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Modeling the Influence of Dynamic Zoning of Forest Harvesting on Ecological Succession in a Northern Hardwoods Landscape

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ABSTRACT / Dynamic zoning (systematic alteration in the spatial and temporal allocation of even-aged forest management practices) has been proposed as a means to change the spatial pattern of timber harvest across a landscape to maximize forest interior habitat while holding timber harvest levels constant. Simulation studies have established that dynamic zoning strategies produce larger tracts of interior, closed canopy forest, thus increasing the value of these landscapes for interior-dependent wildlife. We used the simulation model LANDIS to examine how the implementation of a dynamic zoning strategy would change trajectories of ecological succession in the Great Divide Ranger District of the Chequamegon–Nicolet National Forest in northern Wisconsin over 500 years. The components of dynamic zoning strategies (number of zones in a scenario and the length of the hiatus between successive entries into zones) and their interaction had highly significant impacts on patterns of forest succession. Dynamic zoning scenarios with more zones and shorter hiatus lengths increased the average amount of the forest dominated by early successional aspen (*Populus* sp.). Dynamic zoning scenarios with two zones produced more late successional mature northern hardwoods than scenarios with four zones. Dynamic zoning scenarios with very short (30 years) or very long (120 years) hiatus lengths resulted in more late successional mature northern hardwoods than scenarios with intermediate hiatus lengths (60 and 90 years). However, none of the dynamic scenarios produced as much late successional mature northern hardwoods as the static alternative. Furthermore, the amounts of all habitat types in all dynamic zoning scenarios fluctuated greatly in time and space relative to static alternatives, which could negatively impact wildlife species that require a stable amount of habitat above some minimum critical threshold. Indeed, implementing dynamic zoning scenarios of different designs would have both positive and negative effects on wildlife species and for other objectives of forest management.

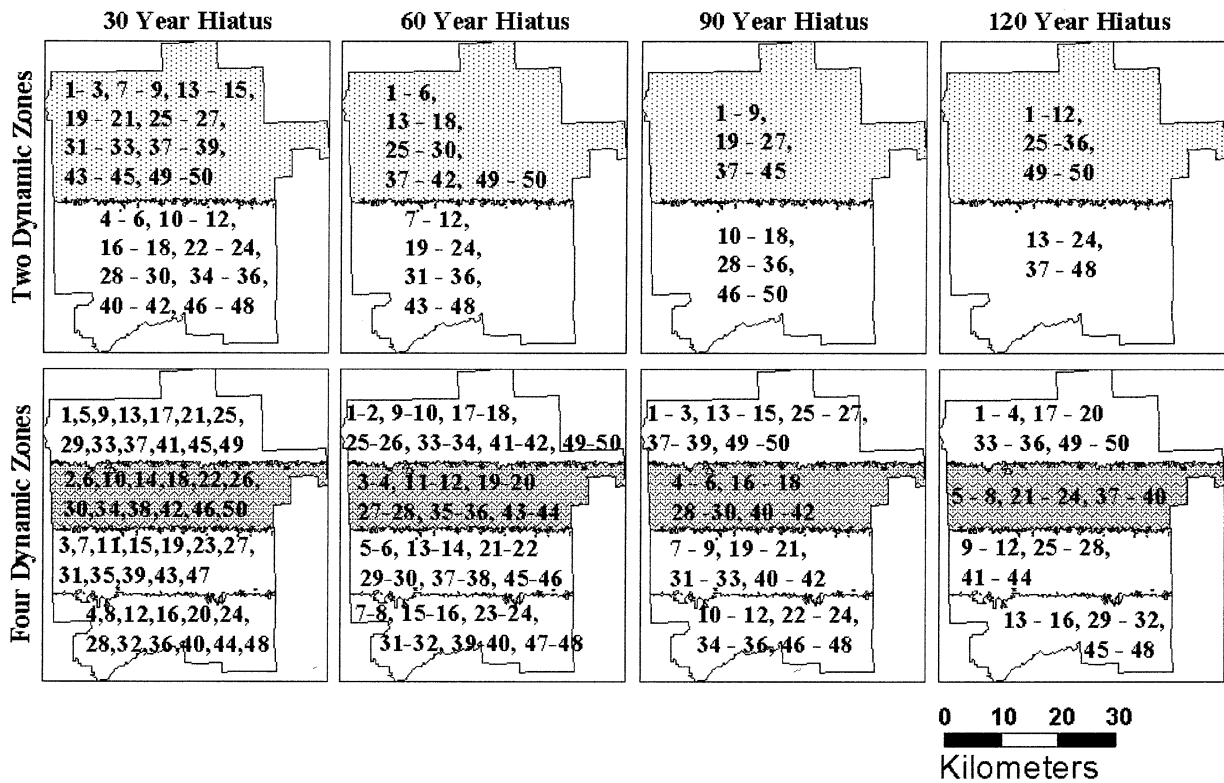*Author to whom correspondence should be addressed; *email:* pzollner@fs.fed.us

Dynamic zoning strategies for timber harvesting have been proposed as an alternative to traditional static forest management practices that distribute even-aged forest management practices (such as clear-cutting) across an entire management area during each time period (Crow and Gustafson 1997). Dynamic zoning approaches change the spatial and temporal allocation of even-aged forest management practices while holding the amount of timber being harvested constant or even increasing it (Gustafson and Crow 1994). This change is accomplished by dividing a management area into spatial subsets or "zones" (Figure 1) and focusing all of the even-aged management practices within a single zone for several decades and then periodically shifting the focus through the remaining zones (Gustafson 1998). Thus, at any point in time, the stands within one zone have a high probability of even-age harvest, whereas stands in the other zones will have a probability of zero. Dynamic zoning scenarios can be described by two key characteristics: (1) the number of zones used and (2) the length of the

Figure 1. Maps of the dynamic zoning scenarios investigated. The numbers on the shaded zones in the figures indicate the decades when 12,000 ha were harvested within that zone. Note that 12,000 ha are equivalent to approximately 16% of the area in a zone for the two-zone scenarios and 32% of the area in a zone for the four-zone scenario.

hiatus between active harvest periods within a given zone. These two factors interact to determine how the pattern of timber harvest changes in time and space and how successful a dynamic zoning strategy is at minimizing forest fragmentation while sustaining timber harvest.

The objective of dynamic zoning is to modify the landscape pattern of forest openings to minimize landscapewide fragmentation of closed-canopy forest conditions (Gustafson and Crow 1994), which can be detrimental to the breeding success of some wildlife species (Thompson and others 1992; Manolis and others 2000; Flaspohler and others 2001). Previous simulation studies have demonstrated that dynamic zoning strategies minimize forest fragmentation while maintaining timber harvest levels (Gustafson and Crow 1996; Gustafson 1998). This is an important result because it implies that strategic allocation of timber harvests in time and space can address concerns about forest fragmentation without compromising timber management objectives. These previous investigations were conducted using simulations that did not track forest

succession, but only seral stage (forest age) (Gustafson 1998). In this article, we hypothesize that implementation of dynamic zoning strategies to change the spatial pattern of forest age structure will also alter successional dynamics and forest composition. Differences in the abundance of different tree species and the spatial arrangement of forest types could have a great influence on ecological communities and forest management objectives (Mladenoff and Pastor 1993; Mladenoff and others 1994). For example, in northern Wisconsin, there are concerns about the influence of forest management on the recruitment of white pine (*Pinus strobus*) relative to its historic occurrence (Landres and others 1999). It is unclear how a dynamic zoning strategy would affect the occurrence of white pine or the response of other tree species of interest such as balsam fir (*Abies balsamea*), which is an important resource for local bough gatherers (Mickman 2002). Finally, the implementation of a dynamic zoning strategy should alter the spatial and temporal patterns of forest cover types on the landscape, which would affect the long-term supply of specific timber products.

Table 1.   Response variables used to describe the influence of different aspects of dynamic zoning on forest succession variables of ecological and management interest

Variable description	Question addressed
Area of dominant aspen	Response of early successional cover type
Area of dominant northern hardwoods	Response of late successional cover type
Area containing mature aspen	Quantify stands succeeding to new forest type
Area containing white pine	Response of a species of management concern
Area containing balsam fir	Important resource for local bough gatherers
Area containing mature northern hardwoods	Quantify total occurrence of critical habitat type for marten
Average patch area of mature northern hardwoods	Quantify suitability of critical habitat type for marten
Average connectivity of mature northern hardwoods patches	Quantify spatial influence on suitability of arrangement of critical habitat for marten

An important objective of forest management is the maintenance of suitable habitat to sustain populations of specific wildlife species (Marcot and Murphy 1996). The effects of dynamic zoning on wildlife are largely unknown. We selected two wildlife species with very different habitat requirements as case studies to examine the impacts of dynamic zoning on the availability of suitable habitat. The American marten (*Martes americana*) was extirpated from Wisconsin but was reintroduced within the last 30 years. However, American marten populations have not spread, and simulation analyses indicate that the spatial pattern of suitable habitat is a likely explanation for this stagnation (Gardner and Gustafson 2004). Unlike western (Koehler and others 1990) and boreal (Sturtevant and others 1996) populations of martens that inhabit conifer forests, research in northern Wisconsin has demonstrated that suitable habitat in this area consists of large blocks of contiguous late successional northern hardwood forests (Gilbert and others 1997; Wright 1999). Thus, a dynamic zoning strategy that minimized fragmentation could provide marten habitat unless the resulting interior habitat was composed of early successional forest types that marten will not use. Alternatively, the ruffed grouse (*Bonasa umbellus*) is a popular game species that benefits greatly from the presence of early successional aspen forest (Dessecker and Mcauley 2001). Dynamic zoning might create more abundant habitat for ruffed grouse than static scenarios, although the distribution of such habitat would vary in both space and time. We hypothesize that dynamic zoning should produce good grouse habitat (young aspen) in the zones that are actively being harvested and might produce good American marten habitat (large block of interior forest) in the inactive zones.

This article models the influence of dynamic zoning of forest harvesting on ecological succession in a northern hardwoods landscape. Specifically, we considered how hiatus length and number of zones in a dynamic zoning strategy influence the total amount of the landscape that is dominated by early successional (aspen) and late successional (northern hardwoods) forest types, as well as the total area of the forest containing senescing aspen (older than 70 years in age). We also examined the total amount of the landscape containing white pine and balsam fir. Finally, we assessed the influence of dynamic zoning on the suitability of habitat for American marten and ruffed grouse. Our overall null hypothesis was that the number of dynamic zones, the length of hiatus between harvests within each zone, and the interactions between these factors did not influence the average value of or the temporal variation in a suite of variables related to successional dynamics and forest composition (Table 1).

Methods

LANDIS Model

We used LANDIS 3.2 to simulate alternative dynamic zoning forest management scenarios. LANDIS simulates spatial forest dynamics, including forest succession based on the vital attributes of tree species and natural and anthropogenic disturbances (Mladenoff and He 1999; He and Mladenoff 1999; Gustafson and others 2000). The design and behavior of the model and model testing are described in detail elsewhere (Mladenoff and He 1999; He and others 199a, 1999b; He and Mladenoff 1999; Gustafson and others 2000). The purpose of LANDIS is to simulate the effects of fire, wind, and vegetation management on patterns of forest vegetation across large (10^4–10^7 ha) landscapes and long timescales (50–1000 years) and it incorporates feedbacks between disturbance and species response (Mladenoff and He 1999). The model operates

on a raster (grid) map, where each cell contains information on the presence or absence of tree species by their 10-year age cohorts (i.e., a list of species by age classes), but not information about the number or size of individual stems. The model requires mapped land types and parameters for species establishment, fire characteristics, and fuel accumulation regimes for each land type.

LANDIS allows simulation of anthropogenic disturbance, including timber harvest. Harvest activity can be specified independently for different management areas. The user specifies the details about how timber management activities selectively remove age cohorts of each species on harvested cells. The order in which stands are selected for harvest is based on ranking algorithms that can be related to specific management goals. These features provide the ability to simulate a wide variety of vegetation management activities. The timber harvest module of LANDIS is described in detail by Gustafson and others (2000).

The LANDIS model simulates wind and fire disturbance regimes based on historical distributions. The user specifies several parameters for the size and frequency of wind and fire events on each land type. These parameters are spatially implemented on the landscape using a stochastic algorithm to approximate a desired return interval across the land type over a long temporal scale (e.g., ≥ 100 years) (He and Mladenoff 1999). LANDIS sequentially simulates windthrow, fire, harvesting, and forest succession at each 10-year time step.

Study Area

We investigated dynamic zoning within the area encompassed by the proclamation boundary of the Great Divide Ranger District (150,000 ha) of the Chequamegon–Nicolet National Forest (CNNF), located in northern Wisconsin, USA. The Great Divide Ranger District is located mostly within the Winegar Moraine and Central Wisconsin Loess Plain ecological subsections (Keys and others 1995), characterized by glacial till and mixed deciduous and hemlock forests. Fire was uncommon during presettlement times, and modern fires are routinely suppressed, but disturbance by high-wind events is a regular occurrence (Canham and Loucks 1984).

The landscape we analyzed included a mix of national forest (86%) and private (14%) lands. We applied the simulated treatments across all ownerships because a lack of harvest activity on private lands would produce large blocks dominated by northern hardwoods that could unrealistically alter successional patterns. In the absence of data on harvest practices on

private lands, we assumed that the outer boundary of the Ranger District defined an area that was managed in its entirety by our experimental treatments. We acknowledge that this does not exactly reflect reality, but it better allows us to draw inference about the main effects studied.

Input maps for LANDIS were derived from existing spatial databases and were gridded to a 60-m cell size. Initial forest composition maps (spatially explicit species and age-cohort data) and land-type maps were based on those used by Gustafson and others (2004). The initial forest condition map was created using spatial location of dominant species derived from a classified TM image (Wolter and others 1995) and then age classes and associated species (by land type) were randomly assigned to stands to match the statistical distributions found in US Forest Service Forest Inventory and Analysis data (Hansen and others 1992) as described by He and others (1999b). The eight land types were the same as those used by Gustafson and others (2004), which were derived from an ecosystem classification system developed by Host and others (1996), based on soils and monthly average temperature and precipitation data for this region. The probabilities of species establishment on cells within each land type were derived by He and others (1996) using the LINKAGES model (Pastor and Post 1986). Windfall return intervals (approximately 1200 years) were derived from a regional historical and empirical study (Canham and Loucks 1984). Our fire disturbance values were not based on the historical fire regime (He and others 1999b), but on the modern era of fire suppression with mean fire return intervals ranging from 100 to 700 years depending on land type (Gustafson and others 2004; Cardille and others 2001).

Experimental Design

For each of the five random number sequences used in this study, the fire probability coefficients for each land type were adjusted according to the techniques described by He and Mladenoff (1999) to ensure that the mean fire return intervals were similar across replicates. We used the same random number sequences for all experimental treatments (combinations of number of zones and hiatus length) to control for the influence of natural disturbances such as fire and wind on the patterns of succession observed in the simulation.

To investigate the influence of the components of dynamic zoning, we applied even-age treatments (clearcutting that reset the stand age to zero) in a fully crossed factorial design with two main factors. In the

spatial main effect, the spatial configuration of the timber cutting zones consisted of two or four spatially delineated Management Areas (MAs) (Figure 1). The second main effect, hiatus length (i.e., the length of time after a zone was harvested with even-aged practices before that zone was harvested again) was set at either 30, 60, 90, or 120 years. In order to achieve these hiatus lengths in the scenarios with both two and four zones, it was necessary to modify the duration (number of decades) of the even-aged harvesting period within zones among scenarios. Figure 1 provides a detailed schedule of when and where even-aged harvests were implemented in each scenario to accomplish these objectives. We simulated each combination of these two effects, and a traditional static (even-aged harvests spread throughout the entire study area during each decade) scenario with five replicates defined by random number sequences, and all simulations were run for 500 years. Disturbance and succession in LANDIS are stochastic processes governed by probability distributions, and five replicates were deemed sufficient based on the results of prior studies.

The area harvested by even-aged management each decade was held constant for all scenarios at approximately 12,000 ha (8% of the forested portion of the entire study area). Stands to be harvested during each decade were selected either from within a particular zone (dynamic scenarios) or from within the entire study area (static scenario) according to the specifications of the relevant stand ranking algorithm. The stand ranking algorithm we employed used weighting values to increase the likelihood that stands containing certain species would be selected for harvest as long as those stands contained that species above minimum critical ages (Table 2) (Gustafson and others 2000). During each decade, 8000 ha of the clear-cuts were targeted (by the stand ranking algorithm; Table 2) toward stands dominated by aspen. The remaining 4000 ha of clear-cuts were targeted toward stands containing conifers (Table 2). In addition to the even-aged management, for all scenarios across all management zones, approximately 6000 ha (4% of the forested portion of the entire study area) were treated with individual tree selection harvest each decade. The stands were selected by a stand ranking algorithm that focused harvests on stands that contained northern hardwood tree species (Table 2) where at least 20 years had elapsed since the previous entry into that stand. This uneven-aged management was included in the simulation to reflect the fact that forest management in this area uses such a silvicultural prescription to maintain northern hardwood forest types and preserve interior forest conditions.

For dynamic scenarios with longer hiatus lengths (where a single zone was harvested for multiple decades before shifting to a new zone), the schedule of even-aged harvests within zones occasionally necessitated that a subset of stands within a zone be harvested several times before harvesting was shifted to a new zone. For example, the zones in the four-zone scenario were each approximately 37,500 ha in size. Thus, during the 120-year hiatus length scenario, 12,000 ha were cut in each zone for four successive decades. This required that in the fourth decade of harvest, 10,500 ha of the harvested stands would be 30-year-old stands that had been harvested during the first decade of activity in that particular zone. See Figure 1 for a schedule of even-aged harvesting activities in each of the dynamic scenarios investigated.

Outputs from LANDIS include raster maps of the presence and absence of all age cohorts of all specified tree species during each time step of the simulation, as well as raster maps classifying the dominant forest types within cells based on the relative age of each species cohort present in each cell. We used these maps to estimate the total area containing white pine and balsam fir. We also calculated the total area of forest containing cohorts of senescing (over 70 years) aspen and mature (over 60 years) northern hardwoods (sugar maple, basswood, or white ash) and the amount of the study area where the dominant forest type was either aspen or northern hardwoods.

Analysis of Model Outputs

All response variables (Table 1) were calculated using APACK (DeZonia and Mladenoff 2002). The total area dominated by aspen was used to assess the availability of suitable habitat for ruffed grouse. Three measures (total area, average patch size, and average patch connectivity) of mature northern hardwoods stands were used to assess the availability of suitable habitat for American martens. Average patch connectivity uses a gravity-based method to calculate the interaction between patches as the product of the mass of the patches divided by the square of the distance between them (Forman and Gordon 1986). This metric assesses connectivity as the spatial proximity of suitable habitat, which should be correlated with the abilities of animals to move between patches of such habitat.

All analyses were limited to simulated data between years 250 and 500 to allow the effects of each scenario to reach equilibrium and to diverge completely from the common initial condition (Wallin and others 1994). The average value over time and the coefficient of variation over time were calculated for each re-

Table 2.   Values used by stand selection algorithm within LANDIS to select stands for harvest during each decade of the simulation

Species	Minimum cohort age (years) considered when selecting stands	Species weighting coefficients for selecting stands for selective cut	Species weighting coefficients for selecting stands for aspen clear-cut	Species weighting coefficients for selecting stands for conifer clear-cut
Abies balsamea	30	30	25	25
Acer rubrum	30	99	25	25
Acer saccharinum	30	99	25	25
Betula alleghaniensis	30	50	25	25
Betula papyrifera	30	25	50	50
Carya cordiformis	30	25	10	10
Fraxinus americana	30	50	10	10
Picea glauca	50	10	25	75
Pinus banksaiana	30	10	50	50
Pinus resinosa	50	10	25	95
Pinus strobus	70	10	25	95
Populus grandidentata	30	5	99	50
Populs tremuloides	30	5	99	50
Prunus pensylvanica	30	1	75	45
Prunus serotina	30	1	75	45
Quercus alba	30	25	10	10
Quercus ellipsoidalis	30	25	10	10
Quercus macrocarpa	30	25	10	10
Quercus rubra	30	25	50	50
Quercus velutina	30	25	10	10
Thuja occidentalis	50	10	10	10
Tilia Americana	30	40	10	10
Tsuga Canadensis	100	5	1	1

sponse variable for each replicate (1–5) in each of the scenarios. We analyzed all of the response variables together in a multivariate analysis of variance (MANOVA) for the mean values and again for the coefficient of variation over that last 250 years of the simulation. These analyses tested the global hypotheses that the length of hiatus between entries into each zone, the number of zones, and the interactions between them did not influence the average value or the temporal variation of each response variable. The MANOVA was computed using PROC GLM by SAS (1988) using a randomized block, 2×4 factorial design. Treatments employing the same sequence of random numbers were treated as blocks, and length of hiatus (30, 60, 90, or 120 years) and number of dynamic zones (two or four) were treated as factors. We used the Pillai's Trace statistic to test our hypotheses because it is the least sensitive of the four multivariate tests provided by SAS to the heterogeneity of variance assumption of MANOVA (Zar 1999). Additionally, each response variable was decomposed into a separate ANOVA to examine response to the experimental factors, and Ryan–Einot–Gabriel–Welsch multiple range tests were used to conduct multiple comparisons and look at the influence of different levels within each factor. However, these multiple comparisons only investigated the influence of levels within each factor independently and not the interaction of the factors (number of zones and length of hiatus). The interactions between levels of factors were explored by plotting all possible combinations of factors and comparing the levels of the response variables to the static alternative. The results of the static alternative were not included in the ANOVAs or MANOVAs to maintain the fully factorial design. Instead, the static results are plotted in the figures to serve as a reference point for comparison to the dynamic zoning scenarios.

Results

The MANOVA analyses revealed a significant effect of the length of hiatus, the number of dynamic zones, and the interactions between these two factors on the average value of all response variables over the last 250 years of the simulation (Table 3). Inspection of the F statistics reveals that the number of dynamic zones contributed the most to explaining the variance in the response variables in the MANOVA, but it was most important in only three of the eight ANOVAs.

The MANOVA analyses also revealed a significant effect of the hiatus length, the number of dynamic

Table 3. MANOVA and individual ANOVA results for the mean value of seven landscape pattern metrics of forest succession as a function of number of zones and length of hiatus period between even-aged harvests within a dynamic zone

	MANOVA global test of hypotheses			
Effect	df (n, d)	Pillai's Trace	F	Prob > F
Hiatus	24, 69	2.99	708.03	<0.0001
No. of zones	8, 21	0.99	6,393.67	<0.0001
Hiatus * No. of zones	24, 69	2.99	918.62	<0.0001
	Individual ANOVA tests of hypotheses			
Source of variation	df	Type III SS	F	Prob > F
Total area dominated by aspen: Model R^2 = 0.9974				
Replicate	4	2,190,190	34.23	<0.0001
Hiatus	3	119,768,881	2,495.46	<0.0001
No. of zones	1	21,227,033	1,326.84	<0.0001
Hiatus * No. of zones	3	25,822,327	538.02	<0.0001
Error	28	447,950		
Total	39	169,456,382		
Total area dominated by northern hardwoods: Model R^2 = 0.9993				
Replicate	4	2,702,315	28.53	<0.0001
Hiatus	3	614,097,872	8,645.17	<0.0001
No. of zones	1	102,435,203	4,326.20	<0.0001
Hiatus * No. of zones	3	212,912,444	2,997.35	<0.0001
Error	28	662,980		
Total	39	932,810,816		
Total area containing aspen older than 70 years: Model R^2 = 0.9998				
Replicate	4	51,742	5.42	0.0023
Hiatus	3	256,198,043	35,758.2	<0.0001
No. of zones	1	59,919,696	25,089.4	<0.0001
Hiatus * No. of zones	3	59,635,635	8,323.5	<0.0001
Error	28	66,870		
Total	39	375,871,989		
Total area containing white pine: Model R^2 = 0.9993				
Replicate	4	153,940	7.33	0.0004
Hiatus	3	157,800,585	10,023.6	<0.0001
No. of zones	1	2,548,735	485.69	<0.0001
Hiatus * No. of zones	3	58,957,871	3,745.05	<0.0001
Error	28	146,933		
Total	39	219,608,066		
Total area containing balsam fir: Model R^2 = 0.9982				
Replicate	4	2,200,460	16.31	<0.0001
Hiatus	3	167,766,740	1,657.76	<0.0001
No. of zones	1	136,911,100	4,058.60	<0.0001
Hiatus * No. of zones	3	75,906,827	2,250.19	<0.0001
Error	28	944,540		
Total	39	535,543,325		
Total area containing northern hardwoods older than 60 years: Model R^2 = 0.9995				
Replicate	4	3,567,803	29.21	<0.0001
Hiatus	3	804,558,613	8,783.29	<0.0001
No. of zones	1	528,507,190	17,309.0	<0.0001
Hiatus * No. of zones	3	386,904,561	4,223.80	<0.0001
Error	28	854,944		
Total	39	1,724,393,113		
Average patch area of northern hardwoods older than 60 years: Model R^2 = 0.9964				
Replicate	4	0.1	1.00	0.4241
Hiatus	3	148.2	1,976.00	<0.0001
No. of zones	1	28.9	1,156.00	<0.0001

Table 3.   Continued

Effect	df (n, d)	MANOVA global test of hypotheses Type III SSS	F	Prob > F
Hiatus No. of zones	3	17.7	236.00	<0.0001
Error	28	0.7		
Total	39	195.6		
Connectivity (CCI) of northern hardwoods older than 60 years: Model R^2 = 0.9868				
Replicate	4	0.043	3.61	0.0172
Hiatus	3	2.97	326.41	<0.0001
No. of zones	1	1.57	518.12	<0.0001
Hiatas ∗ No. of zones	3	1.78	195.72	<0.0001
Error	28	0.085		
Total	39	6.45		

Note. Evaluation period covers simulation years 250–500.

zones, and their interactions on the coefficient of variation (Table 4) for all response variables. Inspection of the F statistics reveals that the number of dynamic zones also contributed the most to explaining the variation in the response variables over time for the MANOVA. However, the variation over the last 250 years for total area containing balsam fir, mature northern hardwoods, and the connectivity of patches of mature northern hardwoods was best explained by hiatus length in the ANOVAs. Examination of trends (Figures 2 and 3) suggests that longer hiatus lengths cause more variation in response variables over time than shorter hiatus lengths, whereas scenarios with more zones tend to have lower levels of variation than those with fewer zones.

Static management scenarios produced more late successional forest (mature northern hardwoods) than did dynamic scenarios (Figure 2). The static scenarios resulted in the most American marten habitat by producing mature northern hardwoods in patches that were larger and more connected (Figures 3 and 4). Interestingly, increasing the number of dynamic zones in dynamic scenarios had a negative effect on the total amount of mature northern hardwoods habitat (Table 5). Scenarios with either very short (30 years) or very long (120 years) hiatus lengths produced more mature northern hardwoods than scenarios with intermediate hiatus lengths (60 and 90 years; Figure 5a). Dynamic scenarios with short hiatus lengths (30 or 60 years) resulted in the most ruffed grouse habitat (areas dominated by aspen; Figure 5b). Static scenarios produced the second most ruffed grouse habitat, followed by dynamic zoning scenarios with longer hiatus lengths (90 or 120 years). Dynamic zoning scenarios with four dynamic zones produced more ruffed grouse habitat than those with two zones.

Discussion

Many landscape ecology studies have investigated how alterations in the spatial and temporal dynamics of timber harvesting can change the spatial patterns of forest openings (Franklin and Forman 1987; Li and others 1993; Ohman and Eriksson 1998; Gustafson 1998). However, the influence of these changes on the trajectories of ecological succession and the resulting patterns of forest composition have rarely been investigated (Kurz and others 2000; Klenner and others 2000). Our results demonstrate that implementation of a dynamic zoning strategy can change trajectories of ecological succession. Although the details of these changes are also subject to factors that we did not consider in our simulations (e.g., global climate change) and the responses might be different in other ecosystems, our results provide evidence that the impact of the spatial and temporal distribution of timber harvest strategies on forest succession is worthy of more study.

The relative quantities of late successional mature northern hardwood forest found on the landscape were strongly influenced by the hiatus length. The conventional wisdom that longer rotation lengths should produce more late successional forests might not provide obvious insight into our results because convention is based on work at local scales (e.g., gap or stand scale) and the phenomena we simulated illustrate a landscape effect. In our static zoning scenario, even-aged and uneven-aged treatments were dispersed across the entire study area by the stand ranking algorithm during the initial decades of the simulation. These treatments changed the composition of stands such that the stand selection algorithms tended to maintain the initial trajectory of harvested stands for the duration of the simulation; that is, even-aged stands

Table 4. MANOVA and individual ANOVA results for the coefficient of variation of seven landscape pattern metrics of forest succession as a function of number of zones and length of hiatus period between even-aged harvests within a dynamic zone

	MANOVA global test of hypotheses			
Effect	$df\ (n,d)$	Pillai's Trace	F	Prob $> F$
Hiatus	24, 69	2.91	88.80	< 0.0001
No. of zones	8, 21	1.00	3,092.23	< 0.0001
Hiatus $*$ No. of zones	24, 69	2.85	55.07	< 0.0001
	Individual ANOVA tests of hypotheses			
Source of variation	df	Type III SS	F	Prob $> F$
Total area dominated by aspen: Model R^2 = 0.9973				
Replicate	4	0.57	1.86	0.1463
Hiatus	3	535.36	2,319.46	<0.0001
No. of zones	1	195.41	2,539.77	<0.0001
Hiatus $*$ No. of zones	3	70.78	306.68	<0.0001
Error	28	2.15		
Total	39	804.28		
Total area dominated by northern hardwoods: Model R^2 = 0.9717				
Replicate	4	1.02	4.64	0.0053
Hiatus	3	22.25	134.74	<0.0001
No of zones	1	8.58	155.95	<0.0001
Hiatus $*$ No. of zones	3	21.15	128.09	<0.0001
Error	28	1.54		
Total	39	54.55		
Total area containing aspen older than 70 years: Model R^2 = 0.993				
Replicate	4	1.75	0.55	0.7009
Hiatus	3	12,536.62	5,221.53	<0.0001
No. of zones	1	16,436.64	20,537.7	<0.0001
Hiatus $*$ No. of zones	3	3,278.52	1,365.51	<0.0001
Error	28	22.41		
Total	39	32,275.96		
Total area containing white pine: Model R^2 = 0.9459				
Replicate	4	1.05	3.44	0.0209
Hiatus	3	20.94	91.23	<0.0001
No. of zones	1	8.05	105.28	<0.0001
Hiatus $*$ of zones	3	7.39	32.22	<0.0001
Error	28	2.14		
Total	39	39.59		
Total area containing balsam fir: Motel R^2 = 0.9941				
Replicate	4	1.17	7.48	0.0003
Hiatus	3	153,43	1,299.86	<0.0001
No. of zones	1	15.96	405.79	<0.0001
Hiatus $*$ No. of zones	3	14.83	125.68	<0.0001
Error	28	1.10		
Total	39	186.51		
Total area containing northern hardwoods older than 60 Years; Model R^2 = 0.995				
Replicate	4	0.86	3.43	0.0211
Hiatus	3	278.36	1,466.71	<0.0001
No. of zones	1	43.14	682.06	<0.0001
Hiatus $*$ No. of zones	3	32.11	169.21	<0.0001
Error	28	1.77		
Total	39	356.26		
Average patch area of northern hardwoods older than 60 years: Model R^2 = 0.9928				
Replicate	4	2.17	1.05	0.3993
Hiatus	3	1,442.71	735.49	<0.0001

Table 4.   Continued

Effect	df (n, d)	MANOVA global test of hypotheses Pillai's Trace	F	Prob > F
No. of zones	1	416.64	804.50	<0.0001
Hiatus * No. of zones	3	439.23	282.71	<0.0001
Error	28	14.51		
Total	39	2,015.26		
Connectivity (CCI) of northern hardwoods older than 60 years: Model R^2 = 0.9711				
Replicate	4	166.63	0.63	0.6462
Hiatus	3	51,069.36	256.81	<0.0001
No. of zones	1	6,014.30	90.73	<0.0001
Hiatus * No. of zones	3	5,010.11	25.19	<0.0001
Error	28	1,856.06		
Total	39	64,116.47		

Note. Evaluation period covers simulation years 250–500.
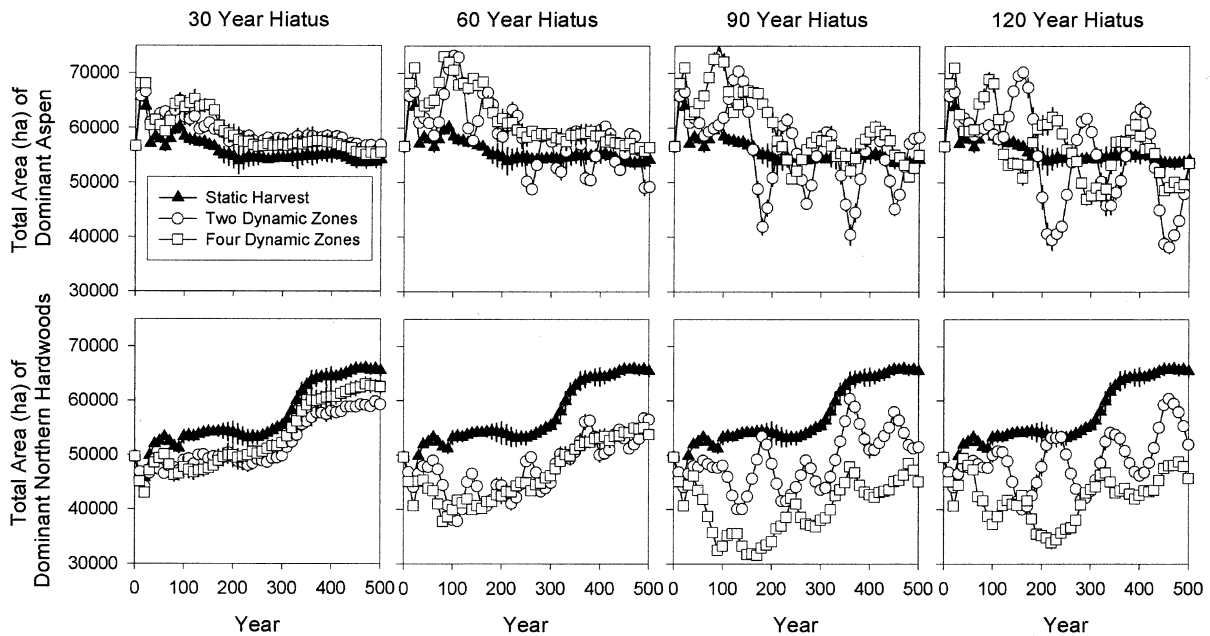
Figure 2. Total area classified as dominated by aspen and northern hardwoods over simulated time for each of the scenarios investigated. Error bars represent 95% confidence intervals for five replicate simulations. Where error bars are not apparent, they are smaller than the symbols representing the mean value.

tended to be maintained as even-aged stands dominated by aspen, and uneven-aged stands tended to be maintained as such, eventually developing into mature northern hardwood stands. In contrast, dynamic zoning scenarios with very long hiatus periods converted all of the stands within a particular zone to even-aged aspen, with the long hiatus providing enough time for the remaining zones to succeed into mature northern hardwoods prior to harvesting shifting between zones. This results in large contiguous blocks of early successional aspen and northern hardwood forest types of various ages in separate zones. Alternatively, dynamic

zoning scenarios with intermediate hiatus lengths (60 and 90 years) did not provide sufficient time for succession to convert stands into mature northern hardwoods before harvests returned. Finally, scenarios with a very short hiatus length (e.g., 30 years) did not completely cut each zone by even-aged harvests, so a subset of stands could develop into the mature forest type. These stands were subsequently maintained in this forest type by the stand ranking algorithm for the duration of the simulation.

The amount of the landscape where early successional aspen forest type dominated was higher with
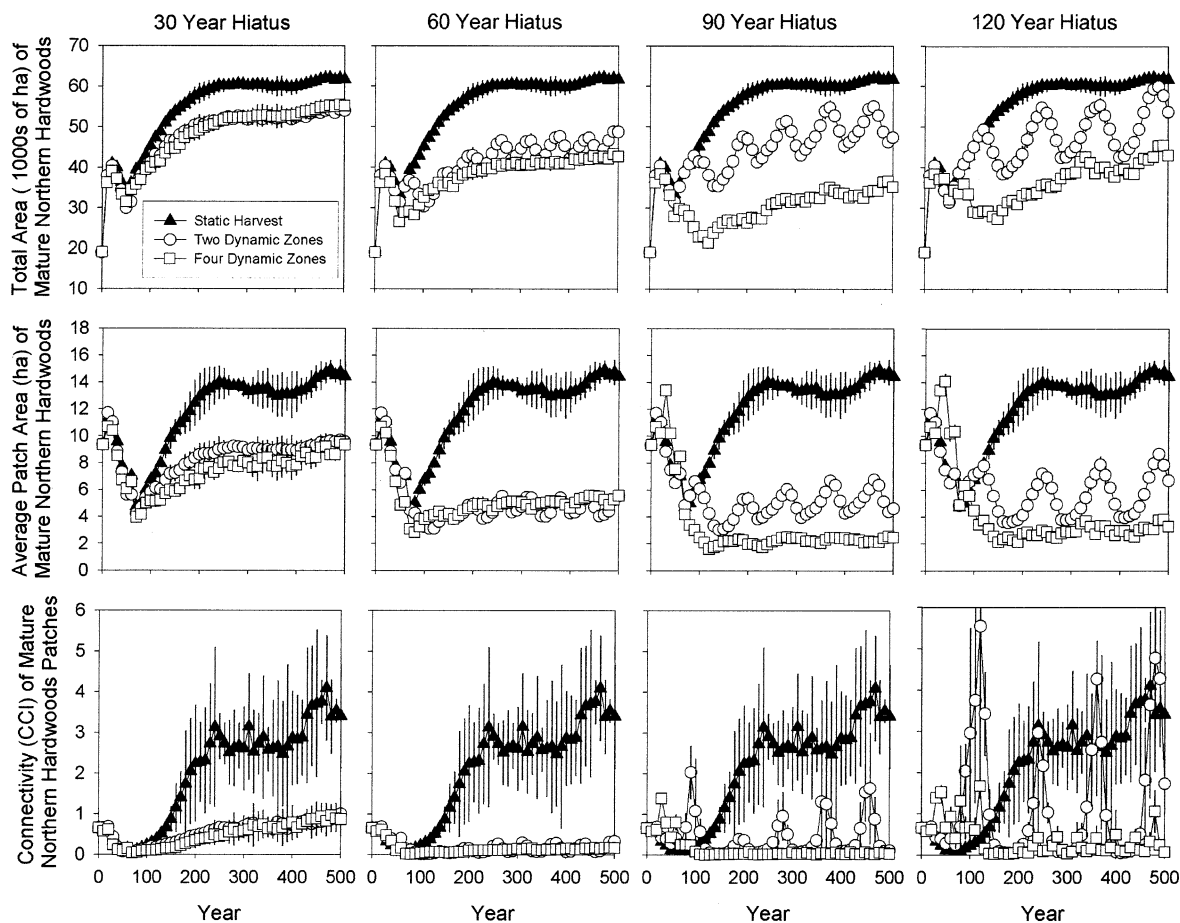
Figure 3. Response of the mature (> 60 years old) northern hardwoods habitat type to each of the scenarios over simulated time. Error bars represent 95% confidence intervals for five replicate simulations. Where error bars are not apparent, they are smaller than the symbols representing the mean value.

more zones and also with shorter hiatus lengths (Table 5). More zones increased the density of harvest units within each zone, leaving fewer stands untouched by even-aged treatments. Shorter hiatus lengths limit the opportunity for forest succession to proceed without interruption. Static harvesting scenarios produced an amount of early successional aspen that was intermediate to shorter- and longer-hiatus scenarios. Overall, hiatus length had a larger influence on the amount of dominant aspen in the landscape than either the number of zones or the interaction of these terms (Table 3).

The influence of hiatus length and number of zones on the relative amounts of early and late successional forest types is not an artifact of the model. The spatial arrangements of harvest blocks in the real world would encounter the same constraints on the allocation of harvests in time and space, and these allocations would interact with the dispersal behavior of each tree spe-

cies. This implies that dynamic zoning scenarios employing hiatus lengths that greatly exceed (e.g., > 180 years) the time it took early successional species to senesce might produce more late successional habitat than static scenarios. However, we did not simulate such long hiatuses because it is unclear whether it would be feasible to implement vastly longer hiatuses on public forests (Crow 2002).

Changes to ecological succession and forest composition resulting from dynamic zoning had both positive and negative ecological consequences for wildlife species of management interest. American martens need large blocks of forest interior, thus dynamic zoning should favor their persistence. However, martens in northern Wisconsin are strongly associated with stands of northern hardwoods that are older than 60 years in age (Gilbert and others 1997; Wright 1999), and the static scenarios produced more of that habitat than did any of the dynamic scenarios. Furthermore,

Figure 4. Spatial arrangement of northern hardwood age classes at simulation year 500 for one replicate. Scenarios shown were chosen for display because they represent the range of conditions found in our results.

among the dynamic zoning scenarios investigated, those with shorter hiatus lengths produced the most marten habitat. Conversely, ruffed grouse require early successional habitat (Dessecker and Mcauley 2001) and we predicted *a priori* that they would benefit greatly from dynamic zoning scenarios that produce more aspen forests. We found that, on average, grouse habitat is most prevalent in dynamic strategies with shorter hiatus lengths, whereas static scenarios provide close to the same amount of grouse habitat as intermediate hiatus scenarios. These results suggest that whereas marten would benefit most from the continuation of static harvest practices, dynamic zoning scenarios with shorter hiatus lengths would be beneficial for both of these species relative to scenarios with longer hiatuses. However, many wildlife species might have some critical threshold quantity of habitat for their persistence in a landscape and dynamic zoning scenarios might fail to maintain populations of such wildlife species of interest because dynamic zoning scenarios create temporally fluctuating quantities of habitat that could occasionally drop below such threshold.

Implementation of dynamic zoning strategies also impacts the occurrence of individual tree species across the landscape. This impact might be important for some management objectives. For example, the CNNF is actively managing to increase the abundance of white pine because it is less common in the modern landscape relative to its historic abundance (Landres and others 1999). Although our dynamic zoning scenarios achieved some management objectives for habitat size and area, our results indicate that dynamic zoning could have unintended consequences for the prevalence of white pine. Managers concerned with encouraging white pine might favor dynamic zoning scenarios with longer hiatuses and more dynamic zones. These impacts might extend to other tree species as well. A dynamic zoning strategy with longer hiatuses would hinder recruitment of balsam fir, whereas scenarios with more zones should increase the quantity of senescing aspen. Aspen senescence has implications for a stable supply of raw material for the paper industry (Einspahr and Wyckoff 1990).

Table 5. Results of Ryan–Einot–Gabriel–Welsch multiple range tests of multiple comparisons between the influence of the number of zones and the length of hiatus period at an alpha level of 0.05 for both the mean values and coefficients of variation over years 250–500 of the simulation

ANOVA test	Factor	Comparison of levels[a]
Total area dominated by aspen	Hiatus	30 yr > 60 yr > 90 yr > 120 yr
Mean value last 250 years	Hiatus	30 yr > 60 yr > 90 yr > 120 yr
	No. of zones	4 zones > 2 zones
Coefficient of variation last 250 years	Hiatus	120 yr > 90 yr > 60 yr > 30 yr
	No. of zones	2 zones > 4 zones
Total area dominated by northern hardwoods		
Mean value last 250 years	Hiatus	30 yr > 60 yr > 120 yr & 90 yr
	No. of zones	2 zones > 4 zones
Coefficient of variation last 250 years	Hiatus	120 yr > 90 yr > 30 yr & 60 yr
	No. of zones	2 zones > 4 zones
Total area containing aspen older than 70 years		
Mean value last 250 years	Hiatus	90 yr > 120 yr > 60 yr > 30 yr
	No. of zones	4 zones > 2 zones
Coefficient of variation last 250 years	Hiatus	120 yr 90 yr > 60 yr > 30 yr
	No. of zones	2 zones > 4 zones
Total area containing white pine		
Mean value last 250 years	Hiatus	120 yr > 90 yr > 60 yr > 30 yr
	No. of zones	4 zones > 2 zone
Coefficient of variation last 250 years	Hiatus	30 yr > 60 yr > 90 yr > 120 yr
	No. of zones	4 zones > 2 zones
Total area containing balsam fir		
Mean value last 250 years	Hiatus	30 yr > 60 yr > 90 yr > 120 yr
	No. of zones	2 zones > 4 zones
Coefficient of variation last 250 years	Hiatus	120 yr > 90 yr > 60 yr > 30 yr
	No. of zones	2 zones > 4 zone
Total area containing northern hardwoods older than 60 years		
Mean value last 20 year	Hiatus	30 yr > 120 yr > 60 yr > 90 yr
	No. of zones	2 zones > 4 zones
Coefficient of variation last 250 years	Hiatus	120 yr > 90 yr > 60 yr > 30 yr
	No. of zones	2 zones > 4 zone
Average patch area of northern hardwoods older than 60 years		
Mean value last 250 years	Hiatus	30 yr > 60 yr > 120 yr > 90 yr
	No. of zones	2 zones > 4 zones
Coefficient of variation last 250 years	Hiatus	120 yr > 90 yr > 60 yr 30 yr
	No. of zones	2 zones > 4 zones
Connectivity (CCI) of northern hardwoods older than 60 years		
Mean value last 250 years	Hiatus	120 yr & 30 yr > 90 yr > 60 yr
	No. of zones	2 zones > 4 zones
Coefficient of variation last 250 years	Hiatus	120 yr > 90 yr > 60 yr > 30 yr
	No. of zones	2 zones > 4 zones

[a] > indicates that the level of the factor on the left was significantly greater than the level of the factor on the right at an alpha level of 0.05 in the REGW multiple range test. & indicates that the levels of the factor were not significantly different from each other at an alpha level of 0.05 in the REGW multiple range test.

Conclusion

Dynamic zoning scenarios create large blocks of closed-canopy forest (Gustafson and Crow 1994), but they also alter patterns of forest succession in ways that differ greatly from static alternatives and are not always intuitive. The characteristics (number of zones and length of hiatus) of dynamic scenarios determine the quantity and arrangement of early and late successional forest types across the landscape as well as the occurrence of other tree species of interest. The resulting spatial patterns of early and late successional forest directly impact many of the objectives of forest management favoring some and hindering others.
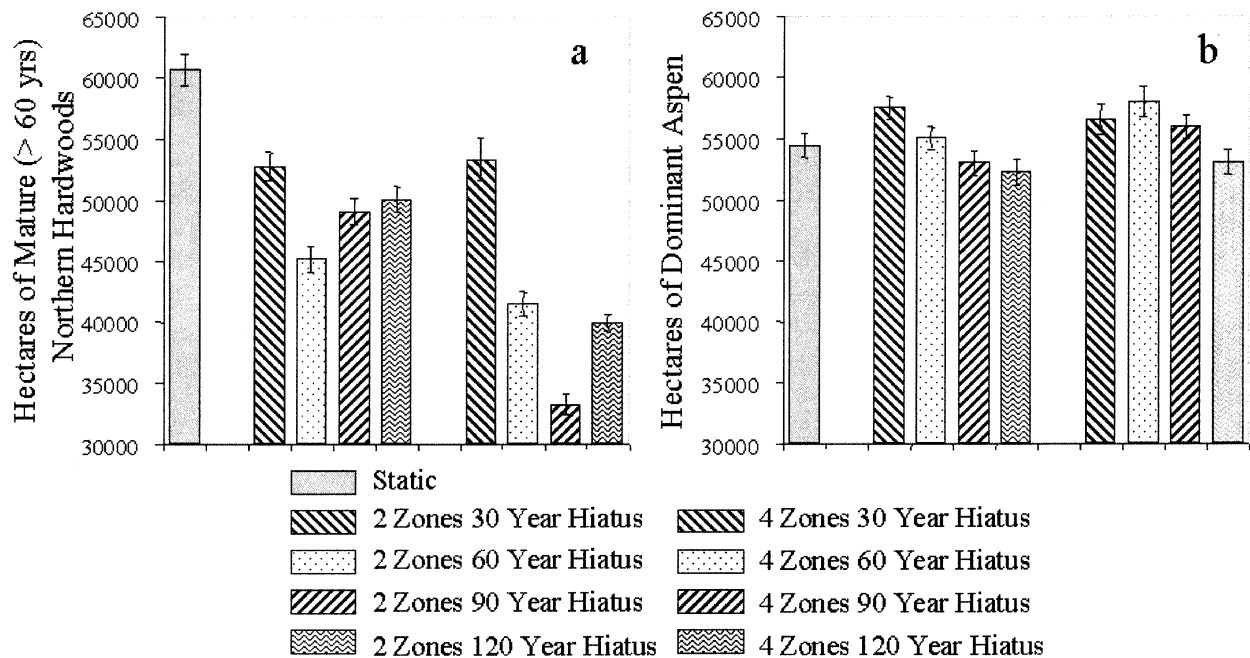
Figure 5. Average amount of (a) pine marten habitat and (b) ruffed grouse habitat over the last 250 years of the simulation for each of the scenarios. Error bars represent two standard deviations around the mean of the five replicates. Within the dynamic zoning scenarios, there was considerable temporal variation (see Figures 2 and 3).

These trade-offs between management objectives produced by different dynamic zoning scenarios illustrate the utility of the LANDIS model for investigating the response of complex, interacting phenomena to novel management strategies, and emphasize the importance of considering the impacts of such strategies upon trajectories of succession when evaluating them.

Acknowledgments

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