

# Disturbance and Temporal Dynamics

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## Key topics addressed in this chapter

- ◆ *A review of scientific findings about the role of disturbance and other kinds of temporal dynamics in ecosystems*
- ◆ *A definition of disturbance and a review of descriptors of disturbance regime*
- ◆ *An overview of the kinds of natural disturbance in North American ecosystems*
- ◆ *A discussion of interactions and feedbacks among disturbances, the influence of landscape pattern on the process of disturbance, the concept of equilibrium with regard to disturbance, and ecosystem responses to disturbance*
- ◆ *An identification of emerging issues in disturbance ecology, including the relationship of disturbance and climate, Native American influences on disturbance rate, the human imposition of new scales on ecosystems through habitat fragmentation, the invasion of exotic species, and the relationship of ecological variation and resilience*

**Keywords:** Disturbance, temporal dynamics, feedbacks and interactions, landscape mosaics and patterns, dynamic equilibrium, managing disturbance, habitat fragmentation, ecosystem dynamics

## 1 INTRODUCTION

All ecosystems are dynamic. Relatively sudden and dramatic changes result from natural disturbances like fire, windstorm, flooding, catastrophic drought, avalanche, coastal erosion, insects, and pathogens (White 1979). Ecosystems also undergo gradual changes due to succession (Olson 1958), climate variation (Davis 1981, Clark 1988), and geomorphic processes (Swanston and Swanson 1976, Swanson 1981). Change is intrinsic and inevitable; ecosystem management must be based on an understanding of this change, whether an ecosystem is managed for harvest of natural resources or preservation (White and Bratton 1980).

While disturbances characterized the evolutionary setting of organisms before the human era, humans have also influenced disturbance regimes and introduced new forms of disturbance. Most management actions involve intentionally disturbing ecosystems (e.g., logging, prescribed fire) or suppressing disturbance (e.g., fire, flood, and insect control). Human activities like logging and livestock grazing may superficially resemble natural disturbances but may differ in important ways (Hansen et al. 1991). In addition to these direct effects, humans have indirectly altered the propagation of disturbances by changing the spatial structure of landscapes (Turner et al. 1989, 1993). Even when disturbances are not under human control (e.g., hurricanes, earthquakes, volcanic eruptions), management actions which alter landscape pattern and successional state may influence ecosystem response. Natural and human-caused disturbances have social and economic consequences, affecting natural resources like timber and fisheries and non-resource values like aesthetics and biodiversity. Although public perceptions focus on negative aspects of large "natural disasters" (e.g., fires, floods, and hurricanes), disturbances often play a crucial positive role in maintaining ecosystem variability and biological diversity (Christensen et al. 1989). The suppression of disturbances leads to the loss of biological diversity and may contribute to larger and more severe disturbance events later.

In this paper, we review principles of disturbance and ecosystem dynamics. Because ecosystem structure and productivity depend largely on primary producers, our focus is on vegetation. We begin by reviewing definitions and characteristics of disturbance, the kinds of disturbance as they vary with climate and site, and the concept of disturbance regime.

We then discuss disturbance interactions and feedbacks, effects of landscape-level patterns on disturbance processes, concepts of equilibrium, and species and community responses to disturbance. We then turn to five emerging issues that will affect how we

incorporate disturbance into ecosystem management: climate variability and disturbance regimes, Native American disturbance, habitat fragmentation and the human imposition of new scales on management, exotic species invasions, and the restoration of ecological variation.

## 2 HISTORICAL CONTEXT

Ecologists have long recognized disturbance as a factor shaping ecological communities. For example, Darwin (1859) noted that when mowing of a meadow ceased, plant diversity declined. During the late 19th and early 20th centuries, much research focused on succession (Cowles 1899, Clements 1916). Disturbance was viewed primarily as a force moving systems away from a stable late-successional condition in which climatic, topographic, and soils determine composition and structure. However, a few early workers emphasized the importance of disturbance itself in shaping ecosystems (Cooper 1926, Raup 1941) or argued that successional concepts of the day did not apply well to vegetation with frequent disturbance (Churchill and Hanson 1958). The work of Watt (1947) drew attention to small-scale disturbances such as treefall gaps in mature forests and suggested that understanding patterns in plant communities required an understanding of dynamic processes, including disturbances. Watt's ideas have been extrapolated through computer simulations (Shugart 1984) and empirical studies (Bormann and Likens 1979, Christensen and Peet 1984, Peet and Christensen 1987) and form the basis for much of modern successional theory.

In the 1970s, attention focused on describing disturbances and documenting their effects, and evidence accumulated that disturbances play an important role in determining the structure of many communities, landscapes, and ecosystems (Dayton 1971, Heinselman 1973, Bormann and Likens 1979, White 1979, Runkle 1982). Empirical and conceptual studies suggested that disturbances may maintain species diversity (Connell 1978, Huston 1979), and increasing awareness of natural disturbances prompted interest in the effects of fire suppression on community and ecosystem structure (Kilgore and Taylor 1979, Harmon 1984). In the 1980s, the emerging discipline of landscape ecology (Forman and Godron 1986, Turner 1989) turned Watt's formulation around, examining ways in which spatial patterns (particularly coarse-scale patterns) influence disturbance processes. Research also focused on the role of residual structures such as logs and snags in post-disturbance recovery (Harmon et al. 1986, Franklin 1989). The 1988 fires in the Yellowstone area and the

debate over logging practices in the Pacific Northwest drew public attention to disturbance ecology. Emerging topics in the 1990s include effects of climate on disturbance regimes (Swetnam and Betancourt 1990), influence of disturbance history on the occurrence and outcome of subsequent disturbances (Schowalter and Filip 1993), and approaches to integrating natural disturbances and management activities (Swanson and Franklin 1992, Christensen et al. 1996).

### 3 CHARACTERIZING DISTURBANCE AND DISTURBANCE REGIMES

We define a disturbance as a relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment (White and Pickett 1985). This "absolute" definition of disturbance stresses disturbance as a measurable physical event and suggests the need for mechanistic studies of disturbance effects and ecosystem recovery. A Forest Service definition is similar but somewhat less specific: disturbance is "a discrete event, either natural or human induced, that causes a change in the existing condition of an ecological system" (Kaufmann et al. 1994).

The alternative to this definition is the "relative" definition of disturbance: disturbance as a departure from the "normal" range of conditions. However, the applicability of this relative definition is limited by problems in defining "normal" conditions. Some disturbance regimes are unstable, and many are poorly known. Even disturbance regimes that appear stable in the short-term vary over longer time periods or in the face of changing climates. Our understanding of "normal" conditions is further complicated by variable and incompletely known histories of human influence. For these reasons, a physical and absolute definition of disturbance provides a better basis for understanding, prediction, and management. As we will argue below, even when the goal is to quantify the range of variation within an ecosystem, we are better off with an absolute measure which stresses the physical characteristics of disturbance and the mechanisms of ecosystem response than an approach that focuses solely on the bounds of variation.

#### 3.1 Kinds of Disturbance in North America

The kinds of natural disturbances that are important vary with climate, topographic position, substrate, and successional age (Table 1, White 1979). Some disturbances are endemic to particular climates. Examples are cryogenesis in arctic and alpine tundra soils, freeze

damage in subtropical and warm temperate vegetation, ice storms in temperate areas with continental climates and high precipitation, ice battering on shores, and flash floods after intense rain storms. Fire is important in climates with ignition sources, sufficient biomass to carry a fire, and long enough dry periods to permit burning. Dry sites in humid areas (e.g., pine barrens on sand deposits and pine stands on well drained ridges in humid mountains) also permit fires which may be severe in drought years. Other disturbances occur in a variety of climates but are specific to particular topographic settings: landslide and avalanche in mountainous areas, alluvial erosion, deposition, and flooding, wave battering of shores, water level fluctuation in basins, and salinity encroachments in coastal rivers. In general, disturbance varies along topographic gradients (Fig. 1) (Romme and Knight 1981, Harmon et al. 1983, White 1994), as do other physical factors like insolation, temperature, and precipitation. Some disturbances are associated with particular geological settings and substrates; these include volcanic eruption, earthquake, sand dune dynamics, and coastal erosion and deposition. Some disturbances are biological in origin; examples are the activities of burrowing mammals, grazers, and ants in the prairie, beaver activity along streams, and insect and pathogen outbreaks in forests. Most ecosystem types experience not only several kinds of disturbance, but a range of disturbance impacts within each kind (Fig. 2) (Harmon et al. 1983, Lang 1985).

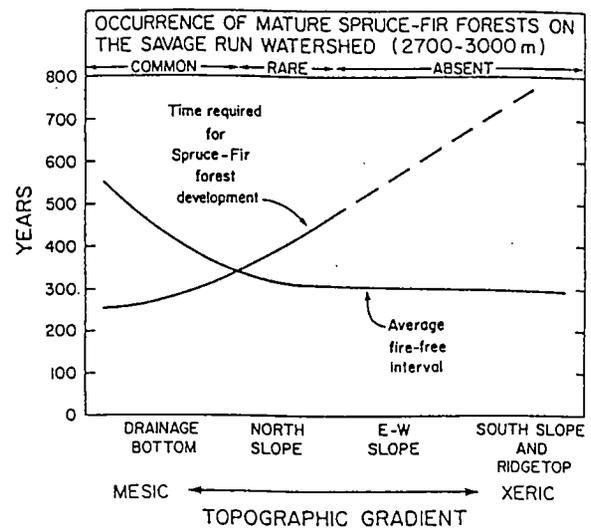


Fig. 1. The average fire free interval decreases from moist to dry sites, while the time for succession to spruce-fir forest increases along the same gradient. As a result, spruce-fir forests will probably never develop on the driest slope positions (from Romme and Knight 1981).

Table 1. Natural disturbances in North America. The kinds of disturbances vary geographically, and by topographical position and substrate.

Eastern mixed and deciduous forests	Gap dynamics: Runkle 1982, 1985; Forcier 1975; Lorimer 1980 Hurricane, catastrophic wind: Foster 1988, Foster and Boose 1992 Fire: Komarek 1974, Harmon 1982, 1984; Abrams 1992; Clark and Royall 1996 Landslide: Hupp 1983 Insects and pathogens: Schowalter 1985, Harmon et al. 1983, Daughtry and Hibben 1994 Ice storm: Lemon 1961, Whitney and Johnson 1984 Catastrophic drought: Hough and Forbes 1943
Southeastern pine forests	Fire, beetles: Komarek 1974, Rykiel et al. 1988, Frost 1993
Appalachian spruce-fir forests	Gap dynamics, wind: White et al. 1985a,b; Sprugel 1976 Debris avalanche: Flaccus 1958
Central grasslands	Fire, grazing, burrowing animals: Vogl 1974, Collins 1987, Hobbs et al. 1991, Vinton et al. 1993 Catastrophic drought: Weaver 1968
Deserts	Rare rain storms, flash floods: Zedler 1981
Western conifer forests	
Rocky Mountains	Fire, insects: Knight 1987, Romme and Knight 1981, Romme 1982, Romme and Despain 1989, Veblen et al. 1994 Cryogenesis in alpine communities: Johnson and Billings 1962
Sierra Mountains	Fire: Kilgore and Taylor 1979, Stephenson et al. 1991, Stephenson 1996, Swetnam 1993
Pacific Northwest	Fire, windstorm: Stewart 1986, Franklin and Forman 1987, Hansen et al. 1991 Landslides: Swanson and Dyrness 1975 Volcanic eruption: Franklin et al. 1985
Western shrublands	Fire: Biswell 1974, Minnich 1983, Christensen 1985 Debris flows: Biswell 1974
Boreal forest	Fire, insects: Heinselman 1973, 1981; Dansereau and Bergeron 1993
Arctic tundra	Cryogenesis: Churchill and Hanson 1958
Subtropical areas	Freeze damage: Silberbauer-Gottsberger et al. 1977
Lakes	Fluctuating water levels: Shipley et al. 1991 Ice battering on shorelines: Raup 1975
Streams	Floods and erosion: Hemphill and Cooper 1983, Resh et al. 1988, Pringle et al. 1988 Beaver: Ives 1942 Debris flows: Lamberti et al. 1991
Coastal areas	Dune movement: Schroeder et al. 1976 Hurricanes and other storms: Chabrek and Palmisano 1973 Salinity changes: Chabrek and Palmisano 1973
Rocky intertidal communities	Wave action, storms, predation, dessication, drift log battering: Paine and Levin 1981; Sousa 1984, 1985; Dayton 1971
Mangroves	Hurricanes, salinity changes: Thom 1967

Disturbances interact with each other and are imposed on more gradually acting sources of ecosystem change, such as soil development, geomorphological changes, and climate change. For example, the distribution and availability of phosphorus on Australian sand dunes shifts dramatically over the course of long-term soil development (Walker and Syers 1976, Vitousek and White 1981). Initially, phosphorus is relatively abundant in the mineral soil; over millennia,

availability declines and the element becomes largely restricted to soil organic matter. Walker and Syers (1976) argue that these changes in soil chemistry will lead to changes in ecosystem response to disturbance; nitrogen fixers, which require relatively high phosphorus levels, will respond more strongly to fires on young soils than on older ones. In Everglades National Park, fire frequency varies with topographic position relative to the water table (White 1994). The water table

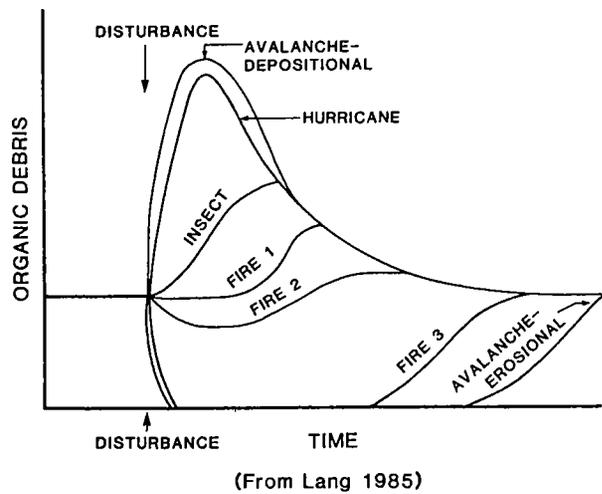


Fig. 2. Within a single ecosystem (in this example, northern Appalachian fir forests), different disturbances produce widely different effects on organic debris (redrawn from Lang 1985).

rises as the sea level rises (which it has been doing over the last few thousand years) and is also influenced by impoundments upstream from the National Park. Topography in this low elevation landscape is partly controlled by the amount of organic matter present. Intense fire removes peat and lowers topographic position; lowered water table (because of impoundments, droughts, or the high evapotranspiration of an introduced tree, *Melaleuca*) leads to a higher decomposition rate and lowers the topography. The incidence of fire is one of many interacting sources of change in this ecosystem.

### 3.2 Disturbance and disturbance regime descriptors

Not all disturbances are equivalent. Disturbances differ in six categories of descriptors (Table 2): kind, spatial characteristics, temporal characteristics, specificity, magnitude, and synergisms (Sousa 1984; White and Pickett 1985; Runkle 1985; White and Harrod 1997). Each of these categories is described below. Taken together, the attributes of all the disturbances occurring in a system, the interactions between them, and their linkages with biotic and abiotic factors, define the disturbance regime.

Disturbances not only affect the sites where they occur, but they also can affect nearby ecosystems. For example, fire in the upper part of a forest watershed can affect nutrients and siltation downstream. Romme and Knight (1981) speculated that a recent downward trend in fish populations in a watershed in Yellowstone National Park was the result of long absence of fire.

Immediately after fire, they suggested that nutrient inputs to streams would be high, causing relatively high aquatic productivity and higher fish populations. Fire also influences wildlife movement patterns, thus changing the level of herbivory at sites that were not burned. Although offsite effects like these are important, in this section we focus on onsite effects.

Table 2. Parameters of disturbance regimes (from Sousa 1984; White and Pickett 1985; Runkle 1985; White and Harrod 1997).

Kind	
Spatial characteristics	Size: patch size, area per event, area per time period, area per event per time period, total area per disturbance per time period Shape Distribution: spatial distribution including relationship to geographic, topographic, environmental and community gradients Landscape context: patch dispersion, contiguity, matrix
Temporal characteristics	Frequency: Number of events per time period Rotation period: Time needed to disturb an area equivalent to the study area Return interval, cycle, or turnover time: Interval between disturbance events Predictability: A scaled inverse function of the variance in return interval Contagion: Rate and probability of spread Seasonality: Seasonal distribution
Specificity	To species: Probability of disturbance by species To age or size classes: Probability of disturbance by age or size classes and feedback between community state and disturbance rate To landforms: Probability of disturbance by landform element
Magnitude	Intensity: Physical force of the event per area per time Severity: Impact on the organism, community, or ecosystem Ecosystem effects: Internal heterogeneity: Degree of internal patchiness within disturbed areas Ecosystem legacies: Structures, dead, and living biomass remaining
Synergisms	Interactions between disturbances Feedbacks through successional state Coupling with climate

### 3.2.1 Kind

The types of disturbance that occur within ecosystems, landscapes, or regions vary with climate, topography, substrate, and biota (Table 1).

### 3.2.2 Spatial characteristics

Disturbances differ in size (patch size, area per event, area per time period, area per event per time period, total area per disturbance type per time period), in distribution (on geographic, topographic, environmental and community gradients), and landscape pattern (patch shape and dispersion, contiguity, and relationship to the surrounding matrix). The size of individual disturbances (few large versus several small disturbances) affects amount of edge, contiguity, and other spatial parameters. Size may also affect the nature of subsequent colonization and succession (lateral expansion versus vertical growth; shade tolerant versus intolerant species; advance regeneration versus the establishment of new individuals) in both terrestrial and marine systems (Fig. 3) (Runkle 1985, Sousa 1985).

The shape of disturbance patches can also be important. The relationship between length of edge and interior area has implications for wildlife and vegetation. Circular or square patches have smaller edge/area ratios than elongate or convoluted patches. The shape and orientation of gaps may affect levels of incident light, particularly in higher latitudes. The distribution of disturbed patches across landscapes, geographic and environmental gradients, and community types is also important. Disturbed patches occur in

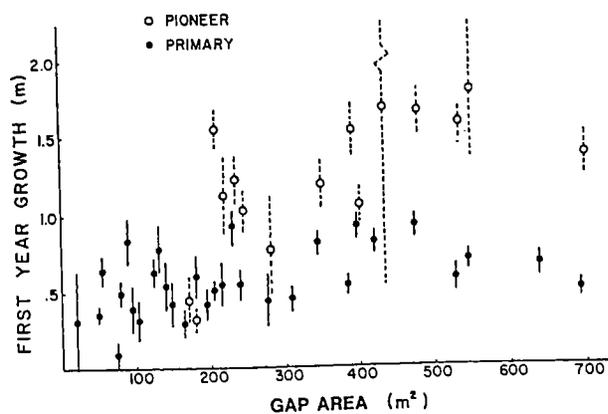


Fig. 3. Height growth (mean and one standard error of annual height increment for stems greater than 1 m tall) of pioneer (open circles) and primary tree species (closed circles) as a function of gap size (from Brokaw 1985). Primary forest species show some response to increased gap size and occur at a wide range of gaps sizes. Pioneer species have the highest growth rates but appear only in the highest light conditions (largest gaps).

the context of a larger landscape which may act as a source of colonists and as a refuge for disturbance-sensitive organisms. The composition and spatial structure of the surrounding landscape will affect post-disturbance recovery and the persistence of biological diversity.

### 3.2.3 Temporal characteristics

Disturbances differ in frequency (number of events per time period), rotation period (time needed to disturb an area equivalent to the study area), return interval, cycle, and turnover time, predictability, regularity, and stochasticity, contagion (rate and probability of spread), and seasonality. The concept of "predictability" has been used in the context of morphological and life-history adaptations to disturbance. From a community or management perspective, "regularity" or "stochasticity" are more useful terms. Temporal stochasticity will contribute to variation between sites in a landscape and may thus increase the diversity of successional states. Management plans can incorporate stochastic factors. For example, when conditions are suitable for prescribed fire, burn/no burn decisions for particular units may be made by applying a probability (e.g., rolling a die or using a random number table). The resulting return interval will reflect a statistical distribution rather than a single value. Periodicity may be driven by endogenous feedback mechanisms (e.g., increasing flammability with stand age) or by exogenous climate factors (e.g., the Southern Oscillation).

Fires, hurricanes, ice storms, and insect outbreaks are among the disturbances which exhibit marked seasonality in their occurrence. Season of disturbance may affect availability of propagules from outside the disturbed area and physiological/phenological response of species within the patch. For example, saplings may be killed outright by a growing season fire, but may resprout if fire occurs during the dormant season; some species like wiregrass on the southeastern coastal plain may only flower in response to properly timed burns. Sousa (1985) reviewed the effects of disturbance timing and seasonality on marine intertidal organisms.

### 3.2.4 Specificity

The susceptibility of organisms to disturbance may vary with species, age or size class, successional time, community state, and landscape position. Some physical disturbances such as lava flows and catastrophic debris slides may obliterate all organisms in their path. Other disturbances, particularly biotic disturbances like insect parasites and fungal pathogens, impact one or very few species. Wind, fire, and vertebrate grazers

tend to be intermediate in specificity. Wind and fire effects vary with species and size/age class (Harmon 1984, Foster 1988). Because disturbance effects are often species- and age class-specific, descriptions of disturbance-induced damage and mortality should be described relative to species and age classes.

### 3.2.5 Magnitude

Disturbances vary in intensity (the physical force per event per area per time) and severity (the impact on organisms and ecosystem structure and composition). This variation is reflected in the percentage of living biomass killed and the amount of dead biomass added to or removed from a patch. Intensity and severity affect resource levels, structural heterogeneity, and mechanisms of recovery. Disturbances rarely remove all biota and organic matter; the amount and nature of living and dead material left in a patch after disturbance may play a key role in determining community and ecosystem response. These residual structures (dubbed the "biological legacy;" Franklin 1989) may include standing live trees, trees knocked over but still alive, seedlings, saplings, herbs, shrubs, buried seeds, standing snags, logs and other coarse woody debris, humus layer and soil biota, including mycorrhizal fungi. These residual organisms and structures may help maintain ecosystem function, moderate fluctuations in temperature and humidity, and restrict nutrient and sediment loss during early stages of post-disturbance recovery (Marks 1974, Franklin 1989). They may also serve as refugia and corridors for disturbance-sensitive species (Franklin 1989) and foci for seed dispersal (McDonnell and Stiles 1983) and contribute to structural heterogeneity and habitat diversity in young, aggrading systems (Hansen et al. 1991). The importance of biological legacies is one reason that we should be careful in accepting management treatments (e.g., logging) as analogs for natural disturbances (e.g., windstorm).

Historic disturbance regimes typically include events of various magnitudes (Lorimer 1980, Barrett et al. 1991). Both high and low intensity disturbances may play roles in maintaining ecosystem structure. On xeric low elevation sites in the southern Appalachians, rare crown fires create canopy and soil conditions necessary for the vigorous growth of pine seedlings; low-intensity surface fires, though more frequent, lead to little pine regeneration (Barden and Woods 1976). However, low-intensity fires help to maintain pine dominance and historic structure by top-killing hardwood seedlings and saplings (Harmon 1984). Intense fires may also be important in sequoia-mixed conifer forests, often termed low-intensity fire systems

(Stephenson et al. 1991). Full characterization of disturbance regimes requires assessment of the range of disturbance magnitudes.

### 3.2.6 Synergisms

At the levels of individuals, stands, and landscapes, the occurrence and outcome of disturbances depend, to some extent, on the history of past disturbance. For example, fire scars may make pine trees more vulnerable to bark beetle attack (Geiszler et al. 1980). As we will argue below, such synergisms are widespread and have important implications for community and ecosystem dynamics.

## 3.3 Characterizing Disturbance Regimes: Approaches and Challenges

Efforts to characterize disturbances and disturbance regimes involve four basic approaches. The historical approach involves documenting past events and ecosystem states through fossil pollen and charcoal (Foster and Zebryk 1993, Clark and Royall 1996), stand origin dates and regeneration patterns (Heinselman 1973, Romme 1982), fire scar analyses (Harmon 1982), detailed reconstructions of stand structure and patterns of release (Henry and Swan 1972, Lorimer 1980), and historical survey records, narratives, and photographs (Seischab and Orwig 1991, Motzkin et al. 1996). Additional information and references on historical methods can be found in the companion management paper (see Engstrom et al., this volume, Section 2.2.1), Agee (1993), and Lorimer (1985; see also Lorimer and Frelich 1989). The observational approach involves description of present-day disturbances, conditions, and responses (Dayton 1971, Runkle 1982, Harmon 1984, Hansen et al. 1991). The experimental approach involves deliberate disturbance of an ecosystem followed by monitoring of disturbance effects (Bormann and Likens 1979, Collins 1987). The simulation approach involves the use of models to examine disturbance behavior and the effects of changes in disturbance regime (Shugart 1984, Franklin and Forman 1987, Turner et al. 1989, Keane et al. 1990, Covington and Moore 1994). These four approaches differ in their spatial and temporal resolution, accuracy, and scope; research programs which integrate multiple approaches will provide the most useful information.

Disturbance regimes can vary considerably between areas with similar vegetation. For example, presettlement lodgepole pine forests supported a range of fire patterns. In the northern Rockies, lower elevation sites burned every 25–150 years; severity ranged from underburns causing little canopy mortality to

stand-replacing fires (Barrett 1994). Higher elevation sites experienced mostly high-severity fires; return intervals ranged from about 200 years on productive andesitic soils (Barrett 1994) to 300–400 years on less fertile rhyolite (Romme 1982, Romme and Despain 1989). In lodgepole pine forests in the Pacific Northwest, fires of variable severity have burned at intervals of 60–80 years (Agee 1993). Although characterizing disturbance regimes involves considerable time, effort, and expense, ecologically sound management requires site-specific information.

### 3.3.1 The historical or natural range of variation

Ecosystem scientists and managers have attempted to use the range of variation that characterizes ecosystems as a guide to understanding and management (Landres 1992, Swanson and Franklin 1992, Hunter 1993, Morgan et al. 1994, Swanson et al. 1994, Landres et al., in press). One might, for example, seek to quantify the "natural range of variation" in biomass or population density over several generations of the dominant organisms. Although this approach may provide valuable information, we cannot assume that all ecosystems have well-defined bounds of variation. The farther back in time we look, the more variation we will see. In addition, recent studies have shown that humans have influenced some ecosystems that were once considered pristine. The "historic range of variation" (Swetnam 1993, Morgan et al. 1994, Wright et al. 1995) is an attractive phrase because it makes no assumption about naturalness or normalcy and accepts the arbitrary and variable duration of the historical record. Documenting historical variation in ecosystems will help us to understand better both disturbance effects and the influences of climate and human activity. The recent history (decades to millennia) tells us about past behavior of the ecosystem and the natural processes with which management actions will have to interact.

## 4 SYNERGISMS: FEEDBACKS AND INTERACTIONS

Here we discuss the potential effects of disturbance history on subsequent disturbance events and include both natural and human caused disturbance. White (1987) identifies two types of synergisms, feedbacks and interactions. A feedback is a situation in which a disturbance influenced subsequent disturbances of the same type. For example, flammability of chaparral may be low immediately after a fire and increase as a stand matures. An interaction is a situation in which a

Table 3. Disturbance feedbacks and interactions by biome.

Eastern mixed and deciduous forests	fire-fire: Harmon 1984
	fire-fungi-wind: Matlack et al. 1993
	lightning-fire-fungi-bark beetle: Schowalter 1985, Schowalter et al. 1981, Rykiel et al. 1988, Flamm et al. 1993
	agriculture-wind: Foster 1988
Central grasslands	fire-grazing: Collins 1987, Hobbs et al. 1991, Vinton et al. 1993
	prairie dog activity-grazing: Coppock et al. 1983
Western conifer forests	fire-fire: Kilgore and Taylor 1979, Agee and Huff 1987, Romme and Despain 1989, Covington and Moore 1994
	lightning-fire-fungi-bark beetle: Geiszler et al. 1980, Knight 1987, Paine and Baker 1993, Schowalter and Filip 1993, Hagle and Schmitz 1993
	fire-parasitic plants: Knight 1987
	fire-weather-large mammal mortality: Turner et al. 1994
	avalanche-fire-bark beetle: Veblen et al. 1994
	fire-grazing: Covington and Moore 1994
	logging-wind: Franklin and Forman 1987
	logging-fire: Franklin and Forman 1987
	logging-landslides: Swanson and Dyrness 1975
	logging-pathogens: Paine and Baker 1993, Hagle and Schmitz 1993
Western shrublands	fire-fire: Minnich 1983, Christensen 1985
	fire-debris slides: Biswell 1974

disturbance influences subsequent disturbances of a different type. For example, fires alter chaparral soils and increase likelihood of landslides on steep slopes. Feedbacks and interactions have been documented in many systems and occur at a range of scales (Table 3).

Individual-level feedbacks and interactions can occur whenever disturbances leave damaged survivors. Wounds caused by fire, lightning, or human activity predispose trees to fungal infection and insect attack. Fungal infection can increase the likelihood of other disturbances. For example, in the New Jersey pine barrens, trees with extensive fungal rot suffered higher rates of wind breakage than sound trees (Matlack et al. 1993). Fungal rot is most common in trees with basal fire scars. Vulnerability to scarring varies with tree age

at time of fire; young trees are particularly vulnerable. Thus, susceptibility of individual trees to wind damage may depend on date of recruitment relative to fire events several decades in the past.

Many other examples of individual level interactions and feedbacks are known. Bark beetles transmit pathogens between trees, and pathogens reduce trees' ability to resist beetles. In general, trees weakened by mechanical injury, disease, or herbivory have fewer resources for growth, maintenance, and defense and are more susceptible to subsequent disturbance. Damage to an individual is often cumulative; a single defoliation by gypsy moths rarely kills an oak, but repeated episodes cause high rates of mortality. Some plants respond to herbivory by increasing toxin levels or reducing nutritional quality of leaves. Such cases provide examples of negative feedback; one defoliation makes another defoliation less likely.

At the stand level, disturbances alter species composition, canopy structure, and fuel levels in ways which affect susceptibility to subsequent disturbances. For example, the distribution of hurricane damage in central New England is largely a function of the history of agricultural disturbance (Foster 1988). Stand susceptibility to wind varies with age and species composition; pine stands over 30 years old are particularly susceptible. The extensive damage caused by the 1938 hurricane can be explained largely by the abundance at that time of 30–100 year old white pine on abandoned agricultural fields.

Fire likelihood and intensity are subject to stand-level feedbacks. In systems in which fires consume most fine fuels, stand flammability is low shortly after a fire, increases in a developing stand, and levels off as the stand matures. The cycle may take 30–50 years in California chaparral or 200–400 years in higher elevation Rocky Mountain lodgepole pine forests. When a fire kills trees without consuming them, post-fire fuel levels and flammability may be high. In western hemlock–Douglas-fir forests in Washington, flammability is highest in the first 20 years after a fire, drops to a low level in ~100-year-old stands, and increases thereafter (Fig. 4) (Agee and Huff 1987). In ponderosa pine/bunchgrass woodlands in the Southwest, frequent surface fires maintain an open stand structure and grassy ground layer and prevent accumulation of woody debris. Surface fires burn grasses and pine needles, but the lack of larger fuels makes crown fires unlikely. Fire suppression results in increases in stand density and woody fuels and decreases in grass abundance. For example, since the onset on fire suppression, fuel loads in forests near Flagstaff, Arizona have increased by 20-fold, while grass and forb production has fallen by 90 percent (Covington and Moore 1994). As

grasses decline and woody fuels accumulate, the potential for low-intensity surface fires decreases and catastrophic crown fires become more likely. Fire suppression may produce even more dramatic effects in ponderosa pine communities in the inland Northwest; there, increases in the densities of fire-sensitive Douglas-fir, grand fir, and white fir have contributed to high-intensity fires and outbreaks of spruce budworms and pathogens (Anderson et al. 1987, Keane et al. 1990, Arno et al. 1995).

Disturbance feedbacks and interactions also include the interplay of landscape pattern and process as discussed below. Interactions may propagate individual and stand-level phenomena to larger areas. For example, a pine beetle infestation may spread from a lightning-damaged tree through a stand to other stands in the landscape (Rykiel et al. 1988).

Stand- and landscape-level feedbacks and interactions between insects, wildfire, and plant pathogens have become management issues on public lands. In stands dominated by susceptible species, insect and pathogen outbreaks may produce large quantities of dead woody fuel. But the effects of insects and pathogens on fire regimes are complex and incompletely understood. In some forests, fire risk actually decreases in the first few decades following a beetle outbreak (Knight 1987). Moderate levels of insect and pathogen activity may reduce the risk of catastrophic fire by thinning stands and preventing excessive fuel buildups; insects and pathogens may also promote forest health by gradually culling weakened trees (Schowalter and Filip 1993).

The stand- and landscape-level effects of fires on insects and pathogens are also complex. The presence of fire-damaged trees may allow bark beetles to persist

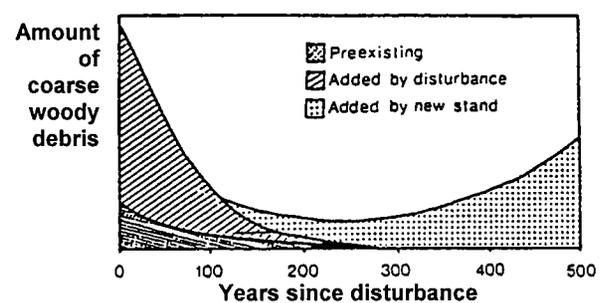


Fig. 4. A general model for changes in coarse woody debris after disturbance (from Agee and Huff 1987). Some coarse woody debris survives the disturbance ("Preexisting"). Some disturbances (including many fires) actually create woody debris through heavy tree mortality ("Added by disturbance"). Decomposition reduces these pools of debris, but succession gradually reestablishes pre-disturbance levels. During the thinning phase of forest succession, woody debris may surpass pre-disturbance levels, but larger size classes of logs would be absent.

at low levels until undamaged trees are made vulnerable by competition or drought (Schowalter 1985). But a regime of low-intensity surface fires may also maintain an open stand structure; with lower densities and more vigorously growing trees, open stands may be less susceptible to insect outbreaks. Hotter fires initiate patches of young trees which do not become vulnerable to bark beetles until they are several decades old (Schowalter 1985, Veblen et al. 1994). As components of a larger landscape, these non-susceptible patches may limit spread of insect outbreak.

Forest management activities also influence insects and pathogens. In parts of the southeastern and western United States, fire suppression and the conversion of natural forests to plantations have led to dense stands with low diversity and poor vigor which are susceptible to severe insect and pathogen outbreaks (Anderson et al. 1987, Schowalter and Filip 1993, Hagle and Schmitz 1993). Thinning treatments may reduce crowding and improve vigor but may also promote insect and disease spread by wounding trees and damaging roots (Paine and Baker 1993). Airborne spores of some root pathogens infect cut stumps; the pathogens may then spread to adjacent trees. The appropriate management response will vary with stand characteristics and the species of insects and pathogens involved. Hagle and Schmitz (1993) discussed options for managing insect-pathogen interactions.

Disturbance interactions play a role in water, nutrient, and sediment dynamics. In many forests, ecosystem function recovers rapidly after a single disturbance. Even though fires, windstorms, insect outbreaks, and even logging may damage or kill large numbers of organisms, biological legacies — the trees, shrubs, and herbs which survive — continue to transpire water, cycle nutrients, and stabilize soils. But if a second disturbance such as salvage logging, herbicide application, or mechanical site preparation compromises the system's ability to compensate, nutrient and sediment losses will increase. In some ecosystems, disturbance interactions lead to conservation of nutrients. In tallgrass prairie, grazing prevents nitrogen losses from the burning of plant biomass (Hobbs et al. 1991). Grazers reduce the amount of biomass available to be burned and return nitrogen to the soil as waste.

Disturbance interactions may also play a role in maintaining biological diversity. For example, in tallgrass prairie in Oklahoma (Collins 1987), fire and grazing create four patch types: undisturbed, grazed, burned, and both burned and grazed. These patch types differ in vegetation structure and species composition. Burning stimulates growth of many grass and forb species. But unless burning is followed by grazing, fast-growing grasses such as big bluestem crowd out

other species, and diversity declines. Cattle and bison prefer these grasses; grazing keeps the grasses in check and allows other species to persist. Thus, while burned, ungrazed patches are least diverse, burned, grazed patches are most. Fire and grazing act together to maintain variety of patch types in the landscape and high levels of diversity within patches.

Feedbacks and interactions are important but poorly documented aspects of disturbance regimes. Although these synergisms occur in many vegetation types, they have been explored in detail in only a few. In most systems, additional research on both mechanisms and long-term consequences is needed before management recommendations can be made. Managers should be aware of the potential for feedbacks and interactions; present activities may have unintended consequences decades in the future. Multiple, interacting disturbances may play an important role in maintaining vegetation structure, ecosystem health, and species diversity. Actions which simplify the disturbance regime may compromise biological integrity. The widespread occurrence of feedbacks and interactions suggests that disturbances should not be studied or managed as independent events. Rather, it argues for a historical, synthetic approach to ecosystem dynamics.

## 5 THE LANDSCAPE MOSAIC AND THE INFLUENCE OF PATTERN ON PROCESS

The early literature on patch dynamics emphasized the effects of processes on compositional and structural patterns. Over the past 20 years, ecologists and land managers have become increasingly interested in the effects that spatial patterns (particularly the size, shape, and arrangement of patches) exert on ecological processes. Among the processes influenced by landscape pattern are seed dispersal, exotic species invasions, and the propagation of fires and insect outbreaks. This recognition of the importance of spatial pattern, and the accompanying focus on phenomena occurring over large areas, have given rise to the discipline of landscape ecology (Turner 1989). The rapid development of landscape ecology has been facilitated by new technology, including geographic information systems (GIS) and high-resolution satellite images. The landscape perspective provides new insight into the dynamics of ecosystems and the impacts of management activities.

A landscape can be envisioned as a mosaic of patches which differ in history, environment, and species composition. A central paradigm in landscape ecology is that processes create landscape patterns, which, in turn, control subsequent processes. For

example, the practice of "checkerboard" cutting in the forests of the Pacific Northwest produces a pattern of small (10–15 ha) clearcuts dispersed across the landscape (Franklin and Forman 1987). Windthrow damage is concentrated along the edges of clearcut patches. Compared with a landscape with a few large patches, a landscape with many small patches has a greater length of edge per area of clearcut. Thus, dispersed cutting creates a pattern (many small patches with high total edge length) which promotes a disturbance process (windthrow along forest edges).

Natural disturbances create new patches, modifying the existing landscape pattern. Landslides in the Pacific Northwest tend to occur on unstable soils, forming wedge- or bullet-shaped scars. Growing pine beetle infestations in the coastal plain of the southeastern United States often form circular "spots" of dying trees. Wildfires in the Rockies may burn over several square kilometers, following prevailing winds, topography, and fuels. A single fire may create patches of several types, consuming some stands in intense crown fires, burning others with cooler surface fires, and leaving unburned islands within burned areas. The effects on landscape pattern will depend on disturbance type, intensity, size, shape, relationship to other patches, and position along environmental gradients. Human activities also shape landscape patterns. Logging, mining, agriculture, road building, and construction fragment existing patches and create new ones. Although natural disturbances usually produce irregular patterns, human activities often create geometric patches with straight boundaries.

Landscape patterns also change through succession. As a clearcut or burned stand matures, it becomes more similar to the surrounding undisturbed forest. Eventually, it may no longer appear as a distinct patch. Landscapes dominated by stand-destroying fires are made up of even-aged stands, each of which develops through a sequence of successional stages. The proportion of the landscape in each stage may change through time; during periods when little area burns, more of the landscape passes into older stages. Figure 5 shows fluctuations in the composition of a landscape in Yellowstone National Park over the past 250 years (Romme and Despain 1989).

Landscapes can be characterized by the number of patch types and the proportion of the total area in patches of each type. The spatial arrangement of patches may also be important. Is the landscape made up of many small patches, or a few large ones? How remote are patches of the same type from each other? What patch types occur together? Are patches compact or elongate in shape? Are their boundaries simple or complex? What are the dimensions of patch edges?

Increasingly, ecologists and resource managers are using geographic information systems (GIS) to address such questions. GIS allows a researcher to analyze a digital map and quantify aspects of landscape structure. Used properly, GIS provides a powerful tool for evaluating management alternatives. However, caution is required in interpreting results. Not all patch boundaries are equal in their ecological significance. For example, adjacent stands of pine and hardwood show far smaller contrasts in light, temperature, humidity and wind speed than either stand does with a clearcut, yet the GIS may show both kinds of boundaries with equal clarity. Landscape attributes will depend on the way in which the landscape is classified. If forest patches are classified simply as "hardwood" or "pine," a landscape may appear homogeneous, with large, continuous tracts of each type. Using a finer scheme which differentiates oak-hickory, beech, and young and mature pine forests, the same landscape will appear more complex. Different management questions warrant different levels of classification.

Both the nature of the pattern and the processes which create it will differ with scale. As one examines areas of increasing size, details are lost but broader patterns emerge. At the scale of a few hundred square meters, the spatial pattern of tree crowns in a southern Appalachian forest depends on the birth and death of individual trees. At the scale of many hectares, single trees are no longer visible; the pattern of stands reflects minor landforms and stand-level disturbance history. At the scale of tens of square kilometers, individual stands merge into larger land-cover units, and vegetation patterns follow broader physiographic gradients

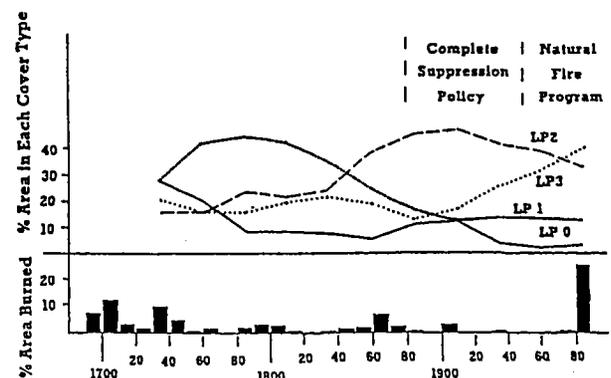


Fig. 5. Disturbance and succession on a 129,600 ha study area in Yellowstone National Park (Romme and Despain 1989). Changes in the percent of the study area in each of four successional types (top) and the percent of the study area burned each decade (bottom) over the past three centuries. LP0 are lodgepole pine stands less than 40 years old; LP1 are even-aged stands 40–150 years old; LP2 are even-aged stands 150–300 years old; and LP3 are mixed-age pine/fir/spruce stands.

and boundaries between public and private land. Many factors act simultaneously to shape the landscape; the scale of observation determines which appear most prominent. No one scale is best for all management applications; the scale used will depend on the questions asked and the resolution of the available data.

Dynamic processes can homogenize a landscape or make it more complex. For example, cattle in unburned tallgrass prairie create a mosaic of small grazed patches (Hobbs et al. 1991). Cattle prefer to graze on the young grass in these patches and thus maintain the initial pattern through time. Prairie fires erase the fine-scale pattern of grazed and ungrazed patches and produce a more uniform landscape. In other systems, the vagaries of fire or wind behavior may increase landscape heterogeneity. Successional processes may in some cases erase the patterns created by disturbance. In other cases, landscape heterogeneity will increase with succession as mature communities develop to reflect local site conditions (Werner and Platt 1976, Christensen and Peet 1984).

Rates of disturbance and succession vary along environmental gradients. These dynamic processes may create and maintain associations between vegetation patterns and features of the physical environment. For example, in southeastern Wyoming (Romme and Knight 1981), lower elevation spruce-fir forests are restricted to ravines and valley bottoms, while lodgepole pine forests dominate slopes and ridges. Lodgepole pine, an early-successional species, typically establishes after fire and forms even-aged stands. Given sufficient time, the later-successional spruce and fir can replace pine on both upland and lowland sites. However, upper slopes and ridges have shorter fire-return intervals and slower rates of succession. On these sites, fires destroy stands before spruce-fir forests can develop. The landscape pattern of pine forests on the uplands and spruce-fir in the valleys and ravines results from a dynamic tension between disturbance and succession.

How do landscape patterns shape processes? In some cases, the composition of an individual patch will be the major factor determining the changes that patch undergoes. In the North Carolina Piedmont, abandoned agricultural fields pass through a successional sequence from grasses and forbs to pines to mature oak-hickory forest. Successional state depends on time since abandonment; landscape changes are largely a function of the proportion of area in each age class. But, even in this case, the size, shape, and arrangement of patches can influence processes. For example, low rates of seed dispersal and poor seedling establishment lead to slower pine invasion on larger fields (Pinder et al. 1995).

In some cases, the dynamics of one patch may be dominated by its relationship with other patches. Some disturbances tend to originate at patch boundaries. In forests of the Pacific Northwest, windthrow may be most severe in forests adjacent to clearcuts (Franklin and Forman 1987), and a disproportionate number of landslides occur near roads (Swanson and Dyrness 1975). Human-caused fires often start near roads or campsites and spread into wildlands; when these patch types are juxtaposed, the likelihood of ignition increases. In the southeastern United States, some exotic species, including Japanese honeysuckle and kudzu, thrive along forest edges but do poorly in the shade of the forest interior. Activities such as dispersed-patch clearcutting and road construction, which fragment the landscape, magnify such edge effects.

In other cases, large, continuous patches of susceptible habitat may promote disturbance spread. The disturbance regime of California chaparral is characterized by stand-destroying fires. Stands accumulate woody fuels as they mature and reach extreme flammability at 30–50 years of age. Minnich (1983) compared fire size and frequency in southern California, where there are active fire control efforts, with nearby Baja California, where there are not. He found that while there were fewer fires in California, the total area burned in both regions is similar. The suppression of small fires appears to lead to large patches of highly flammable older chaparral and larger, more difficult to control fires.

The effects of fire suppression on fire size and intensity have become management issues in many western landscapes. In 1988, fires burned nearly 3,000 square kilometers in the Greater Yellowstone Area of Wyoming, Idaho, and Montana. To gain a historical perspective on the 1988 fires, Romme and Despain (1989) reconstructed fire history and past landscape composition for a portion of Yellowstone National Park (Fig. 5). They found that fires comparable to those in 1988 had occurred in the early 1700s. For the next 200 years, the landscape was dominated by relatively non-flammable early- and mid-successional forests. Although ignitions occurred every decade, the size of burned patches remained small. By the mid 20th century, most of the landscape had developed into highly flammable older forest. The 1988 fires occurred in unusually dry and windy weather, but also in a landscape which was particularly susceptible to fire spread. With or without fire suppression, large fires probably would have occurred in the Greater Yellowstone Area in the mid or late 20th century. The period of effective fire exclusion (mid 1940s–mid 1970s) was short relative to the ~300 year cycle of forest

development. Fire suppression may thus have delayed the burning of some areas and led to one year with particularly extensive fires, but in the long run probably had little effect on the total area burned.

Studies of lodgepole pine forests in the Yellowstone area (Romme 1982, Barrett 1994) suggest that in systems in which infrequent crown fires dominated the presettlement disturbance regime, recent fire suppression has not fundamentally altered landscape dynamics. Other systems, such as Douglas-fir woodlands in Yellowstone, sequoia-mixed conifer forests in California, and ponderosa pine woodlands throughout the West, were maintained historically by frequent low-intensity surface fires. Fire suppression in these systems has led to increases in stand density and fuel loads, creating the conditions for high intensity crown fires (Kilgore and Taylor 1979, Barrett 1994, Covington and Moore 1994, Arno et al. 1995).

Large, homogeneous tracts dominated by a single species may also facilitate insect outbreaks. Several hundred years ago, the coastal plain of the southeastern United States was a complex mosaic of hardwood forests, shrub bogs, and open pine savannas (Frost 1993). Over large areas, that mosaic has now been replaced by commercial pine plantations in which high densities of physiologically stressed trees create ideal conditions for the spread of the southern pine beetle. In the boreal zone of Alaska and Canada, where species-poor spruce-fir forests dominate the landscape, large outbreaks of spruce budworm are common.

Simple computer models suggest that the proportion of a landscape susceptible to a disturbance such as fire or insect outbreak influences the nature of disturbance propagation (Turner et al. 1989). Modeling landscapes with a random pattern, Turner et al. found that when less than about 60 percent of the landscape is made up of susceptible cells, susceptible patches are disjunct, and disturbance spread is limited by patch boundaries. In such a landscape, the amount of area disturbed is sensitive to the number of disturbance initiations (e.g., lightning strikes). When the proportion of susceptible cells exceeds 60 percent, susceptible areas coalesce into a few large patches. Because a single disturbance can then spread across much of the landscape, the number of initiations becomes less important. The extent to which susceptible patches are connected with each other appears to be a critical factor in disturbance spread. Real-world landscapes tend to have higher connectivity than random ones; thus, the threshold at which actual disturbances can spread over large areas is probably lower than 60 percent.

Both patches of non-susceptible vegetation and geomorphic features may act as barriers to disturbance spread. In the Boundary Waters Canoe Area in

Minnesota, large fires tend to burn from west to east, following prevailing winds; lakes, particularly large lakes with north-south orientation, interrupt the spread of fires (Heinselman 1973). Fire regimes on islands in boreal forest lakes differ from that of the surrounding mainland (Bergeron and Brisson 1990). On the mainland, a fire started from a single lightning strike can spread across large areas of forest. Islands, isolated from fire spread, burn far less frequently.

In subalpine forests in the Rocky Mountains, spruce beetle outbreaks, fires, and snow avalanches shape and are shaped by the pattern of susceptible patches and barriers to disturbance spread (Veblen et al. 1994). Spruce do not become susceptible to beetles until about 70 years of age. Thus, sites of severe fires and beetle outbreaks are unlikely to support subsequent infestations for several decades. Avalanche paths lack the mature spruce attacked by beetles. They also have little fuel accumulation and thus check fire spread.

Landscape pattern influences the dynamics of wildlife populations. Some species thrive along edges of disturbed patches, where a mix of habitats provides forage and cover. As a landscape becomes increasingly fragmented, these species increase. Others prefer the moist, shady conditions found in the interior of mature forest patches. In western coniferous forests, the spotted owl, varied thrush, and red-backed vole are among the species more common in interior habitats. For these species, the suitability of forest patches depends on their size. Because edge influences on microclimate may extend two to three tree heights into the forest, patches below a certain size are, in effect, all edge (Franklin 1989). Forest fragmentation brings increased contact with predators and parasites with which interior species have little evolutionary experience. For example, brown-headed cowbirds, brood parasites which lay their eggs in the nests of songbirds, are more active near forest edges than in the interior of large forest patches.

The density and placement of roads may affect wildlife. Roadkill is a major source of mortality for some species (Schoenwald-Cox and Buechner 1992). Roads also increase access for legal and illegal hunting and off-road vehicle use. The presence of roads may reduce the quality of otherwise suitable habitat. Grizzly bears in the northern Rockies avoid areas within 100 m of roads. Because the roads often run along streams in valley bottoms, they limit the bears' use of those productive areas (McLellan and Shackleton 1988).

Some conservation biologists have advocated wildlife corridors, strips of suitable or semisuitable habitat which connect larger patches. Corridors may allow species to recolonize areas from which they have disappeared and facilitate movement of animals that

require large areas or multiple kinds of patches. However, the value of corridors remains controversial (Mann and Plummer 1995). The extent to which most species will use them is unknown. High ratios of edge to interior may promote invasion by exotic species and bring wildlife into increased contact with humans and natural predators and parasites. Perhaps the best case for corridors can be made when they provide multiple benefits. For example, a strip of undisturbed vegetation along a stream will protect fish habitat and water quality whether or not it is used by terrestrial wildlife.

Studies of landscape-level phenomena have drawn attention to functional linkages across large areas. The size, shape, and spatial configuration of patches may influence the initiation and spread of disturbance and the abundance of wildlife species. Logging, road building, and fire control may have effects in areas far removed from the site of activity. When evaluating alternatives, managers need to consider implications for landscape-scale patterns and processes.

## 6 DISTURBANCE AND THE DYNAMIC EQUILIBRIUM

One of the most important questions for understanding and managing ecosystems is whether processes, such as disturbance and succession, are consistent with and can sustain observed patterns (the frequency of various compositional and structural states) (White 1987). Consequences for management are clear: if process and pattern are in equilibrium (we introduce several definitions of equilibrium below), structure, process, and composition will persist across many locally fluctuating patches. Shugart (1984) used simulation models to suggest that biomass would be in equilibrium across patches if patch size was 1/50th or less of landscape size, i.e., if 50 or more patches with independent dynamics comprised the simulated landscape (Fig. 6); see also below for the model of Turner et al. (1993) that incorporates both disturbance and recovery rate.

A steady state equilibrium exists most likely where patch size is small relative to landscape size, where recovery time is much less than average recurrence interval, and where disturbance regimes are stable (White and Pickett 1985). If the probability of disturbance increases with patch age, and these other conditions are met, a steady state equilibrium is also more likely. An exception to this statement may be contagious disturbances such as fire and insect outbreak. In a landscape with a high proportion of susceptible patches, such disturbances may spread over large areas. A large disturbance will create a cohort of

patches which will increase in susceptibility as they mature. The result may be long periods during which little disturbance activity occurs punctuated by shorter periods of widespread disturbance.

Whether or not landscapes and regions ever had equilibrium disturbance regimes, human management has drastically changed the scale of many ecosystems. The natural or original patch size of disturbance may exceed the scale of the remnant natural area. The result may be the complete disturbance of the area in a single disturbance event. If there are no refuges for species vulnerable to disturbance, disturbance will cause an immediate loss of diversity even though it is essential to the persistence of other biota (Pickett and Thompson 1978, Baker 1992a,b).

Ideas of stability, constancy, and steady-state are deeply ingrained in our concepts of nature (Botkin 1990), and we have a tendency to expect equilibrium within the wildlands that we manage. However, ecological research during the last two decades has shown that equilibrium is not a simple concept; in many situations we cannot unambiguously determine that an ecological system is or is not in an equilibrium state (DeAngelis and Waterhouse 1987). There are at least three reasons for this uncertainty: (i) multiple definitions of equilibrium, (ii) multiple parameters for measuring equilibrium, and (iii) effects of spatial and temporal scale. Nevertheless, the idea of equilibrium is useful in characterizing and understanding the long-term dynamics of these landscapes. In the next section we review the various ways in which the concept of equilibrium can be fruitfully applied.

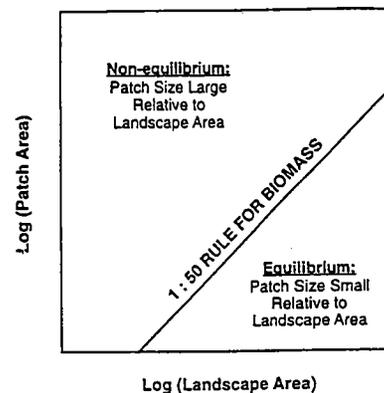


Fig. 6. Shugart's (1984) depiction of the effects of patch size and total landscape area on the nature of dynamic equilibrium in ecosystems. In his simulation models, patch sizes which were less than one-fiftieth of landscape area produced an overall equilibrium of biomass values at the landscape scale because the independent dynamics of individual patches produced a stable average.

## 6.1 Equilibrium, Change, and Scale

Scale refers to the spatial or temporal dimensions of an observation. The components of scale include grain, which is the level of resolution or smallest entity that can be recognized within a data set, and extent, which is the size of the study area or the time frame being considered (see Caraher et al. and Haufler et al., this volume; Allen and Starr 1982; O'Neill et al. 1986; Turner et al. 1989, 1993).

Some controversies over equilibrium versus non-equilibrium characteristics can be resolved simply by specifying the relevant spatial and temporal scales and ecological parameters. Consider a 100 m<sup>2</sup> plot within the deciduous forest of Great Smoky Mountains National Park. Such a plot is about the median size of treefall gaps in this ecosystem, and treefalls are likely to occur about every 100 years (Runkle 1982). If we monitored above-ground living biomass, biomass of large dead boles, or canopy cover for 200 years, we would conclude that this plot was a non-equilibrium system, because all of these parameters would change abruptly when a treefall occurred and continuously as smaller trees grew into the gap during the next 100 years. However, our perceptions change when we view this situation from a different scale. Treefall gaps affect about 1 percent of entire park annually (Runkle 1982). Living biomass, coarse woody debris, and canopy cover, averaged over the larger area, remain nearly constant even though dramatic changes are occurring within the smaller units; thus, the larger system appears to be in equilibrium. If we reduce the temporal scale within the original 75 m<sup>2</sup> plot to a single decade and if a tree-fall does not happen to occur during this short time period, the system may appear to be in equilibrium during the time of observation. Finally, consider another parameter of the system, richness of vascular plants on the forest floor, which may remain essentially constant at all of the scales of time and space described above, or may vary in response to other factors. The first step in any assessment of equilibrium/nonequilibrium dynamics is to specify the spatial and temporal scales of analysis and the parameters of the system that are being considered.

The equilibrium concept probably is most useful at intermediate scales. We would not expect to find equilibrium at the scale of a few plants, nor would this kind of equilibrium provide much insight for managers responsible for areas of hectares or square kilometers. Yet if we expand the spatial scale too far, we begin to encompass regions having fundamentally different climate and soil properties, in which different disturbance regimes and ecological dynamics prevail. Clearly, the equilibrium concept is not particularly meaningful

at a scale that crosses biomes. Generally, a landscape scale, i.e., a spatial extent of tens to hundreds of kilometers, is most useful for consideration of equilibrium disturbance regimes (Risser 1987, Forman 1990). Similarly, equilibrium is not very meaningful to most managers within time frames shorter than several decades, and if we try to deal with many thousand of years, we encounter profound changes in climate and soils related to glacial cycles and long-term geologic processes. Thus, the appropriate temporal scale for assessing equilibrium generally is in the range of decades to centuries, though it may be appropriate to use millennia in very long lived trees (Stephenson 1996).

## 6.2 Concepts of Equilibrium

Various definitions of equilibrium have been used to assess ecological systems. Let us first dispense with two concepts that are not particularly useful to wildland managers. One of these is the idea of equilibrium as complete absence of change; clearly this notion is not applicable to ecosystems. The other is the idea that a system is in equilibrium only when it returns to its original set point after being disturbed. This definition assumes that stasis is the norm and that disturbance necessarily moves the system into an "unnatural" or otherwise inappropriate state. Moving beyond these overly simplistic concepts, however, we can identify four general classes of definitions of equilibrium that provide useful insights into the workings of ecological systems:

(1) *Persistence or qualitative equilibrium* — A system may be regarded as in equilibrium if none of its characteristic elements becomes extinct during a specified period of time (DeAngelis and Waterhouse 1987, DeAngelis and White 1994). These elements might be species, successional stages, surface water, or any other ecological parameter of interest. This is the least rigorous of the four concepts of equilibrium discussed here, but it is useful nonetheless: at a bare minimum, an equilibrium system must not lose any of its components, and a system that does lose components is clearly not in equilibrium, at least with respect to those components. This definition allows much local fluctuation in abundance, as long as elements persist.

(2) *Shifting mosaic, steady-state, or quantitative equilibrium* — A system may be regarded as in equilibrium if the abundance of specific elements or the rates of specific processes remain more or less constant throughout a specified time period. Some temporal variation is allowed, but it must be small, and the levels of the parameters of interest must remain close to some average value. For example, Bormann and Likens (1979) suggested that total biomass in watersheds or

landscapes dominated by northern hardwoods forests varied only slightly during the period before European settlement, despite large fluctuations within smaller units of the landscape. Bormann and Likens described this situation as a shifting mosaic steady-state. Similar equilibria, defined as constancy of biomass or of proportions of the landscape occupied by each successional stage, have been suggested for wave-regenerated fir forests in New England and elsewhere (Sprugel 1976), for riparian woodlands disturbed by recurrent floods (Everitt 1968; cited in Baker 1989a), and for fire-regenerated boreal forests in northern Sweden (Zachrisson 1977) and Isle Royale in Lake Superior (Cooper 1913).

This type of equilibrium is strongly dependent on the spatial and temporal characteristics of the disturbance regime. Based on simulation studies, Shugart (1984) suggested that a quasi-steady-state landscape was likely only in situations where the total extent of the landscape was at least fifty times the average size of a disturbance event. Zedler and Goff (1973), Connell and Sousa (1983), and DeAngelis and Waterhouse (1987) also suggested that stable mosaics of successional stages are more likely to occur when the landscape is large relative to the size of disturbed patches.

Shifting mosaic steady-state systems may be fairly rare because large, infrequent disturbances are a feature of many ecosystems. Baker (1989a) did not detect equilibrium in the mosaic of successional stages in the Boundary Waters Canoe Area in northern Minnesota even at a spatial scale 87 times as large as the average disturbance-patch. The relative proportions of post-fire successional stages in subalpine forests of Yellowstone National Park have not exhibited constancy during the last 250 years at any spatial scale up to 130,000 ha because of the persistent effects of infrequent large fires (Fig. 5) (Romme 1982, Romme and Despain 1989).

(3) *Stable trajectory or stationary-dynamic equilibrium* — Loucks (1970) suggested that although individual communities at particular locations are continually changing through time as a result of disturbance, the long-term process of disturbance and recovery constitutes a stable system because the same successional sequence occurs after each disturbance event. The system never reaches any final, undisturbed state, but it does return along the same trajectory of change, i.e., the same dynamics occur after each disturbance (O'Neill et al. 1986).

(4) *Statistical equilibrium* — A system or subsystem can be regarded as in equilibrium if the distribution of individual disturbance events does not deviate significantly from the expected statistical distribution, and if a normal successional sequence follows each

disturbance. If disturbance intervals, intensities, sizes or responses fall outside the expected distribution, then the system may be out of equilibrium or it may have shifted to a new equilibrium. Probability density functions of disturbance intervals and disturbance sizes in fire-dominated systems have been described quantitatively using the Weibull model (Johnson and Van Wagner 1985, Baker 1989b, Johnson and Gutsell 1994).

The statistical distribution of disturbance intervals is sensitive to the spatial and temporal scales at which the disturbance regime is described. For example, the Weibull model assumes that the largest individual disturbances are much smaller than the total extent of the study area (Johnson and Van Wagner 1985); where this assumption is not true, the Weibull distribution may be an inappropriate model for landscape dynamics (Baker 1989b). Statistical distributions of disturbance intervals also may be complicated by the presence of subregions, having somewhat different disturbance regimes, that lie within the larger landscape unit being analyzed. Subtle spatial heterogeneity in disturbance regimes may not be apparent until it is teased out by means of cluster analysis or some other analytical method (Baker 1989b).

### 6.3 Management Implications of Equilibrium/Nonequilibrium Disturbance Regimes

Given the complexity of the equilibrium concept as applied to ecological systems, few managers will be able to determine unambiguously whether their particular parcel of land is an equilibrium or nonequilibrium system. Fortunately, it probably is not necessary to categorize specific areas as equilibrium or nonequilibrium with respect to every ecological parameter. However, it is important for managers to explicitly recognize the spatial and temporal dynamics of disturbance regimes and to be aware of the scale of the landscape processes that characterize their systems.

For example, it is helpful to understand that most crown-fire ecosystems are not in quantitative equilibrium, although such landscapes may meet the criteria for qualitative or stable-trajectory equilibrium (Baker 1989b, 1992b; Turner and Romme 1994). The proportion of successional stages in Yellowstone National Park was drastically altered in 1988. Prior to the fires, the landscape was dominated by middle and late successional stages, and early successional habitat was rare. The fires transformed nearly 30 percent of the landscape to early successional stages and reduced middle and late stages correspondingly. A change of this magnitude would be regarded as a catastrophe if

the expectation was for a quantitative equilibrium. However, the characteristic spatial and temporal scales of Yellowstone's disturbance regime indicate that fires like those in 1988 are infrequent but expected events in this kind of ecosystem. Although proportions of successional stages were altered by the 1988 fires, no landscape elements were eliminated entirely, and historical landscape reconstructions indicate that qualitatively similar disturbances and recovery have occurred in the past (Romme and Despain 1989). From a historical perspective, the 1988 fires were not a unprecedented catastrophe but a normal feature of the area's disturbance regime.

We need a practical method by which managers can assess whether the landscapes for which they are

responsible are characterized by equilibrium vs. non-equilibrium or stable vs. unstable dynamics. Turner et al. (1993) have developed a model that can help to answer this question. A state-space diagram (Fig. 7) depicts qualitatively different kinds of landscape dynamics in relation to spatial and temporal scales of disturbance. The ecological parameter upon which this model is based is the relative proportion of the landscape occupied by each successional stage. If we have reasonably reliable empirical data with which to characterize the disturbance regime of a particular landscape, then we can locate that system within the state-space shown in Fig. 7.

The horizontal axis (S) represents the spatial scale, i.e., the ratio of disturbance extent to landscape extent.

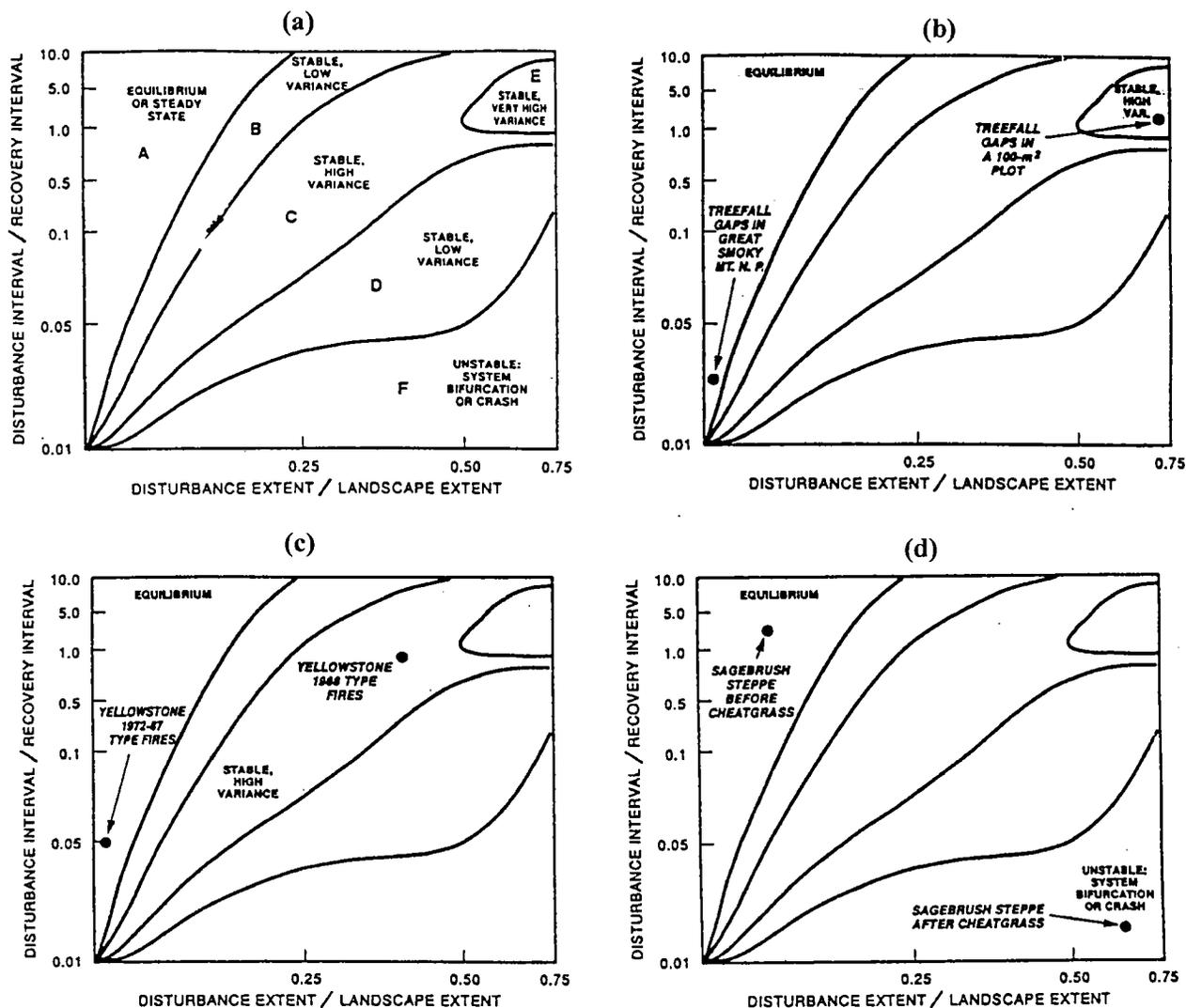


Fig. 7. State-space diagram of qualitatively distinctive types of landscapes in relation to spatial and temporal scales of disturbance (adapted from Turner et al. 1993). (a) The regions of six different kinds of landscape dynamics (see text). (b) Effects of scale on landscape dynamics of mesic forests in Great Smoky Mountains National Park (adapted from Runkle 1982). (c) Two types of disturbance regimes in Yellowstone National Park (adapted from Romme and Despain 1989). (d) Effects of introduction of exotic cheatgrass in sagebrush-steppe landscapes of western North America (adapted from Whisenant 1990). See text for further explanation.

Disturbance extent refers to the mean, median, or some other measure of the size of individual disturbances (for some landscapes the maximum likely disturbance extent might be most appropriate here). There are two qualitatively different regions along this axis: regions where disturbances are small relative to the size of the landscape (i.e., low ratios) and regions where disturbances are large relative to the landscape (i.e., high ratios).

The vertical axis (T) represents the temporal scale, i.e., the ratio of disturbance interval to recovery interval. Disturbance interval might be expressed as the mean, median, or some other measure of the time between successive disturbance events (the expected interval between large disturbances might be most appropriate for some systems). Recovery interval refers to the time required for succession to reach some late or "climax" stage of development if there were no further disturbance. There are three qualitatively different regions along the vertical axis: regions where the interval between successive disturbances is longer than the time required for recovery ( $T > 1$ ); regions where disturbance and recovery intervals are equal ( $T = 1$ ); and regions where the disturbance interval is shorter than the time required for recovery ( $T < 1$ ).

The region in the upper left-hand corner (A) is characterized by disturbances that are small, relative to the total extent of the landscape, and that occur at intervals longer than the time required for recovery. This is the region in which we find systems traditionally regarded as equilibrium or steady-state (e.g., the northern hardwood forest or the Great Smoky Mountains landscape). To the right of the equilibrium zone is a region where disturbances are a little too large and too frequent to allow a true equilibrium state as defined by the constancy concept described above, but where the variation in proportion of successional stages over time is relatively low (region B). This is a stable landscape state, where all elements persist, but where there is a small amount of fluctuation over time. The landscape in region B is dominated by late successional stages. Region C extends through the center of the Fig. 7, and is a state in which the landscape is stable, in the sense that all elements persist, but in which relative proportions of landscape elements fluctuate strongly over time as a result of relatively infrequent but large disturbance events. Many crown-fire ecosystems fall into this kind of landscape (e.g., the Boundary Waters Canoe Area and Yellowstone National Park). Below and to the right of region C is an area where variance is again low, and all elements persist, but this kind of landscape (region D) is dominated by early successional stages because disturbances tend to be both large and frequent. In the

upper right-hand corner (region E) is a landscape characterized by very great fluctuation in landscape structure, resulting from very large disturbance events (affecting  $> 50\%$  of the landscape). Nevertheless, this kind of landscape does not lose any of its elements because these large disturbances occur only at very long intervals. Finally, we see the region where disturbances are both large and frequent (region F).

<sup>4</sup> This is an unstable kind of landscape, susceptible to irretrievable loss of one or more of its elements (e.g., late successional stages). Such a landscape is likely to "crash" or "bifurcate," i.e., to shift to a qualitatively different ecological state or developmental trajectory. We do not see many systems in region F because they do not persist for very long. However, it is useful to recognize that alterations of the spatial and temporal dimensions of a disturbance regime can cause profound and probably irreversible changes in the structure and dynamics of an ecosystem. For example, chronic air pollution in Copper Basin, Tennessee, transformed a deciduous forest landscape into a sparsely vegetated landscape that has not recovered even after the pollution sources were eliminated (Turner et al. 1993).

Long lasting effects of infrequent, large disturbances may overshadow the effects of more frequent small disturbances (Turner and Romme 1994). A possible reason why Baker (1989a) found no evidence of a steady-state patch mosaic in the Boundary Waters Canoe Area, despite a study area 87 times the size of an average fire-created patch, was because the largest fire in the 141-year period of study burned nearly  $1/5$  of the 400,000 ha study area. In the Yellowstone landscape before 1988, the most abundant elements were middle and late successional stages that had developed following extensive fires around 1700 A.D. (Romme and Despain 1989). Even though smaller fires occurred in every decade thereafter, the imprint of those early large fires was still evident. The fires of 1988 created a new landscape pattern that will persist until the next extensive fire event. Romme (1982) simulated landscape changes in Yellowstone during the last 200 years under three scenarios: (i) actual fire history (documented from fire scars and current stand ages), (ii) all fires excluded, and (iii) large fires excluded but small fires allowed to occur. Interestingly, the landscape patterns generated in the second and third scenarios were almost indistinguishable, and both were strikingly different from the patterns produced by the actual fire history. Based on these considerations, the location of a landscape in the state-space diagram of Fig. 7 probably should be based on the size of the largest disturbance events rather than on mean, median, or modal disturbance patch sizes. The Weibull distribu-

tion can be used to estimate the occurrence of very large or infrequent disturbance events.

Landscapes having disturbance regimes that place them in the upper right-hand portion of the state-space diagram shown in Fig. 7 pose special challenges to managers. These are systems that require large land areas to retain all of their ecological elements because the spatial scale of disturbances is so great. In a very small management unit having this kind of disturbance regime, a single large disturbance could affect the entire landscape and eliminate all but the earliest successional stages. The result would be complete loss of the species and ecological processes that characterize later successional stages. Even in a very large management unit, we cannot be 100 percent certain that a single disturbance event will not affect all or most of the area. Large wilderness areas and national parks in western North America contain some of the most extensive remaining tracts of old-growth forest, but many of these protected areas are crown-fire ecosystems in which a single fire event could eliminate most of the old forests. In such systems, it is important to maintain or restore mature forests in surrounding multiple use lands as well as in designated nature reserves. In contrast, even a small tract of land may support equilibrium conditions if it has a disturbance regime that places it in the upper left-hand corner of the state-space diagram.

Managers should seek to avoid situations in which a system is shifted into a region of the state-space diagram dramatically different from its natural or historical norm. This may be difficult in the world of the early 21st Century, given the variety and magnitude of stresses being imposed on our wildland ecosystems. For example, consider the semi-arid sagebrush steppes, which cover thousands of square kilometers in the Great Basin of western North America (West 1988). Prior to the late 1800s, this region was characterized by infrequent, small fires, placing it in the upper left-hand corner of the state-space diagram (Fig. 7). Fires, whether ignited by lightning or by humans, rarely spread over large areas because the scattered shrubs and bunchgrasses, separated by patches of bare ground, formed a discontinuous fuel bed (Whisenant 1990). In the early 1900s this region was invaded by the Eurasian cheatgrass, which spread with alarming speed through plant communities already stressed by heavy livestock grazing (Leopold 1966, Mack 1981, Billings 1990). A winter annual, cheatgrass grows quickly in the early spring then dies and becomes dry by early summer, creating a highly flammable, continuous fuel bed. Cheatgrass is not injured by fire; on the contrary, fire creates an ideal seedbed for cheatgrass germination. Since its arrival, fires have become more

frequent and have begun to burn over thousands of hectares. Changes in the spatial and temporal parameters of the fire regime have moved the system into the lower right-hand corner of the state-space diagram (Fig. 7). Neither native shrubs nor bunchgrasses can withstand such frequent burning; they have disappeared over large areas and been replaced by cheatgrass and a few other fire-tolerant species (Whisenant 1990). The original sagebrush-steppe system has "crashed" following the change in disturbance regime, and the original post-fire succession has been replaced by a new trajectory dominated by cheatgrass.

In addition to the stresses posed by biological invasion and legacies of unsustainable land-use practices in the past, managers of the 21st century will have to contend with the impact of elevated atmospheric CO<sub>2</sub>, altered global nitrogen dynamics, and possible climate change (Vitousek 1994). It is therefore important not only to document past disturbance regimes in wildland ecosystems, but also to monitor current and future disturbance regimes in order to detect changes in intensity, kind, frequency, or size of disturbance — changes that could push a system into an unstable region of the state-space diagram. Even if future changes in disturbance regimes do not cause systems to crash, they may cause quantitative or qualitative changes in landscape dynamics (Baker 1995). For example, warmer and drier conditions will likely be associated with more frequent fires (Romme and Turner 1991), which could shift the Yellowstone landscape from a stable system with high variability in proportions of successional stages (region C in the state-space diagram) to a stable system with low variability dominated by early successional stages (region D). Such a change would have obvious implications for long-term persistence of species associated with old forests, such as pine marten and goshawk (Romme and Turner 1991). Flannigan and Van Wagner (1991) coupled global predictions for precipitation and temperature under conditions of doubled atmospheric CO<sub>2</sub> with the Canadian Forest Fire Weather Index System, which provides an index of fire intensity. Their results suggest that a doubling of atmospheric CO<sub>2</sub> could lead to a 40 percent increase in the annual area burned in Canada.

Spatial and temporal parameters of disturbance regimes have important implications for the existence and nature of equilibrium. Steady-state equilibrium is most likely to occur where disturbances are infrequent and small relative to recovery time and the total extent of the landscape. Where disturbances tend to be frequent or large, other kinds of landscape dynamics will occur. Although these landscapes are not in quantitative equilibrium, they may nonetheless exhibit quali-

tative and stable-trajectory equilibrium. An increase in disturbance size or frequently resulting from biological invasion, global climatic and atmospheric changes, or unsustainable land use practices may cause a qualitative shift in landscape structure and dynamics. Whether a particular land unit is in equilibrium or not, managers need to document past disturbance regimes and monitor potential future changes in the scale, intensity, and kinds of disturbances that shape the structure and dynamics of the landscape.

## 7 ECOSYSTEM RESPONSES TO DISTURBANCE

By definition, disturbances alter the physical environment or the availability of resources or space. Levels of available light, moisture, and nutrients often increase as a result of reduced uptake and enhanced decomposition (Vitousek 1984). For example, treefall in most temperate and tropical forests increases understory light levels (Canham et al. 1990), and fires in tallgrass prairie release phosphorus sequestered in dead biomass (Knapp and Seastedt 1986). Disturbances may also make available a range of substrates such as logs, tip-up mounds, and mineral soil. Conversely, the physical effects of disturbance may reduce resource availability. Overall moisture availability may decrease in large forest gaps as increased wind speeds and temperatures offset reduced water uptake by vegetation. Disturbances that remove soil, leaf litter, or coarse woody debris reduce the availability of these resources to species which require them (Hansen et al. 1991). In addition to altering absolute levels, disturbances may change the distribution of resources and increase or decrease spatial heterogeneity (see section on pattern and process above).

Response to disturbance involves several mechanisms. In forests, these include expansion of crowns of surviving canopy trees, release of suppressed individuals in the understory (advance regeneration), sprouting from roots and stumps of damaged individuals, establishment of new seedlings, and suppression of trees by vigorously growing shrubs, herbs, and vines (Woods and Shanks 1959, Runkle 1985, Everham and Brokaw 1996). Which of these mechanisms dominates depends on the characteristics of the disturbance (particularly size, specificity and severity) and the structure and composition of the community. For example, small gaps in eastern deciduous forests are typically filled by crown expansion and advance regeneration (Runkle 1985). Because light levels are fairly low and gap closure is rapid, new seedlings have little chance of reaching the canopy. In larger, more

persistent gaps, new seedlings of fast-growing, shade-intolerant species such as tulip-poplar can compete for space in the canopy. A dense understory of shrubs such as rhododendron and mountain laurel may inhibit tree regeneration (Clinton et al. 1994) and slow gap closure.

Longer term changes following large disturbances have been described using a four-phase model (Oliver 1980, Peet and Christensen 1987). The establishment phase, which immediately follows disturbance, is characterized by open conditions and the germination and rapid growth of herbs, shrubs, and tree seedlings. Resource availability often exceeds uptake; the result may be a pulse of nutrient runoff in ground water. During the establishment phase, competition is reduced, and fine-scale species diversity is often high.

As seedlings grow up to form a closed canopy, the stand enters the thinning phase. Biomass continues to accumulate, but growth of the more vigorous trees is offset by death of weaker competitors. Most of the trees which die have been overtopped by stronger competitors and thus do not create gaps in the canopy. The few small gaps which form are filled rapidly by expansion of adjacent trees. Competition for light and nutrients is intense, and nutrient runoff drops to very low levels. The initial, even-aged canopy is typically dominated by fast-growing, shade-intolerant species. After the canopy closes, opportunities for new establishment are limited, and only species tolerant of low resource levels persist in the understory. As a result, fine-scale species richness is often low. Living biomass typically peaks toward the end of the thinning stage.

After several decades, canopy trees become large enough to form gaps which cannot be filled by lateral expansion, and the stand enters the transition phase. At this point, death of canopy trees creates patches of resource availability which promote seedling and sapling growth. As the initial even-aged canopy breaks up, the stand begins to develop a multi-age size structure. Although individual trees continue to increase in size, total biomass may decline. Gap formation increases structural diversity, and reduced competition in gaps may lead to an increase in fine-scale species diversity.

In the final, steady-state phase, the breakup of the initial even-aged canopy is complete, and the stand has developed an all-aged, all-sized structure. Barring subsequent large disturbance, formation of small gaps will be balanced by germination and growth. At a scale many times that of individual gaps, structure, composition, and biomass will be in rough equilibrium. The model also suggests that nutrient runoff during this phase will be balanced by inputs from atmospheric and geologic sources. Although it is often assumed that biomass and productivity in this phase will converge on pre-disturbance values, other relationships are pos-

sible (Reiners 1983). For example, erosion or nutrient losses immediately following a disturbance may lead to long-term reductions in productivity.

The four-phase model, originally developed to explain secondary succession in eastern forests following clearcutting or agricultural abandonment, applies with minor modifications to secondary forest succession following other large, severe disturbances such as crownfires in Rocky Mountain forests (Peet 1992). The model suggests that stands of different ages will differ fundamentally in structure, dynamics, and diversity; thus, observed effects of disturbance will vary with successional age. In addition, the model provides insights into mechanisms by which disturbances alter community composition. For example, Meier et al. (1995) suggest that reduced densities of some vernal herb species in logged southern Appalachian forests relative to unlogged sites may reflect mortality incurred during logging itself, inability of these species to tolerate the open, high-light environment of the establishment phase, or intense competition, low resource levels, and lack of gaps during the thinning phase.

The four-phase model can be generalized to explain forest response to disturbances of low and medium severity. Disturbances which remove light-demanding canopy trees but leave shade-tolerant advance regeneration more or less intact move can stands toward steady-state composition; examples of such "accelerated succession" include logging in oak forests (Abrams and Nowacki 1992), beetle outbreaks in southern Appalachian pine stands (Kuykendall 1978), and hurricane damage on old agricultural fields in New England (Foster 1988). Systems in which frequent, low-intensity disturbances such as surface fires maintain open conditions and create opportunities for regeneration of light-demanding species may never leave the establishment phase. In such systems (e.g., longleaf pine savannas), fine-scale species diversity is often very high (Walker and Peet 1983, Peet et al. 1983).

Understanding the role of disturbance in maintaining biological diversity requires knowledge of the characteristics of individual species. Species differ in dispersal ability, mode of reproduction, and ability to survive, grow, and reproduce under various conditions. Most ecosystems contain species which require the open conditions and resources made available by disturbance. Some, such as fireweed, flourish briefly following disturbance and disappear as succession proceeds (Agee 1993). Others, such as tulip-poplars and giant sequoias, require disturbance for initial establishment but persist for centuries. In ecosystems throughout the United States, the suppression of natural fires and floods has led to declines of open, early successional habitats and the species that require them (see Eng-

strom, this volume, Sections 9.01-9.09). Most systems also contain species that can establish and survive under both early and late-successional conditions. Although the abundance of such species may change through successional time, they occur on both recently disturbed and undisturbed sites. The existence of species which require late-successional habitats is less well documented. The best examples come from the Pacific Northwest, where concern over the loss of mature forests has prompted extensive study (Hansen et al. 1991).

Determining species' successional requirements is not always straightforward. Some species which require disturbance for establishment or survival over much of their ecological range may be able to persist on extreme sites in the absence of disturbance (Barden 1988). Some species require microenvironments or structures such as large snags rather than particular successional states (Hansen et al. 1991); even though such species may thrive in both mature stands and stands recently disturbed by natural fire or windthrow, they may disappear from clearcut stands which lack those structures. And populations of some species which occur in both early and late successional managed stands may gradually decline if logging rotations are too short to allow recovery to pre-disturbance levels.

The relationship between species diversity and the frequency and intensity of disturbance is the subject of the intermediate disturbance hypothesis ("IDH", below; Connell 1978), which suggests that diversity peaks at some intermediate frequency and intensity of disturbance. Huston (1979) made a similar prediction, proposing that diversity is highest at intermediate disturbance frequencies and population growth rates. Intermediate levels of disturbance create opportunities for species which require early-successional conditions without eliminating disturbance-sensitive species. Thus, the IDH should be true in a qualitative sense, at least in systems which contain both groups of species. However, in systems with no history of a particular disturbance, all species might be sensitive, and in systems with a very high frequency of disturbance, there might be no species which require late-successional conditions. Even in systems in which the IDH applies, the model lacks much predictive value. Does diversity show a distinct peak or a broad plateau with increasing frequency or intensity of disturbance? And at what levels is diversity maximized? For most systems, the answers to these questions are not known. The hypothesis that diversity is highest at the disturbance levels which characterized the system over its ecological and evolutionary history has received some anecdotal support (Peet et al. 1983).

The effects of disturbance on species diversity also vary with scale (Palmer and White 1994, White and

Harrod 1997) and with simple changes in stem density (Busing and White 1997). The number of species in a single square meter is often much higher in a recent clearcut than in an intact forest. But if all the species that establish in the clearcut were already present in the watershed before clearcutting, the total number of species in the watershed remains unchanged. And if clearcutting in the watershed leads to loss of mature forest species, increases in the number of species at fine scales will be accompanied by a decline in species numbers at coarser scales. For these reasons, statements on the relationship between disturbance and diversity need to specify the scale of observation.

## 8 MANAGING DISTURBANCE: EMERGING ISSUES

Because species show a wide range of responses to disturbance, and because historical composition and structure are themselves products of past disturbance, changes in disturbance regimes often threaten biological diversity and ecosystem function. The two natural disturbances most manipulated by people are fire and hydrology. In North America, fire frequency has been greatly reduced in the 20th century (Kilgore and Taylor 1979, Covington and Moore 1994). Channelization, damming, and draining have affected many river systems. Reintroducing fire and hydrologic fluctuation are key to the restoration of many ecosystems (Baker 1994, Dahm et al. 1995). Where suppression has led to major changes, it will often be necessary to modify ecosystem structure (e.g., thinning treatments or fuel reduction burns) before reintroducing natural processes. Restoration of natural structure and dynamics may occur only gradually over the course of several disturbance cycles.

To what extent do management activities mimic natural events? Human-caused disturbances resemble natural disturbances in some ways, but differ in others. Clearcutting might resemble windthrow in patch size and return interval, but differ in its effects on woody debris, soils, and salamander populations. Prescribed fire might mimic the seasonality and average intensity of natural fires, but differ in the patchiness of effects. Meaningful comparisons require accurate, detailed information on both natural and human-caused disturbances. They also require us to specify which aspects of the disturbances are being compared.

Human-introduced disturbances, including logging and grazing, may also threaten species and ecosystems. The study of natural disturbances suggests ways to modify management activities to balance commodity production with ecosystem health and diversity. The

restoration of ponderosa pine forests in western Montana provides one example of the application of disturbance ecology in ecosystem management (Arno et al. 1995). There, managers are using prescribed fire and thinning treatments (including commercially-oriented harvests) to restore open stand structure, enhance canopy and understory vigor, and reduce wild-fire and insect hazards. Disturbance ecology also forms a foundation for "New Forestry" in Douglas-fir forests of the Pacific Northwest (Franklin 1989, Swanson and Franklin 1992). To mimic the effects of natural disturbances more closely, managers have modified clearcutting practices to retain more coarse woody debris and standing live trees. Managers are also modifying the traditional pattern of dispersed 10–15-ha cutting units to reduce fragmentation of mature forest tracts and create patches of variable size. In both regions, management actions have been informed by historical, observational, and simulation studies and are treated as ongoing experiments subject to monitoring and evaluation.

Application of disturbance ecology to management of ecosystems is complicated by several factors. In the next sections we summarize five major challenges: the relation of disturbance regime to climate variability and climate change, the influence of Native Americans, habitat fragmentation and the human imposition of new scales on ecosystems, exotic species invasions, and documenting and understanding the role of ecological variation.

### 8.1 Climate Variability, Regional Scales, and Disturbance Regimes

Documenting the connection between climate and disturbance will improve our ability to predict ecosystem dynamics and assess the potential impact of climate change. Natural climatic fluctuations occurring at time scales of decades may have broad impacts on terrestrial ecosystems; examples of such events include multiyear droughts in the 1930s in the Great Plains and the 1950s in the North American subtropics (Betancourt et al. 1993). These events may affect disturbance and recovery rates and suppress or amplify human impacts on terrestrial ecosystems. For example, range conditions in much of the American Southwest have improved over the last 20 years. Does this improvement reflect better management or simply rebounding precipitation levels following the 1950s drought? And to what extent does interdecadal variability explain changes in flood regimes (Webb and Betancourt 1992), fire behavior (Fig. 8) (Swetnam and Betancourt 1990, Swetnam 1993) and outbreaks of forest pests (Swetnam and Lynch 1993)?

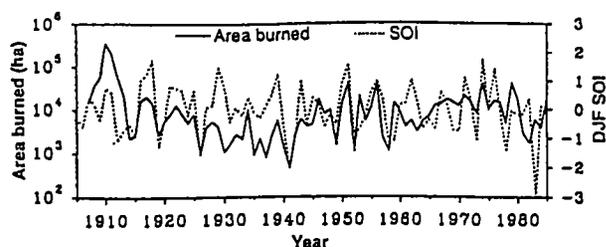


Fig. 8. The association between area burned in Arizona and New Mexico between 1905 and 1985 and an index of the Southern Oscillation (SOI) for the December to February (from Swetnam and Betancourt 1990). High values of SOI are associated with droughts and higher fire incidence across large areas.

Documenting effects of interdecadal variability on the demography of trees presents several challenges. Data on tree recruitment and mortality must be regional in geographic extent and both long-term (much longer than 100 years) and high resolution (preferably annual) in temporal coverage. Few such studies have been attempted (e.g., Villalba 1995), in part because the necessary resolution and sample size are often prohibitive.

The extent to which climate synchronizes ecological processes at regional scales has implications for management. For example, in years of severe drought, intense fires may affect many units and land-managing agencies and strain management resources. In addition, regional synchronization of the dynamics of wildlife populations would make rare species more vulnerable to extinction. The spatial scale of this synchronization is likely to vary from one part of North America to another. Documenting responses to decade-scale climatic variation may also help to predict the ecological effects of human-induced climate change.

## 8.2 Native American Disturbance

Ecologists and land managers once assumed that ecosystem dynamics prior to European settlement of North America were influenced only locally or in minor ways by Native Americans. It is now becoming clear that at some times and places, Native American populations had important direct and indirect impacts on ecosystem processes. These impacts include cultivation, the use of fire, and the direct harvest of wild plants and animals. Impacts on disturbance regimes and temporal dynamics varied with the size, location, and evolving cultural practices of these populations. In some areas these influences were relatively minor (e.g., occasional hunting and gathering activities), whereas in others they were significant (e.g., frequent burning and large agricultural areas; Delcourt et al. 1986). Evidence of widespread Native American influence

suggests that we re-evaluate the "naturalness" of pre-Columbian ecosystems (see also Bonnicksen et al., this volume.)

Understanding the effects of Native American activities may also provide insights into ongoing ecological change. In the 1950s through 1970s, chaining of southwestern pinyon-juniper woodlands to improve forage and water yield proceeded on the assumption that pinyon and juniper had recently invaded grasslands as a result of overgrazing and fire suppression. However, midden records suggest that at least some of the areas chained were impacted by intensive prehistoric fuel harvesting (Betancourt and Van Devender 1981). These so-called invasions may in fact represent recovery from prehistoric human impact (Samuels and Betancourt 1982).

## 8.3 Habitat Fragmentation and the Human Imposition of New Scales

Managers must be concerned not only with the characterization of disturbances, but also with the scale of managed systems. The size of disturbance events may exceed that of management units, and the boundaries of management units may not necessarily correspond to natural boundaries. In areas where several agencies oversee adjacent units with similar ecology, ecosystem management on a scale appropriate to the disturbance regime may require coordination among agencies. In other situations, we may need to ask if management can reduce disturbance size and still maintain the desired patch mosaic.

Scale-dependence of ecological variables such as species richness has important consequences for how we observe and manage ecosystems. Different ecosystem parameters (e.g., leaf area, biomass, downed woody debris, species richness) change at different rates with scale. As a consequence, there is no single optimum scale of observation and management for an ecosystem, although particular management goals may be best addressed at particular scales. Although finer scales (e.g., patches, stands and watersheds) have received more attention in the past, coarser scales (e.g., landscapes and regions) may be critical for managing biological diversity (Swanson and Franklin 1992).

Reduction in the size of natural areas because of habitat loss and fragmentation may threaten the persistence of both early and late successional species. Early-successional species that disappear from older patches can persist in a landscape only if newly disturbed patches occur within dispersal distance (Pickett and Thompson 1978; Baker 1992a, b). The alteration of spatial context may thus impair response to distur-

ance itself. Similarly, the loss of late-successional refuges for disturbance-sensitive species may jeopardize their persistence. Human alteration of the landscape matrix will also affect the propagation of disturbances. Changes in the size and spatial context of natural areas represent an important challenge for the management of biological diversity in the future.

#### 8.4 Exotic Species Invasions and Disturbance Regimes

One of the most troubling problems in the management of ecosystems is the invasion of exotic species, sometimes called the least reversible of human impacts (Coblentz 1990). Humanity is now engaged in a massive experiment involving purposeful and accidental transport of species across natural barriers to their dispersal (Drake et al. 1989, Groves and Burdon 1986, Mooney and Drake 1986, Pycek et al. 1995). Exotics may exert direct impacts on native species through competition, predation, and pathogenesis, and may affect communities indirectly by altering habitat structure, resource availability (e.g., the invasion of nitrogen fixers in Hawaii, Vitousek 1990), hydrology, and ecosystem function. Dogwood anthracnose, an exotic fungus, has devastated populations of flowering dogwoods in eastern North America (Daughtrey and Hibben 1994). In doing so, it has removed a major component of the small tree stratum and an important source of fruit for migratory songbirds. Because flowering dogwoods act as "calcium pumps," extracting the nutrient from the subsoil, anthracnose may alter soil nutrient status and thus the abundance of other plant species.

Exotic species invasions change disturbance regimes. Exotic insects and pathogens such as the gypsy moth, hemlock aphid, and chestnut blight kill or damage trees and thus represent a new source of disturbance to the forest canopy. The introduction of Eurasian cheatgrass to semi-arid sagebrush steppes, discussed above, has caused a fundamental shift in disturbance regime, increasing the size and frequency of fires and threatening native species (Billings 1990). In south Florida, the exotic tree *Melaleuca* transpires so much water that it lowers the water table; the result is an increase in fire intensity (Bodley et al. 1994).

Rates of exotic species invasion can be hastened by both human and natural disturbances. For example, many exotic plants common in the eastern United States, such as Japanese honeysuckle, princess tree, and kudzu, thrive in open and edge habitats but are slow to invade intact forest. Human-caused habitat fragmentation and natural disturbances such as hurricanes allow these species to spread by creating

gaps and edges. The invasion of *Potamocorbula amurensis*, an Asian filter-feeding clam, in San Francisco Bay provides an example of the effects of disturbance on exotic species invasions (Carlton et al. 1990, Nichols et al. 1990). The 1986 introduction of this clam in ballast water coincided with a major flood which disrupted benthic communities. By 1988, the clam was the dominant organism in the north section of the bay and had begun spreading into the southern section.

The spread of exotic species will affect our ability to restore historical processes in certain landscapes. Management of exotic species may involve direct removal, reduction of human activities which promote their spread, and testing and release of biological control agents. Biological control agents which are themselves exotics must be introduced with caution; managers must seek to minimize the risk that new exotic pests will be released.

#### 8.5 Ecological Variation, Scale Dependence, and Resilience

In many ecosystems, disturbance maintains ecological variability. However, we can also turn this formulation around: ecosystem response to disturbance is itself a function of the ecological variability present. For example, some species and patch types require disturbance to persist, and some of these disturbance-dependent elements are critical to ecosystem function (Marks 1974, Hansen et al. 1991). The interrelationship of disturbance and variability thus has implications for ecosystem resilience. Effects of ecological diversity on resilience have only recently attracted rigorous empirical study (e.g. Tilman 1996, Tilman et al. 1996, Huston 1997). Relationships between disturbance, diversity, and ecosystem dynamics represent an important research frontier.

Results of ecological studies depend, sometimes critically, on spatial and temporal scales of observation (Busing and White 1993, Reed et al. 1993, Zedler and Goff 1973). One implication of scale dependence in a patchy ecosystem is that small samples may contain only a subset of ecosystem states. For example, studies which position relatively small plots in areas of large trees typically overestimate biomass in southern Appalachian old growth forests (Busing et al. 1993). If the time span of a historical study is too short, extremely large and destructive disturbance events which are an infrequent part of a system's dynamics may appear unprecedented. Rather than relying on a narrow range of states defined by a few small samples or reference points, managers should seek to characterize and understand the full range of spatial and temporal variation in their systems (White and Walker, in press).

## 9 CONCLUSIONS AND KEY POINTS

1. A disturbance is a relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment. Natural disturbances occur in all ecosystems, and in many cases, play an important role in maintaining species diversity and community and ecosystem structure. Describing disturbance regimes is an important step towards understanding the natural dynamics of ecosystems.
2. Most management activities involve disturbing ecosystems (e.g., logging, prescribed fire) or suppressing disturbance (e.g., fire and pest control). These alterations of the disturbance regime may affect ecosystem health and productivity, biological diversity, and aesthetics.
3. Disturbances are not all equivalent, but differ in spatial parameters (e.g., size and shape), temporal parameters (e.g., return interval and seasonality), magnitude (e.g., proportion of living biomass removed), and specificity (relative impacts on different species and size classes). Historical, observational, experimental, and simulation approaches have been used to document disturbance regimes and effects. Considerable geographic variation in disturbance regimes, even within single vegetation types, suggests the need for site-specific data.
4. Climate change, the pervasive influence of human cultures, and low-frequency events make it difficult to fully document disturbance regimes. Because disturbance regimes are ultimately coupled to climate, differences between past and present climates may limit the application of historic disturbance data to present situations. Human-induced changes in climate and atmospheric chemistry are likely to further complicate the situation in the future. Historical and prehistorical land-use have affected disturbance regimes in both direct (burning and clearing) and indirect (e.g., changes in landscape structure) ways. Disturbance regimes are not necessarily stable, and any demonstration of stability is contingent on temporal scale. For these reasons, we should be careful in our interpretation of and reliance on "natural," "original," or historical (e.g., presettlement) disturbance regimes.
5. Community and ecosystem responses to disturbance reflect the impacts of the disturbance on resource availability and the structure of the post-disturbance community. "Biological legacies" (e.g., standing live trees, coarse woody debris, and buried seeds which remain following disturbance) often play an important role in response. Patch structure and dynamics change as a function of successional time.
6. Species show a range of responses to disturbance. Some require open, early-successional conditions, some require mature communities, and some can survive in both early and late-successional habitats. Increases or decreases in disturbance levels relative to historical conditions may threaten biological diversity.
7. In many ecosystems, the occurrence and outcome of disturbance depend on the history of previous disturbances. These synergisms occur at the levels of individual organisms, patches, and landscapes and may profoundly influence parameters such as species richness, community composition, and the likelihood and intensity of fires and insect outbreaks.
8. The effects of 20th-century fire suppression vary considerably between ecosystems. In vegetation types with historical disturbance regimes dominated by high-intensity, stand-regenerating fires, fire suppression may lead to an increase in fire size but otherwise have little effect on ecosystem dynamics. In some vegetation types (e.g., ponderosa pine) in which the historical disturbance regime was characterized by frequent, low intensity fires, fire suppression may lead to increases in stand density and fuel levels; as a result, likelihood of high-intensity fire may increase. In other frequent-fire systems, fire suppression may lead to replacement of fire-prone vegetation (e.g., long-leaf pine and wiregrass) with a fire-resistant type (closed canopy mesic forest).
9. Disturbance interacts with climate, topography, geology, and successional processes to create landscape-level patterns. The size, shape, and spatial configuration of patches in a landscape, in turn, influence the initiation and spread of disturbance and the dynamics of ecosystem response. Disturbances may increase or decrease landscape heterogeneity. Large, continuous tracts of susceptible vegetation promote the spread of fires and insect outbreaks. Other disturbances, such as windthrow, may increase in more heterogeneous landscapes. Landscape patterns influence wildlife populations (e.g., area-sensitive forest interior species, "edge" species) and ecological processes (e.g., seed dispersal, spread of exotics).

10. The spatial and temporal characteristics of a disturbance regime have important implications for the existence and nature of equilibrium. Steady-state equilibrium is most likely to occur where disturbances are small and infrequent relative to recovery time and total landscape size. While landscapes with large or frequent disturbances may not be in quantitative equilibrium, they may nonetheless exhibit qualitative or stable-trajectory equilibrium. Habitat loss and fragmentation alter the scales of landscapes, making it more difficult to preserve species and maintain historical disturbance regimes.
11. Applying disturbance ecology to ecosystem management will require investigation of the relation between climate and disturbance regime, the effects of Native Americans, the influence of habitat fragmentation on the spatial and temporal characteristics of disturbance, the relationship between exotic species invasions and disturbance, and the relation of ecological variation and resilience.
12. The study of natural disturbances provides guidelines for balancing commodity production with the maintenance of ecosystem health and biological diversity. However, our ability to incorporate disturbance ecology into ecosystem management is currently restricted by the limitations of historic data, a lack of site-specific information, and the inherently stochastic nature of disturbance occurrence and response. The current gaps in our knowledge about disturbance suggest that we treat human management as an iterative, adaptive process linked to long-term monitoring and research.

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# Ecological Stewardship

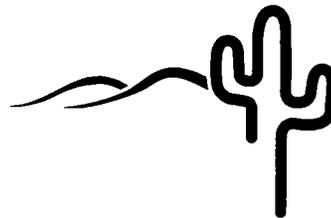
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