long-distance dispersal event if suitable cells are lo-

cated within the proper range; successful colonization by random dispersal in the wind-dispersed model is a chance event that depends on the receptivity class of the recipient cell.

Applying these rules, if no suitable edge cells existed in the dispersal range, migration only could occur by local dispersal, 200 m per generation. In order to portray more realistic patch dynamics, it was assumed that if no edge cells existed in an extensive region of closed forest, at least one permeable cell would open sometime in the generation time of the oaks and be inoculated with an acorn by the jays. This “patch” dispersal was modeled by assuming that one randomly-selected permeable cell within 1.1 km from the current range would be colonized when no suitable edge cells were present.

The model runs were terminated when colonization of a cell in the top row of the grid occurred. Figs. 4 and 5 show sample runs for the bird-dispersal model, in a forested landscape and fragmented landscape, respectively.

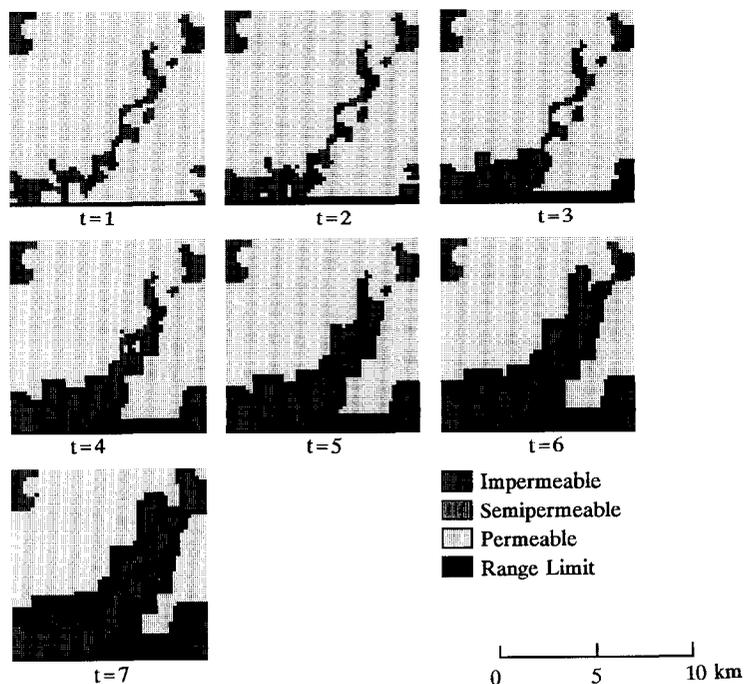


Fig. 4. Sample run for the bird-dispersal model in the same forested landscape as shown in Fig. 2. Rapid colonization of edges is apparent, with slower infilling of uniform blocks of cells. Random long-distance dispersal events are also evident. Through-migration occurs in 7 generations.

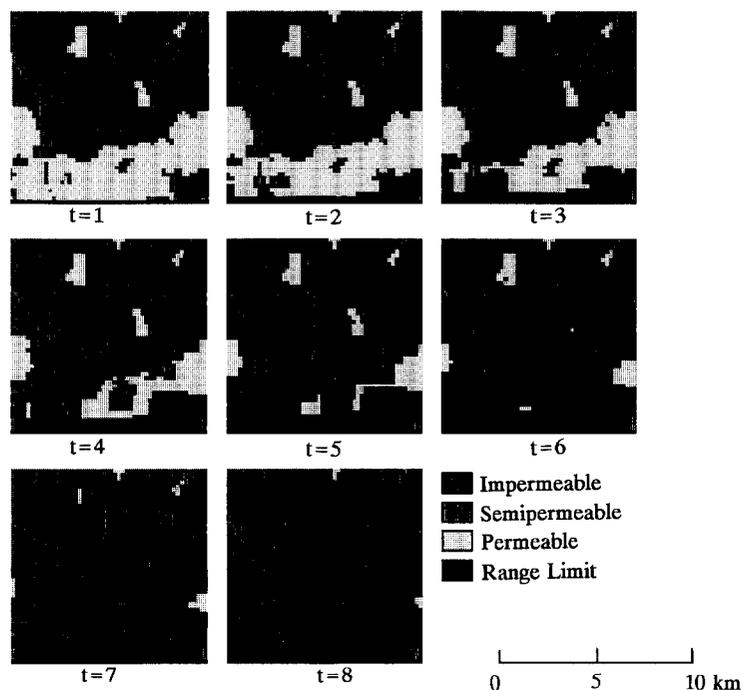


Fig. 5. Sample run for the bird-dispersal model in the same fragmented landscape as shown in Fig. 3. Due to both the directional nature and the greater distances of bird dispersal, the barrier to wind-dispersed migration is overcome, and through-migration occurs in 8 generations.

Sensitivity analysis

After completion of the landscape-scale analysis, model parameters were adjusted independently and the models were rerun on a small subset of the grids. This allows an assessment of the sensitivity of the models to their specifications. When the models were rerun, only one parameter was changed at a time, the others maintained their original value.

For both models, the number of random dispersal events per generation was increased from one to three, and then to five. Local dispersal distance was increased from 200 m to 400 m, and maximum random dispersal distance from 2500 m to 5000 m. In addition, the rules for establishment in a semipermeable cell also were changed. First, only one neighboring cell was required to be colonized instead of two. Second, semipermeable cells became colonized after being inoculated during two different time intervals, regardless of the status of neighboring cells. For the bird-dispersed model, additional changes were

made wherein bird dispersal distances were increased from 1100 m to 2200 m, and then to 5000 m. Maximum random dispersal distances in the bird-dispersed model were increased from 5000 m to 10000 m. Finally, migration was performed north-to-south through the grids (instead of south-to-north) to assess the importance of specific grid configuration on migration success.

3.2. Landscape scale results

Based on the rules of migration in the models and the specific cell configuration within the 987 potential grids, it was determined that through-migration was possible in 690 grids for the bird-dispersed model, and 669 grids for the wind-dispersed model. However, because of the random nature of wind dispersal, colonization of a cell within the top row of the grid did not occur within the imposed 50-generation time limit for all the wind-dispersed model runs, even though successful colonization was possible. The proba-

bility of through-migration was deemed sufficiently low for those grids which experienced zero successful runs in the three iterations that these were dropped from analysis, resulting in a sample size of 471 for the wind-dispersed model. The grids that experienced one through-migration ($n = 31$) and those that experienced two successful migrations ($n = 21$) were rerun without any imposed time limit. Migration rates in excess of 50 generations were then rank-ordered for the two groups, and the median values were used as the “missing” value(s) in computing average grid mi-

gration rates within the respective groups. Average migration times for all 471 grids therefore were based on three values.

Wind dispersal model

Correlation analysis revealed a strong negative relationship ($r = -0.81$) between average number of generations for wind-dispersed through-migration (WIND_AVG) and permeable land use (PERM). This correlation substantiated an intuitive expectation, that as the proportion of “favorable” permeable cover increased, the num-

Table 4
Fifty by fifty-cell grids with the fastest and slowest average migration times for the wind-dispersal model

Study area ^a	Migration time (generations)	Percent land use cover:			Moran's I	Permeable edge cells:		
		Impermeable	Semipermeable	Permeable		Total (km)	Centroid (row)	Radius (cells)
<i>Fastest wind-dispersed average migration times</i>								
C/C	12.3	1	0	98	0.28	57.6	24	22
C/C	13.0	3	0	97	0.48	62.8	22	19
C/C	13.0	3	1	96	0.52	68.8	26	22
C/C	14.3	8	1	91	0.34	130.4	21	21
C/C	15.0	6	0	94	0.51	81.6	25	20
C/C	15.0	0	0	100	1.00	40.0	-	-
C/C	15.3	10	0	90	0.54	102.4	32	20
C/C	15.3	0	0	100	0.50	44.4	30	8
C/C	15.7	3	1	96	0.30	89.6	25	18
C/C	15.7	26	0	74	0.61	156.4	26	19
C/C	15.7	16	0	84	0.57	134.8	22	17
C/C	15.7	4	2	94	0.56	89.2	23	21
C/C	15.7	1	0	99	0.41	49.2	5	16
C/C	15.7	3	3	94	0.47	93.6	21	21
N/W	15.7	2	0	97	0.55	57.6	24	18
<i>Slowest wind-dispersed average migration times</i>								
N/W	76.0	62	20	18	0.49	142.4	28	20
N/W	76.0	17	68	15	0.47	105.2	24	18
N/W	76.0	37	38	26	0.65	116.0	22	21
N/W	75.7	78	1	21	0.53	141.6	21	17
N/W	75.7	49	18	33	0.53	195.2	27	20
N/W	75.3	22	53	25	0.55	143.2	23	20
F/M	75.3	76	0	22	0.75	78.0	18	19
N/W	74.3	50	31	18	0.62	96.0	19	19
N/W	73.7	58	17	25	0.66	122.4	25	20
N/W	73.7	30	40	30	0.58	158.8	28	20
N/W	73.0	74	3	23	0.52	152.8	18	18
N/W	73.0	36	39	25	0.50	169.6	18	19
N/W	72.7	46	23	31	0.57	175.6	30	20
N/W	72.3	57	7	36	0.54	189.6	26	19
N/W	72.3	73	12	14	0.48	118.0	21	20
F/M	72.3	81	2	17	0.72	66.4	31	20

^a C/C = Clarksburg/Charleston, F/M = Fort Wayne/Muncie, N/W = Newark/Wilmington.

ber of generations required for through-migration would decrease. Grids with the lowest values of WIND_AVG all had PERM values of 90% or greater, while grids with the highest WIND_AVG had PERM values under 35%. This relationship held true for the entire data set, and for the individual study areas.

Table 4 lists the characteristics of the grids with the fastest and slowest wind-dispersed migration rates; Figs. 6 and 7 depict these grids with the fastest and slowest rates, respectively. It can be seen that the grids with the fastest wind-dispersed migration rates not only have high amounts of permeable cover, but also that the permeable cover forms continuous tracts within the grids. In contrast, the grids with the slowest wind-dispersed migration rates were highly fragmented and

tended to have a mixture of land use classes. The permeable cover existed in isolated tracts, which did not provide good “targets” for wind-dispersed seed. All of the “slow” grids in Fig. 7 experienced only one successful migration in three model runs.

A plot of WIND_AVG vs. PERM for the entire data set indicated a logarithmic relationship, and a power function transformation offered the greatest improvement in explaining the variance in the dependent variable when a bivariate regression was performed. The resulting equation for the entire data set was:

$$\text{WIND_AVG} = 640.52 (\text{PERM})^{-0.78},$$

$$R^2 = 0.80.$$

Regression coefficients were significant at the

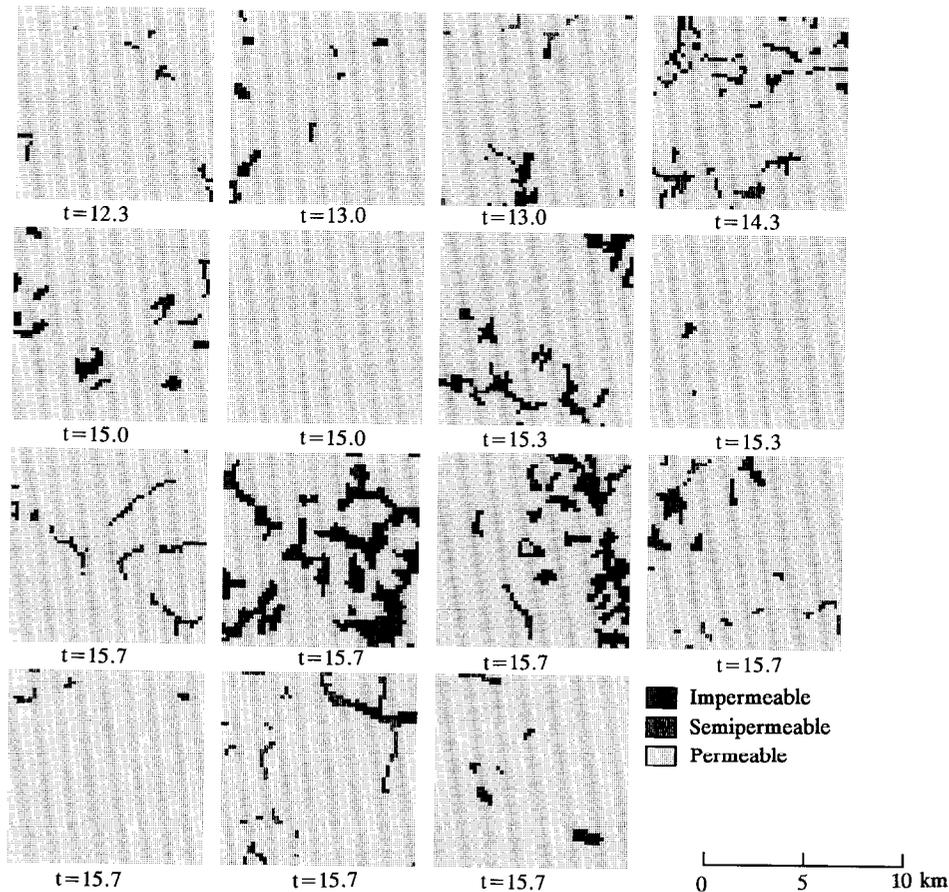


Fig. 6. Grids with the fastest wind-dispersed average migration times, in generations. All contain high percentages of permeable cover, which forms continuous tracts within the grids.

0.0001 level; residual analysis revealed no notable anomalies.

When model parameters were adjusted independently and the model rerun on a subset of the grids, results indicated that migration rates are most sensitive to the number of random dispersal events per generation. Increasing the number of such events diminishes land use differences between the grids; as the number of random dispersal events increases, the probability of successful colonization increases, even in highly fragmented landscapes. Increasing local and random dispersal distances, as well as changing the colonization rules for semipermeable cells had a lesser influence on migration rates; differences in migration

rates between grids largely were maintained when these other model parameters were varied.

Bird dispersal model

Average bird-dispersed migration times ranged from 3.7 to 27.7 generations; the distribution of these values was extremely skewed and leptokurtic: 89% occurred between 5 and 8 generations. This clustering of data points made modeling of migration difficult.

Correlation analysis revealed very weak relationships between average bird-dispersed migration time and all of the land use variables (permeable, semipermeable, or impermeable cover). Bird-dispersed migration rates for the entire data

Table 5
Fifty by fifty-cell grids with the fastest and slowest average migration times for the bird-dispersal model

Study area ^a	Migration time (generations)	Percent land use cover:			Moran's I	Permeable edge cells:		
		Impermeable	Semipermeable	Permeable		Total (km)	Centroid (row)	Radius (cells)
<i>Fastest bird-dispersed average migration times</i>								
F/M	3.7	99	0	1	0.41	6.4	9	14
F/M	3.7	91	8	1	0.57	10.4	13	21
F/M	4.0	87	11	2	0.66	10.8	9	14
N/W	4.3	8	0	92	0.75	66.8	11	17
C/C	4.7	7	0	92	0.43	106.0	21	20
C/C	4.7	5	0	95	0.54	74.8	23	22
C/C	4.7	11	1	89	0.62	103.6	14	14
C/C	4.7	3	1	96	0.36	78.0	15	16
C/C	4.7	7	1	91	0.61	84.8	13	15
F/M	4.7	98	1	1	0.40	14.0	16	17
N/W	4.7	69	1	29	0.87	52.8	19	18
N/W	4.7	60	9	31	0.78	90.4	26	20
N/W	4.7	60	25	16	0.73	111.2	11	19
<i>Slowest bird-dispersed average migration times</i>								
C/C	27.7	0	0	100	1.00	40.0	–	–
C/C	27.3	0	0	100	0.15	40.8	48	1
C/C	24.0	2	0	98	0.28	58.8	42	5
C/C	20.0	0	0	100	0.50	44.4	30	8
C/C	18.7	2	0	98	0.53	53.6	41	11
C/C	16.3	2	0	98	0.45	61.6	26	12
C/C	14.0	6	4	90	0.59	96.0	36	15
C/C	13.7	1	0	99	0.37	49.2	24	12
C/C	13.3	5	0	95	0.27	104.4	30	20
C/C	13.3	1	0	99	0.41	49.2	5	16
C/C	13.3	3	0	97	0.49	66.4	33	20
C/C	13.0	2	0	98	0.50	50.0	24	17
C/C	12.0	2	0	98	0.56	48.8	19	23

^a C/C = Clarksburg/Charleston, F/M = Fort Wayne/Muncie, N/W = Newark/Wilmington.

set were actually slowest in those grids with the greatest proportion of permeable cover. The amount of permeable edge, which represents the target cells for long-distance dispersal, measures of permeable edge central tendency and dispersion, and Moran's I also were poor indicators of bird-dispersed migration rates. Table 5 lists characteristics of grids with the fastest and slowest bird-dispersed migration times, and Figs. 8 and 9 depict these grids with the fastest and slowest times, respectively.

A visual inspection of these grids reveals the reason for this lack of association between average migration rates and any of the independent variables. Fastest rates occur when suitable target

(permeable edge) cells are located at the center and also the top of the grid, such that in each generation the migration front is compelled to take extended jumps toward the top of the grid. In other words, rapid migration is forced by a lack of appropriate target cells. The configuration of target edge cells in these "fast" grids range from isolated woodlots surrounded by agriculture, to small openings in extensive forest cover. Thus, any measure of "total" cell type within a grid is inadequate as a predictive tool; the grids with the fastest bird-dispersed migration rates ranged from 99% impermeable to 96% permeable. In contrast, the grids with the slowest bird-dispersed migration rates all had PERM values of

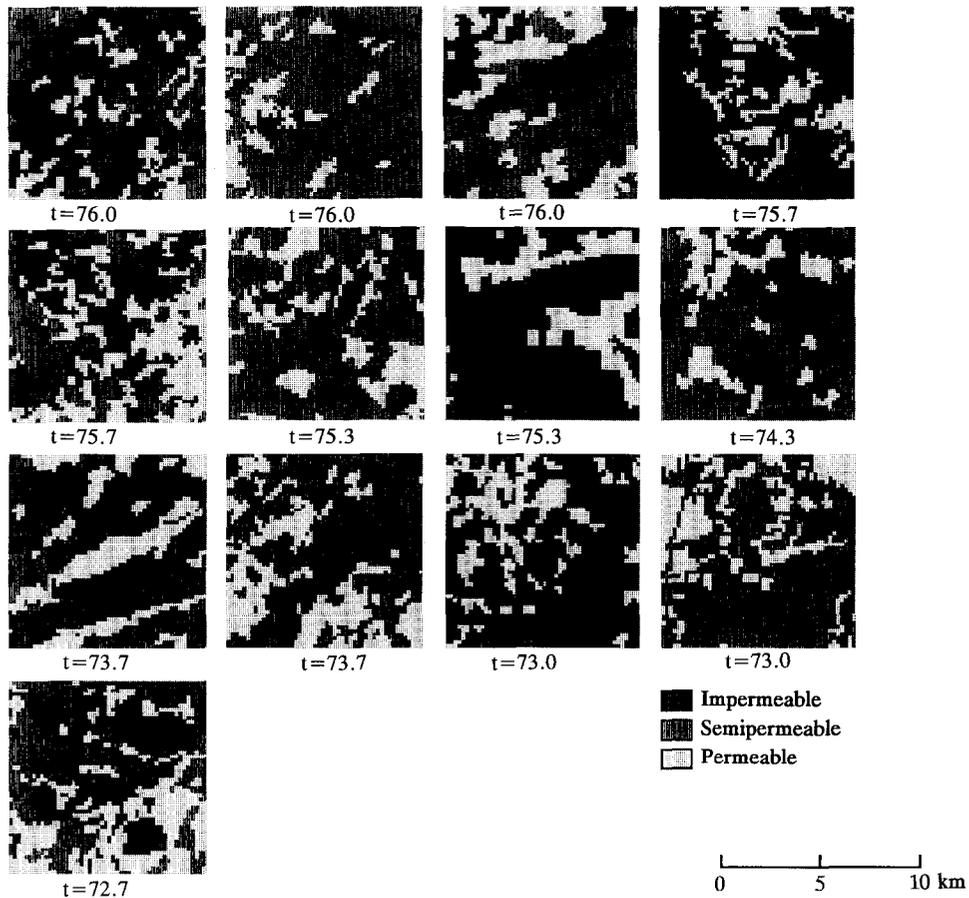


Fig. 7. Grids with the slowest wind-dispersed average migration times, in generations. The grids are highly fragmented, with a mixture of land use classes. Permeable cells are isolated and do not form continuous tracts within the grids.

90% or greater (Table 5). (Three of the grids in the slowest bird-dispersal group also emerged in the fastest wind-dispersal group.) In these grids the permeable cover was continuous with either few edge cells to act as target cells for long-distance dispersal, or with edge cells situated such that long migration jumps to the top of the grid were not possible (Fig. 9).

Bird dispersal distance proved to be the variable to which migration rates were most sensitive when model parameters were varied independently with a subset of the grids (doubling the bird dispersal rate had an effect similar to increasing the number of random dispersal events per gen-

eration five-fold); general differences in migration rates between the grids were maintained when other parameters were adjusted.

As with the wind-dispersed model, the key factor influencing migration rate was landscape configuration; the model parameter that most influenced migration success frequently depended on the internal cell configuration within a particular grid. When migration was reversed and performed north-to-south through a subset of the grids, grids with the fastest migration rates (both wind- and bird-dispersed) were slower; migration through the slowest grids for both models was faster (or migration was no longer possible). These

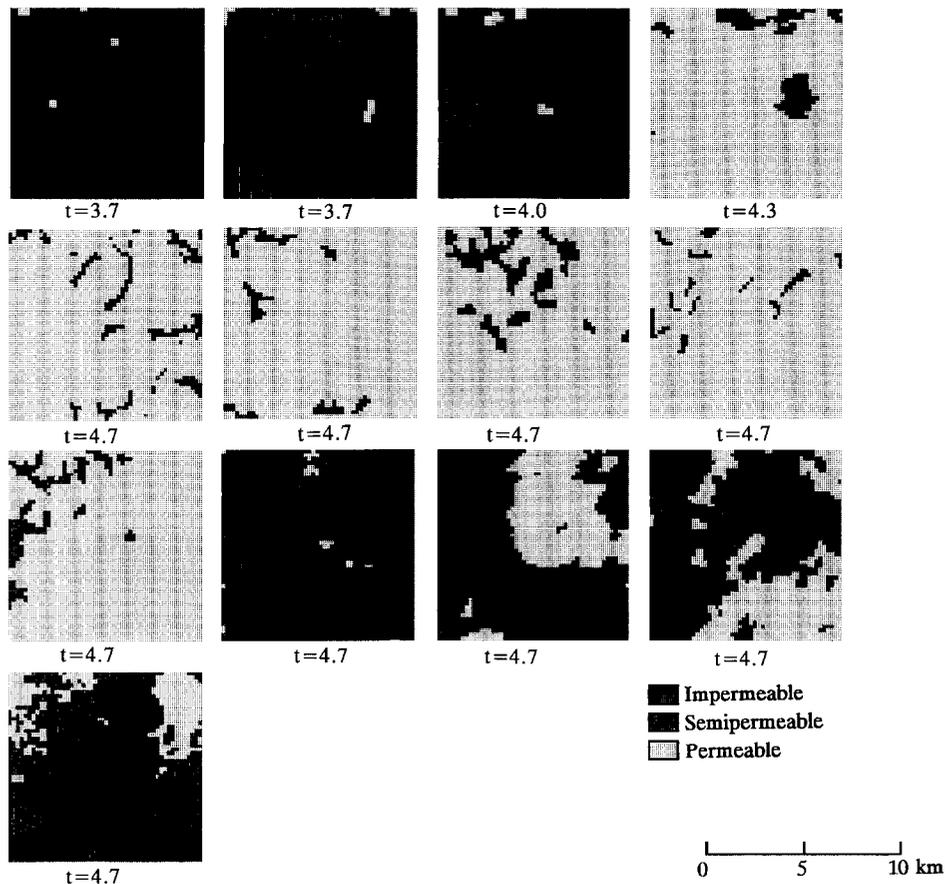


Fig. 8. Grids with the fastest bird-dispersed average migration times, in generations. Permeable edge cells are located near the center and top of the grids, facilitating rapid “jump” dispersal.

changes canceled out regionally however. Average migration rates for all grids was virtually unchanged.

4. Mesoscale analysis

4.1. The model

The next phase in the analysis was to examine potential migration patterns at a larger scale. To accomplish this, the three original study areas again were divided into 50×50 -cell (10-km square) grids. As defined earlier, “cell” refers to the 200-m square area to which the original land use and land cover values were assigned, and is

the smallest unit of observation in the landscape-scale analysis. A “grid” is a square of 2500 cells, and is the smallest unit of observation in the “mesoscale” analysis. A “typical” $2^\circ \times 2^\circ$ study area would be composed of 22×18 grids. For both the wind- and bird-dispersed models, each grid was assigned a value representing the number of generations that were required for through-migration. If through-migration was not possible for the grid, it was assigned a unique fixed value.

The initial range limit for both oaks and pines was assumed to be an additional row of grids added across the bottom of each study area, excluding those grids situated over an ocean or bay (Newark/Wilmington study area). Each gen-

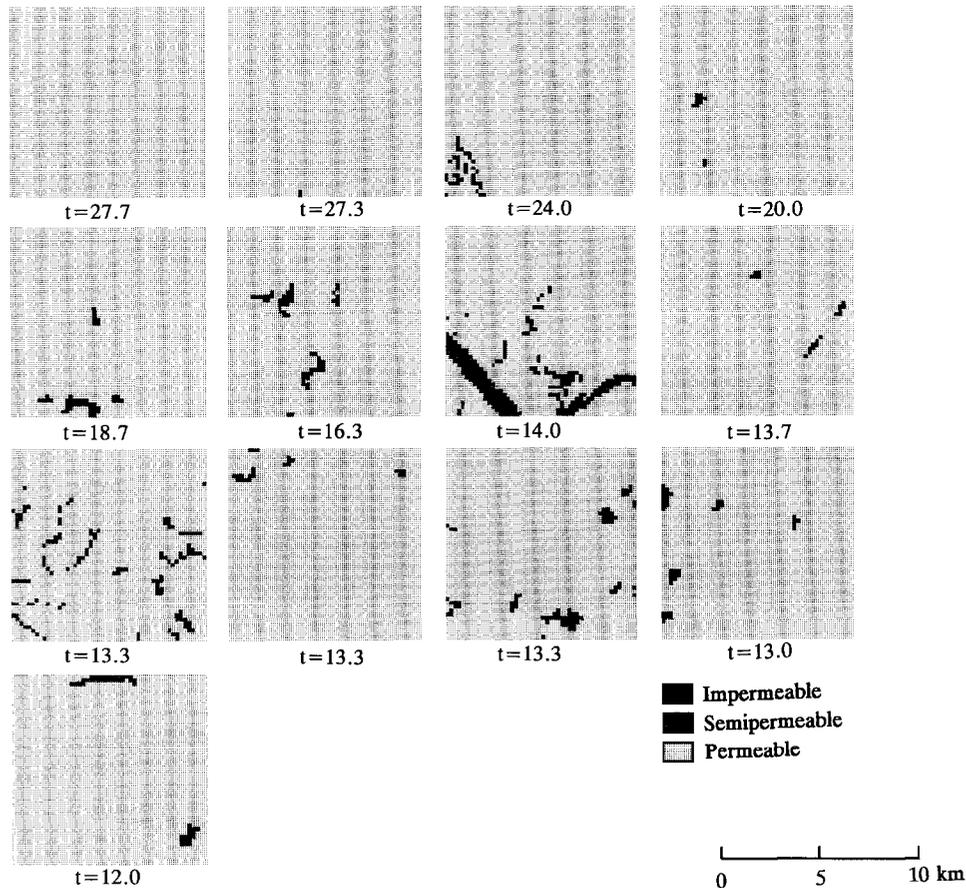


Fig. 9. Grids with the slowest bird-dispersed average migration times, in generations. Permeable edge cells are either absent or located such that long migration jumps to the top of the grids are not possible.

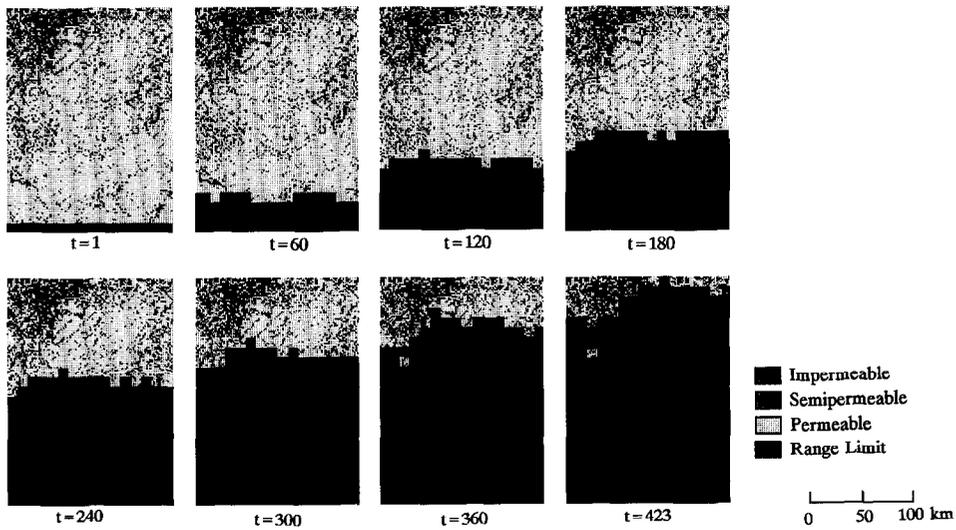


Fig. 10. Wind-dispersed migration through the Clarksburg/Charleston study area. Little impediment to migration is encountered and migration occurs in a uniform wave. Through-migration occurs in 423 generations.

eration, the migration value of the grids adjacent to the current range (including diagonal grids) was reduced by one; when a grid's value reached zero, it was assumed through-migration occurred, and that grid was incorporated into the range of the given species. Grids in which through-migra-

tion was not possible were constantly reset, and never became part of the species range.

This process was repeated until the range occupied one of the grids along the top tier of the study area, or until an impermeable barrier was encountered. Impermeable barriers resulted when

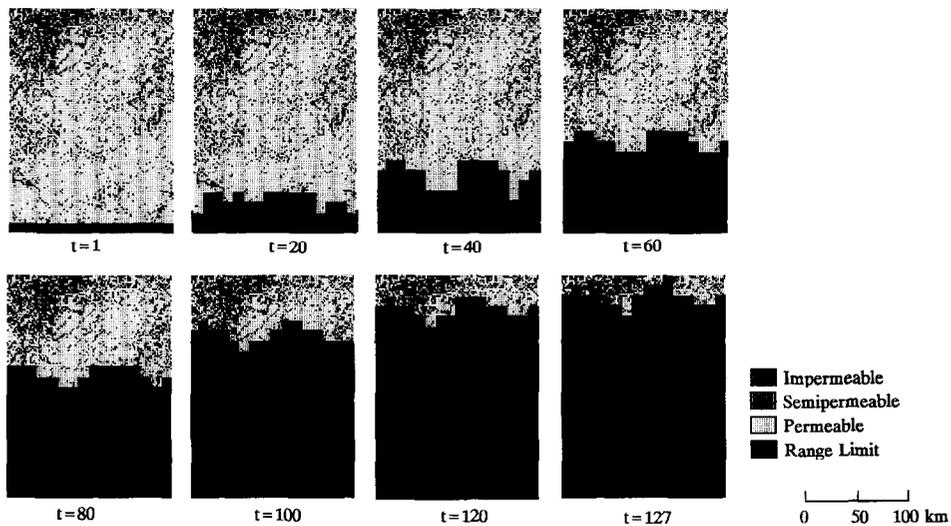


Fig. 11. Bird-dispersed migration through the Clarksburg/Charleston study area. Migration through the study area is uniform and occurs in 127 generations.

a contiguous section of grids in which through-migration was impossible laterally traversed the study area.

This approach to “scaling up” species migration modeled at the 50×50 -cell landscape scale is intended to provide a “first approximation” of species migration at larger spatial scales. Several shortcomings are evident in this initial approach, however. For example, at the landscape scale, the initial range limit was assumed to be the row of cells along the bottom of the grid, and through-migration occurred when a single cell at the top of the grid was colonized. At the mesoscale a grid is assigned species presence, which enables it to influence adjoining grids, regardless of the extent to which the grid was permeated before through-migration occurred. Similarly, relevant patterns of diffusion at larger spatial scales are lost with the 10×10 -km units of observation at the mesoscale. Dyer (1994) has run migration models using the 200×200 m unit of observation utilized in the landscape analysis on larger areas (150×150 km grids). Models also are being developed which utilize the landscape approach, utilizing a 1-km^2 unit of observation, and incorporating the influence of soils, disturbance, and additional biological characteristics to simulate migration at the biome scale (Dyer, in prep.).

4.2. Mesoscale results

Clarksburg / Charleston study area

Figs. 10 and 11 show the progression of both the wind-dispersed and bird-dispersed migrations, respectively. In both instances, little impediment to migration is encountered, as each modeled species moves through this heavily-forested study area as a uniform wave. Through-migration occurred for the wind-dispersed model at 423 generations, and for the bird-dispersed model at 127 generations. The minimum seed-bearing age for most individuals is about 10 years for pines, and 20 years for oaks (Schopmeyer, 1974; Burns and Honkala, 1990). Thus, using pine and oak as analogues for the wind-dispersed and bird-dispersed species, respectively, these migration rates translate to approximately 50 m/yr for pine and 83 m/yr for oak.

Fort Wayne / Muncie study area

The Fort Wayne/Muncie study area, dominated by agriculture, has been so intensively modified that very little suitable habitat remains to foster species migrations. Neither the wind-dispersed nor the bird-dispersed species were able to migrate through this study area due to the lack of suitable habitat at the southern end of the

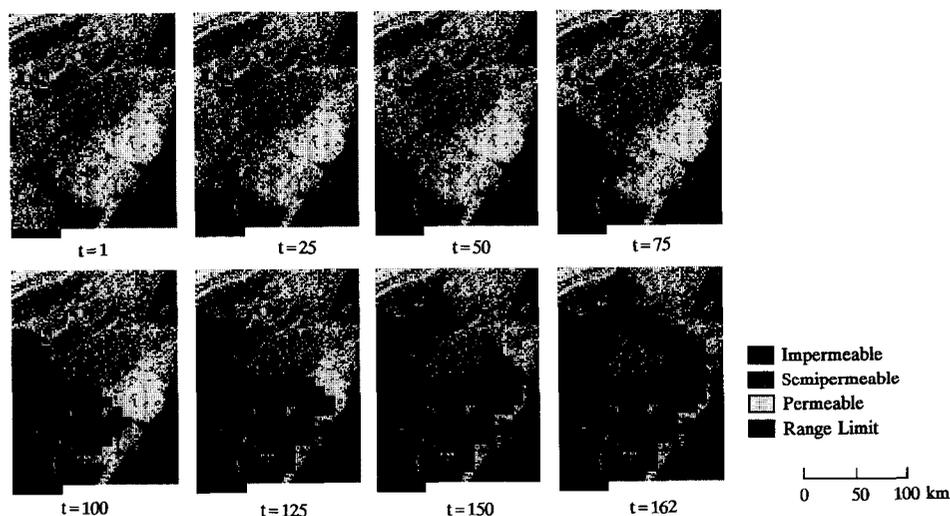


Fig. 12. Bird-dispersed migration through the Newark/Wilmington study area. Migration is circuitous through this fragmented study area, but successful in 162 generations.

study area. The wind-dispersed migration was halted in one generation, the bird-dispersed migration after seven generations.

Newark / Wilmington study area

A mosaic of human influence is presented with the Newark/Wilmington study area, as forested tracts are interspersed with intensively modified areas. The migrating species that encountered this patchwork in the models met with varying success.

The wind-dispersed species was unable to traverse the metropolitan area centered on Wilmington, Delaware, and migration was halted after 225 generations. The bird-dispersed species was able to migrate successfully through to the top of the study area. Fig. 12 shows the progression. Unlike migration in the heavily forested Clarksburg/Charleston study area, migration in this fragmented study area took a much more circuitous route. The “stepping-stone” nature of bird dispersal enabled the species to traverse the metropolitan areas west of the Delaware River and Bay, unlike the wind-dispersed species. The migration front then was able to fan out into New Jersey. Through-migration occurred at 162 generations, which translates to approximately 65 m/yr for oaks.

5. Discussion

Inherent to any modeling exercise are limitations imposed by the data which could affect model results. The use of quadrangles as study areas with their arbitrary boundaries, the resolution of mappable features, and the accuracy of the LULC data all potentially could limit the interpretation of the results. Likewise, simplifications necessitated in model assumptions could influence migration outcomes. Despite these limitations, general patterns of potential future species migrations are indicated by the current models.

5.1. Comparison with post-glacial migration rates

Since past migrations cannot provide direct analogues for comparison with anticipated future

conditions, true model validation is not possible with the present research. However, post-glacial migration rates can be used as a benchmark to determine if model results lie within reasonable expectations. Delcourt and Delcourt (1987) provide post-glacial migration rates for several eastern North American taxa, derived primarily from palynological evidence. These values represent the responses of various species to a relatively recent climatic warming, before extensive human modification of the landscape.

The average migration rates for oaks and southern pines as presented in Delcourt and Delcourt (1987) were 126 m/yr and 81 m/yr, respectively. Average migration rates from the Clarksburg/Charleston study area for bird-dispersed (oak) and wind-dispersed (pine) species were 83 m/yr, and 50 m/yr, respectively. This study area is the least modified by human influence, and thus is most suited for direct comparison. The figures indicate that although migration rates for both taxa are slower with the model, the ratio of the migration rates are similar between the model and the palynological record. The results of the model, which employs actual dispersal values cited in silvics literature, therefore appear to be in accord with realistic expectations.

The fact that average migration rates for both pines and oaks are slower in the model than those seen in the palynological record could indicate a short-coming of the model. The differences in rates could also reflect real differences in today's landscapes compared to the early Holocene. As the continental glacier retreated at the close of the Pleistocene, the newly-opened sites for colonization would have presented a very different environment for any migrating species, as compared for instance to the closed forest characteristic of much of the Clarksburg/Charleston study area. Open parkland vegetation with scattered woodlots occurred south of the ice sheet (Jacobson et al., 1987), and should have provided ideal habitat for early successional species such as pine, or edge-favoring species such as oak. Jays migrating north behind the retreating glacier could have greatly facilitated the advancement of oaks (Johnson and Webb, 1989); it is also possible that steeper pressure

gradients also could have resulted in greater wind dispersal distances, and hence more rapid migration of pines.

5.2. *Future migrations*

The models presented here were designed to examine the potential roles which land use pattern and means of dispersal could play if species are forced to migrate in response to future climatic warming. Because of the complex nature of such a scenario, many confounding factors by necessity were excluded from the models. The omission of these factors was for the sake of model tractability, and was not an attempt to ignore their potential role in future species migrations. Some salient factors in addition to land use and dispersal which invariably would influence migration rates and which themselves would vary with a climatic warming include seasonal climatic variations which could affect seed crop size and dispersal, disturbance (Overpeck et al., 1990), pest and pathogens (Dewar and Watt, 1992), soils (Pastor and Post, 1988; Perry et al., 1990), atmospheric pollution (Perry et al., 1990), CO₂ fertilization (Tolley and Strain, 1984; Williams et al., 1986), and interspecific competitive relationships (Solomon, 1986; Bazzaz, 1990). Predicting the effect of any of these additional external factors in a future warmer world would prove extremely difficult, especially considering their potential interactive effects. Also, it is likely that species would respond to the suite of factors described above individualistically. For these reasons, the present models included only the effects of land use pattern and dispersal means, thus facilitating interpretation of the potential role of a single factor, and also preserving the general applicability of the models.

Shifts in species ranges are a virtual certainty with a warming climate. Results of this modeling exercise indicate that some species may have difficulty migrating in response to climatic warming, when only the means of dispersal and land use variables are considered. Even when the modeled species were able to traverse the study areas successfully, migration times were long relative to

the anticipated rate of future climatic warming. If pine and oak are used as analog species for the wind- and bird-dispersed species, respectively, the models indicate that approximately 4230 years for pine and 2540 years for oak would be required to migrate through the forested Clarksburg/Charleston study area (based on generation times of 10 years for pine and 20 years for oak). It would take approximately 3240 years for oak to migrate through the fragmented Newark/Wilmington study area. These rates indicate that species capable of negotiating today's landscapes may not be able to do so quickly enough. If species are unable to migrate to their new ranges in conjunction with a climatic warming, the vegetation cover is likely to be in a widespread climatic disequilibrium for several centuries, or perhaps millennia.

6. **Conclusion**

Migration models were developed which maintained the spatial structure of modern landscapes, in order to investigate forest species' abilities to respond to a potential climatic warming. At a fine (landscape) scale of analysis, it was found that continuous tracts of "favorable" permeable land use would be required to facilitate the migration of a wind-dispersed species through the landscape. Results indicate a negative logarithmic relationship between average wind-dispersed migration rate and percent permeable cover. Since bird dispersal is a much more directed event, as jays preferentially transport acorns to suitable edge habitat, results indicate that bird-dispersed species could be maintained with only a series of favorable habitat "islands" interspersed at distances within the birds' foraging range; other factors such as the size of such woodlots, or issues of biological and genetic diversity were not considered. To these ends, continuous tracts of favorable habitat may benefit both the wind- and bird-dispersed species; both species met with greatest success in the heavily forested study area. Although model results indicate that widely-spaced permeable edge habitat

may be sufficient to enable migration of bird-dispersed species through a landscape, the quantification of this relationship was not possible. Thus, no good correlation was obtained between bird-dispersed migration rates and measures of land use dominance, edge, central tendency, or spatial configuration. Other indices of landscape pattern recently have been put forth (O'Neill et al., 1988; Turner et al., 1989); however, due to the sensitivity of modeled bird-dispersed migration rates to slight differences in landscape geometry, it is unlikely that other measures would have offered significant improvement.

Aggregating results from the landscape-scale analyses, and using pine and oak as analogues for wind-dispersed and bird-dispersed species, respectively, average migration rates in the least disturbed study area (Clarksburg and Charleston quadrangles) were approximately 5.0 km per century for pine, and 8.3 km per century for oak; if significant global warming occurs next century, these migration distances would fall short of projected range shifts by at least an order of magnitude. The fastest migration rates for any model landscape were 8.1 km per century for pine, and 13.6 km per century for oak. These rates are significantly faster than average rates, but still appear inadequate to match the rate of northward displacement of isotherms over the next several centuries.

This research demonstrates the importance of incorporating spatially explicit, probabilistic processes into simulation modeling efforts. Indications are that the interaction of rapid climate change, current land use patterns, and dispersal limitations may cause the majority of temperate forest taxa to persist in relatively inhospitable circumstances, maintaining a climatic disequilibrium for some time after the cessation of a warming trend. Such a condition may lead to enhanced susceptibility to natural disturbances such as disease or pest infestation, as well as to both direct and indirect anthropogenic influences. These conclusions point to the general need to include a more regional, landscape perspective in land-use planning, as well as a specific need to create a mosaic of greenspaces suitable for the migration of forest taxa.

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