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Implications of Habitat Fragmentation on Climate Change-Induced Forest Migration

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A rapid warming caused by the release of greenhouse gases could result in the displacement of climatic controls that limit the current ranges of many species. Projected northward displacement for loblolly pine is over 400 km, with only a narrow region of overlap between the current and projected future range limits. A model of dispersal developed for loblolly pine is presented. The model utilizes a GIS to assess the critical influence of land use patterns on climate change-induced migration through modern landscapes. Results from two relatively large (150 × 150 km) study areas in the eastern United States suggest that potential migration rates may fall short by at least an order of magnitude of that necessary to track projected range shifts. Management options of species transplanting and the establishment of greenways are explored with the model. Species that are unable to keep pace with changing range limits may experience a reduction in population size and exist in climatic disequilibrium. **Key Words:** forest migration, land use patterns, climatic warming, range limits.

Introduction

Global mean surface temperatures are projected to rise 4.2 ± 1.2 °C with the anticipated doubling of atmospheric CO₂ during the

next century. The magnitude of this warming approximates that which occurred following deglaciation 18,000 years ago (5 ± 1 °C) (Webb 1992). Major changes in the distribution of vegetation accompanied climate changes in the

past. For example, Webb (1988) has used pollen data to construct maps showing the changing location, abundance, and association of individual taxa for eastern North America since the last glacial maximum. Although these maps cannot be used to define precise range boundaries, they can provide valuable estimates of the magnitude of range changes over time. For example, the maps indicate that the greatest northward range expansion of southern pines in the last 6,000 years, for which the best pollen record exists, occurred between 6,000–4,000 years ago (6–4 ka) along the Atlantic Coastal Plain. A longitudinal line (77° W) along the east coast intersects the 6 ka northern range boundary just south of the current Virginia–North Carolina border and intersects the 4 ka northern range boundary at the current Pennsylvania–Virginia border. This northward movement of approximately 370 km would necessitate an average migration rate of 185 m/yr.

At broad spatial scales, climate is the primary control on the distribution of most plant species (Mather and Yoshioka 1968; Rosenzweig 1968). In an effort to project future range changes, many studies have attempted to define specific climate controls on current range limits (e.g., Jacobson et al. 1987; Davis and Zabinski 1992). To have biological significance, the assigned limiting factors should be physiologically based. Actual evapotranspiration (AE), the actual loss of water from plant and soil surfaces, is a potentially useful variable for explaining plant distributions because of its simultaneous incorporation of precipitation, temperature, and soil moisture at a site (Stephenson 1990). Manogaran (1975) has demonstrated that a mean annual AE value of 762 mm delimits the northern and western range limit of the most commercially important forest species in the southern U.S. loblolly pine (*Pinus taeda*). Although it is more difficult to assign a climatic limiting factor for the southern range limit of a species physically constrained by the Gulf of Mexico, Manogaran (1975) used an annual AE value of 1,050 mm to define the climatic limit of loblolly pine in Florida. Figure 1 shows the native range of loblolly pine east of 85° W. Also shown in Figure 1 are projected 762 mm (potential northern range limit) and 1,050 mm (potential southern range limit) AE isolines obtained

from double-CO₂ scenarios of two general circulation models, GFDL (Manabe and Wetherald 1987) and GISS (Hansen et al. 1983). These projections were derived by first calculating a ratio (2×CO₂/1×CO₂) of AE change (Willmott 1977) and interpolating between model grid points. Modern AE estimates interpolated from a 1° × 1° grid (Willmott et al. 1985) were then multiplied by the AE change factors.

The models show remarkable similarities in their projections of the northern displacement of the potential range limit (cf Overpeck et al. 1991). In the eastern United States, northern displacement along a longitudinal line (77° W) is over 400 km. For the species to track this displacement if warming were to occur in the next 100–200 years, populations would need to migrate at the average rate of 2,000–4,000 m/yr. Projected northward displacement is even greater through the Appalachian Mountains to the west, but it is possible that the shallow, steep-sloping, coarse-textured upland soils would support only limited populations of loblolly pine (Miller et al. 1987). The potential southern range limit is also displaced substantially, resulting in a relatively narrow zone of overlap between the current and projected future ranges. It is unlikely that loblolly pine could adjust rapidly to these changes, especially in the context of extensive habitat fragmentation and the establishment of migration barriers by current land use practices (Peters and Darling 1985). If a species is unable to track a climatic change, it will experience a reduction in range and, therefore, a reduction in population size (Davis and Zabinski 1992).

This study attempts to assess the influence of land use on the ability of a wind-dispersed tree species to migrate in response to climatic warming. Previous studies have explored the magnitude of range adjustments in response to potential future warming; this study seeks to assess explicitly the ability of trees to migrate through actual landscapes. Typical models of dispersal by wind include specific micrometeorological and seed density components (Johnson et al. 1981; McClanahan 1986; Greene and Johnson 1989) or require explicit assessments of physical characteristics and biological interactions at a site (Hanson et al. 1990). The model presented here differs in scale and approach (Dyer, forthcoming). An

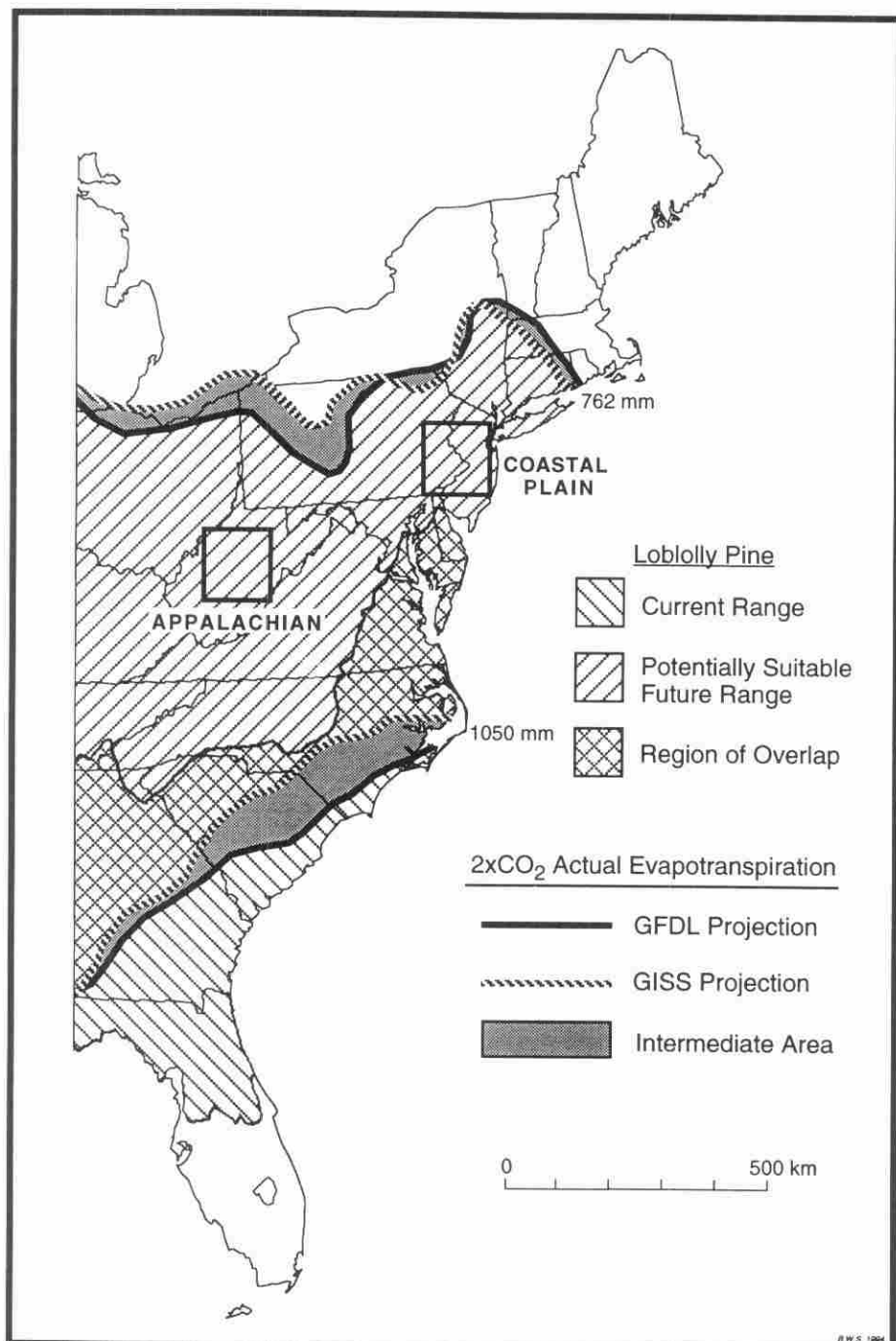


Figure 1: Study areas with current range of loblolly pine (Little 1971) and potentially suitable range with doubled CO₂, east of 85° W. Field capacity is assumed to be 300 mm for actual evapotranspiration computations.

objective in developing the model was to study range expansion, so only presence/absence is modeled. By excluding density effects and modeling the cumulative effect of thousands of dispersal events over many years, the model is able to examine migration over extensive geographic areas. Additionally, since the model is coupled with a geographic information system (IDRISI) (Eastman 1990), explicit spatial relationships within the landscape are maintained. This feature enables the assessment of possible management options, such as the establishment of "greenways" to mitigate negative consequences of climate change or the transplanting of species to new sites well beyond their current range. To date, there have been few attempts at bringing a GIS perspective to global change issues.

Local processes that would influence colonization success are not included in the model. For instance, the model currently does not include (1) disturbance, which might influence the rate of forest response to climatic warming (Overpeck et al. 1990); (2) biotic interactions between species, such as competition for light or symbiotic relationships between plants and soil micro-organisms (Perry et al. 1990); or (3) physical and chemical properties of soils (Pennington 1986; Pastor and Post 1988), although these factors are being incorporated into a revised version of the model currently in preparation by the author. It is important to realize, however, that ecological responses differ with the spatial and temporal scales at which they are studied, and that controlling variables at each scale are likely to be different (Graham et al. 1990). As the spatial extent is increased, the number of important variables tends to decrease, and these important variables tend to be abiotic rather than biotic (Meentemeyer 1984; Meentemeyer and Box 1987). Despite its shortcomings, the current model can provide a useful means to move from the site-specific scale to a more regional scale, so that broad-scale questions of biotic responses to climate change can be addressed (Graham et al. 1990).

Methods

To explore the potential ability of a forest species to migrate through modern-day landscapes, two study areas were selected which

exhibit a range of human impact on the landscape (Fig. 1). Each measures 150 × 150 km. The first is located in the Appalachian Plateau province of West Virginia. This area possesses minimal fragmentation of forest cover and would be expected to offer minimal resistance to a migrating species, based on land use. The second area is located primarily in the Atlantic Coastal Plain and contains metropolitan areas centered around Philadelphia and New York, extensive forested areas in the Ridge and Valley province and in New Jersey (the Pinelands), and large areas devoted to agriculture. A wind-dispersed species would be expected to meet greater resistance to migration in this dissected study area (Gardner et al. 1991).

A model of dispersal was developed for loblolly pine (Dyer, forthcoming). A literature review was conducted to determine estimates of seed production, seed dispersal distances, and generation time (number of years for adult seed-bearing trees to develop from seed). The first objective was to define a distance that loblolly pine could routinely disperse seed into new areas in such quantities as to establish a viable population. A number of studies present estimates of annual production of sound seed per acre (0.4 ha) over a number of years (Allen and Trousdell 1961; Lotti 1956; Lotti and LeGrande 1959; Pomeroy and Korstian 1949). These values were used to approximate the potential number of seeds which could be produced over a 10-year period, which represents an estimated minimum generation time for loblolly pine (Krugman and Jenkinson 1974). The range was from 1.3 million to 3.7 million sound seeds per acre. Estimates of viable seed densities dispersed to various distances were then obtained from published results of a long-term study of dispersal from a loblolly forest stand (MacKinney and Korstian 1938 (covering a one-year period); Jemison and Korstian 1944 (two four-year periods); Pomeroy and Korstian 1949 (one five-year period)). These data were fitted to a negative exponential curve to model seed density as a function of distance from the forest stand (Peart 1985). Greatest dispersal distances are reported in Jemison and Korstian (1944). Using this dispersal curve and the range of estimates of seed production, a maximum distance over which dispersal could reasonably occur within a generation was es-

tablished as 1 km. At this distance, a 4 ha plot (the smallest unit of observation in the dispersal model, as described below) would be inoculated with five to 13 viable seeds from a stand of monoecious loblolly pine. This potential migration rate of 1 km per generation, therefore, represents a probable maximum distance over which wind-blown pine seed could be dispersed routinely and is significantly farther than a value used in a previous modeling exercise (Dyer, forthcoming). Greater maximum dispersal distances are possible although much less common; Reynolds (1933) reports an apparent dispersal distance for loblolly pine of 4 km.

In each time interval, which represents a generation for the migrating species, two classes of dispersal are modeled. Local dispersal occurs 1 km in all directions from the current range. In addition to local dispersal, random long-distance events also are modeled in an attempt to simulate those chance dispersal events that nevertheless could influence range expansion (Van der Pijl 1982). In the absence of empirical data on the frequency of such events for loblolly pine, 10 random long-distance dispersal events were assumed to occur each generation (arbitrarily set at one event per year for a 10-year period). Random dispersal distance is 1–4 km from the current range. This value is significantly farther than that used in a previous modeling exercise (Dyer, forthcoming).

As an initial modeling condition, the southern edge of each study area was established as the species range limit. Digital land use land cover (LULC) maps were obtained from the U.S. Geological Survey for each study area. These maps are divided into 4 ha (200 × 200 m) cells, and each cell is assigned the value of the level II category of the Land Use and Land Cover Classification System (Anderson et al. 1976) feature located at its center. Although a 4 ha resolution may mask important landscape variability, such generalization should not obscure the dominant pattern of regional land use. To simplify migration modeling, LULC categories were reclassified according to their likelihood of successful colonization by advancing tree species. Cells were designated as (1) impermeable, with a very low probability of successful colonization by mi-

grating species (e.g., cropland, CBDs, water bodies); (2) semipermeable, with an intermediate probability (e.g., highway right-of-ways, residential areas); and (3) permeable, which would have a very high probability of successful establishment (e.g., forest, forested wetland). Table 1 provides general land use characteristics for the two study areas by presenting level I LULC category summaries. The Appalachian site is clearly dominated by forest, whereas the Coastal Plain site has a mixture of land use classes.

Local and random long-distance dispersal occur each generation, inoculating those 4 ha land use cells within the dispersal range. Successful establishment occurs if the seed inoculates 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 is colonized when at least two cells alongside of it already are colonized or when one side and all four adjoining diagonal cells already are colonized. Previous research has determined that reducing the necessary number of colonized neighboring cells to one or changing colonization rules such that semipermeable cells became colonized after being inoculated during two different time intervals, regardless of the status of neighboring cells, did not have a major effect on migration rates (Dyer, forthcoming). Impermeable cells are never colonized. Random dispersal results in successful colonization only when the seed reaches a permeable cell. Through-migration occurs when colonization of the top row of the study area takes place.

To explore two possible management options aimed at mitigating the effect of habitat fragmentation on migration, the dispersal model first was run again for the Coastal Plain

Table 1 Level I Land Use Land Cover (%) in the Two Study Areas

Land Use	Appalachian	Coastal Plain
Urban	1.82	22.75
Agriculture	11.38	39.33
Rangeland	0.01	<0.01
Forest	85.70	31.26
Water	0.29	1.83
Wetland	0.04	3.61
Barren Land	0.76	1.22

site after the establishment of two continuous north-south corridors. These corridors are 200 m wide and link existing cells of permeable land use. They are configured to minimize land use conversion from semi- or impermeable land uses to permeable land use. The corridors occupy 63.2 km², of which 5.2 km² (0.02% of the study area) were converted from another land use. A second modified run was then performed for the Coastal Plain site. In addition to the initial condition in which the southern edge of the study area was established as the range limit, the modeled species also was "transplanted" to a single 4 ha cell located north of a large urban area which would be expected to hinder migration through the study area.

Results

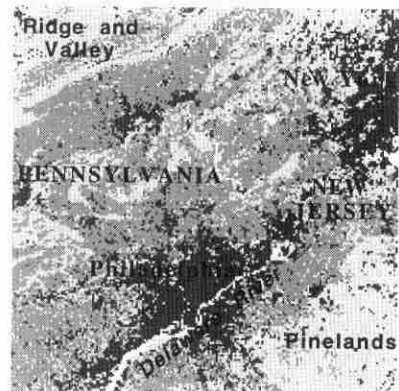
The modeled species is able to traverse the heavily forested Appalachian site as a uniform wave front, colonizing 18,767 km² (83%) of the study area when through-migration occurs. This supports findings from an earlier study performed at smaller spatial scales (Dyer, forthcoming) which found that wind-dispersed migration rates were highly correlated with the percentage of forested land within the landscape. Since this study area is minimally affected by human action when compared to other areas in the eastern United States, modeled migration rates should approximate the estimated northward displacement for southern pines (including loblolly pine) of 185 m/yr which occurred 6–4 ka, assuming that this Holocene migration rate was constrained solely by dispersal limitations. The average migration rate for the modeled species, assuming a generation time of 10 years, is 160 m/yr (150 km in 940 years). Considering the difficulty in defining precise range boundaries for southern pines from the pollen record, it is felt that the model result is an acceptable rate, and that the model can provide useful information concerning migration through landscapes influenced by human activity.

Figure 2 illustrates range expansion through the Coastal Plain study area. The species is able to migrate through the forested New Jersey Pinelands in the eastern portion of the study area within 50 generations. In the west,

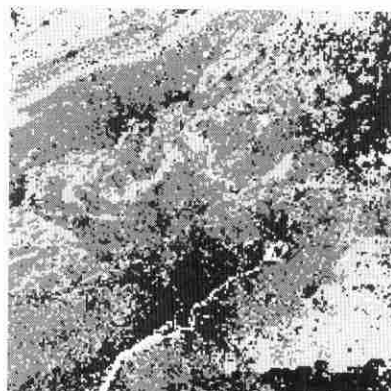
the species requires over 130 generations to join up with the eastern migration wave north of Philadelphia. A single front then slowly migrates northward through the center of the study area, west of the large New York urban area. The modeled species is forced to migrate around the perimeter of both large metropolitan areas, Philadelphia and New York, by a lack of continuous habitat. The species colonizes 6,463 km² of the 22,500 km² study area when through-migration occurs. The average migration rate through the entire study area is 86 m/yr (150 km in 1,740 years).

To explore the role which greenways could play in facilitating migration through areas of fragmented habitat, two continuous north-south corridors, 200 m wide, were established in the study area, one west of the Delaware River through Pennsylvania and the other east of the river through New Jersey. Figure 3 depicts the pattern of range expansion when the model is run with corridors. The pattern and rate of migration are very similar to that in the original study area as the species migrates to the west and east of the Philadelphia metropolitan area. North of this area, however, the pattern changes dramatically. In the west, the corridor enables the species to colonize and disperse through the extensive forested tracts of the Ridge and Valley province in the northwestern section of the study area. In the east, the species is no longer forced to take such a circuitous route around the New York metropolitan area. In addition to these new migration routes opened with the corridors, the original migration route is followed also. The average migration rate through the study area is 117 m/yr (150 km in 1,280 years). Although the species migrates through the modified study area 460 years faster, virtually the same amount of area (6,164 km²) is occupied by the species when through-migration occurs because additional habitat is opened with the corridors.

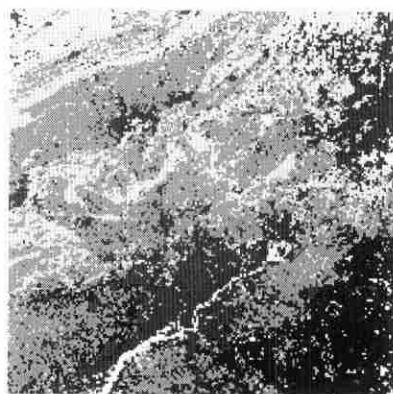
Also shown in Figure 3 is the pattern of range expansion after the species has been transplanted ahead of the current range at the onset of the model run. The transplant site, circled in Figure 3, is north of the large Philadelphia metropolitan area which hindered migration in the initial model run. As expected, through-migration occurs much more rapidly



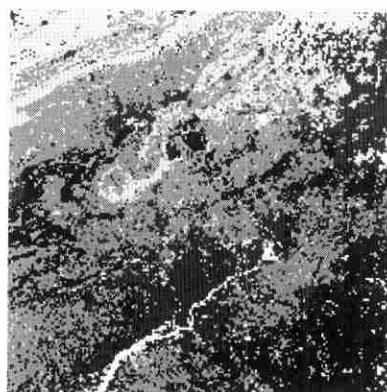
t = 0



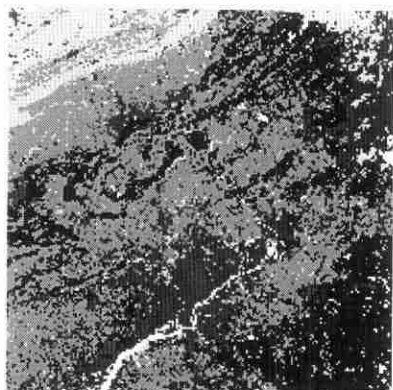
t = 10



t = 50



t = 130



t = 174

-  Urban
-  Agriculture
-  Forest and Wetland
-  Water and Barren Land
-  Species Range

0 150 km

Figure 2: Migration of loblolly pine shown with level I land use land cover in the Coastal Plain study area. Time intervals are generations.

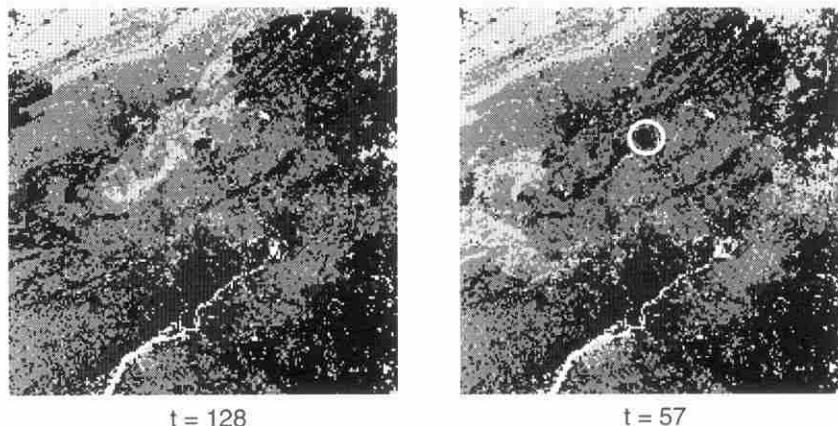


Figure 3: Pattern of loblolly pine range expansion through the Coastal Plain study area after the establishment of corridors (left) and after transplanting (right). The 4 ha transplant site is within the circle. Time intervals are in generations. Legend is the same as in Figure 2.

with the transplanting (57 generations or 570 years). Compared to the initial model run, the species reaches the northern edge of the study area in a third of the time, yet it colonizes 5,089 km² of the study area, or 79% of the area colonized after 1,740 years in the initial run. Occupied sites are virtually the same for the two model runs except for the central-west and central-east portions of the study area which had not yet been colonized in the transplant scenario.

Conclusions

The model was designed to examine the potential role which land use patterns could play if a species is forced to migrate in response to future climatic warming. As noted earlier, many factors which could influence the biotic response to climatic warming are not considered in the current model. Because species undoubtedly will respond individually to future climate change as they have in the past (Davis 1989), it will be necessary to understand how additional climate-dependent factors that affect forest dynamics can influence the vegetation response (Pacala and Hurtt 1993). Many species will be unable to respond at the rate at which mean temperatures will increase with global warming, which is expected to be faster than any time since the last glacial maximum (Webb 1992). This is especially true consider-

ing the barriers to dispersal caused by habitat fragmentation by human land use patterns (Peters and Darling 1985). Thus, it is important to evaluate the role that land use may play as a limit to migration. It is believed that general patterns of range expansion through relatively large regions can be ascertained from the model, despite simplifications in model assumptions and limitations imposed by the land use data.

Assuming a generation time of 10 years for loblolly pine, simulated migration through the 150 × 150 km Appalachian study area occurs in 940 years; 1,740 years are required to migrate through the Coastal Plain study area. Forested land accounts for over 85% of the Appalachian site; this figure is under 35% in the Coastal Plain site (Table 1). Migration rates through the two study areas indicate that even in areas of extensive favorable habitat, migrating species are unlikely to keep pace with a projected climate change. This is especially true in areas which have undergone extensive habitat modification. These findings are consistent with the results of percolation theory applied to the spread of populations through heterogeneous landscapes. Gardner et al. (1991) concluded that when forest accounts for less than 60% of the landscape, habitat becomes highly fragmented and a dispersing population is unable to reach much of the available habitat. Thus factors which or-

ganize landscape patterns, including land use, produce landscape-specific results. Although only one species was modeled in this exercise, it would seem that urbanization and agriculture may act as selective filters on species migrations.

The establishment of corridors linking habitat remnants is an important issue in resource management (Noss and Harris 1986), especially in the context of climatically driven migrations (Peters and Darling 1985). The establishment of corridors through the Coastal Plain study area did significantly increase the rate of migration. However, the improvement still would not allow species to track anticipated range shifts caused by a rapid climate change. If species are unable to keep pace with changes in their range limits, widespread disequilibrium between vegetation and climate is likely and could continue for long after climate stabilizes.

Other mitigating actions which may be pursued include large-scale transplants of species to new sites if they are unable to migrate naturally. The transplanting of the modeled species in the Coastal Plain site greatly accelerated overall northward migration while still allowing the colonization of large areas. Although wholesale transportation of soil and seed banks may be a future management option, it is difficult to conceive of this "stepping stone" approach being utilized to preserve all species threatened by climate change. Potential future climatic conditions should be a siting factor in the establishment of any new reserves; intensive management of existing reserves (e.g., irrigation) also may be necessary.

Critical gaps in our knowledge prevent specific actions with regard to biotic response to climate change. Immediate research needs include (1) an increased understanding of how species respond to climate and climatically altered ecosystem dynamics, and how climate change could alter species distributions and relationships with other organisms; and (2) improved techniques of habitat management and restoration (Peters 1988). The rapidity of climate change, current land use patterns, and dispersal limitations may interact to put many species at risk if preventative measures are not instigated. Although many uncertainties regarding climatic warming remain, the significance of the potential erosion of biotic re-

sources lends credence to the development of contingency plans now. ■

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Geographical Dimensions of Environmental Restructuring in New Zealand*

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During the 1980s, New Zealand underwent a period of dramatic economic, social, and administrative restructuring. The reform extended to the administrative arrangements for environmental management. A geographic restructuring model is used in this paper to establish the context in which the reforms were carried out. A combination of economic, environmental, and social influences operating at different geographic scales can be identified. These influences are subsequently illustrated through reference to three aspects of the restructuring that have distinct geographical dimensions: the definition of human-environment relations, the spatial definition of planning regions, and the implications of spatial differentiation for resource management policy and practice. **Key Words:** environmental planning, resource management, local government, administrative restructuring, New Zealand.

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Introduction

Shifts in the global economy and a deeply set domestic economic crisis were the preconditions to a period of dramatic restructuring in New Zealand. Begun in the 1980s, sweeping social, economic, and administrative reforms have been the most far-reaching and radical in New Zealand's history. As a part of this restructuring, administrative arrangements for environmental management have been thoroughly reorganized and strengthened. Against the background of right-wing economic, social, and administrative reforms, the strong commitment to environmental priorities is somewhat paradoxical. Indeed, the reform of environmental administration itself has at times been a potentially uneasy mix of free marketeering and government intervention.

This paper examines the context in which restructuring has taken place in New Zealand, with specific reference to the reform of the administrative arrangements for environmental management. Our analysis is framed by

the "geographic restructuring model" developed initially by Britton et al. (1992). This model helps to contextualize the various influences that have contributed to the restructuring process, emphasizing the relevance of geographic scale. Within this paper, three specific aspects of the reform of environmental administration which have strong geographical elements are discussed in detail: (1) the definition of human-environment relations; (2) the spatial delineation of planning areas; and (3) the implications of spatial differentiation in respect of environmental management. The restructuring model provides explanations for the manner in which these elements have been treated in the reform of environmental administration, while the issues themselves provide specific contexts within which to extend the description of the model.

The Restructuring Context

New Zealand's restructuring imperative was derived from a crisis of global capitalism and a

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