Land use pattern, forest migration, and global warming

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Abstract

Range limits of many plant species are expected to shift dramatically if climatic warming, driven by the release of greenhouse gases, occurs in the next century. The ability of species to migrate in response to the range shifts has been questioned, especially in the context of extensive habitat fragmentation which occurs in modern-day landscapes.

Simulation models are presented which incorporate two factors, land use pattern and means of dispersal, to assess potential responses of forest species to climatic warming. Study areas displayed a range of human influence on the landscape, from heavily forested areas to areas dominated by urbanization and agriculture. The effect of establishing corridors (greenways) through fragmented landscapes is also assessed.

Results indicate that many species may be unable to track shifts in climatically-controlled range limits, resulting in widespread disequilibrium between vegetation and climate. A variety of mitigating options likely will be necessary to offset the negative consequences of climatic warming on biological diversity. Land use planners and managers are encouraged to incorporate climate warming into long-term planning.

Keywords: Forest migration; Global warming; Land use pattern

1. Introduction

With the expected doubling of atmospheric carbon dioxide in the next century, global mean surface temperatures are projected to rise 4.2 ± 1.2 °C. The magnitude of this warming approximates that which occurred (5 ± 1 °C) since the last glacial maximum (Webb, 1992). The biotic environment has undergone dramatic transformations in response to the changing climate of the last 18 000 years. For example, the northern range limit of oak (*Quercus*) in North America has extended from 37–38°N at the full glacial to 47–49°N today (Delcourt and Delcourt, 1987), a distance of 800–900 km. The rate of potential future warming, 3°C per century or faster, will be more rapid than that which oc-

curred in the last 18,000 years (Webb, 1992) Given the rapidity of this climate change and the magnitude of the biotic response, there is concern over the ability of vegetation to shift into any new climatically-defined ranges. This is especially true given the highly fragmented landscapes of today.

Models were developed to explore the ability of plants with different means of dispersal (by wind and bird) to migrate through present-day landscapes. Although previous research has addressed the potential rate and magnitude of range adjustments to future warming, no studies have explicitly sought to assess the ability of tree species to migrate under current landscape conditions.

Several authors have developed computer

models to simulate seed dispersal. These models usually include micrometeorological conditions, seed densities, life-history characteristics, and behavioral characteristics of dispersing animals (e.g. Johnson et al., 1981; McClanahan, 1986; Greene and Johnson, 1989). The complexity of these models necessitates that applications be restricted to individual plants and relatively short time periods. A more general approach was sought for this project. Only presence/absence of the migrating species was modeled, density effects were excluded. In this way, the models were able to examine range expansion over extensive areas resulting from the cumulative effect of many dispersal events over many years. In addition, the models were coupled with a geographic information system (IDRISI) which enabled explicit spatial relationships to be maintained and visual inspection of the simulations. The results of the analyses may prove to be useful for resource planners and land managers who face the difficult task of developing and implementing strategies to mitigate the negative impacts of climatic warming on biotic resources.

2. Methodology

Three study areas were selected which reflected the range of human impact upon the landscape. Each measured 2° of latitude by 2° of longitude (approximately 270×180 km), and consisted of two 1:250 000 U.S. Geological Survey quadrangles. The first study area is situated in the Appalachian Plateau and is comprised of the Clarksburg and Charleston quadrangles. This area is primarily in woodland and forest, with some cropland and pasture. It represents one of the largest regions in the United States with minimal fragmentation of forest cover, and as such would be expected to offer negligible land-use resistance to species migration. At the other extreme in terms of land use is the study area consisting of the Fort Wayne and Muncie quadrangles, in the Central Lowlands. This area is mostly cropland with only scattered woodlots and strands of riparian forest. The third study area, intermediate in land use intensity, con-

sisted of the Newark and Wilmington quadrangles situated primarily in the Atlantic Coastal Plain. This area contains large expanses of continuous forest and wetland, as well as extensive agriculture and some of the most heavily urbanized areas on the eastern seaboard.

U.S. Geological Survey digital Land Use Land Cover (LULC) maps were obtained for each study area. These maps portray the level II categories of the Land Use and Land Cover Classification System (Anderson et al., 1976). The maps are divided into 4 ha cells (200×200 m), with each cell assigned the value of the LULC feature located at its center.

To simplify the migration process, LULC categories were reclassified according to their likelihood of successful colonization by advancing tree species. Cells were designated as follows: (1) impermeable, with a low probability of successful establishment by migrating species (e.g. cropland, water bodies, central business districts); (2) semipermeable, with an intermediate probability (e.g. residential areas, highway right-of-ways); and (3) permeable, which would have a high probability of successful establishment (e.g. forest, forested wetland).

Each study area was divided into contiguous 10×10 km grids (50×50 cells), for a total of 987 grids. For each grid, the percent cover of the three permeability classes was calculated, as well as Moran's I, an index of spatial autocorrelation based upon the covariance of juxtaposed cell values. As with a classical correlation coefficient, Moran's I approaches 1 when similar values cluster, and approaches −1 as cells with dissimilar values become juxtaposed. Finally, measures of permeable "edge" were calculated. Edge cells are defined as permeable cells which border either semipermeable or impermeable cells. As described below, these cells are "targets" for bird dispersal. Both total edge and dispersion of edge cells were computed for each grid.

Details of the migration models are described in Dyer (1994a). The initial condition assumes the species range limit is at the bottom of the grid. Each time interval represents one generation for the particular species (the time for seed-bearing adults to develop from seed). Dispersal param-

eters were obtained from a review of forestry literature (e.g. Schopmeyer, 1974; Burns and Honkala, 1990). Acknowledging their ecological and economical importance, pines served as the model for the wind-dispersed tree and oaks served for the bird-dispersed tree.

In each generation there are two components of dispersal for the wind-dispersed tree: local and random long distance. Local dispersal extends the current range 200 m to any adjoining cell. Successful establishment occurs if the propagule lands in a permeable cell, or in a semipermeable cell with two neighboring cells, or one neighbor and all four diagonal cells already colonized. This minimum perimeter requirement for colonization reflects the difficulty migrating species would encounter in semipermeable cells. Impermeable cells are never colonized. A random long-distance event disperses seed to a single cell located 200 m to 2.5 km beyond the current range. This results in successful colonization only when the recipient cell is permeable.

Three components of dispersal occur each generation for the bird-dispersal model: local, long distance, and random long distance. Local dispersal, performed by gravity and rodents, extends the range 200 m to any adjoining cell. Long distance dispersal is accomplished by birds, notably blue jays, and extends the range 1.1 km. Since jays cache acorns primarily in edge environments (e.g. the border of forest and an agricultural field), only "edge" cells are considered receptive to jay dispersal. Since blue jays are known to fly longer distances than the average 1.1 km (Darley-Hill and Johnson, 1981), one

random long-distance dispersal event occurs from 1.1 to 5.0 km beyond the current range. Colonization rules for inoculated cells are the same as for the wind-dispersal model.

Major differences in dispersal characteristics between the two models are (1) the greater distances birds are capable of transporting seeds compared with wind dispersal, and (2) the directed nature of bird dispersal. Whereas dispersal of seed to suitable habitat by wind is largely a chance event, jays cache acorns in sites which are highly suitable for successful establishment (Darley-Hill and Johnson, 1981); suitable habitat within the transport distance of the blue jay always is colonized.

Through-migration occurs when at least one cell in the top row of the grid is colonized within an imposed time limit. Three iterations of each model were run on each grid.

3. Results

A logarithmic relationship was found between average wind-dispersal migration rates and percentage of permeable cover in the grid ($R^2 = 0.80$, $n = 471$). This substantiated an intuitive expectation, that as the proportion of "favorable" permeable cover increased, the number of generations required for through-migration would decrease. When only successful iterations (i.e. those resulting in through-migration) are considered, slowest grids ($n = 32$) average 28% permeable cover, and have an average migration rate of 23 m year^{-1}, assuming a generation time

Table 1
Characteristics of 10×10 km landscape grids with fastest and slowest average migration rates

Subset	Number, by study area[a]				Average migration rate (m year^{-1})	Percent land use		
	C/C	F/M	N/W	Total		Urban	Agriculture	Forest (range)
Fastest bird	15	5	16	36	104	10	31	44 (1–97)
Slowest bird	22	4	4	30	37	4	15	76 (6–100)
Fastest wind	33	0	1	34	64	2	6	92 (60–100)
Slowest wind	3	4	24	31	26[b]	20	51	23 (7–45)

[a] C/C, Clarksburg and Charleston; F/M, Fort Wayne and Muncie; N/W, Newark and Wilmington.
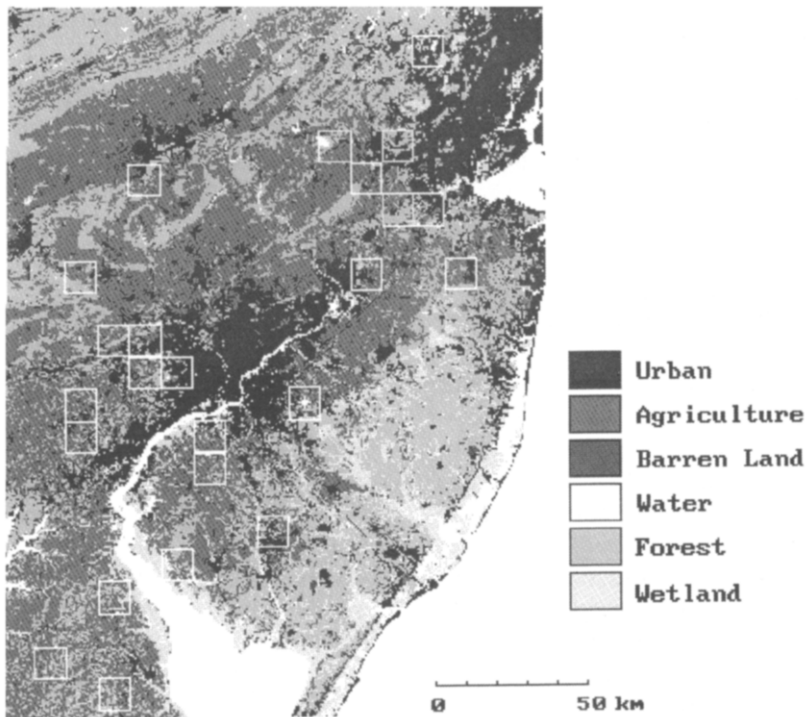[b] Average based on the fastest of three model iterations.

Fig. 1. Level I land use in the Newark and Wilmington quadrangles. The majority of grids with the slowest wind-dispersal migration rates occur in this study area (Table 1) and are indicated by the large white squares. None has continuous north–south corridors. The grid to the east of the Philadelphia metropolitan area marked with an asterisk is depicted in Fig. 2.
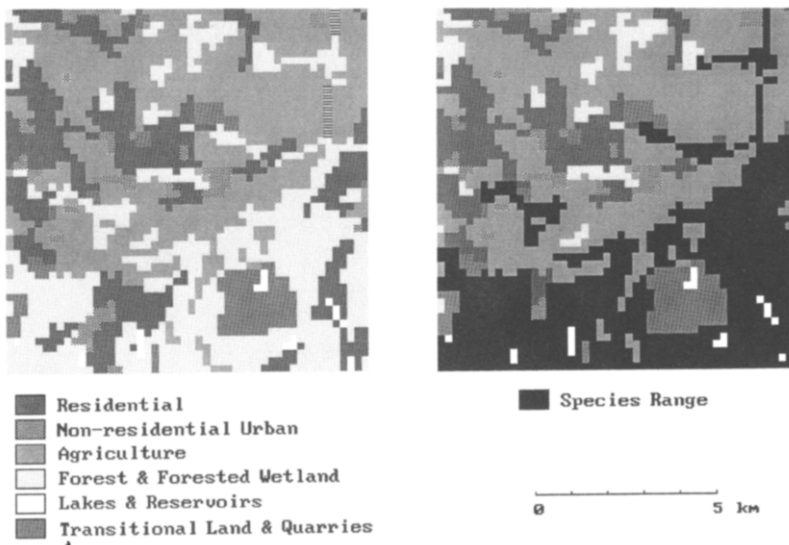

Fig. 2. Land use in a sample 10×10 km grid. Left: parcels converted from agriculture (44 ha) to establish a continuous north–south forested corridor are indicated by horizontal lines (upper right of grid). Right: range expansion of the wind-dispersed species through the modified grid. Average migration rate through the grid was 24 m year^{-1}.

of 10 years for pines (Krugman and Jenkinson, 1974). The fastest grids ($n=35$) average 82 m year^{-1}, and have an average of 88% permeable cover. This relationship holds for the entire data set as well as for the individual study areas. In addition, the permeable cover in the fastest grids is also highly "connected", existing in continuous tracts throughout the grids. Slowest grids are highly fragmented, with a mixture of permeability classes.

In contrast, no good relationship was found between average bird-dispersal migration rates and the percentage or configuration of permeable cells. Bird-dispersal migration rates are sensitive to the specific configuration of cells within the grids; fastest rates occur when suitable cells are situated at distances near the maximum dispersal ranges of the birds, allowing the migrating species to quickly disperse through the grid in a "stepping stone" manner. Although fastest bird-dispersal migration rates often occur in fragmented grids with a low percentage of permeable cover, this should not be construed to suggest a low percentage of favorable habitat is beneficial to migration. Grids in which successful bird-dispersal migration is not possible ($n=297$) average only 3% permeable cover; the majority of these are located in the agriculturally-dominated Fort Wayne/Muncie study area (68.7%) or the urbanized Newark/Wilmington study area (30.6%). In contrast, grids which experience successful through-migrations ($n=690$) average 52% permeable cover. Over half of these grids exceed 50% permeable cover, although a great range exists. The fastest bird-dispersal grids ($n=36$, average migration rate = 104 m year^{-1}) have permeable land use ranging from 1–97%, while slowest grids ($n=30$, average rate is 104 m year^{-1}) range between 6–100% permeable cover. These average migration rates assume a generation time of 20 years for oaks (Olson, 1974), and closely approximate the average migration rate for oaks of 126 m year^{-1} determined from the post-glacial palynological record (Delcourt and Delcourt, 1987).

Subsets of the fastest and slowest grids for both the wind-dispersal and bird-dispersal models were examined to explore the effects of land management practices within these grids. Specifically, corridors (greenways) were emplaced in all grids which did not contain continuous north-south tracts of permeable land use. Corridors were 200 m wide, and linked existing cells of permeable land use. They were configured to minimize land use conversion from semi- or impermeable land uses to permeable land use.

3.1. Corridor analysis

Grids with the fastest and slowest average migration rates were selected. Characteristics of these subgroups are summarized in Table 1. Data in Table 1 suggest that bird-dispersal migration is largely insensitive to land use configuration. Fastest and slowest bird-dispersal grids display a similar range of forested land percentage. In addition, this forested land does not exist as continuous north–south tracts in 21 of 36 fastest bird-dispersal grids, yet 23 of 30 slowest bird-dispersal grids have continuous tracts of forest. A visual inspection of these grids reveals that fastest rates occur when suitable target (permeable edge) cells are located at the center and also at 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. The configuration of target edge cells in these fast grids range from isolated woodlots surrounded by agriculture, to small openings in extensive forest cover. (When corridors were added to the grids which lack continuous forest, average migration rates are actually slowed significantly.) In contrast, slowest bird-dispersal rates occur in grids when "jump dispersal" is not facilitated, either by lack of forest cover, or a lack of openings within forested grids.

It is apparent that corridors could play a significant role in the successful migration of wind-dispersed species (Table 1). Fastest wind-dispersal grids have a high percentage of forest land, and in all cases it exists in continuous tracts. The slowest wind-dispersal grids have low percentages of forest, with none containing continuous north–south tracts of forest. The majority of these occurred in the Newark/Wilmington study area (Fig. 1). When corridors are added to these grids,

migration rates increase modestly but significantly (from 26 m year^{-1} to 29 m year^{-1}). Figure 2 presents a grid in which a corridor is added, and the subsequent pattern of migration through the grid.

4. Discussion

The models presented were designed to examine the potential roles which land use patterns and means of dispersal could play if species are forced to migrate in response to future climatic warming. It is apparent that the models omit factors which could affect the outcome of such a scenario. It is believed, however, that general indications of potential future migrations are possible with the current models. Indications are that some species may have difficulty adjusting to range shifts, resulting from inability to disperse through modern landscapes which have been altered by human activities. The establishment of corridors connecting parks and reserves has been proposed to facilitate migration in the face of global change (Peters and Darling, 1985). Riparian areas, especially if they include a topographic gradient to upland habitats, provide an excellent opportunity for corridor development (Noss and Harris, 1986). Corridors should be wide enough to support interior species of the reserves (Burke and Kiester, 1990); ideally corridors should serve as reserves in their own right (Peters, 1985; Jordan et al., 1988). However from this modeling exercise at relatively small spatial scales, as well as at larger scales (Dyer, 1994b), it is apparent that corridors alone can not mitigate the deleterious biological effects of climatic warming — many species still will not be able to keep pace with climatically-controlled range shifts. Other possible alternatives include the intensive management of existing reserves (Peters and Darling, 1985), transplanting species to restored habitat (Jordan, 1988) or the establishment of new reserves (Peters, 1988). The magnitude of potential changes probably will necessitate a variety of management options, and likely only will be feasible for a selected set of target species.

The most effective means for preserving future biological diversity is to minimize ongoing habitat fragmentation and the encroachment of development; however, there is little economic incentive to preserve biological diversity, despite its economic importance (Peters, 1990). Landscape planners and managers must be informed of the potential effects of climatic warming and incorporate climate change into their long-term planning. Although many uncertainties regarding the timing and magnitude of climatic warming exist, it is clear that the potential losses are significant enough to deserve action now.

5. Conclusion

Models were developed to assess the influence of land use pattern and means of dispersal on the ability of forest species to migrate through 10×10 km landscapes in response to climatic warming. The wind-dispersed species are dependent on the percentage and connectivity of favorable forested habitat in the landscape. The bird-dispersed species are less sensitive to these factors, exhibiting the ability to migrate through the landscapes in a "stepping stone" manner.

Corridors (greenways) were established in a subset of the landscape grids. These significantly increase average rates of wind-dispersal migration. However, they probably are insufficient as a sole means of preserving biological diversity in the context of climatic warming. Landscape planners are encouraged to incorporate climatic warming in long-term planning.

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