



Fire and forest landscapes in the Georgia Piedmont: an assessment of spatial modeling assumptions

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Abstract

Landscape simulation models are widely used to study the behavior of ecological systems. As computing power has increased, these models have become more complex and incorporated more realistic spatial representations of landscape patterns and ecological processes. The goal of this research was to examine the sensitivity of simulated landscape patterns to fundamental spatial modeling assumptions. The LANDIS simulator was parameterized for forests of the Georgia Piedmont and used to model landscape-scale community dynamics at fire return intervals from 20 to 100 years. A base scenario incorporating localized seed dispersal along with landform-related variation in species establishment rates and disturbance regimes was contrasted with three alternative scenarios. The uniform habitat scenario applied the same set of species establishment coefficients across all landforms. The uniform dispersal scenario removed the effects of seed source abundance and pattern on species establishment. The uniform disturbance scenario assumed identical disturbance regimes on all landforms.

At the shortest fire return intervals, fire severities were low and the stand age distribution was dominated by older forests. At longer fire return intervals, fire severities were high and the stand age distribution was skewed toward younger forests. Species composition generally followed a gradient from fire-resistant species at short fire return intervals to fire-sensitive species at longer fire return intervals. However, some species exhibited bimodal distributions with high abundances at both short and long fire return intervals. Landscape responses to fire were similar in the uniform habitat scenario and the base scenario. Communities were less sensitive to fire return interval and had more fire-sensitive species in the uniform dispersal scenario than in the base scenario. Species composition in the uniform disturbance scenario was similar to the base scenario for the longest fire-intervals, but was more sensitive to changes in the fire regime at shorter fire return intervals. In models of Piedmont forest landscapes, accurate spatial representations of dispersal and fire regime heterogeneity are essential for predicting landscape-scale species composition under changing fire regimes. In contrast, the precise spatial representation of species–habitat relationships may be considerably less important.

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1. Introduction

The development of landscape simulation models and their application in forest management and land use planning have increased considerably over the past decade. Models have emerged as important tools in landscape research because other scientific approaches, such as experiments and observational studies, are often fundamentally limited in spatial extent, temporal scope, or the number and levels of variables that can be assessed (Caswell, 1988; Baker, 1989). Modeling provides a framework for synthesizing information about multiple ecological processes and their interactions to make predictions about system behavior across large areas and over long time periods. Landscape simulation models have been used to predict the influences of climate change on species distributions (He et al., 1999; Schwartz et al., 2001), to compare vegetation patterns and habitat suitability under different forest management scenarios (Gustafson and Crow, 1994; Hansen et al., 1996; Li et al., 2000), and to reconstruct past landscape patterns based on historical disturbance regimes (Wimberly et al., 2000; Wimberly, 2002). Modeling has also advanced our theoretical understanding of ecological thresholds and other emergent properties that can arise in complex, large-scale systems (Gardner et al., 1989; With and Crist, 1995; Fahrig, 2002). Because of the prevalence of simulation modeling in large-scale research, it is crucial that landscape ecologists have a strong conceptual grasp of the strengths and limitations of different modeling approaches, along with an understanding of how modeling assumptions and parameterization errors may influence model behavior.

The increasing accessibility of inexpensive computing power, geographic information systems (GIS) software, and broad-scale spatial datasets has brought about a major paradigm shift in the development of landscape models. Modeling efforts have evolved from non-spatial approaches such as whole-landscape and distributional landscape models (Baker, 1989) to spatial landscape simulators with more ecological realism (Mladenoff and Baker, 1999). Spatial modeling typically incorporates patterns of land cover and environmental heterogeneity, along with the movement of organisms, water, nutrients, and other ecosystems components. For example, environmental variables may structure the spatial distribution of species along gradients or into discrete community types (Cowell, 1993).

Frequencies, sizes, and intensities of fire and other disturbances can change with environmental setting, further influencing the spatial variability of forest structure and community composition (Kushla and Ripple, 1997; Shinneman and Baker, 1997; Heyerdahl et al., 2001). The distributions of plant species may also be mediated by seed dispersal, which can limit establishment in otherwise suitable habitat (Clark et al., 1998). Comparisons of spatial and non-spatial models often demonstrate that spatially explicit simulations capture critical feedbacks and other important system properties that are not fully expressed in non-spatial models. For example, the SORTIE model, a spatially explicit stand-level forest simulator, predicted higher basal area and species diversity than a mean-field variant that eliminated spatial heterogeneity (Pacala and Deutschman, 1995). These differences arose because the presence of low-density forest gaps in the spatial simulations allowed for more rapid growth of younger trees and greater recruitment of shade-intolerant species.

Although spatial simulation models provide a more realistic representation of landscape processes than their non-spatial counterparts, they also entail greater uncertainty in model specification and parameterization. Critical elements of model structure, such as the shape of seed dispersal curves (Greene and Johnson, 1996) or movement rules for animals (Byers, 2001), may be difficult to define. Modeling biotic processes in a heterogeneous landscape may require multiple estimates of parameters across a range of habitat conditions. Furthermore, it may be difficult to obtain sufficient data at the spatial and temporal scales necessary to provide initial conditions for model runs, parameterize key functions, and corroborate model predictions. Given these limitations, the predictions of landscape models are often viewed with a healthy skepticism. Do simulation results provide a valid representation of how real forest landscapes behave, or are they artifacts of assumptions made in model development and uncertainties in model parameterization (Xu et al., 2004)?

This study seeks to address these general questions through structural analysis of a spatially explicit landscape simulator of disturbance and forest community dynamics in a heterogeneous landscape. Structural analysis is analogous to the commonly used techniques of sensitivity and uncertainty analysis, but involves the comparison of predictions under alternative model

formulations rather than changes in parameter values (Loehle, 1997). The specific goal was to simulate changes in landscape-scale tree species composition in response to varying fire return intervals, and to determine whether predictions of species distributions along this fire regime gradient were contingent upon the underlying assumptions used to model spatial relationships. The analysis focused on three key spatial elements: heterogeneity of species–habitat relationships, dispersal limitations to species establishment, and heterogeneity of disturbance regimes.

The LANDIS forest landscape simulator (Mladenoff and He, 1999) was used in this analysis. LANDIS incorporates a cohort-based succession algorithm derived from the earlier LANDSIM model (Roberts, 1996) to provide a phenomenological representation of vegetation dynamics at the patch level. This approach is simpler and more computationally efficient than the individual-tree based method used in forest gap models such as JABOWA, FORET, and their descendants (Botkin et al., 1972; Shugart, 1984). In contrast to many of these gap models, however, LANDIS explicitly simulates the spatial relationships between landscape patterns and large-scale ecological processes. Vegetation patterns and landform heterogeneity constrain the rate and direction of fire propagation across the landscape. Fires in turn influence vegetation by destroying existing cohorts and creating new opportunities for recruitment. Fire effects are linked to fire frequency through fuel accumulation curves that predict changes in fire severity as fuel accumulates following the last fire. Habitat constraints link potential species distributions to environmental heterogeneity, and the spatial pattern of seed sources imposes an additional limitation on species establishment. These spatial and temporal feedbacks create a system with strong “ecological memory” (Peterson, 2002) and the potential to exhibit nonlinear threshold responses. Thus, LANDIS provides an ideal platform for assessing the relative importance of key spatial processes when modeling forest dynamics in complex, disturbance-driven landscapes. A general description of the ecological and computational aspects of LANDIS is provided by Mladenoff and He (1999). A more detailed explanation of the fire disturbance simulator is provided in He and Mladenoff (1999a), and a description and analysis of the seed dispersal algorithms is given in He and Mladenoff (1999b).

The generalized framework of LANDIS allows it to be readily adapted to new ecosystems. LANDIS has been used to model forested landscapes in northern Wisconsin (He and Mladenoff, 1999a), the Missouri Ozarks (Shifley et al., 2000), northeastern China (He et al., 2002), and boreal Fennoscandia (Pennanen and Kuuluvainen, 2002), as well as chaparral shrublands in southern California (Franklin et al., 2001). For the purposes of this study, LANDIS was parameterized to simulate oak–pine forests in the Piedmont physiographic province of the southeastern United States. The large number of dominant tree species, complex terrain, and high historical fire frequencies in these forests make them an appropriate system for examining forest community responses to changes in disturbance regimes. The objective of this modeling exercise was not to make and validate specific predictions of past or future landscape conditions for any particular area. Instead, the aim was to use southern Piedmont forests as an archetypical system for understanding the implications of spatial modeling assumptions in forests with strong feedbacks linking landscape-scale disturbances and vegetation patterns.

2. Methods

2.1. Study area

Landscape maps and species lists for the parameterization of LANDIS were based on a 57,000 ha section of the Georgia Piedmont (~33°08'N, 83°37'W), encompassing portions of Jasper, Putnam, and Jones counties. The Piedmont physiographic province is a region of rolling hills bordered to the north by the Appalachian Mountain Chain, and to the south by the Atlantic and Gulf Coastal Plains (Fig. 1a). Elevations range from 100 to 400 m, and the deeply dissected terrain is characterized by narrow to broad upland ridges, short hill-slopes, and narrow valley floors (USDA Soil Conservation Service, 1981). The climate of the Piedmont is characterized by relatively mild winters and hot humid summers with precipitation distributed evenly throughout the year. Within the study area, soils are primarily Typic Kanhapludults, and the predominant soil series include Cecil, Madison, Davidson, and Pacolet (Payne, 1976). These soils generally consist of a surface layer of reddish-brown sandy loam underlain by red, clay-rich

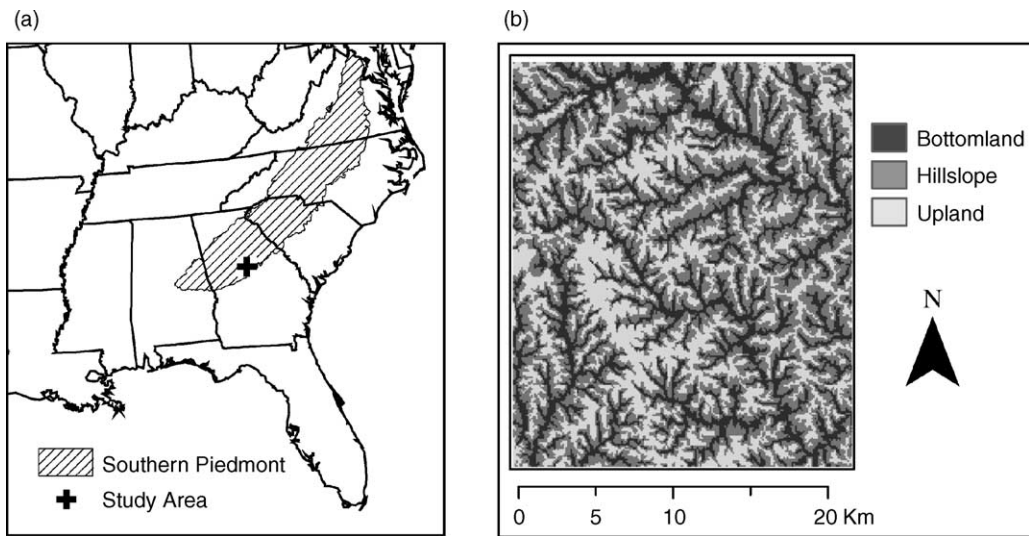


Fig. 1. (a) Study area location. (b) Distribution of landtypes within the study area.

horizons. Most of these soils have experienced significant erosion resulting from past land clearing and land use practices.

Prior to the arrival of European settlers, Piedmont forests were dominated by *Pinus* spp., *Carya* spp., and *Quercus* spp. (Cowell, 1995, 1998). The occurrence of frequent fires likely played an important role in shaping historical vegetation composition, as did large Native American populations (Williams, 1989). An analysis of pre-settlement forest vegetation based on Georgia land-lottery surveys from the early 19th century suggested that the species composition of pre-settlement forests was commensurate with a fire return interval in the range of 20–50 years (Cowell, 1995). Following European settlement, large portions of the Piedmont were cleared for agriculture. Soil degradation and erosion eventually led to widespread farm abandonment, and forest cover increased over most of the 20th century as trees reestablished on former agricultural lands. Presently, forests are once again the prevalent land cover across much of the Piedmont. Major forest types include naturally regenerated hardwood and mixed pine/hardwood stands, as well as intensively managed pine plantations. The current land use trend is a gradual loss of both forested and agricultural lands to development, and forest fragmentation is projected to increase in the future (Wear, 2002).

2.2. Parameterization of LANDIS

Parameterization of LANDIS (Version 3.6) for oak–pine forests of the Georgia Piedmont involved three major steps: development of landtype maps, estimation of species vital attributes and establishment coefficients, and calibration of disturbance regimes. Simulations were carried out on a landscape grid comprised of 100 m × 100 m (1 ha) cells. Topographic moisture gradients have been identified as a key factor influencing community composition and fire frequency in Piedmont forests (Jones, 1988; Cowell, 1998), and topography was therefore used as the basis for delineating landtypes. The landscape was classified into bottomlands, hillslopes, and ridges (Fig. 1b) using a slope position index derived from a 30 m digital elevation model (Hatfield, 2000). Bottomlands (index values 0–25) encompassed hydric and mesic sites on flat terrain adjacent to major streams. Hillslopes (index values 26–85) were relatively steep with intermediate moisture status. Ridges (index values 86–100) included the driest sites located on gently sloping uplands.

A total of 22 tree species were incorporated into LANDIS (Table 1). Only species that have the potential to attain a dominant status in the forest canopy and are relatively common within the study area were included in the final species list. Thus, common subcanopy

Table 1
Vital attributes and establishment coefficients for 22 Piedmont tree species

Species	Lng	Mat	Shd	Fire	Effd	Maxd	Vegp	Vega	Ec1	Ec2	Ec3
<i>Acer negundo</i>	100	20	4	2	150	300	0.5	50	0.9	0.2	0.05
<i>Acer rubrum</i>	150	30	2	3	150	300	1	100	0.3	0.5	0.3
<i>Betula nigra</i>	100	10	1	2	200	400	0.5	50	0.9	0.2	0.05
<i>Carya cordiformis</i>	300	30	2	3	50	3000	1	100	0.3	0.3	0.3
<i>Carya ovata</i>	300	40	3	3	50	3000	1	100	0.3	0.6	0.3
<i>Carya tomentosa</i>	500	25	3	3	50	3000	1	150	0.5	0.8	0.5
<i>Fagus grandifolia</i>	300	30	4	2	50	300	1	100	0.3	0.6	0.3
<i>Fraxinus pennsylvanica</i>	150	15	3	3	150	300	0.5	30	0.9	0.2	0.05
<i>Liquidambar styraciflua</i>	300	25	2	2	100	200	1	50	0.5	0.8	0.5
<i>Liriodendron tulipifera</i>	250	15	1	4	150	300	0.5	50	0.5	0.8	0.5
<i>Nyssa sylvatica</i>	250	5	4	3	100	200	0.5	50	0.3	0.6	0.3
<i>Pinus echinata</i>	300	20	1	5	100	200	0.5	30	0.1	0.6	0.8
<i>Pinus taeda</i>	250	15	1	5	100	200	0	0	0.5	0.8	0.5
<i>Plantanus occidentalis</i>	500	25	2	3	150	300	0.5	50	0.7	0.1	0.05
<i>Prunus serotina</i>	100	20	1	2	–1	–1	0.5	60	0.05	0.4	0.6
<i>Quercus alba</i>	500	20	2	5	50	3000	1	80	0.5	0.8	0.5
<i>Quercus falcata</i>	250	25	3	4	50	3000	1	80	0.05	0.4	0.6
<i>Quercus nigra</i>	200	20	2	3	50	3000	1	150	0.3	0.6	0.3
<i>Quercus rubra</i>	400	25	3	4	50	3000	1	150	0.1	0.6	0.8
<i>Quercus stellata</i>	400	25	2	5	50	3000	1	130	0.1	0.6	0.8
<i>Quercus velutina</i>	300	20	2	5	50	3000	1	100	0.1	0.6	0.8
<i>Ulmus alata</i>	125	15	3	3	150	300	0.5	50	0.3	0.5	0.3

Lng: maximum longevity (years); Mat: age of reproductive maturity (years); Shd: shade tolerance (1: least shade tolerant, 4: most shade tolerant); Fire: fire tolerance (2: least fire tolerant, 5: most fire tolerant); Effd: effective seeding distance (m); Maxd: maximum seedling distance (m); Vegp: vegetation propagation coefficient; Vega: maximum age of vegetative propagation; Ec1: establishment coefficient for bottomlands; Ec2: establishment coefficient for hillslopes; Ec3: establishment coefficient for ridges.

species such as *Celtis occidentalis*, *Cornus florida*, and *Carpinus caroliniana*, as well as less common over-story species such as *Quercus phellos* and *Magnolia acuminata*, were not modeled. Species vital attributes were estimated based on published summaries of autecological characteristics. Maximum age, minimum reproductive age, relative rankings of shade tolerance and fire susceptibility, resprouting probabilities, and maximum resprouting ages were derived from a variety of sources (Burns and Honkala, 1990; Prasad and Iverson, 1999; Fire Sciences Laboratory, 2003).

LANDIS models seed dispersal as a function of two distance parameters: the effective and maximum dispersal distances (He and Mladenoff, 1999b). Probability of dispersal up to the effective distance is assumed to be relatively high. Dispersal between the effective and maximum distances declines along a negative exponential curve, and dispersal events at the maximum range are relatively infrequent. Estimates of these seed dispersal parameters were based on a generalized classification of seed dispersal mechanisms. Effective

seed dispersal ranges were 50 m for gravity-dispersed species, 100 m for large wind-dispersed winged seeds, 150 m for small wind-dispersed winged seeds, and 200 m for small plumed seeds (Sutherland et al., 2000). For wind-dispersed seeds, maximum dispersal distances were assumed to be double the effective dispersal distance. For seeds with animal or bird dispersal vectors, maximum dispersal distance was assumed to be 3000 m to reflect the potential for rare, long-distance dispersal events. *Prunus serotina* was unique among the tree species modeled in that it forms a soil seed bank, in which animal- and bird-dispersed seeds can persist for a number of years (Fire Sciences Laboratory, 2003). Because LANDIS does not explicitly simulate seed banking, *P. serotina* was parameterized with global dispersal to more realistically model its extensive regeneration from stored seeds following disturbance.

Species establishment coefficients were estimated from published summaries of species characteristics (Burns and Honkala, 1990; Iverson et al.,

Table 2
 Characteristics of the simulated fire regimes

Scenario	Target FRI	Mean FRI	Ridge FRI	Hillslope FRI	Bottomland FRI	Mean fire size (ha)
Base	20	22.2	14.4	26.7	35.9	483.6
	30	31.6	21.8	35.1	52.0	629.6
	40	43.5	32.5	47.0	61.3	736.8
	50	53.9	38.2	59.8	82.1	685.4
	70	70.4	54.4	74.8	96.7	802.1
	100	102.9	81.2	110.0	132.8	859.5
Homogeneous habitat	20	22.2	14.4	26.8	35.9	483.2
	30	31.2	21.4	34.9	51.0	628.4
	40	43.1	32.0	46.9	61.1	742.9
	50	53.8	38.2	59.9	81.1	699.3
	70	72.3	55.9	76.6	100.3	791.5
	100	105.3	83.7	111.0	138.4	815.7
Global dispersal	20	22.5	14.5	27.3	36.2	477.9
	30	31.4	21.4	35.1	52.2	628.2
	40	42.5	31.8	46.1	59.0	754.2
	50	54.5	38.8	60.4	83.0	672.9
	70	72.2	55.3	77.3	99.4	797.8
	100	106.9	85.2	112.9	138.9	800.4
Homogeneous disturbance	20	23.2	23.1	23.3	23.3	857.4
	30	29.6	28.3	30.3	30.2	852.4
	40	43.7	43.5	43.8	43.8	1052.3
	50	54.9	54.9	55.0	54.8	1040.2
	70	73.6	72.9	73.9	74.0	1083.3
	100	107.6	108.4	107.6	106.5	1010.0

All fire return interval (FRI) values are in years. Mean FRI and mean fire size are aggregate values computed across the entire landscape. Ridge, hillslope, and bottomland FRI values are computed separately for the three landtypes.

1999; Sutherland et al., 2000; Fire Sciences Laboratory, 2003) and from studies of community patterns along environmental gradients in present-day and pre-settlement forests (Cowell, 1993, 1995). The 22 modeled species were first classified as being either common or uncommon within the study area based on their relative frequencies of occurrence in the present-day and pre-settlement landscape. Individual species were further characterized by their association with bottomland, hillslope, or ridge habitats. Relative values of species establishment coefficients were then assigned based on these classifications (Table 1).

The fire return interval for a LANDIS simulation is based on user-specified parameters that determine the number and sizes of fires to be modeled. Simulated fire regimes may not achieve these user-specified values, however, because the sizes of individual fires are limited by the abundance and spatial distribution of fuels. Therefore, fire regimes must be calibrated to achieve the desired fire return interval by adjusting a

parameter that influences the probability of fire spread into adjacent cells (He and Mladenoff, 1999a). Six target fire regimes were specified for the LANDIS simulation experiment based on 20, 30, 40, 50, 70, and 100-year fire return intervals. Default calibration parameters were initially specified for each fire regime, and actual fire return intervals were computed for 2000-year simulations and compared to the target fire return intervals (Table 2). The calibration parameters were iteratively adjusted until the simulations consistently produced actual fire return intervals that were within $\pm 10\%$ of the target values. All six fire regimes were parameterized with a mean fire size of 1000 ha. Because historical evidence suggested that fire return intervals increased along a gradient from ridges to bottomlands (Cowell, 1995), fire regimes were varied across the individual landforms to produce fire return intervals approximately twice as long in the bottomlands as on the ridges. Fuel accumulation curves were also varied across landforms so that the rate of fuel accumulations

Table 3
Fuel accumulation curves by landtype, specified as the years since fire needed to reach each fire severity class

Landtype	S1	S2	S3	S4	S5
Bottomland	0	10	50	80	120
Hillslope	0	10	40	60	90
Ridge	0	10	30	40	60

S1–S5 represent the fire severity levels simulated by LANDIS. As fire severity increases, older cohorts and species with high fire tolerance become increasingly susceptible to mortality (He and Mladenoff, 1999a).

following a fire, along with the commensurate rate of increase in fire severity, was highest on ridges, lower on hillslopes, and lowest in the bottomlands (Table 3).

2.3. Landscape simulations

Individual LANDIS runs were carried out for 2000 simulation years. The goal of the simulations was to model quasi-equilibrium community composition for the specified disturbance regimes, not to predict transient dynamics from a particular initial configuration. Simulations were initialized with an arbitrary landscape pattern in which cohorts were distributed based on a map of conifer-dominated, hardwood-dominated, mixed conifer–hardwood, and open patches derived from the 1992 National Land Cover Data Set (Vogelmann et al., 2001) along with the previously described landtype map. Hardwoods and/or conifers were assumed to be present in the appropriate land cover classes, and individual species were assumed to be initially present on landforms where their establishment coefficients were greater than 0.1. Cohort ages were assigned based on the range of expected ages given the fire regimes on each landform. Open areas were mapped as recently disturbed forest, with 10-year old cohorts of all potential species present.

The first 1000 years of each run served as an initialization period during which the simulated disturbance, dispersal, and establishment processes overwrote these initial landscape patterns. A preliminary analysis indicated that the 1000-year initialization period was sufficient to erase the initial landscape pattern, and that multiple simulations under the same disturbance regime converged to similar conditions after 1000 years even when the initial landscape configuration was varied. Following the initialization period, land-

scapes were sampled every 100 years, yielding a total of 10 sample landscapes for each simulation run. Temporal autocorrelation analysis indicated that the 100-year sampling interval was sufficient to ensure independence of the samples.

All six of the fire return interval treatments (20, 30, 40, 50, 70, and 100 years) were simulated for each of the four scenarios. In the base scenario, all major spatial processes in the model (including spatial variability in species–habitat relationships, spatially explicit seed dispersal, and spatial variability in fire regimes) were implemented. In the three alternative scenarios, these spatial assumptions were relaxed one at a time. In the uniform habitat scenario, a single establishment coefficient was computed for each species by taking an average of the three landtype-specific coefficients weighted by the area of each landtype. The expected rate of species establishment at the landscape scale was therefore the same as in the base scenario, but establishment rates did not vary across landforms. In the uniform dispersal scenario, distance-limited dispersal was replaced by global dispersal (propagules for every species were always available in every cell) by changing the options in the LANDIS parameter file. In the uniform disturbance scenario, the same mean fire return interval was simulated on all three landtypes, rather than allowing fire frequency to vary with landtype. In addition, the fuel accumulation curves for the hillslope landtype were used on all three landtypes, removing spatial variability in rates of fuel accumulation.

For each sampled landscape, the age distribution of forest cells (determined by the age of the oldest cohort in each cell) and the severities of all fires occurring within the past decade were recorded. Frequency distributions of forest age classes were plotted as histograms and compared with the expected age-class distributions under a negative exponential model of fire return intervals (VanWagner, 1978). This model represented the expected age-class distribution under the assumption of a stand-replacing fire regime with age-invariant fire susceptibility, and served as a neutral model for assessing the influences of internal system feedbacks on the forest age structure.

The landscape-level frequency of each species was computed as the percentage of cells in the landscape occupied by that species. These values were normalized to relative frequency based on the sum of frequencies of all species in each landscape. Non-metric

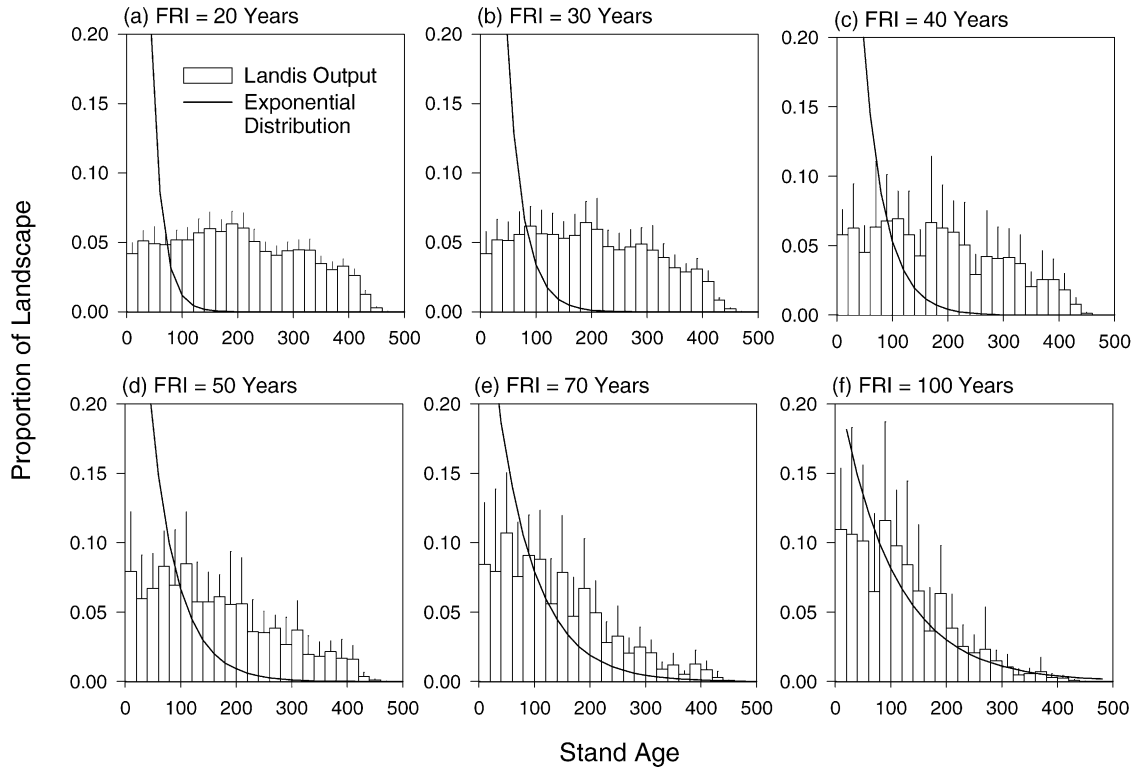


Fig. 2. Age-class distributions generated from LANDIS simulations of the base scenario at six fire return intervals. Error bars represent the standard deviations of each age-class over time. Lines represent the theoretical negative exponential age-class distribution, based on the assumption of stand-replacing disturbances and age-invariant susceptibility to fire.

multidimensional scaling (NMS), computed with PC-ORD Version 4.25 (McCune and Mefford, 1999), was used as an ordination technique to compare trends in species composition across the different scenarios and fire regime treatments. The Sorenson coefficient, based on species relative frequency, was used as a measure of compositional distance among the simulated landscapes. The NMS Autopilot function was used to search for a solution that explained a large portion of the between-landscape dissimilarities based on a small number of ordination axes. The amount of variance explained by the NMS ordination was assessed using the correlations of ordination distances with Sorenson distances in the original species space. The relationships of species with the ordination axes were assessed using the correlations of species relative abundances with the axis scores, and by visual inspection of species distributions within the ordination space.

3. Results

3.1.1. Fire regime calibration

Although the simulated fire return intervals varied slightly from their target values, the fire regime simulations were consistent across the different scenarios (Table 2). For clarity, these fire regimes will be referenced by their target values (e.g. 20-year fire return interval) rather than the actual simulated fire return intervals. In practice, it was not possible to maintain precise ratios among the fire return intervals on individual landforms while calibrating a landscape-level fire return interval. Therefore, the relative distribution of fire return intervals across landforms varied slightly among the different fire regimes, although there was always a clear gradient from ridges to hillslopes to bottomlands. In the homogeneous disturbance scenario, the fire return interval on each landform was simi-

lar to the aggregate fire return interval for the entire landscape.

Calibration parameters for the simulated fire sizes were not adjusted for the different fire regimes because of the difficulty of simultaneously calibrating multiple components of the fire regime. Mean fire size generally decreased with the fire return interval because of increasing fragmentation of vegetation and fuels which reduced the maximum extent of individual fires. Fires were largest in the homogeneous disturbance scenario, reflecting the elimination of the relatively fire-resistant riparian areas that served as firebreaks in the scenarios with spatially heterogeneous disturbance regimes.

3.2. Disturbance regimes and landscape age structure

In the base scenario, forest area had a relatively even distribution across age classes at the 20-year fire return interval (Fig. 2). The frequency distribution of age classes exhibited a weak mode at approximately 200 years, with frequencies gradually decreasing as forest age increased above this point. Compared to the hypothetical distribution from a negative exponential model, the area of younger age classes (<60 years) was much lower and the area of older age classes (>100 years) was much higher than would be expected under a stand-replacement fire regime with age-invariant disturbance susceptibility. The age-class distribution at the 30-year fire return interval was very similar to the 20-year fire return interval. At 40-, 50-, and 70-year fire return intervals, the simulated age-class distribution began to develop a negative skew, but there was still notably less young forest and more old forest than would be expected under a stand-replacement fire regime. The simulated age-class distribution was similar to the negative exponential curve at a 100-year fire return interval, although some deviations in the frequencies of young and old forest age-classes were still apparent.

The distribution of area burned by fires of differing severities also varied with fire return interval (Fig. 3). In the 20-year fire return interval simulation, more than 90% of all fires were in the lowest two severity classes. The frequency distribution of fire severities shifted toward the higher-severity classes as fire frequency decreased. At the 100-year fire return interval, nearly 50% of the total area disturbed was burned by fires in the highest fire severity class. In the three alternative sce-

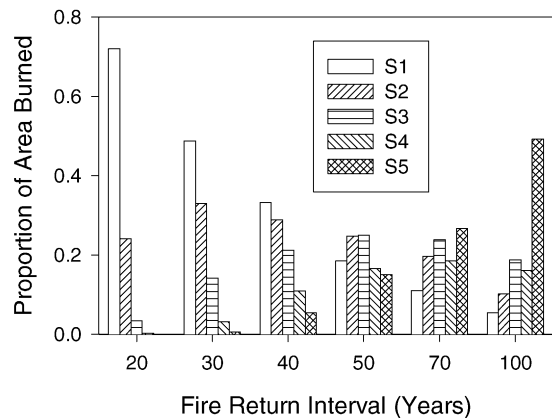


Fig. 3. Distribution of fire severities generated from LANDIS simulations of the base scenario at six fire return intervals. S1–S5 are the fire severity levels simulated by LANDIS. As fire severity increases, older cohorts and species with high fire tolerance become increasingly susceptible to mortality (He and Mladenoff, 1999a).

narios, changes in the age-class and fire severity distributions with fire return interval were similar to those documented for the base case (M.C. Wimberly, unpublished data).

3.3. Comparisons of base run with alternative scenarios

The NMS ordination of species relative abundances for simulated landscapes under the four scenarios resulted in a two-axis solution (Fig. 4). The first axis accounted for 87% of the total variation in species relative frequencies among the simulated landscapes. This axis described a gradient from landscapes dominated by *Betula nigra*, *Carya cordiformis*, *Carya ovata*, *Fagus grandifolia*, *Liquidambar styraciflua*, *Prunus serotina*, *Quercus nigra*, and *Quercus velutina* at low axis scores to landscapes dominated by *Liriodendron tulipifera*, *Nyssa sylvatica*, *Pinus echinata*, *Pinus taeda*, *Quercus alba*, and *Quercus rubra* at high axis scores (Table 4). Species that were negatively correlated with axis 1 had low fire resistance and occurred most frequently at longer fire return intervals (Fig. 5a). In contrast, species that were positively correlated with axis 1 had high fire resistance and occurred most frequently at shorter fire return intervals (Fig. 5b). *Quercus velutina* was a notable exception to this trend, as it was in the highest fire resistance class, but had the greatest abundance at the

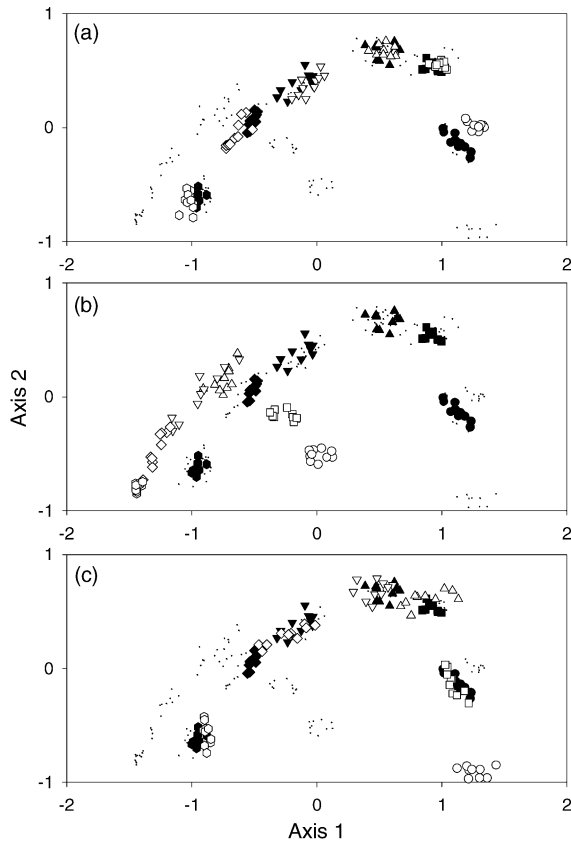


Fig. 4. NMS ordination of landscape-level relative species abundances for six fire return intervals and four scenarios. Each graph highlights a comparison between the base scenario (solid symbols) and one of the alternative scenarios (hollow symbols) with results from the other scenarios displayed as dots. (a) Base vs. uniform habitat; (b) base vs. uniform dispersal; (c) base vs. uniform disturbance. Symbol shapes represent different fire return intervals (circles = 20, squares = 30, triangles = 40, inverted triangles = 50, diamonds = 70, and hexagons = 100).

longest fire return intervals (Fig. 5c). *Quercus falcata* and *Quercus stellata* had weak correlations with axis 1, and were relatively insensitive to the fire return interval (Fig. 5d).

The second NMS axis captured an additional 11% of the total variation in species relative abundances. The distribution of landscapes along the second axis created a distinctive arched shape in the responses for each of the simulation scenarios (Fig. 4). This arch was not a computational artifact of a sparse community matrix (Beals, 1984), but instead captured a true bimodal

response of several species to the fire frequency gradient. Species that exhibited a strong negative correlation with axis 2, such as *Carya ovata*, *Carya tomentosa*, and *Plantanus occidentalis* (Table 4), had bimodal distributions along the first ordination axis. These species occurred most frequently at the highest and lowest fire return intervals, and less frequently at intermediate fire return intervals (Fig. 5e). Their distributions were reflected in the arch that bent each end of the fire return interval gradient toward the lower end of axis 2. Other species that had strong positive correlations with axis 2, such as *Acer negundo*, *Fraxinus pennsylvanica*, and *Ulmus alata*, exhibited unimodal responses that peaked near the center of axis 1. These species occurred most frequently at intermediate fire return intervals and less frequently at higher and lower fire return intervals (Fig. 5f).

For each scenario, the simulated landscapes exhibited similar responses in the ordination space (Fig. 4). Landscapes modeled at long fire return intervals had the lowest axis 1 scores, whereas landscapes modeled at short fire return intervals had the highest scores. Landscapes modeled at intermediate fire return intervals had the highest axis 2 scores, whereas landscape

Table 4
Pearson correlation coefficients between tree species and ordination axes

Species	Axis 1	Axis 2
<i>Acer negundo</i>	0.36	0.96
<i>Acer rubrum</i>	0.09	-0.41
<i>Betula nigra</i>	-0.83	-0.35
<i>Carya cordiformis</i>	-0.63	-0.52
<i>Carya ovata</i>	-0.88	-0.78
<i>Carya tomentosa</i>	-0.33	-0.92
<i>Fagus grandifolia</i>	-0.97	-0.48
<i>Fraxinus pennsylvanica</i>	0.51	0.90
<i>Liquidambar styraciflua</i>	-0.85	-0.68
<i>Liriodendron tulipifera</i>	0.72	-0.09
<i>Nyssa sylvatica</i>	0.97	0.38
<i>Pinus echinata</i>	0.61	0.31
<i>Pinus taeda</i>	0.61	0.31
<i>Plantanus occidentalis</i>	0.07	-0.80
<i>Prunus serotina</i>	-0.57	-0.17
<i>Quercus alba</i>	0.97	0.55
<i>Quercus falcata</i>	-0.46	0.56
<i>Quercus nigra</i>	-0.61	-0.47
<i>Quercus rubra</i>	0.91	0.65
<i>Quercus stellata</i>	0.42	0.21
<i>Quercus velutina</i>	-0.93	-0.20
<i>Ulmus alata</i>	0.23	0.84

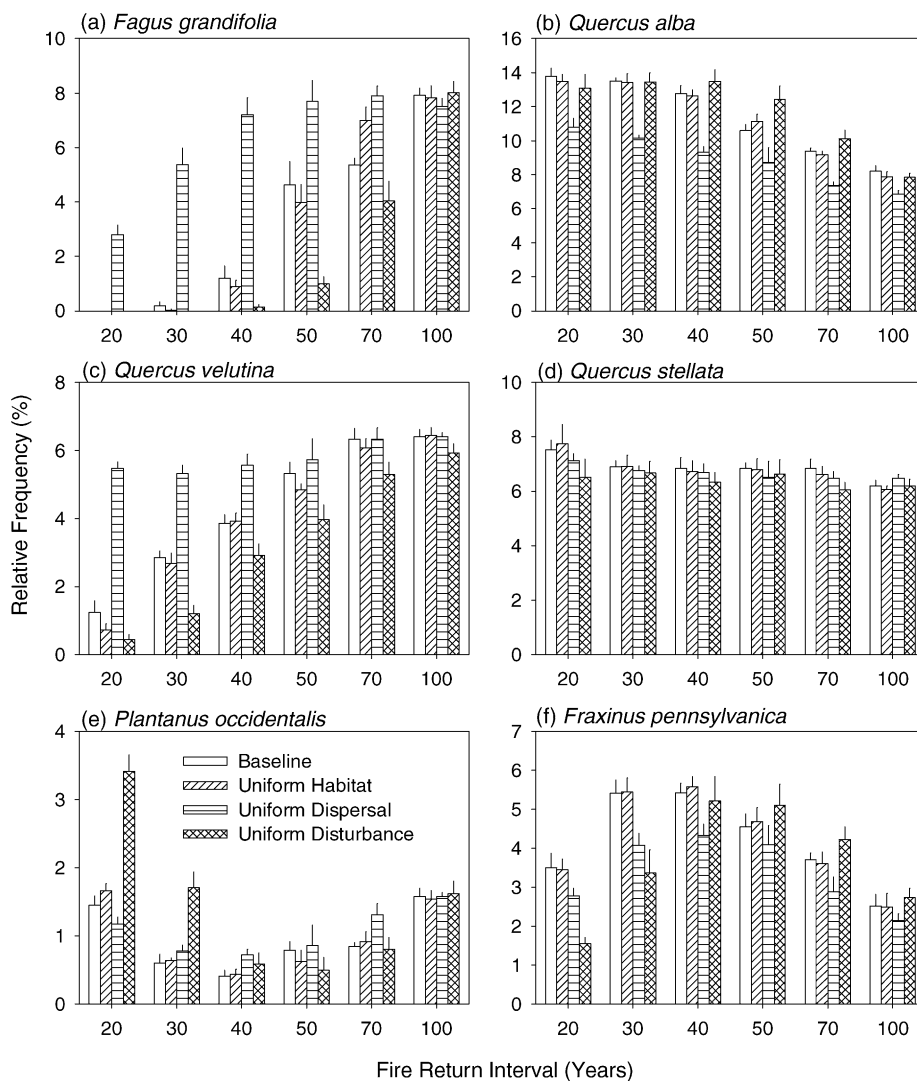


Fig. 5. Relative frequencies of six tree species simulated with LANDIS under alternative modeling assumptions and at different fire return intervals. Error bars represent the standard deviations of relative frequency over time. The six species shown were selected to illustrate a variety of responses to changes in fire frequency.

modeled at shorter and longer fire return intervals had the lowest scores. However, the shape and breadth of these responses varied across the different scenarios. In the uniform habitat scenario (Fig. 4a) species responses to the fire return interval were not substantively different from the base scenario. In the uniform dispersal scenario (Fig. 4b), the amount of compositional change in response to the fire return interval was reduced relative to the base scenario. This difference

was reflected in the tighter clustering of simulated landscapes in the ordination space under the uniform dispersal scenario. In addition, overall species composition in the uniform dispersal scenario was shifted toward fire-sensitive species at the lower end of axis 1. In the uniform disturbance scenario (Fig. 4c), the relative frequencies of species were very similar to the base case at a fire return interval of 100 years. As fire return intervals decreased, species composition in the uniform

disturbance scenario shifted compared to the base scenario. For example, species composition for a 20-year fire return interval under the base case was similar to species composition for a 30-year fire return interval under the uniform disturbance scenario.

4. Discussion

4.1. Landscape-level responses to fire disturbance

The simulated forest age-class distributions differed considerably from the expected distributions under a stand-replacing fire regime with age-invariant fire susceptibility. At shorter fire return intervals, fuel accumulations remained low and most fires were low severity burns that left the oldest age classes undisturbed. Under these short fire return intervals, most of the landscape was comprised of multi-cohort stands that contained at least one cohort of old, large trees. When fire return intervals were longer, more fuels accumulated between fires, leading to higher-severity burns that could potentially destroy all the cohorts within a stand. The decrease in area of older forests with increasing fire return interval contradicts the predictions of the negative exponential model, and suggests that shifts in fire severity are having a stronger influence on the age-class structure than are changes in fire frequency. Simple analytical models such as the negative exponential curve (VanWagner, 1978) and landscape simulators that have been derived from them (Boychuk and Perera, 1997), are based on an assumption of strong external controls on fire frequency and severity. Although these models can be used to predict forest age structure in landscapes where these assumptions are valid (Johnson et al., 1995; Lesica, 1996), they will produce misleading results in systems where strong linkages between fire return interval, fuel conditions, and fire severity mediate the effects of fires on forest vegetation.

Responses of most species to changing fire return intervals were predictable based on their fire tolerance parameters, with fire-tolerant species most abundant in landscapes with frequent fire and fire-sensitive species most prevalent in landscapes with infrequent fire. However, *Q. velutina* was a notable exception, exemplifying the kinds of ecological “surprises” that can arise in systems with strong feedback loops. Both *Q. stellata* and *Q. velutina* were parameterized to have identical shade

tolerance, fire resistance, dispersal attributes, and establishment coefficients. *Q. stellata* exhibited a slight, but discernable decrease in relative abundance with increasing fire return interval, whereas *Q. velutina* increased in relative abundance with increasing fire return interval. Although these species were generally ecologically similar, competitive interactions combined with small differences in their life history attributes led to distinctive distributions of these species along the fire return interval gradient. Additional simulation experiments have demonstrated that *Q. velutina*'s shorter lifespan is the key parameter limiting its abundance relative to *Q. stellata* at the lowest fire return intervals (M.C. Wimberly, unpublished data).

C. tomentosa, *C. ovata*, and *P. occidentalis* exhibited distinctive bimodal responses to fire frequency. Bimodal distributions are assumed to occur only rarely in species–environment relationships, as they fundamentally conflict with basic tenets of niche theory and conceptual models of species distribution along environmental gradients. However, this type of response may be realistic in the context of a disturbance gradient where there is a trade-off between disturbance frequency and disturbance severity. Species can persist through a resistance strategy in high-frequency, low-severity disturbance regimes if mature cohorts can survive low-intensity fires. The same species may also be able to maintain a widespread distribution in low-frequency, high-severity disturbance regimes if cohorts can successfully establish in disturbance-created openings and then remain undisturbed long enough to reach reproductive age. At intermediate disturbance frequencies, the species may be at a competitive disadvantage if disturbances are severe enough to kill mature cohorts, but fire frequency is too short to allow cohorts to reach reproductive age.

Commonly used ordination methods such as NMS, detrended correspondence analysis (DCA), and canonical correspondence analysis (CCA) do not have the capability to model bimodal species responses along compositional gradients. In the ordination of the simulation results from this study, bimodal distributions were instead captured by an arching of plots along the second axis. Researchers should therefore use caution when analyzing simulation results or field data that encompass vegetation responses to a fire frequency gradient. Analysis methods that implicitly model species distributions as monotonic or unimodal curves may fail

to capture the complexity of community responses to changes in disturbance regimes.

4.2. *Habitat heterogeneity*

The application of structural analysis techniques to the LANDIS model provided insights into the relative influences of various spatial processes on landscape responses to shifts in fire frequency. The relative frequencies of species in the simulated landscapes were not sensitive to assumptions about the spatial homogeneity or heterogeneity of species–habitat relationships. At a landscape scale, the impacts of disturbance-driven mortality and dispersal-limited recruitment appear to override the influence of spatial variability in rates of species establishment on species composition. This insensitivity to habitat heterogeneity may arise in part from the spatial grain of landtypes in the southern Piedmont. Landforms form narrow bands that follow topographic contours (Fig. 1b), and the continual movement of seeds and disturbances from adjacent landtypes may dilute the influences of habitat distribution on landscape-scale species composition.

The model's insensitivity to habitat pattern is not surprising, given that previous empirical and modeling studies have found that habitat amount, rather than spatial pattern, is the most important determinant of species abundances in large landscapes (e.g. Fahrig, 1998; Trzcinski et al., 1999). The results of this study indicate that this general result also holds true at the community level. The uniform habitat scenario removed the effects of habitat pattern by altering the spatial distribution of establishment coefficients, but kept overall habitat amounts constant by maintaining the expected rates of species establishment at the landscape scale. It is important to note, however, that the predicted spatial distributions of species with strong habitat associations (particularly bottomland species) do change when assumptions of habitat heterogeneity are relaxed. Even though the relative frequencies of species at the landscape scale do not change appreciably under the uniform habitat scenario, a considerable amount of finer-scale spatial detail is lost.

This result is significant in light of the fact that the species establishment coefficients may be among the most difficult parameters to directly quantify in LANDIS and similar models. Changing from an individual-based to a cohort-based modeling approach is an

efficient means for limiting the amount of fine-scale detail, thereby increasing computational efficiency and allowing a focus on large-scale processes. However, the definition of a “cohort” is more ambiguous than that of an individual tree, and ecological studies do not typically quantify vegetation change in terms of decadal probabilities of cohort establishment. Relative values of establishment coefficients can be inferred from field observations of species distributions along environmental gradients, but it is often unclear how much observed vegetation patterns are a function of environmental gradients, as opposed to disturbance regimes or land use history. It is possible to use a meta-modeling approach to derive establishment coefficients from individual-tree based models of forest gap dynamics (He et al., 1999), but the results of this approach will still depend on the assumptions and uncertainties of the underlying gap model. In Piedmont forests, a precise quantification of species establishment patterns across different landforms may not be critical when the goal is to predict changes in species composition at broad scales in response to disturbance.

4.3. *Seed dispersal*

In contrast to the uniform habitat scenario, species responses to changing fire return intervals shifted considerably under the uniform dispersal scenario. When uniform dispersal was simulated, propagules of all species were available everywhere in the landscape, and simulated vegetation dynamics were primarily a function of disturbance-driven mortality and competition from remnant cohorts that limited regeneration. Under the base scenario with distance-dependent dispersal, the spatial pattern of vegetation following a fire exerted an additional constraint on post-fire establishment. This spatial relationship created a self-reinforcing mechanism through which widespread dispersal helped to maintain the broad distributions of abundant species, whereas dispersal limitations constrained the potential for less common species to increase in abundance. Thus, species composition exhibited a much greater shift toward fire-resistant species with decreasing fire return interval in the base scenario than in the uniform dispersal scenario. These results indicate that assumptions about dispersal and uncertainty in the estimates of dispersal parameters have the potential to significantly influence prediction

of species responses to disturbance at a landscape scale.

Unlike the establishment coefficients, seed dispersal parameters can be directly measured through field experiments and observational studies. Dispersal curves can be estimated by directly measuring seed-fall (Greene and Johnson, 1996) or by inferring seed rain from patterns of seedling establishment (Johnson, 1988). However, there are still challenges associated with quantifying these parameters. Difficulties arise in areas where multiple seed shadows overlap or where habitat limitations influence spatial patterns of regeneration (Ribbens et al., 1994; Clark et al., 1998). Dispersal ranges for a particular species can also vary depending on the environmental context. For example, seeds of *Tsuga heterophylla* disperse considerably farther in large openings than in closed-canopy forests (Wimberly and Spies, 2002). The frequency and spatial distribution of rare, long-distance dispersal events may be particularly difficult to predict, especially for species with animal or bird dispersal vectors. In the future, it will be important to obtain dispersal data for a larger number of Piedmont tree species and to gain a better understanding of model sensitivity to uncertainties in parameter estimates and the assumptions inherent in the dispersal functions.

4.4. Spatially heterogeneous disturbance

Landscape-level species composition was also sensitive to the spatial heterogeneity of disturbance regimes. Under the base simulation, the fire return interval at the landscape scale was the aggregate of a range of fire return intervals on the different landtypes. Each landtype exhibited a distinctive temporal disturbance pattern, favoring species with a different set of vital attributes. However, eliminating this disturbance heterogeneity did not always result in different landscape-level responses. Species composition under spatially heterogeneous and spatially homogeneous disturbance scenarios was nearly identical at the 100-year fire return interval, and was very similar at the 70- and 40-year fire return intervals. Distinctions between spatially heterogeneous and spatially homogeneous fire regimes were expressed most clearly at the 20-, 30-, and 50-year fire return intervals, indicating a general trend of increasing landscape-scale sensitivity to disturbance heterogeneity with decreasing fire return interval.

Spatial variability in disturbance regimes has been documented in many forested ecosystems (Kushla and Ripple, 1997; Shinneman and Baker, 1997; Heyerdahl et al., 2001). The frequencies, sizes, and severities of fires may vary as a function of landform characteristics, climate, or the presence of water bodies, rock outcrops, or other natural and anthropogenic fire breaks. The influence of fire on forest community composition has been modeled at the stand level (e.g. Keane et al., 1990; Miller and Urban, 1999), but the aggregate influences of spatial variability in fire regimes at the landscape level have not been directly addressed. To effectively simulate landscape-level patterns of species abundance, it may be necessary to accurately parameterize multiple disturbance regimes across different landforms rather than just a single, global disturbance regime. Dendroecological methods have been used to elucidate spatial patterns of fire frequency in historical landscapes (Heyerdahl et al., 2001), and can be a valuable source of data for modeling heterogeneous fire regimes (Wimberly et al., 2000; Wimberly, 2002). Alternately, fire frequencies or timber harvest rotations may be specified by the modeler when the goal is to assess the relative impacts of different hypothetical management scenarios. In these situations, it may be worthwhile to consider varying the spatial distribution of disturbances across the landscape as a component of these alternative management strategies.

5. Conclusions

As forest landscape models have become more realistic and spatially explicit, the amount of information required to initialize and parameterize these models has increased considerably. In many cases, existing data suitable for quantifying key landscape-level processes is limited. Modelers are often forced to make decisions based on qualitative results of prior research, expert opinion, and personal judgment. Although this uncertainty cannot be entirely eliminated, evaluation techniques such as structural analysis allow modelers to determine which of these decisions are likely to have the greatest impact on model predictions. These assessments can also guide future research by identifying the types of information that would be most useful for reducing model uncertainty. In LANDIS simulations of Piedmont forest landscapes, the predicted relationships

between landscape-scale species composition and fire return interval were insensitive to the spatial pattern of habitats, moderately sensitive to the spatial pattern of fire regimes, and highly sensitive to the assumption of distance-limited versus global seed dispersal. Future refinements of the model will therefore focus on obtaining more precise estimates of seed dispersal distances, and better quantifying the relationship between fire regimes and topography.

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