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).

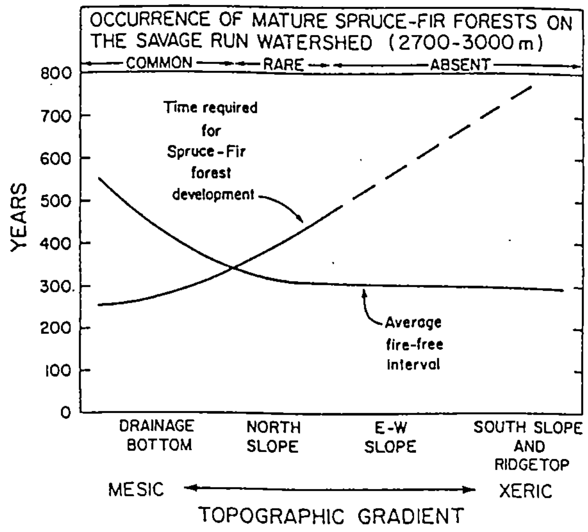
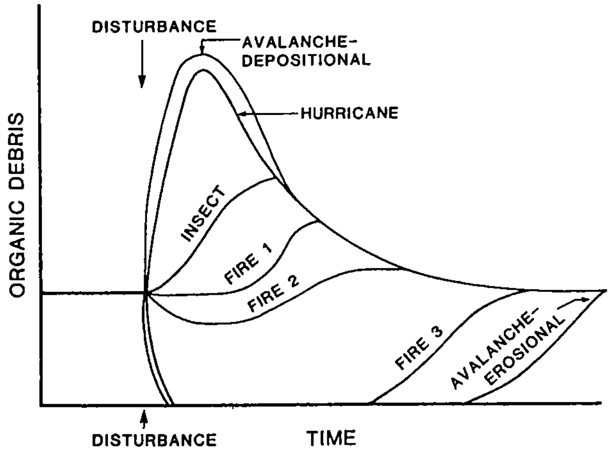


Fig. 1. The average fire free interval decreases from moist to dry sites, while the time for succession to spruce-fir forest increases along the same gradient. As a result, spruce-fir forests will probably never develop on the driest slope positions (from Romme and Knight 1981).

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
	Cryogensis 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



(From Lang 1985)

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 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.

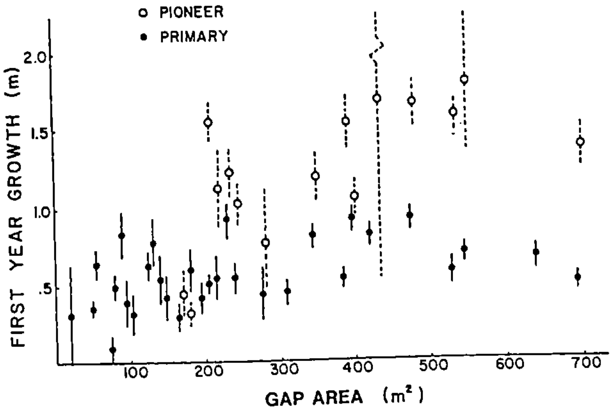


Fig. 3. Height growth (mean and one standard error of annual height increment for stems greater than 1 m tall) of pioneer (open circles) and primary tree species (closed circles) as a function of gap size (from Brokaw 1985). Primary forest species show some response to increased gap size and occur at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

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 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).

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

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

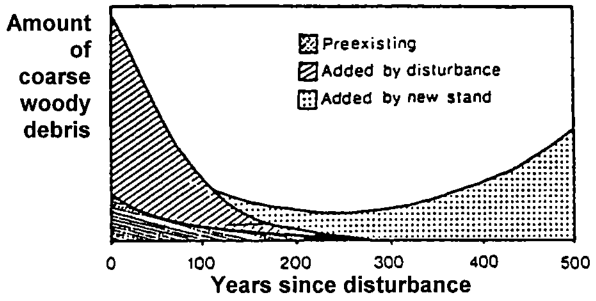


Fig. 4. A general model for changes in coarse woody debris after disturbance (from Agee and Huff 1987). Some coarse woody debris survives the disturbance ("Preexisting"). Some disturbances (including many fires) actually create woody debris through heavy tree mortality ("Added by disturbance"). Decomposition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

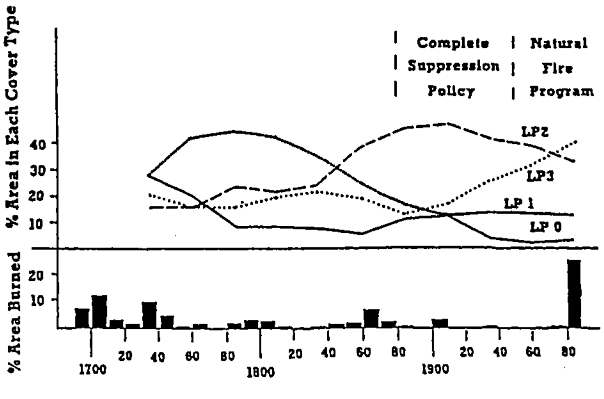


Fig. 5. Disturbance and succession on a 129,600 ha study area in Yellowstone National Park (Romme and Despain 1989). Changes in the percent of the study area in each of four successional types (top) and the percent of the study area burned each decade (bottom) over the past three centuries. LP0 are lodgepole 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.