Landscape Disturbance Models and the Long-term Dynamics of Natural Areas

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ABSTRACT: The management of natural areas in disturbance-prone landscapes poses many challenges for which spatially explicit models can provide useful guidance. We have incorporated disturbance processes into simple landscape models and applied the results to two management issues. First, alternative disturbance scenarios were simulated as a function of landscape pattern and the frequency, spread, and severity of disturbance. The model simulates disturbance on random landscapes and for various levels of landscape connectivity on subsections of Yellowstone National Park. Simulation results suggest that when the habitat that is susceptible to a disturbance is well connected, the probability of disturbance spread is most important in controlling the amount of habitat disturbed. A critical threshold of habitat connectivity was observed in random landscapes, but the actual landscape maps did not exhibit this threshold effect for the particular frequency and spread values used here. For a given proportion of the landscape occupied by susceptible habitat, the variability in the amount of habitat affected by simulated disturbances was much greater in the real landscapes than in the random landscapes. This difference suggests a strong interaction between the spatial configuration of susceptible habitat and the point of initiation of the disturbances. Second, the results of a model that incorporates disturbance and recovery dynamics suggest that qualitative shifts in landscape behavior (e.g., from steady state to nonequilibrium) may occur, with important implications for natural area management.

INTRODUCTION

Many landscapes are influenced by disturbances (i.e., any relatively discrete events in time that disrupt ecosystem, community, or population structure and change resources, substrate availability, or the physical environment [White and Pickett 1985]). Fires, storms, outbreaks of pests or pathogens, mass movements, and even climatic changes play important roles in controlling natural landscape dynamics. Disturbance creates patterns in vegetation by producing a patch mosaic of seral stages, and ecologists have long recognized the importance of these patterns (e.g., Cooper 1913, Leopold 1933, Watt 1947). Natural disturbances may increase biological diversity and may be essential for persistence of some species and ecological processes. Considerable attention has been focused recently on disturbance-generated patch dynamics (e.g., Pickett and White 1985a), the role of landscape heterogeneity in controlling the spread of disturbance (e.g., Turner 1987, Turner et al. 1989), and biotic responses to disturbance events (e.g., Knight and Wallace 1989). Disturbances occur at a variety of spatial and temporal scales, from frequent small events, such as gap formation in deciduous forests, to rare large events, such as extensive stand-replacing fires or hurricanes. Because disturbance is a ubiquitous feature of natural landscapes, disturbance must be recognized as an integral system component in the design and management of nature reserves.

As was particularly evident with the 1988 fires that occurred in Yellowstone National Park, the managers of natural areas in disturbance-prone landscapes face a variety of challenges. The future conditions of a landscape that may be affected by one or more disturbances may be difficult to predict. Even though a particular disturbance is "natural," it may have undesirable effects on a natural area of finite size and rigid political boundaries. Thus, natural area managers face many difficult questions. What is the extent, frequency, or severity of disturbance that can be tolerated by the system without irretrievable loss of biotic elements (e.g., species) or processes? What are the ecological effects of a particular disturbance? Could a disturbance qualitatively change the system? How large should a reserve be in a disturbance-prone environment? Should management seek to alter natural disturbance dynamics? The answers to these questions are neither straightforward nor simple.

Landscape simulation models can be a valuable aid in the design and management of natural areas in disturbance-prone landscapes for several reasons. First, it is difficult or impossible to conduct controlled experiments with large-scale disturbances in natural areas. Although the experimental manipulation of a large portion of a natural area would seldom, if ever, be permitted, such a disturbance could be simulated using a model. In addition, replicating large-scale experiments or sampling regimes is often prohibitively expensive. For example, it is unlikely that a large manipulation in a natural area could be replicated to obtain a statistically satisfying sample. Even if treatments could be repeated, pseudoreplication remains a potential problem. However, stochastic simulations with a model can be replicated many times and the results summarized statistically, thereby providing an estimate of the range of potential effects. Thus, modeling allows the manager to explore the implications of events for which landscape-level experiments are not feasible, within the constraints of the assumptions built into the model.

Modeling and analytic methods also are needed to better understand fundamental interactions between landscape pattern and disturbance regimes (Turner and Dale 1991). In general, models can offer a variety of useful insights into ecological systems because they can be used to generate and explore testable hypotheses and identify potentially sensitive parameters or parts of a system. Simulations can be used to delimit the range and magnitude of potential system dynamics in response to some stimulus. The use of models may aid in extrapolating results from small study areas to large landscapes or from short to long time periods. Finally, because models are quantitative expressions of our knowledge of ecological dynamics, comparisons made between model results and empirical data are extremely valuable in testing our understanding of the system.

APPLICATIONS OF DISTURBANCE MODELS

A variety of model types can be developed for landscape-level disturbances (see Turner and Dale 1991). In this paper, we review two applications of disturbance models to illustrate their potential use in natural area design and management. These examples include models of (1) the dynamics of a disturbance and (2) long-term landscape dynamics as influenced by disturbance and recovery processes. We focus on simple models that are general and include simulations conducted with real landscape patterns.

Disturbance Dynamics

Determining how much area will be affected by a specified disturbance in a landscape is important to natural area managers. Disturbance regimes are characterized by a variety of parameters (e.g., spatial extent, frequency, return interval, rotation period, intensity, severity; see Pickett and White 1985b for definitions) that can be used in landscape disturbance models. Simulation experiments that use ranges of values for these parameters can offer general insights into the interactions between landscape pattern and disturbance spread and can generate an expectation of potential disturbance effects.

A simple model of disturbance spread

Methods of percolation theory (Stauffer 1985, Gardner et al. 1987) have been used to develop simple probabilistic models of disturbance spread (Turner et al. 1989, Turner and Dale 1991) based on disturbance regime descriptors. The landscape is considered as a grid that contains only two types of habitat: habitat that is susceptible to a particular disturbance, and habitat that is not susceptible to that disturbance. The proportion, p, of the landscape occupied by susceptible sites is specified (e.g., $p = 0.1$, ..., 0.9) and generated on the landscape at random by drawing a random number, x, for each grid cell; if $x \leq p$, then that grid cell is considered susceptible to the disturbance. The model includes three disturbance parameters: frequency, probability of spread, and severity. Each parameter is represented as a probability that can range from zero to one. Disturbance frequency (f) is defined as the probability that a new disturbance will be initiated in a grid cell of susceptible habitat during the time period represented by the simulation (e.g., the probability of lightning striking a hectare of pine forest during a particular time period). Probability of spread (i) is defined as the probability that the disturbance, once initiated, will move to an adjacent site of susceptible habitat. Disturbance severity (h) is the probability that the site is altered by the disturbance such that it cannot be revisited by the disturbance during the simulation. When $h = 1$, all disturbed sites are altered (e.g., vegetation is completely consumed), whereas when $h < 1$, some sites are not altered and can be disturbed again. It is assumed that the disturbance can spread a distance of one grid cell per time step.

Simulations with this simple model have generated interesting results. Most important, the proportion of the susceptible habitat that is affected by a disturbance with a given i, f, and h is controlled largely by whether the susceptible habitat occurs above or below a critical threshold of connectivity. In large random maps, the cells of susceptible habitat will become connected from one end of the map to the other at approximately $p = 0.6$ (Gardner et al. 1987). When the amount of susceptible habitat occurs above this threshold of connectivity, habitat patches are large and contiguous, and it is the probability of spread (i) that determines the proportion of susceptible habitat that is disturbed. A low frequency disturbance with a high probability of spread can affect approximately 90% of the available habitat (Turner et al. 1989). In contrast, when the susceptible habitat occurs below this critical threshold, patches are small and isolated, and it is disturbance frequency that controls the extent of the disturbances. The spread of a disturbance is constrained by the spatial arrangement of the habitat patches. In order to affect a substantial proportion of the available habitat at low p, a high frequency of disturbance is needed. For a given value of i and p, increased disturbance severity (h) always results in a greater percentage of available habitat being disturbed. However, this effect is not always proportional to the increase in h. In general, as disturbance severity decreases below 0.75, the reductions in the percent of habitat disturbed tend to become smaller (Turner and Dale 1991).

Simulation results from this simple model in a random landscape have implications for natural area management (Turner et al. 1989). If a susceptible habitat type is rare and surrounding habitats are not susceptible to the disturbance, management should focus on the frequency of disturbance initiation. Disturbances with low frequencies will have little impact, even at high probabilities of disturbance propagation, because there is insufficient landscape connectivity. In contrast, high frequencies of disturbance initiation can substantially change landscape structure. However, if a susceptible habitat type is common, management must consider both frequency and intensity. The proportion of a landscape affected by disturbance can be predicted at the extreme ends of the ranges of frequency and probability of spread. Disturbances with a low probability of spread and low frequency will have little effect, whereas disturbances that spread easily will cause substantial changes. At intermediate probabilities of spread, however, responses can be quite complicated and more difficult to predict. A common habitat type can be easily fragmented and qualitatively changed by disturbances with low to moderate probability of spreading and low to high frequency.

Simulations using a real landscape

The spatial distribution of habitat types in real landscapes is not random, however, so it is reasonable to ask how these results might translate to a real landscape. To examine the influence of structured landscape patterns on the spread of the disturbance, we conducted simulations with this simple model on forested subsections of the Yellowstone National Park (YNP) landscape. YNP encompasses 9000 km^2 in the northwest corner of Wyoming and is primarily a high, forested plateau. Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine (Despain 1990). As in most other parts of the Rocky Mountains, fire has a strong influence on the fauna, flora, and ecological processes of the Yellowstone area (Houston 1973; Romme 1982; Romme and Knight 1981, 1982; Romme and Despain 1989; Despain 1990). Large portions of the landscape burned during the early 1700s and the 1860s (Romme 1982), and although the fires of 1988 were the most extensive observed since the park was established, the fires appeared to be similar in extent and severity to those that burned around 1700 (Romme and Despain 1989).

Observations of fires in Yellowstone during the past two decades suggest that the connectivity of habitat susceptible to burning is controlled by both stand age and weather (Romme 1982; Romme and Despain 1989; Renkin and Despain 1992; Turner and Romme, in press). Between 1972 and 1987, most of the 235 lightning-ignited fires that were allowed to burn without interference under YNP's natural fire program went out without intervention before burning more than a hectare; the largest single fire (in 1981) burned about 3100 ha (Despain 1990). The summer weather was usually too wet for fires to spread over large areas (Renkin and Despain 1992). When summer weather was drier, the larger fires that occurred generally were constrained by the spatial pattern of forest successional stages on the landscape; fires burned readily in late-successional forests, but often died down when they reached early or middle successional stands (Despain and Sellers 1977, Despain 1990; our Table 1 summarizes forest successional stages in YNP). Fires in the early part of 1988 behaved much like the fires that had been observed between 1972 and 1987. However, fires that burned during the latter part of the 1988 season spread rapidly through all forest successional stages and appeared to be influenced more by wind speed and direction than by subtle patterns in fuels or topography (Renkin and Despain 1992, Turner et al. in press). Thus, the connectivity of the YNP forests with respect to fire spread appears to vary with meteorological conditions. Under moderately dry conditions, only the older forest stands appear flammable, whereas under extreme burning conditions with both dry fuels and high winds, all forest age classes appear flammable.

To explore the effects of changing the connectivity of susceptible habitat on the spread of a disturbance, we ran the disturbance model on nine 100 x 100 grid-cell subsections of the YNP landscape under a series of aggregations of successional stages (Table 1). The spatial distribution of stand age classes was obtained from National Park Service data stored in the geographic information system GRASS, and each cell represented 10 ha. The abundance and connectivity of susceptible habitat were varied as follows. First, we considered only the oldest forest stands (LP3) to be susceptible, and all other age classes were considered to be unsuitable. Disturbance spread then was simulated only in these oldest stands on each of the nine maps. Next, we combined the oldest (LP3) and the moderately old stands (LP2) into the susceptible class and

Table 1. Generalized successional stages in subalpine forests of Yellowstone National Park, developed from sampling of a chronosequence of stands that originated following fires at various times in the last 400 years (from Despain 1990).

Stage	Approximate Age (yrs)	Description
LP0	0–40	Recently burned lodgepole pine stands in the grass to seedling/sapling stage before canopy closure. Trees usually less than 2 m in height.
LP1	40–150	Closed canopy of even-aged, often very dense lodgepole pine; young pole successional stage.
LP2	150–300	Closed canopy dominated by lodgepole pine. Overstory still largely intact. Understory may contain small to medium conifers, but tends to be open and parklike.
LP3	300 +	Canopy quite irregular, predominantly of old lodgepole pine trees but containing some Engelmann spruce, subalpine fir, and whitebark pine in the pole-sized class. Understory usually dense.

again simulated disturbance spread on the nine maps. Following that, we assigned LP3, LP2, and LP1 to the susceptible category, and finally, we simulated disturbance spread with all forest habitats considered as susceptible habitat. Nonforest habitat was not susceptible in all runs. Disturbance parameters were fixed at $f = 0.002$, $i = 0.6$, and $h = 1.0$. Because the model is stochastic and disturbances are initiated at random points in the landscape, simulations were replicated 10 times and the results summarized statistically. Results from the simulations on the YNP landscape were compared with simulations run on random landscapes with comparable values of p. The random landscapes serve as a neutral model (Gardner et al. 1987) in which the effects of spatial pattern are minimized.

The initial p of susceptible habitat on the nine maps ranged from 0.08 to 0.45 when only the oldest age classes were included, and ranged from 0.50 to 0.85 when all forest age classes were included (Figure 1). For a given value of p, a higher percent of available habitat was disturbed in the real landscape than in the random landscape (Figure 1). This is not surprising because habitats in real landscapes are generally more connected with fewer, larger patches than observed on random maps (Gardner et al. 1987, Gardner and O'Neill 1991, Gardner et al. 1991). However, the percent of available habitat disturbed on the random landscape increased dramatically when p approximately equalled 0.8, whereas the portions of the real landscape show a more continuous and linear response that begins at lower values of p. However, note that critical thresholds in landscape connectivity in the real landscapes may be observed at other values of i than used here. For intermediate values of p, there was substantial variation in the percent of available habitat disturbed on the various maps. For example, when $0.4 < p < 0.5$, the percent disturbed varied from less than 20% to more than 70%. Landscape maps that had connected patterns of suitable habitat were most affected by disturbance. When suitable habitat was discontinuous at the same value of p, disturbance had less effect on the landscape.

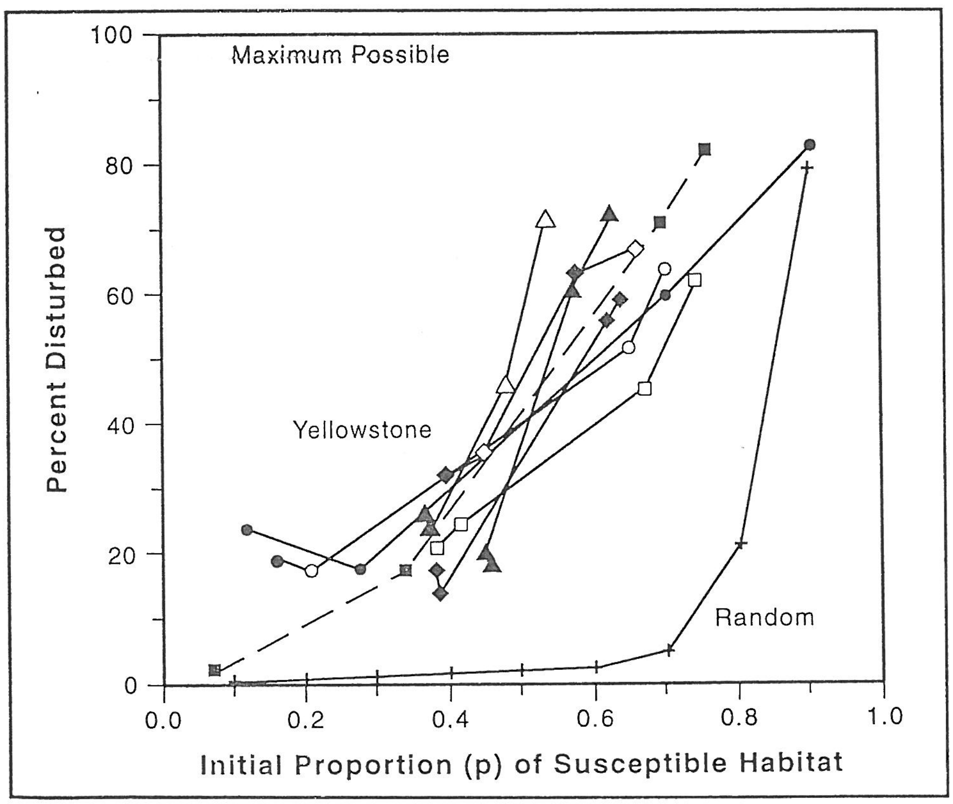

Figure 1. Mean percent of available habitat disturbed (n = 10) when disturbance spread was simulated on nine 100 x 100 grid cell maps obtained from Yellowstone National Park and on random maps. Each line represents one map in which stand age classes were combined sequentially to represent increased abundance and connectivity of disturbance-susceptible habitat.

The minimum and maximum percentages of the landscape that was disturbed were recorded from the ten replicate simulations for each of the nine landscape maps. The real landscapes exhibited a much wider range of variation than did the random landscapes (Figure 2). When only the most flammable stands (LP3) were susceptible, the percent of the landscape that was disturbed ranged as much as 40% for a given disturbance (Figure 2a). When all forest stands were susceptible to disturbance, the range between the minimum and maximum disturbed during the simulations was lower (Figure 2b). Differences between the real and random landscapes were greatest at intermediate values of p and least when p was very low (e.g., 0.1) or very high (e.g., 0.8).

The simulation results from the real landscape maps suggest a strong interaction between the locations of disturbance initiations and the spatial arrangement of susceptible habitat. In addition, these results suggest that alternative spatial arrangements of habitat may have a greater effect on disturbance effects at intermediate values of p for a given value of i. When the proportion of susceptible habitat is high, there are fewer opportunities for spatial patterns to vary substantially.

These simulations were not designed to be realistic predictors of fire spread, but rather to illustrate the use of models to identify the range of potential disturbance effects for a given set of rules or assumptions. Identifying the magnitude of variability in potential effects of disturbance and when the uncertainty in the outcome is greatest may be very important for a land manager. In the simulations presented here, the location of disturbance starts differed among the replicate simulations, and these locations had a greater effect on the real maps than on the random maps. Of course, the probabilistic spread of the disturbance also contributes to the variation among the replications. These simulations also point out the importance of understanding the spatial scales and rules used to represent the disturbance dynamics. The results reported here would

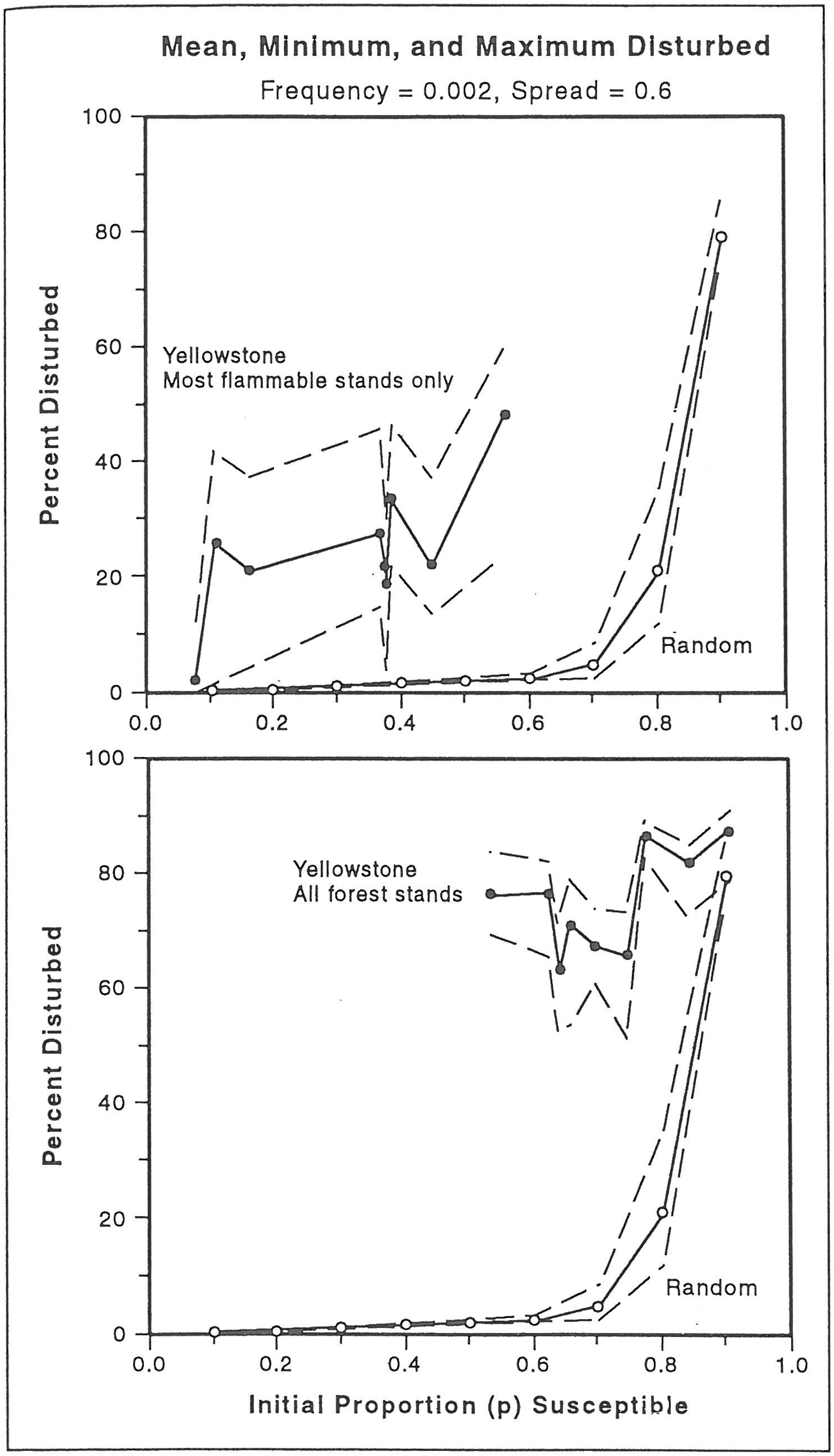

Figure 2. Mean, minimum, and maximum percent of available habitat disturbed in 10 replicated simulations of disturbance spread on nine 100 x 100 grid cell maps obtained from Yellowstone National Park and on random maps. Upper panel: only the oldest forest stand-age classes were considered to be susceptible to disturbance. Lower panel: all forest stands were considered to be susceptible to disturbance.

only be expected to hold for the disturbance parameters used in the model, and the use of a different scale or rule to control the disturbance spread (e.g., disturbances can spread to eight neighbors of a cell, or disturbance can "jump" across some number of cells) would substantially change the results. However, the same results could be generated with a rule that allowed disturbance to spread to eight neighbors if the value of i was reduced. Research is in progress to expand this modeling approach and to develop realistic rules for projecting fire spread in YNP.

Long-term Dynamics of Disturbed Landscapes

The dynamic mosaic observed in many landscapes results from a complex interplay between disturbance and recovery processes. Because the mosaic constantly changes, understanding the long-term dynamics of disturbance-prone landscapes is very important for a natural area manager. For example, a manager would be very interested in knowing the probability of the natural area remaining more-or-less in its current state or undergoing some dramatic changes. The answer obtained is a function of the disturbance regime, recovery processes, and the spatial and temporal scales considered.

We developed another simple model of landscape dynamics that considers the spatial-temporal scales of disturbance and recovery (Turner et al. 1993). Five major factors characterizing the dynamics of landscapes were included: (1) disturbance frequency, or its inverse, the interval between successive disturbances; (2) rate of recovery from disturbance, or its inverse, the length of time required for a disturbed site to recover; (3) disturbance severity, i.e., the amount of damage inflicted on the biota; (4) the size or spatial extent of the disturbance events; and (5) the size or spatial extent of the landscape. Because the functional effects of these factors are interrelated, we reduced them to two key parameters representing time and space that can be used to describe potential disturbance dynamics.

The temporal parameter (T) is defined by the ratio of the disturbance interval (i.e., the time between successive disturbances) to the recovery time (i.e., the time required for a disturbed site to achieve recovery to a "mature" stage). Disturbance severity is incorporated into recovery time such that a low-severity disturbance would be associated with rapid recovery, and a high-severity disturbance with slow recovery. Defining the temporal parameter as a ratio permits the evaluation of three qualitatively different states, regardless of the type or time scale of the disturbance. These states are (1) the disturbance interval is longer than the recovery time ($T > 1$), so the system can recover before being disturbed again; (2) the disturbance interval and recovery time are equal ($T = 1$); and (3) the disturbance interval is shorter than the recovery time ($T < 1$), so the system is disturbed again before it fully recovers.

The spatial parameter (S) is defined by the ratio of the size of the disturbance to the size of the landscape of interest. There are two qualitatively different states of importance here, again regardless of the type of disturbance. These states are (1) disturbances that are large relative to the size of the landscape, and (2) disturbances that are small relative to the extent of the landscape. The use of ratios in both parameters permits the comparison of landscapes across a range of spatial and temporal scales. We use the parameters to describe a landscape state-space in which the temporal parameter is placed on the y-axis, and the spatial parameter is displayed on the x-axis. Note that the reduction of the landscape dynamics to two general parameters subsume an enormous amount of spatial and temporal variation in where and when disturbance events occur. There may be many different physical manifestations of a landscape that map into a given time/space ratio.

A simple simulation model was developed to explore landscape dynamics within the state space described above (Turner et al. 1993). The landscape again was represented as a square grid of 100 x 100 cells, but eight seral stages or stand-age classes were included. Initially, the entire landscape is covered with mature vegetation (seral stage 8). At a fixed interval, square disturbances of a fixed size are imposed on the landscape. In contrast to the previous model, disturbances can occur in all seral stages, and the effect of the disturbance is to return each disturbed cell to seral stage 1. The location of each disturbance is randomly chosen, and the disturbance events are "wrapped" from one edge of the map to the opposite edge so that boundary effects (Gardner et al. 1987) are eliminated. Disturbed sites recover deterministically through succession, passing through a seral stage at each time interval and achieving full recovery eight time steps (chosen arbitrarily) following the disturbance. The seral stages followed one another sequentially, and we assumed that seed sources for each stage remained present in the landscape. The disturbance-recovery process was simulated for 100 time intervals.

Under different combinations of T and S, qualitatively different landscape dynamics were observed. We used the mean and variability of proportion of the landscape covered by each seral stage during the simulations to define different regions within the state space (Figure 3). When disturbances were small in size and disturbance interval was long relative to recovery time, landscape equilibrium was observed. That is, a landscape may show small local changes but very little change through time in the overall abundance and variability of each seral stage (region A in Figure 3). A landscape may also appear relatively stable, exhibiting low variance in p values of each seral stage, as disturbance size increases but disturbance events are still relatively infrequent (region B in Figure 3). We then see a stable system with low variance in which much of the landscape is still occupied by mature vegetation. This region of the state space may be comparable to the stochastic or relative constancy as defined by Botkin and Sobel (1975), where a system changes but remains within reasonable bounds. The landscape may also appear stable with low variance when disturbance sizes increase even further, although the early seral stages will dominate (region D in Figure 3). The landscape begins to show very high variance with intermediate values of S and T (region C in Figure 3) and extremely high variance when disturbance size exceeds 50% of the landscape and the disturbance interval is very long (region E in Figure 3). Landscapes in this region of the state space are characterized as non-equilibrium systems. Under conditions of

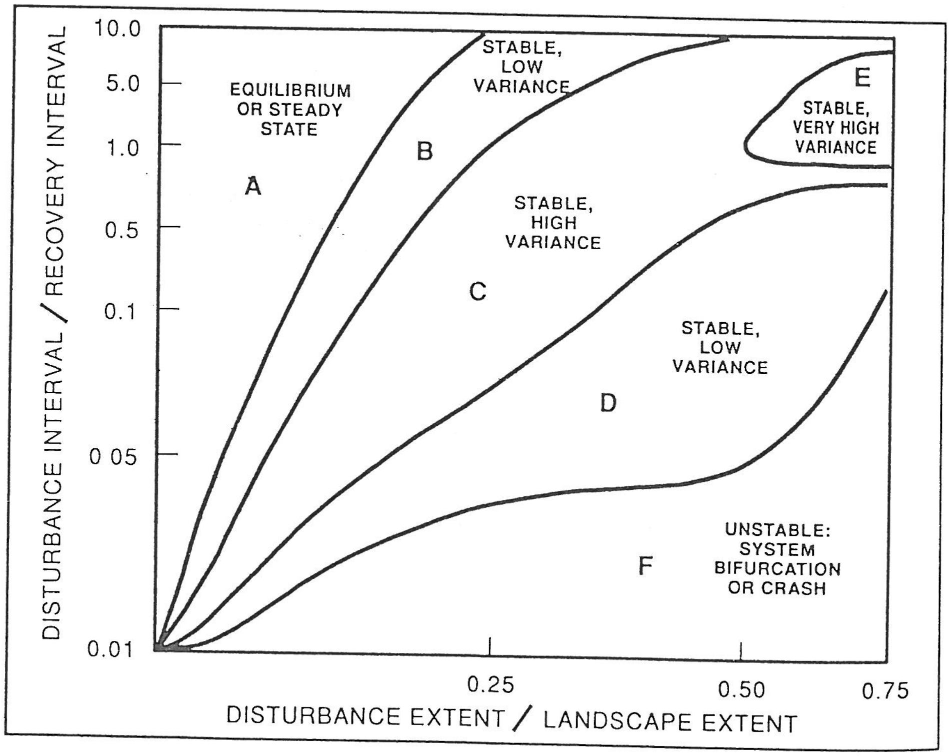

Figure 3. State-space diagram of the temporal and spatial disturbance and recovery parameters, illustrating regions that display qualitatively different landscape dynamics (from Turner et al. in press).

very large and frequent disturbance, there exists also the potential for unstable or catastrophic change (region F in Figure 3). If the disturbance is sufficiently large and/or sufficiently frequent, the landscape may not recover to the preperturbation trajectory. An alternative system often exists, and the disturbance may change the nature of the system if the species cannot become reestablished. Subsequently, the landscape may tend to recover along a new trajectory.

Consider the dynamics of fire in the YNP landscape as an example of how natural disturbance dynamics may fit within this framework. Under YNP's natural fire program, most fires that occurred between 1972 and 1987 went out without intervention before burning more than a hectare. A total of 8300 ha (approximately 1% of the park) burned in 1981, but the area burned in other years was much less (Despain 1990). The return interval for fires of this size in the Yellowstone landscape is approximately 15 years, and the recovery time for burned forests to reach the mature stage is approximately 300 years (Romme and Knight 1982). Thus, for fires observed in Yellowstone between 1972 and 1987, the temporal parameter $T \sim 0.05$, the spatial parameter $S \sim 0.01$. This disturbance regime occurs in the lower left corner of the diagram (Figure 4) and suggests equilibrium conditions of little change. In contrast, the 1988 fires that burned in YNP occurred during an extreme fire year and affected approximately 36% (ca. 321,000 ha) of the park (Despain et al. 1989). The last comparable fires occurred around 1700, and the return interval for fires of this scale is approximately 300 years (Romme 1982, Romme and Despain 1989). Thus, expanding the temporal scale to include fires like those that occurred in YNP in 1988, we observe $T \sim 1.0$ and $S \sim 0.36$. This disturbance regime falls within the region of a stable landscape with high variance (Figure 4), consistent with Loucks's (1970) concept of a stationary process and Romme's (1982) failure to find a shifting-mosaic steady state in the Little Firehole River drainage of YNP.

Results from this simulation model of disturbance and recovery have implications for natural areas. The importance of infrequent disturbances, especially if they are large in size, is noteworthy. If the rare disturbances in a system are neglected, our understanding of landscape dynamics as well as species persistence, energetics, soil, and nutrient relations will be impeded (Franklin and Hemstrom 1981). All disturbances have some size distribution, and large disturbances may be less frequent than small disturbances. In the Boundary Waters Canoe Area, Baker (1989) found that landscape stability or instability was controlled primarily by the largest observed disturbance patch rather than the mean size of the disturbance. Similarly, in Yellowstone National Park, the landscape mosaic is dominated by the effects of the relatively infrequent but large fires (Romme 1982, Romme and Despain 1989). Thus, it is important for landscape managers to anticipate rare disturbance events. Empirical studies designed to describe the disturbance history of a natural area (e.g., Romme 1982, Foster 1988) are extremely valuable.

If a disturbance regime shifts from one region of the state space to another (Figure 3), the dynamics of a natural area might change dramatically. For example, it is hypothesized that global climate change will alter existing disturbance regimes (e.g., Graham et al. 1990). If the frequency and size of disturbances (e.g., fires or storm events) are increased, a landscape may shift from showing low variability to high variability. In a natural area, such a change in the landscape mosaic may have important implications for the persistence of species that require mature habitat (e.g., Romme and Turner 1991). Alternatively, the temporal or spatial scale of the disturbance regime may change but the system may remain in the same qualitative region of Figure 3, in which case no adverse effects may result from the change. The simulation results presented here could be used to inform managers about the potential configurations of their natural areas under future scenarios.

The model also can provide some guidance for the establishment of natural areas in disturbance-prone landscapes. Preservation of natural areas is especially challenging because we seek to preserve areas that are changing (White and Bratton 1980). A variety of authors (e.g., Wright 1974, Sullivan and Shaffer 1975, Pickett and Thomp-

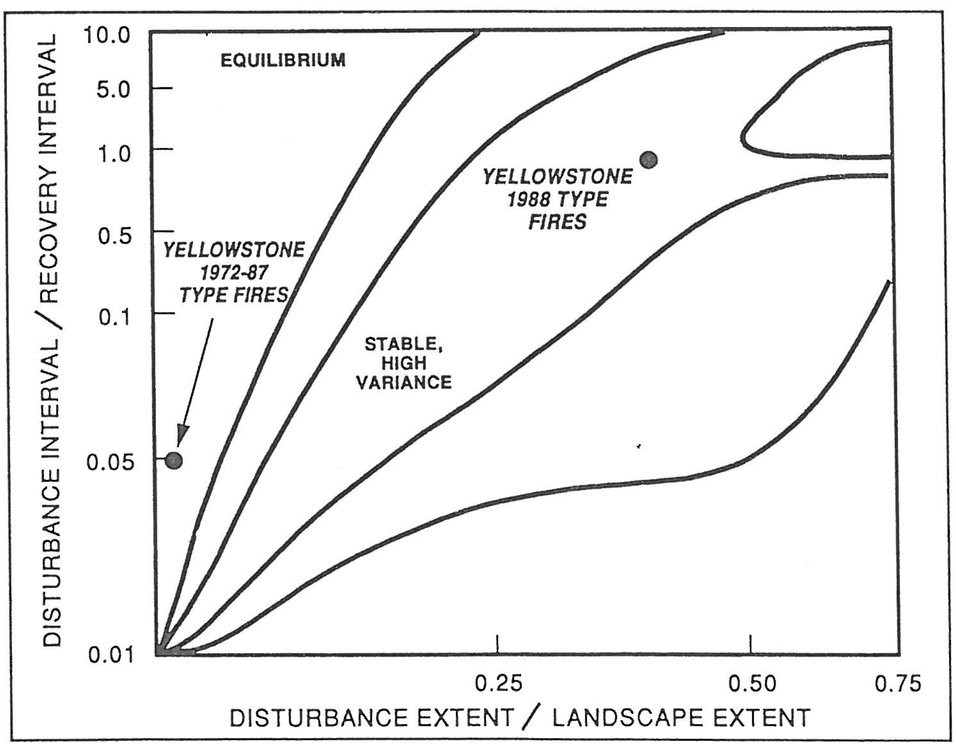

Figure 4. State-space diagram of the temporal and spatial disturbance and recovery parameters, using fire in Yellowstone National Park to illustrate effects of expanding the temporal scale of observations on conclusions regarding landscape dynamics (from Turner et al. in press).

son 1978) have suggested that natural areas should be sufficiently large to include a mosaic of all normal stages in community development, and that natural processes of perturbation and recovery should be allowed to occur without intervention. By knowing the frequency and extent of disturbances within a landscape, the spatial extent necessary to incorporate this disturbance could be determined. Obviously, landscapes characterized by very large-scale patterns of disturbance and recovery would necessitate a much larger natural area than might be required under systems in which perturbations are small and frequent. However, it is important to remember that our projections only address the dynamics of seral stages, and other attributes of a natural area (e.g., species, biomass, etc.) must also be considered. Landscape equilibrium cannot be guaranteed indefinitely by a reserve of any size because unexpected events probably will occur over long time scales. However, increasing the size of a reserve should decrease the probability of a dramatic shift in landscape dynamics due to a rare disturbance event.

CONCLUSION

Models can be extremely useful tools for the managers of natural areas in disturbance-prone landscapes. The two examples we have reviewed illustrate how relatively simple models can be used to explore the potential effects of disturbances under different landscape conditions and the long-term dynamics of a landscape under different disturbance regimes. These examples also illustrate how models can be used to enhance our understanding of disturbance and landscape dynamics. Our simulations have documented the importance of landscape connectivity in controlling disturbance dynamics and of the interaction between landscape configuration and characteristics of a specific disturbance (e.g., point of disturbance initiation). These models are probabilistic, not mechanistic, and are used appropriately to explore the central tendency and ranges of response to disturbance rather than to predict the outcome of a single specific disturbance. Thus, we also underscore the importance of using the appropriate type of model for a particular purpose.

As with the use of any mathematical model, caveats apply to using models (Golomb 1968) in natural area design and management. No matter how complex, a model is always a simplification of a real system. A manager must not believe that the model is reality, nor should reality be distorted to fit the model. The simplifying assumptions on which the model is based should be understood and, if necessary, tested. The limits of applicability of a model must also be known and not surpassed — in other words, don't believe the n^{th}-order consequences of a 1^{st}-order model.

The management of natural areas, especially in disturbance-prone landscapes, is not easy, even in a more-or-less stable environment. Given the finite boundaries and progressive insularization of most nature reserves today, and the potentially dramatic climatic changes that may occur in the coming century, disturbance regimes are likely to change substantially in the future. Land managers should avail themselves of all the techniques available to anticipate the implications of these changes and to aid in their decision making. Because models provide a link between theory and empirical studies, models can be helpful in designing key studies to obtain critical information, especially because funds for research are never infinite. Used appropriately, models are invaluable tools that can enhance our fundamental understanding of natural landscapes and our ability to anticipate changes and provide good stewardship of natural areas long into the future.

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