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Longterm response of disturbance landscapes to human intervention and global change

William L. Baker

Department of Geography and Recreation, University of Wyoming, Laramie, WY 82071, USA

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Abstract

The structure of landscapes subject to patch-forming catastrophic disturbances, or “disturbance landscapes”, is controlled by the characteristics of the disturbance regime, including the distribution of disturbance sizes and intervals, and the rotation time. The primary landscape structure in disturbance landscapes is the structure of the mosaic of disturbance patches, which can be described by indices such as patch size and shape.

The purpose of this research was to use a geographical information system-based spatial model (DISPATCH) to simulate the effects of the initial density of patches on the rate of response to alteration of a disturbance regime, the effects of global warming and cooling, and the effects of fragmentation and restoration, on the structure of a generalized temperate-zone forested disturbance landscape over a period of 400 yr.

The simulations suggest that landscapes require 1/2 to 2 rotations of a new disturbance regime to adjust to that regime regardless of the size and interval distributions. Thus alterations that shorten rotations, as would be the case if global warming increases fire sizes and decreases fire intervals, produce a more rapid response than do alterations that lengthen rotations, such as cooling and fire suppression. Landscape with long rotations may be in perpetual disequilibrium with their disturbance regimes due to a mismatch between their adjustment rate and the rate of climatic change. Landscapes with similar rotation times may have different structures, because size and interval distributions independently affect landscape structure. The response of disturbance landscapes to changing disturbance regimes is governed by both the number and size of patch births.

Introduction

Landscapes subject to catastrophic patch-forming natural disturbances, hereafter called ‘disturbance landscapes’, are common throughout the world, yet their longterm dynamics are poorly understood. Catastrophic disturbances, such as large fires, floods, mass movements, volcanic eruptions, snow avalanches, and windstorms periodically alter the structure of most of the world’s landscapes (White

1979). Over the longterm, disturbances produce a shifting-mosaic of patches (Bormann and Likens 1979). The landscape structure of this shifting mosaic can be described using a variety of indices, such as the amount of patch edge, the density of patches, and the distance between patches (Forman and Godron 1986; Turner 1989).

The structure of this shifting mosaic may not be temporally stable (Romme 1982, Baker 1989a), and the changing pattern of landscape structure has im-

portant implications. The pattern of change in structure may influence the availability of habitat for species sensitive to landscape structure (Romme and Knight 1982). Changing landscape structure can also influence how the landscape functions in terms of nutrient dynamics, energy partitioning, and hydrologic flows (*e.g.*, Ryszkowski 1992).

Disturbances associated with human land uses have replaced natural disturbances in many landscapes. Human disturbance regimes differ from natural disturbance regimes in many respects. Nonetheless, faced with the complexity of managing human-modified landscapes for biodiversity at multiple scales as global change proceeds, there is increasing interest in how natural landscapes have responded and will respond in the future to global change (Kareiva *et al.* 1993). Perhaps if the long-term dynamics of natural landscapes can be understood, then those dynamics could be a guide for patterning human disturbances.

Temporally dynamic landscape models based on geographical information systems (GIS) have been used to some extent to explore how landscapes change on the decade to century time scale. The most complex longterm change spatial models for disturbance landscapes have been described by Baker *et al.* (1991) and Antonovski *et al.* (1992). The Antonovski *et al.* model includes explicit functions driving the effect of climatic fluctuations on the occurrence of catastrophic fires in a landscape, but does not output data on landscape structure. The Baker *et al.* model, called 'DISPATCH', presents a somewhat different conceptual framework for modeling climatic influences on longterm dynamics of disturbance landscapes, but lacks the explicit functions and verification of the Antonovski *et al.* model. However, DISPATCH includes a module for outputting landscape structure as the model runs and can be used in theoretical simulations. A modified version of DISPATCH, lacking a climatic driver, has been used to analyze the effects of fire suppression on the structure of landscapes subject to catastrophic fires (Baker 1992, 1993).

Despite this modeling effort, a theory of landscape change in disturbance landscapes remains rudimentary. Baker (1992) found that when a dis-

turbance regime is altered there may be delays of as much as hundreds of years in the adjustment of landscape structure. This inertia apparently is in part the result of the density of patches in the landscape at the time of the alteration, but it is unclear whether high density or low density landscapes would respond more rapidly. Based only on the pattern of change after a period of large fires, Baker (1992) hypothesized that the response to global warming in the landscape of the Boundary Waters Canoe Area (BWCA), Minnesota, might be a lowered mean patch age, larger mean patch size, lower Shannon diversity of patch ages, and higher angular second moment (a measure of texture, discussed below). However, there was no explicit modeling of the longterm pattern of change or the rate of adjustment of the landscape to potential global warming. It is generally understood how landscape structure in forested regions responds to the fragmentation induced by human land uses (Godron and Forman 1983; Franklin and Forman 1987, Ripple *et al.* 1991; Mladenoff *et al.* 1993), yet it is less clear how rapidly these landscapes might respond to reinstatement of a natural disturbance regime or land use patterns that mimic such a regime (Swanson *et al.* 1992).

The purpose of this paper is to present the results of simulation experiments, using the modified version of DISPATCH, to analyze (1) the effect of initial landscape structure on the rate of response of landscape structure to global change, (2) the long-term effects of global warming and cooling on landscape structure, and (3) the rate and pattern of response of landscape structure to forest fragmentation and its restoration through reinstatement of a natural disturbance regime. Although these are specific experiments, the goal of this set of experiments is to further develop a general theory of the response of disturbance landscapes to alterations in their disturbance regimes.

Methods

The DISPATCH model

The DISPATCH model has been described in detail elsewhere (Baker *et al.* 1991; Baker 1992). A brief

synopsis is presented here. The model consists of three components, the first of which is the disturbance regime, represented here by a negative exponential probability density function for disturbance size and a normal probability density function for disturbance interval (time since last disturbance). These distributions are sampled using a random number generator to produce a temporal sequence of disturbances varying in size and timing. The second component of the model is the GIS, which is used to store and manipulate maps of disturbances and the spatial mosaic of disturbed patches. The GIS is GRASS 4.1 (USA-CERL 1991), and the data are maintained in raster or grid-cell format in GRASS. The third component is a set of new **GRASS** programs, called the *r.le* programs for quantitatively analyzing landscape structure as the model runs (Baker and Cai 1992).

The model operates with a yearly timestep, although the disturbance interval function may result in the passage of several years before a disturbance actually occurs. Disturbances are initiated at particular locations probabilistically and are allowed to spread probabilistically based on the disturbability of each cell in the GIS map of patches. Disturbability is defined differently in the three experiments, and is explained further below. Each year the GIS map of patch ages is updated to reflect the aging (by one year) of undisturbed patches and the reassignment of age 0 to patches disturbed during the year. At 25 yr intervals during the simulation runs the *r.le* programs are used to quantify the structure of the GIS map of patch ages, using several indices described later.

The simulated landscapes

The simulated landscapes are all 200 × 200 pixel square areas, with each pixel representing an area 100 m × 100 m (1 ha). Thus the total area represented is 20 km × 20 km (40,000 ha). The simulated landscapes represent typical temperate zone forested landscapes subject to periodic patch-creating catastrophic fires and/or human disturbances such as timber extraction clearcuts.

The model requires data on fire sizes and fire in-

tervals that are not typically determined or reported in fire history studies, as maps of individual fires must be reconstructed to obtain these data. A useful measure for comparing fire regimes, that can only be obtained from individual fire maps, is the fire rotation time. Fire rotation time can be defined simply as the time required to disturb a land area equal to the area of the landscape in question (Heinselman 1973). The limited data available suggest that a natural fire rotation time of 60–465 yr is typical of landscapes in the western United States and Canada (Table 1). Landscapes affected by fire suppression may have fire rotation times greater than 2700 yr (Table 1).

Monitoring changing landscape structure

The *r.le* programs (Baker and Cai 1992) are used to quantify 8 measures of landscape structure as the model runs. Mean age is the average age of all the patches in the landscape. Mean distance is the average distance, measured from the center of a patch to the center of each patch that shares a boundary with the patch. Mean size is simply the average size of all the patches in the landscape. The mean number of edge pixels is a count of the number of pixels that lie on the boundary between the patches in the landscape. Patch density is a simple count of the number of patches in the 40,000 ha area. The mean angular second moment is a measure of the fine-scale texture of the landscape. Larger values indicate a coarser texture. Mean Shannon diversity of patch ages is a measure of the combined evenness and richness of patch ages. The fraction of old growth is the fraction of the 40,000 ha landscape that is covered by patches whose age is greater than 200 yr. There are many possible definitions of ‘old growth’, but this is one that is commonly used (Norse 1990). These measures are described in more detail in Baker and Cai (1992).

The simulation experiments

There are three simulation experiments, with three treatments in each experiment (Table 2) The first

Table 1. Fire rotations reported for the United States and Canada for a natural fire regime (pre-1900) and a regime affected by European settlement and fire suppression (post-1900). Rotation time is the time required to disturb a land area equal to that of a particular landscape.

Author	Place	Fire rotation (yr)	
		pre-1900	post-1900
Agee <i>et al.</i> (1990)	North Cascades, Wash.	60–208	103
Heinselman (1973)	Northern Minnesota	ca. 100	–
Hemstrom & Franklin (1982)	Mt. Rainier, Washington	226–465	2583
Johnson <i>et al.</i> (1990)	Glacier National Park, B.C.	80–110	–
Masters (1990)	Kootenay Nat. Park, B.C.	60–130	> 2700
Morrison & Swanson (1990)	Central W. Cascades, Ore.	95–149	–
Payette <i>et al.</i> (1989)	N. Quebec-boreal forest	100	–

Table 2. The treatments used in the three simulation experiments and the mean disturbance size, mean disturbance interval, and rotation time for each treatment. Rotation time is calculated as (40000 ha/mean size) X mean interval.

Treatment	Initial map	Mean Size(ha)	Mean Interval(yr)	Rotation(yr)
DENSITY EXPERIMENT				
Initial low density	low density	1280	4.2	131.3
Initial high density	high density	1280	4.2	131.3
Standard	avg. density	1280	4.2	131.3
GLOBAL CHANGE EXPERIMENT				
Warming	low density	3404	5.6	65.8
Cooling	low density	1715	11.3	263.6
Standard	low density	2560	8.5	132.8
FRAGMENTATION EXPERIMENT				
Fragment	unfragmented	640 (40 x 16)	1.0	62.5
Restore	fragmented	3404	5.6	65.8
Standard	unfragmented	3404	5.6	65.8

experiment is to analyze the effects of the initial density of patches in the landscape on the rate of response of the landscape to an altered disturbance regime. The two treatments of interest are ‘initial low density’ and ‘initial high density’. The initial low density map (Fig. 1a) was produced by running the model for 400 years with a disturbance size distribution with a mean of **2560** ha (also **2560** pixels) and a normal disturbance interval distribution with a mean of **8.5** yr (rotation time = **132.8**yr). The initial high density map (Fig. 1b) was derived from a comparable run with a mean size of **256** ha and a mean interval of **2.1** yr (rotation time = **332** yr). Disturbability is assumed for this experiment to increase linearly with increasing patch age, so that older patches have a higher probability of catching

fire, and it is more likely that fires will spread into these older patches. To assess how these two treatments affect the landscape, these treatments are compared with a ‘standard’ treatment, which is initialized with an average density landscape. All three treatments receive the same disturbance regime (Table 2), which is the disturbance regime used to produce the ‘average density’ map. The experiment, then, tests how rapidly the ‘initial high density’ and ‘initial low density’ landscapes will return to the structure represented by the ‘average density’ landscape when subjected to the disturbance regime that produced this average density landscape.

The second experiment compares a ‘warming’ treatment and a ‘cooling’ treatment. There is evi-

Fig. 1. Initial maps for the model runs. (a) low density, (b) high density, (c) unfragmented, (d) fragmented.

dence that higher temperatures, such as might be produced by global warming, are accompanied by larger and more frequent fires, while cooling periods are associated with smaller, less frequent fires (Clark 1988; Johnson *et al.* 1990; Flannigan and Van Wagner 1991). The exact magnitude of this effect is generally unknown for specific locations.

The effect of warming thus cannot be exactly determined, but the direction of change can be analyzed even while the magnitude of change has little relevance to specific locations. The effect of warming is simulated here by an approximately 33% increase in mean size over the 2560 ha mean size used to create the low density landscape that initiates the

experiment, and by a 33% decline in the mean interval between fires compared to the 8.5 yr mean interval used to create the initial low density landscape (Table 2). Cooling is simulated by a 33% decrease in size and 33% increase in interval. This also means a fire rotation of 65.8 yr for the warming treatment and 263.6 yr for the cooling treatment, compared to the 132.8 yr rotation that produced the initial map. These rotations approximately span the range of rotations that has been reported for the western United States and Canada (Table 1 and 2). Disturbability is also assumed for this experiment to increase linearly with increasing patch age. The 'standard' treatment for this experiment begins with the same low density landscape, but simply continues to subject it to the same kind of disturbance regime that produced this landscape.

The third experiment consists of a 'fragment' treatment and a 'restore' treatment. The fragment treatment is designed to simulate a disturbance regime similar to that produced by dispersed-patch clearcutting in forested landscapes (Franklin and Forman 1987; Li *et al.* 1993). The disturbance size is fixed at 16 ha and each year there are 40 disturbances, which produces a rotation of 62.5 yr (Table 2), comparable to the timber management rotation used in more productive western United States forested landscapes. The unfragmented landscape that is used to initiate this treatment is the landscape, of those produced by the warming disturbance regime, with the closest to average landscape structure (Fig. 1c). Although this initial landscape happens to have been produced by the warming fire regime, this regime and this initial landscape are typical of those in landscapes in the more fire prone regions of the western United States at the present time (Table 1). The fragment treatment does not substantially alter the rotation time, but achieves the same rotation through smaller, but more frequent disturbances (Table 2). The restore treatment enables analysis of the rate and pattern of response to restoration of a natural disturbance regime in a fragmented landscape. The initial map for this

treatment is the landscape, of those resulting from the fragment regime, with the closest to average landscape structure (Fig. 1d). Disturbability of a pixel is assumed for this experiment to be $1000/(\text{minimum age in the 8 pixels surrounding the central pixel})$ if age is greater than 60 yr and less than 200 yr; disturbability is assumed to be 1 otherwise. This has the effect of concentrating the initiation and spread of disturbances into pixels that are old enough to be harvested (> 60 yr) in a typical productive western United States forested landscape, but not old growth (> 200 yr), and that adjoin recently disturbed pixels. This is one disturbance strategy that might be employed to continue timber harvest disturbances, but place them in such a way as to minimize further fragmentation and more closely approximate a natural disturbance regime. The 'standard' treatment used in this experiment is the same unfragmented landscape used to initiate the 'fragment' treatment, but in this case this unfragmented landscape is subjected to the same disturbance regime that produced it.

Each treatment in each of the three experiments received 10 replicate runs. Replicates vary because random numbers are used to pick disturbance sizes and intervals, and disturbances are initiated and spread probabilistically. Mean values are calculated from the 10 replicates for each of the 8 landscape structure measures at 25 yr intervals during the 400 yr simulation period. The null hypothesis of no treatment effect was not rejected if the 95% confidence interval for the difference in the means for the 10 replicates, for a particular measure at a particular time, included zero (Bratley *et al.* 1987).

Results

Effect of initial density

The initial density of the landscape affected the rate at which the landscape adjusted to an altered disturbance regime (Fig. 2). The initial low density land-

Fig. 2. Change in measures of landscape structure during the 400 yr simulations of the effect of initial density. Each data point represents the mean of 10 replicates. Means for each treatment that differ from the mean for the standard are starred below the x-axis for the year in which the 95% confidence interval of the difference in means overlaps zero.

scape adjusted more quickly than did the initial high density landscape in the case of every measure. The initial high density landscape required 25–100 more yrs to adjust than did the initial low density landscape. The two initial landscapes had structures comparable to those in the standard landscape after 150 yrs.

The measures that adjusted most rapidly included mean age (Fig. 2a), edge (Fig. 2d), and angular second moment (Fig. 2f), followed by Shannon diversity (Fig. 2g), then fraction of old growth (Fig. 2h), and distance (Fig. 2b). The mean patch size (Fig. 2c) and number of patches (Fig. 2e) were the slowest to adjust.

Effect of warming and Cooling

Warming produced a significant decrease in mean patch age (Fig. 3a), the mean Shannon diversity of patch ages (Fig. 3g), and the fraction of old growth (Fig. 3h). There were inconsistent responses in the other measures. The mean values of distance (Fig. 3b), patch size (Fig. 3c), and angular second moment (Fig. 3f) were often higher than in the standard treatment, but only occasionally was this difference significant. The mean values of edge (Fig. 3d) and number of patches (Fig. 3e) were often lower than in the standard treatment, but only occasionally was this difference significant.

Cooling, not surprisingly, had the opposite effect. Cooling produced a significant increase in mean patch age (Fig. 3a), the mean Shannon diversity of patch ages (Fig. 3g), and the fraction of old growth (Fig. 3h). There were inconsistent responses in the other measures. The mean values of distance (Fig. 3b), patch size (Fig. 3c), and angular second moment (Fig. 3f) were often lower than in the standard treatment, but only occasionally was this difference significant. The mean values of edge (Fig. 3d) and number of patches (Fig. 3e) were often higher than in the standard treatment, but only occasionally was this difference significant.

Where there was a significant response it occurred in the landscape subjected to warming 25–50 yrs earlier than in the landscape subjected to cooling (Fig. 3). In the cases where there was a significant response, it began to be significant within 25 yrs of the onset of warming and within 50–75 yrs of the onset of cooling, but was not fully expressed until about 100 yrs after warming onset and perhaps 100–150 yrs or more after cooling onset (Fig. 3).

Effect of fragmentation and Restoration

The fragmentation regime required only 25 yrs to produce a significant decline in age (Fig. 4a), distance (Fig. 4b), size (Fig. 4c), angular second moment (Fig. 4f), and the fraction of old growth (Fig. 4h), and an increase in edge (Fig. 4d), number of patches (Fig. 4e), and Shannon diversity (Fig. 4g). All of these measures reflect the unusually high density of small, young patches produced by the fragmentation process.

The restoration regime returned the landscape to its original structure within 50–125 yrs (Fig. 4), substantially longer than the time required for fragmentation to become significant. The most rapid restoration was in age, within 50 yrs (Fig. 4a), while it required 75 yrs to restore angular second moment (Fig. 4f) and Shannon diversity (Fig. 4g). It required 100 yrs to restore edge (Fig. 4d) and fraction of old growth (Fig. 4h). The slowest measures to restore were distance (Fig. 4b), size (Fig. 4c), and number of patches (Fig. 4e), which required 125 yrs.

Rate of adjustment

The time required for these landscapes to adjust to an altered disturbance regime is related to the rotation time of the new disturbance regime. Based on the estimates presented above, it appears to require

Fig. 3. Change in measures of landscape structure during the 400 yr simulations of the effect of warming and cooling. Each data point represents the mean of 10 replicates. Means for each treatment that differ from the mean for the standard are starred below the x-axis for the year in which the 95% confidence interval of the difference in means overlaps zero.

between one half and two rotation times for landscape structure to equilibrate with a new disturbance regime. The most rapid adjustment in relation to rotation time was the adjustment of the initial low density landscape, which required only about 75 yrs to adjust, even though the rotation time was 131.3 yrs. The initial high density landscape, in contrast, required about 125–150 yrs to adjust, approximately equal to one rotation. The warming landscape required a little more than one rotation to adjust, while the cooling landscape required less than one rotation. The fragmentation landscape had adjusted within about one rotation. The restoration landscape was the slowest to adjust, in comparison to rotation time, requiring as much as 125 yrs to adjust, even though the rotation time was only 65.8 yrs.

The time required for adjustment is also clearly related to the structure of the landscape at the time the disturbance regime is altered, independent of the rotation time of the new disturbance regime. The density experiment shows that an approximately 2-fold difference in initial patch density resulted in a nearly doubled time required for adjustment even though rotation time was constant. Similarly, the fragmentation experiment showed that a fragmented landscape with numerous patches (1,314 patches in the initial ‘fragmented’ landscape used in the ‘restore’ treatment) requires nearly two rotations to adjust, while an unfragmented landscape with fewer patches (131 patches in the initial ‘unfragmented’ landscape used in the ‘fragment’ treatment) requires a little less than one rotation to adjust, even though the rotation times of the new disturbance regime were comparable (Table 2).

Discussion

Rate of adjustment of disturbance landscapes

Disturbance landscapes adjust slowly to alterations in the disturbance regimes that control their struc-

ture, because the patchiness and structure produced by the old regime must be erased (burned over or obliterated by new patches) before the new structure dominates. Not surprisingly, this requires a significant part of one rotation of the new disturbance regime, but usually more than one rotation, as some of the disturbances during the first rotation may occur on top of others, rather than in new areas.

A simple consequence of the need for 1/2 to 2 rotations before adjustment is that landscape subjected to the shorter rotation warming regime adjust more rapidly than do landscapes subjected to the longer rotation cooling regime (Fig. 3). The exact magnitude of the effect of potential global warming on landscape structure cannot be estimated from this simulation experiment. Nonetheless, the time needed for adjustment to warming will be substantially less than the current natural rotation time of the landscape, assuming that warming increases fire sizes and decreases fire intervals. This means that forested landscapes in the western United States and Canada will require at a minimum several decades to adjust to warming, based on the data in Table 1.

The rate of adjustment was affected significantly by the more than 2-fold difference in the density of the initial landscapes (167 patches in low density vs. 375 patches in high density). High density landscapes require more time to adjust because the new disturbance regime must find and destroy more patches before the new structure produced by this new disturbance regime dominates. Thus the state of the landscape at the time a change in the disturbance regime occurs will influence the rate of response.

The structure of the initial landscape and the rotation time of the new disturbance regime control the rate of adjustment, but disturbance size and interval control the kind of landscape that will result after adjustment. For example, the warming and fragment treatments have nearly equal rotation times (Table 2), yet after 400 yr of simulation, long

Fig. 4. Change in measures of landscape structure during the 400 yr simulations of the effect of fragmentation and restoration. Each data point represents the mean of 10 replicates. Means for each treatment that differ from the mean for the standard are starred below the x-axis for the year in which the 95% confidence interval of the difference in means overlaps zero.

after any effect of the initial landscape has disappeared, their structures are quite different (Figs. 3 and 4).

Restoration of fragmented landscapes

One goal of landscape ecology must be to discover means by which human land uses can occur more sustainably within landscapes with less impact upon the non-human components of the landscape and landscape functioning; there is considerable interest, for example, in finding ways to restore fragmented landscapes (Hobbs and Saunders 1993). The simulation represented by the restore treatment here is a step in what needs to be a more extensive analysis of the most effective ways to continue human land uses, but at the same time move the landscape back within its range of natural variability and toward a healthier functioning (Costanza *et al.* 1992).

It was expected that the restore treatment would complete restoration within only a little more than one rotation, but this was not the case. By definition, exactly one rotation would be required to erase all evidence of the landscape structure produced by the previous regime, if the disturbances in the new regime did not overlap. The restore treatment includes a disturbance initiation and spread algorithm that avoids placing disturbances into areas recently disturbed, thus discouraging disturbance overlap. The failure of the restore treatment to achieve restoration within one rotation must be due to the delaying effect of the high density of patches in the initial landscape. The initial 'fragmented' landscape contained 1,314 patches, compared to the 131–375 patches that were in the initial maps for the other treatments in the set of three experiments. Further research is needed with other restoration algorithms to determine whether restoration of fragmented landscapes can be achieved in significantly less than two rotations.

Caution is also warranted here, as the structure that is being restored is simply a set of measures of the patch structure. Even though these measures and similar measures are commonly used (*e.g.*,

Ripple *et al.* 1991; Li *et al.* 1993), they may not necessarily be the right set, or it may be that other **kinds** of structure are important. There is still only fragmentary and incomplete evidence to support or refute the idea that this particular set of eight measures contains really important features of landscape structure. Part of the difficulty is that we have to ask the question: important for what? The answer may be different for different aspects of landscape functioning, such as nutrient cycling, energy flows, and the provision of habitat for a variety of species. More landscape sensitive wildlife-habitat models, incorporating landscape indices, may help answer the question for animals (Morrison *et al.* 1992), but until there is more research it will remain difficult to answer in general.

Perpetual disequilibrium in long rotation landscapes due to climatic change

Climatic change can clearly alter the size and interval distributions that affect the structure of disturbance landscapes (Clark 1988; Johnson *et al.* 1990, Flannigan and Van Wagner 1991). The studies of Johnson and his colleagues and others (summarized in Johnson 1992) suggest that there may have been declines in fire frequency and/or burned area during the Little Ice Age, although there are problems with the fire cycle model used by these authors to analyze fire history (Baker 1989b). Declines are also evident between 1915 and the 1970s, apparently also due to climatic change (Van Wagner 1988). Climatic changes on the scale of decades to a few hundred years can clearly affect fire regimes, making the concept of a stable fire regime questionable (Suffling 1991).

To complicate matters further, there is not always an equilibrium between the rate of climatic change and the rate of adjustment of landscapes. If a sudden change in climate occurs tomorrow that drastically alters the fire regime, the simulation results reported here suggest that it will still be several decades before most landscapes have adjusted to the new regime. However, before that adjustment is completed, there may be further changes in climate that move the disturbance re-

Fig. 5. General trends in landscape measures resulting from several kinds of human and global change effects on disturbance regimes. Four combinations of changes, in which disturbance size and interval distributions are shifted to the right or left, are illustrated.

gime along a new path. The result is that in some landscapes there may be a perpetual non-equilibrium between the disturbance regime and the structure of the landscape. Unfortunately, we have comparatively few data on fire rotation times in natural landscapes (Table 1). This non-equilibrium is most likely in long rotation landscapes, such as those on Mt. Rainier, Washington (Table 1), where the fire rotation is as much as a few centuries, sufficiently long to intercept climatic changes comparable to those of the Little Ice Age.

A spatially forced disequilibrium, different from this temporally forced disequilibrium, was earlier suggested by Shugart and West (1981). Their modeling results suggested that small islands subject to hurricanes, and other environments where land area is small relative to the size of disturbances, may have landscapes perpetually in disequilibrium. In contrast, the temporal disequilibrium suggested here, and previously by Suffling (1991), may occur even in landscapes that cover substantial land area, as long as the rotation time for the landscape approaches or exceeds the time between climatic fluctuations that are sufficient to modify the disturbance regime.

This temporal disequilibrium, which is between climatic change, the disturbance regime, and the resulting landscape structure, is different from a temporal disequilibrium between disturbance interval and recovery time considered in previous simulation research (Turner *et al.* 1993). Turner *et al.* consider in detail the possibility of catastrophic change in species composition as a result of the temporal disequilibrium between disturbance interval and recovery time, although actual species or population sub-models are not included in their model. There is some evidence for unstable or catastrophic vegetation change in real landscapes (e.g., Laycock 1991; Turner *et al.* 1993), but it is not clear from this simulation work or the work of Turner *et al.* (1993) that temporal disequilibria encourage the possibility of the kinds of catastrophic species change discussed by Laycock or Turner *et al.* The model used here and that used by Turner *et al.* will require the incorporation of succession or population dynamics sub-models before the possibility of catastrophic species change from temporal disequilibria can be evaluated in a modeling framework.

Similarities in landscape response to several kinds of treatment

There are some similarities in the direction of response to several kinds of treatment (Fig. 5). There are four combinations of modifications to the disturbance size and interval distributions that typically occur, although other combinations are possible. When disturbance size or interval is increased or decreased, then certain sets of the 8 landscape structure measures respond similarly (Fig. 5).

In general, human modifications of natural disturbance regimes and human land uses (*i.e.*, traditional clearcut logging) in forested landscapes of the western United States produce a landscape structure response that is similar in direction, but not necessarily magnitude, to that produced by cooling. Cooling, fragmentation, fire suppression, and the traditional use of prescribed fires all tend to produce more numerous, smaller patches that are closer together and that have more edge. This also means a higher angular second moment and higher Shannon diversity. However, disturbance suppression and cooling are accompanied by a longer mean interval between disturbances, which produces a higher mean age and more old growth, while small prescribed disturbances and fragmentation are accompanied by a shorter mean interval between disturbances, which produces a lower mean age and less old growth.

Restoration after either disturbance suppression or fragmentation and warming all produce less numerous, larger patches that are farther apart and that have less edge. This also means a lower angular second moment and lower Shannon diversity. However, restoration after fragmentation typically is accompanied by a longer mean interval between disturbances, which produces a higher mean age and more old growth, while restoration after disturbance suppression and warming typically are accompanied by a shorter mean interval between disturbances, which produces a lower mean age and less old growth.

While the short-term response to suppression of fires may be along the same path as that produced by cooling, the longterm response might be different. Suppression of fires might eventually lead to

larger, more catastrophic fires due to an unnatural buildup of fuel (*e.g.*, Minnich 1983). If this occurs, then the longterm response might be along a path that is similar to that from restoration after fragmentation, in which both disturbance size and interval are increased.

Differences in the response of individual measures of landscape structure

Previous simulation research suggests that landscape structure measures do not all respond at the same rate to alterations in a disturbance regime (Baker 1992, 1993). Fire suppression produced a rapid rise in age and richness, accompanied by a more gradual rise in Shannon diversity and a gradual decline in size and angular second moment. Restoration of a natural fire regime into a landscape affected by suppression produced a rapid readjustment in size and edge, a more gradual readjustment in Shannon diversity, and very slow readjustment in age and richness (Baker 1994), a trend in rates nearly opposite that produced by suppression. In the set of three experiments reported here the trends in rate of adjustment are only partly consistent with these previous results. Age adjusts rapidly in all three experiments, just as in the suppression experiment. Angular second moment adjusts rapidly in the density experiment, but more gradually in the fragmentation experiment, only partly consistent with its slow response in the suppression experiment. Size responded slowly to restoration after fragmentation, but rapidly following restoration after suppression. Shannon diversity appears to respond at an intermediate rate in all cases.

There is no obvious simple explanation for these differences in the rate of response, although the sensitivity of particular landscape structure measures to the size and interval components of a disturbance regime may be part of the explanation (Baker 1994). The value of measures, such as age and number of patches, is more sensitive to patch number than patch size, as each new patch that is added affects these measures the same amount regardless of patch size. The number of patches produced is controlled most directly by the disturbance interval

distribution, although the size distribution also has an effect. In contrast, measures such as distance, size, edge, and angular second moment are more strongly affected by the size of disturbances rather than simply the number of disturbances. For example, when disturbances are suppressed age responds rapidly because existing patches simply get older, even though few of the existing patches are destroyed immediately. When the original disturbance regime is restored in a landscape affected by suppression, then age responds more slowly because the existing patches that are old must first be destroyed by the restored regime before mean age comes back down. However, this explanation is not consistent with the response to the cooling and warming treatments. The landscape should respond more quickly to cooling (which is similar to disturbance suppression) than to warming (which is similar to restoration after disturbance suppression, but just the opposite occurs (Fig. 3a). Thus the reason for differing rates of response by particular measures cannot be fully explained and will require further simulation research.

Spatial fire history data needed for simulating landscape adjustment

The potential longterm response of landscapes to alterations in their disturbance regimes can only be understood if adequate data are available for simulations such as those reported here, as it is not feasible to observe actual landscapes over long time periods. In order to be able to simulate landscape change using the DISPATCH model it is necessary to have sufficient data to be able to estimate the fire size distribution and fire interval distribution, as well as a map of the initial landscape that is to be subjected to the disturbances regime. To meet these needs it is essential to complete fire history studies that include reconstruction of actual maps of individual fires where feasible (e.g., Heinzelman 1973), and to report fire size and interval distributions as well as an estimate of rotation time.

More difficult is the need for an adequate understanding of the factors that control the disturbance of individual locations within the landscape.

General trends have been hypothesized, such as a relationship between stand age and fire susceptibility (Heinzelman 1973), but other factors such as topography and elevation also influence the probability of fire initiation and spread (Fowler and Asleson 1984). More extensive studies are needed of the factors that influence fire initiation and spread probabilities.

Finally, the model used here does not realistically simulate the effect of landscape structure in controlling the size of fires (Turner *et al.* 1989), although there is some control on the pattern of spread. More complex fire spread models with explicit climatic controls (e.g., Antonovksi *et al.* 1992) are needed to refine the findings reported here.

Conclusion

Landscapes require 1/2 to 2 rotations of a new disturbance regime for their structure to adjust to that new regime, regardless of the manner in which the disturbance regime is altered. Alterations that shorten the rotation time, such as the increase in fire size and decrease in fire intervals that might accompany global warming, can be expected to require less time for adjustment than do alterations that lengthen the rotation time, such as cooling. The rate of response to an altered disturbance regime may be enhanced if the landscape at the time of alteration has a comparatively low density of patches. Landscapes with long rotation times may be in perpetual disequilibrium with their disturbance regimes, because climatic change may create a new disturbance regime before the landscape has fully adjusted to the old regime. Two landscapes whose disturbance regimes have similar rotation times and adjust at the same rate may have quite different structure, because the size and interval distributions independently affect landscape structure.

Disturbance suppression, cooling, the use of small prescribed disturbances, and fragmentation from clearcut logging all tend to produce landscapes with smaller, more numerous patches that are closer together. These trends also produce a

smaller value of angular second moment and higher Shannon diversity. In contrast, warming and restoration of a natural disturbance regime after fragmentation or disturbance suppression tend to produce opposite trends. The mean age of the landscape and the fraction of old growth are more dependent upon the interval between disturbances, with longer intervals allowing a higher mean age and more old growth. The temporal order in which the 8 measures adjust to different kinds of disturbance regime alteration is inconsistent and cannot be fully explained.

Understanding the response of landscapes to alterations in their disturbance regimes requires understanding the spatial dynamics of populations of patches. These dynamics are clearly different from the dynamics of a population of organisms. Patch population dynamics are a zero-sum-game in which patch births cause patch deaths because the land area is fixed; as a consequence, larger patch births mean the destruction of more existing patches (Baker 1992). The population density and influence of parents in such a population depends not only on the numbers of babies, but whether the babies are big in relation to their parents.

Understanding the longterm response of landscapes to disturbance regime alteration is also essential to ecosystem management at the landscape scale, where management decisions may have significant longterm consequences. GIS-based landscape simulation can and should play a significant role in the consideration of management alternatives in both wildland and humanized landscapes.

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