



# DISTURBANCE, MECHANISMS OF

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## GLOSSARY

**disturbance** Relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.

**disturbance regime** The collective spatial, temporal, physical, and ecological characteristics of a disturbance process operating in an area.

**resilience** Measure of a system's ability to recover to its original state when subjected to disturbance.

**resistance** A measure of system's ability to remain unchanged when subjected to a disturbance.

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**DISTURBANCES** in ecological systems promote characteristic patterns of environmental heterogeneity and regulate ecosystem processes, population dynamics, species interactions, and species diversity. Ecological disturbances are created by mechanical forces, extreme

physico-chemical conditions, and biological consumers and pathogens. Each of these three classes of mechanisms has somewhat distinctive characteristics in the way it operates, the kinds of organisms affected, and the biological and physical legacies that remain. This article reviews general principles of disturbance ecology and describes and illustrates different disturbance mechanisms and their interactions, concluding with a brief discussion of the role of humans in altering disturbance regimes.

## I. DISTURBANCE ECOLOGY

Ecological communities are subjected to sharp environmental perturbations, such as the passage of a fire, a storm wave, an avalanche, or a large animal, that suddenly reduce standing biomass. Such events also alter ecosystem properties such as energy balance, nutrient fluxes, substrate texture, and chemistry. Generally referred to as "disturbances," these events are distinguished as a special form of environmental variability because they are relatively discrete in both time and space and cause unusual mortality or tissue loss in affected populations. Disturbances promote environmental heterogeneity and free up limiting resources, such as space, light, and nutrients, thereby triggering successional processes of community recovery.

Widespread agents of disturbance in terrestrial ecosystems include fire, wind, extreme temperature, desiccation, gravity (as a force on water, ice, rocks, and soil),

and organisms. With the exception of fire, one can find analogs in aquatic systems, in which the main agents are heat, solutes, currents, desiccation, waves, ice, sediments, and organisms. Disturbance agents operate by exerting mechanical force, altering physico-chemical conditions, or through biological consumption and disease. For example, practically any physical mass can mechanically disturb ecosystems at some scale provided it has sufficient velocity to dislodge organisms or kill tissues. In contrast, disturbance by fire involves chemical combustion of biomass. Disturbance of terrestrial communities by prolonged inundation is largely a chemical disturbance resulting from oxygen depletion. Freshets in estuarine and marine environments are also chemical disturbances. These mechanical and physico-chemical disturbances contrast with biological disturbances such as herbivory or predation, which involve tissue removal and digestion by individual mobile consumers.

During the first half of the twentieth century, ecologists paid more attention to post-disturbance processes of species recovery and community succession than to specific disturbance mechanisms. Disturbance was generally treated as a temporary setback to communities that otherwise would tend to develop toward a relatively steady state or "climax community" whose structure and composition were determined by climate and other physical factors and were regulated by endogenous biological interactions. Recently, disturbance has been recognized as intrinsic to and ongoing in virtually all ecological systems. Closer attention has been paid to disturbance processes and their role in promoting characteristic scales of spatial and temporal environmental heterogeneity and in regulating ecosystem processes, population dynamics, species interactions, and species diversity (Paine and Levin, 1981; Sousa, 1984; Pickett and White, 1985). Disturbance ecology has become a familiar term in the lexicon of ecology and a recognized area of emphasis in ecological research.

In practice, it may not be easy to distinguish disturbances from other environmental variation. Most agents of disturbance operate over a continuum, and environmental perturbation is sudden and severe only relative to some set of reference conditions and from the perspective of the affected organisms. The mound of soil produced by a burrowing gopher is a significant disturbance to the underlying herbaceous plants and soil animals but likely to be of little consequence to a large tree a few meters away. A windstorm that topples trees in an open savanna may have no immediate effect on small herbaceous plants located a short distance outside of the canopy. Thus, it is important to bear in mind that disturbance is a relativistic concept and that distur-

bances can span a very broad range of spatial and temporal scales. Not surprisingly, the term disturbance has been applied somewhat indiscriminately in ecology. The most general definition of a disturbance—any process that causes a sudden decrease in standing live biomass and frees up ecological resources (Sousa, 1984)—is perhaps the most unambiguous.

A disturbance differs from a stress in that the latter is a more chronic condition inhibiting the growth or normal functioning of an organism (e.g., a lack of key nutrients or physical abrasion). A disturbance is termed a catastrophe if it causes extraordinary ecological impact.

Variables commonly used to describe a single disturbance event include timing, extent, and magnitude, where magnitude encompasses both intensity (e.g., energy per area per time) and severity (biological impact). These and other stochastic variables, such as event frequency or recurrence interval between events, have statistical properties that serve to define a disturbance regime. More broadly, a disturbance regime is the collective spatial, temporal, physical, and ecological characteristics of a disturbance process operating in an area. Predictability, which can be defined as the inverse of the variance in disturbance frequency, size, and magnitude (Christensen, 1988), is also an important consideration. In general, predictability increases as the spatio-temporal scale of analysis is expanded from local (the typical size of a disturbance event) to regional (the entire area over which the disturbance regime is manifested).

Because the magnitude of disturbance is defined relative to its ecological impact, it is practically tautological that disturbance regimes are dominated by events of relatively low magnitude and high frequency, whereas higher magnitude events are increasingly rare. However, the impact of a disturbance may not increase linearly with size, frequency, or duration. Romme *et al.* (1998) distinguish three classes of disturbance response: (i) threshold response, (ii) scale-independent response, and (iii) continuous response. Individuals and communities manifest threshold responses when there are discrete limits in their ability to resist a large disturbance (e.g., the wind speed at which a tree is uprooted). Disturbances can have their greatest ecological impact when one or more events follow close on the heels of another, preventing or disrupting normal community recovery (Paine *et al.*, 1998).

Some mechanisms of disturbance, such as earthquakes or storm waves, are exogenous to the biological communities being impacted, whereas others such as treefall or fire could be considered endogenous. In the former, there is little or no feedback between the state of the ecosystem and the likelihood of a disturbance

event so that the disturbance regime depends mainly on location and environmental context. In the latter, the likelihood of a disturbance depends on the state of the ecosystem as well as location. Although the categories of endogenous and exogenous disturbances are somewhat artificial, it is useful to examine the relative strength of coupling between disturbance processes and the biota. In many cases, disturbance processes and their effects are tightly coupled to the biological properties of individual organisms and communities. This coupling may promote the formation of specific scales of ecological pattern and reinforce certain ecological and evolutionary processes (Levin, 1992).

In thinking about patterns and processes, it is also useful to distinguish spatially propagating from non-propagating disturbances. Disturbances such as fire and flood spread from neighboring areas, and the spatial pattern of "susceptible" areas or organisms may have a constraining effect on disturbance dynamics, thereby linking spread to previous disturbance events.

## II. DISTURBANCE AND BIODIVERSITY

The "intermediate disturbance hypothesis" (IDH; Connell, 1978) predicts that maximum levels of biodiversity should be observed under some intermediate disturbance frequency because few species are able to tolerate very intense disturbance regimes, and few are able to compete successfully in habitats that experience little or no disturbance. The IDH also implies that maximum diversity should be found at some intermediate span of time since the last disturbance. The IDH has been expanded to incorporate intermediate levels of disturbance intensity and extent, and it has been tested and supported in a wide variety of ecosystems.

The best experimental examples of the IDH come from the study of sessile species competing for space or some space-associated resource. Counter-examples come largely from the study of mobile consumers (e.g., freshwater invertebrates), for which rapid immigration may override local disturbance effects. Defining "intermediate" in the context of specific organisms and choosing the scale at which to measure diversity are also important issues in assessing the validity of the IDH, about which there is ongoing debate. In general, the IDH applies to small-scale disturbances and to plants and sessile filter feeders. The relationship between disturbance and diversity is more complicated at larger scales and may not apply when interactions among multiple trophic levels are considered.

At spatial scales much larger than the characteristic size of single disturbance events, disturbance regimes

generate disturbance mosaics that maintain beta diversity in landscapes or regions by promoting co-existence of dispersal-limited competing species or prey species and by maintaining environmental heterogeneity and multiple seral stages (Pickett and White, 1985).

If they recur with sufficiently high frequency (e.g., on average at least once per generation), ecological disturbances can be a strong selective force operating on species' morphology, physiology, and/or behavior. Not surprisingly, many organisms are adapted to and/or depend on specific kinds of disturbances and disturbance regimes. Grime (1979) proposed that herbaceous plant life histories can be ordered along three fundamental axes: stress tolerance, competition, and disturbance. Somewhat analogously, animal species are often called r-strategists or k-strategists depending on whether they have high intrinsic rates of reproduction and tend to be favored by disturbances or whether they have lower reproductive rates but exert competitive dominance in the absence of disturbance. Because local abundance of many species is increased or maintained by disturbance, the long absence of specific kinds of disturbances (e.g., fire or floods) may have large negative impacts on biodiversity.

The life history strategies of some organisms may promote specific disturbance regimes (e.g., some fire-adapted shrub species possess canopy structure and foliar chemistry that promote fire spread). Organisms that recover quickly after a disturbance are said to be resilient to that disturbance, as opposed to those that show little response to disturbance and are considered resistant. These concepts are also applied to ecological communities, and the relationship between community diversity and community stability and resilience has long preoccupied ecologists (Holling, 1973). The subject has received renewed attention due to increasing concern over human-caused species extinctions and community impoverishment associated with habitat fragmentation. To date, the hypothesis that community stability to disturbance increases with community richness has met with mixed results in modeling and empirical studies, in part due to differences in spatial and temporal scale and in how stability is measured.

## III. MECHANICAL DISTURBANCES

Most aquatic and terrestrial communities are constantly subjected to mechanical forces that reduce standing biomass at some scale. Avalanches, landslides, and debris flows remove soil, shear off and uproot plants, and bury plants and animals. High winds, snow, and ice uproot trees and break off branches and leaves that

then bury other plants and animals. Ice in the nearshore zone plucks and scours littoral communities. Floodwaters topple riparian vegetation and scour streambeds. Waves dislodge encrusting intertidal organisms and break down branching corals. Large animals break twigs and compact the soil as they move. Humans clear or clip vegetation and plow soils. Burrowing animals excavate plants and animals as they dig. In all of these cases, biomass is dislocated but not immediately chemically transformed or consumed. Most important, space occupied by living tissues is evacuated as those tissues are moved someplace else.

Thus, mechanical disturbances leave conspicuous openings and persistent biological legacies, such as large woody debris embedded in landslides, downed trees next to treefall gaps, floating wracks of detached marine plants and animals, or rubble piles of coral. Materials are often transported to a location where they act to create another disturbance. Thus, the legacy of biological debris from mechanical disturbances not only affects the rate and pattern of community recovery but also may influence the timing and location of subsequent disturbance events.

The spatial distribution of mechanical forces in the environment is highly nonrandom. Features such as substrate, topography, and standing biomass create persistent biophysical pathways in which specific mechanical disturbances are concentrated, thereby compounding existing physical environmental heterogeneity. For example, the location of avalanche paths is strongly associated with topography, geology, and lithologic structure. The impacts of severe wind storms on forest communities varies systematically with topography and soil characteristics as well as vegetation composition and structure (which depend, in part, on disturbance history). Wave energy is concentrated on jutting shorelines. Animal burrowing is concentrated in specific soils and sediments. In other words, many mechanical disturbance processes can have somewhat predictable spatial distributions.

Most mechanical disturbances operate indiscriminately (i.e., they do not target specific organisms, as would selective herbivory, for example) and their impact depends on the ability of organisms to withstand the mechanical force. Thus, mechanical disturbances often winnow biological communities. For example, snow avalanches apply a bending stress on trees in their path that is a function of the snow's density and the avalanche's mass and drag. Susceptibility of woody species to breakage (vs bending) increases with tree size, leading to complex interactions between avalanche recurrence frequency and forest structure and composi-

tion in avalanche paths. Similarly, masses of attached barnacles and mussels in rocky intertidal environments become increasingly susceptible to detachment by waves as organism size and density increase. The same mechanical agent may create different kinds of disturbances depending on the size of the organism. In forests, for instance, woody stems may be most susceptible to breakage by wind when they are very small or very large, whereas intermediate-sized stems may be the most susceptible to uprooting by wind (Everham and Brokaw, 1996). When impacts of mechanical disturbances depend on the size or density of organisms, this produces feedbacks that influence population dynamics and create pronounced spatial patchiness at scales well below that of the disturbing process (Levin, 1992).

#### IV. PHYSICO-CHEMICAL DISTURBANCES

Physico-chemical disturbances, such as extreme cold, prolonged inundation of terrestrial organisms, hypoxic episodes in aquatic systems, freshets in coastal waters, and releases of toxic compounds (e.g., biological exotoxins such as those produced by the dinoflagellate *Pfiesteria piscicida*), reduce biomass by imposing lethal physiological stress. Physico-chemical disturbances do not involve mechanical force (except perhaps in the case of extreme cold when tissue damage is due to intracellular ice formation), and most physical and chemical disturbances leave dead tissues and organisms *in situ*. This contrasts with mechanical disturbances, in which space and resources are freed up through displacement of biological material. There are few studies comparing recovery processes under these two situations, but one might expect differences simply due to the presence or absence of residual detritus that could affect light, nutrient levels, and substrate quality (Reiners, 1983).

Like mechanical disturbances, Physico-chemical disturbances have organism-specific impacts because of species-, age-, and size-specific physiological tolerances to environmental extremes. Thus, like mechanical disturbances, physico-chemical disturbances operate as an environmental filter of biological assemblages.

As mentioned previously, much of the emphasis in disturbance studies has been on sessile organisms such as plants and benthic invertebrates. Some large-scale physico-chemical disturbances may be somewhat distinctive in that they can kill large numbers of highly mobile organisms. For example, episodes of anoxia can

cause massive fish kills in estuaries and lakes. Severe cold weather can selectively kill large numbers of birds. In these instances, the suddenness and magnitude of the events prevent animals from escaping, a phenomenon which can also be observed during extreme wildfires.

Fire is obviously a special case of a physico-chemical disturbance because biomass is both transformed and removed in the combustion process. Fire is also unquestionably one of the most pervasive and obvious disturbances in terrestrial ecosystems, and an enormous scientific literature has been devoted to the subject of fire events and fire regimes. It is discussed here to illustrate in more detail the concepts of disturbance mechanisms and disturbance regimes.

The occurrence of fire requires an ignition, fuel combustion, and spread, each of which in turn depends on many physical and biological factors, notably climate, weather, fuel structure and chemistry, and topography. The most important effects of fire are partial or complete combustion of aboveground vegetation, mineralization and deposition of plant tissues as ash and charcoal, extreme heating of the local atmosphere and topsoil, and killing of selected plants, seeds, spores, and animals both above- and belowground.

Figure 1 presents a simple conceptualization of factors that influence fire dynamics at three distinctive spatial and temporal scales in Mediterranean-climate shrublands. The fire fundamentals triangle (Fig. 1a)

captures essential elements of the actual combustion process, which occurs at minute scales and depends on oxygen, heat, and fuel. The timing, size, and severity of a wildfire (or controlled fire) event, which may last hours to weeks and extend over hectares to thousands of square kilometers, depends on local weather, topography, and fuel bed. Finally, the fire regime of a landscape depends on complex interactions among climate, vegetation, and ignition factors operating over decades to centuries.

Fire creates strong biological patterns over a broad range of spatial scales. At the scale of individual plants, biomass combustion, soil heating, and nutrient removal can vary widely, imposing very fine-grained variation in mortality and postfire conditions that is manifested in equally fine-grained patterns of biological recovery. A coarser pattern can be created at the scale of entire populations (vegetation stands). Fire severity and vegetation removal can vary with topography, soil, vegetation, and wind conditions, and distance from source populations for seeds and animal colonists can influence community recovery. At still broader scales, landscapes are composed of fire mosaics, a patchwork of stands with differing fire histories and biotic communities. This landscape mosaic is one of the factors aiding in the long-term persistence of species with different fire tolerances. The spatial patterns from individual plant distributions to landscape mosaics all affect

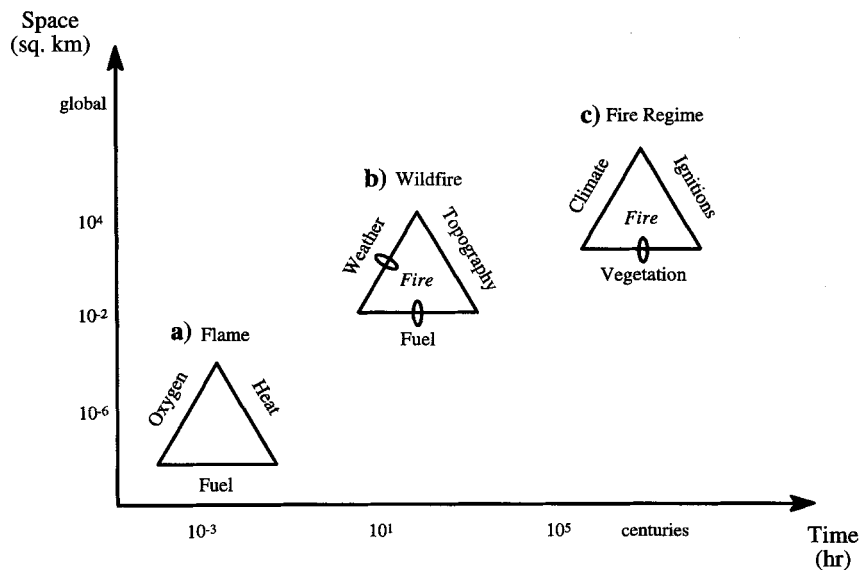


FIGURE 1 Hierarchical model of fire controls at successively coarser scales of space and time. Connections between fire and individual controls indicate potential feedback loops (after Moritz, 1999, with permission).

the location and severity of future fires and their ecological impacts.

Fires are obvious, discrete events, and research on wildfire history has provided many useful models and methods for characterizing temporal and spatial properties of disturbance regimes (Johnson and Gutsell, 1994). Temporal properties such as time-since-fire (survivorship) and fire interval (mortality) are described using probability distribution functions, notably the Weibull and negative exponential distributions. Fire mosaics and their dynamics have been described using spatial Markov chain models, percolation theory, and spatial autocorrelation statistics. These quantitative characterizations are useful for describing changes in fire regime over time, for comparing different areas, and for estimating wildfire risk.

## V. DISTURBANCE BY HERBIVORES AND PREDATORS

In many ways, consumers (and pathogens) have the same effects as other agents of disturbance in that biomass is removed and new opportunities for recruitment are created. There are some distinctive features, however, of disturbances by herbivores and carnivores. Most obviously, they operate at the relatively fine scale of individual consumers, and they leave a very different biological legacy than mechanical and physico-chemical disturbances because biomass is concentrated and converted into heat, new tissues, and discrete waste products. The waste products are frequently deposited away from the disturbed area. For example, frass from defoliating caterpillars in tree canopies falls to the soil surface. Shade-seeking ungulates in African savannas deposit a disproportionate amount of urine and feces under trees. Elk migrations lead to a net transport of nitrogen from summer ranges to winter ranges.

Foraging is also a far more selective form of disturbance than other disturbance mechanisms. Organisms (including humans) preferentially occupy specific sites and microsites and focus on specific plant resources, creating patchiness at many scales. Most plants are unpalatable to most herbivores, and selective herbivory by dominant grazers can exert strong, directional effects on community composition, structure, and ecosystem processes. These effects may be amplified by strong feedbacks between consumption, food quantity, and food quality. For example, moose in boreal ecosystems selectively browse nitrogen-rich deciduous species and avoid coniferous species. Over time this promotes nitro-

gen sequestration in conifer litter and accelerates succession of deciduous to coniferous plant communities (Hobbs, 1996). Disease spread from infected to susceptible hosts and the development of resistance in infected individuals is somewhat analogous in terms of the strong spatio-temporal feedbacks between the disturbance process and the state of the system.

Many consumers act as mechanical, chemical, and biological agents of disturbance. Perhaps the most sensational example is that of beavers, which selectively fell trees, dam streams, and inundate floodplains. Similarly, burrowing animals such as pocket gophers can operate as "physical ecosystem engineers" creating pervasive changes in the abiotic and biotic environment by redistributing soil and nutrients, altering soil hydrology and canopy light regimes, and altering vegetation composition and dynamics.

## VI. INTERACTIONS AMONG DISTURBANCE MECHANISMS

Disturbances can interact in complex, nonlinear ways across space and time. One disturbance may promote another, such as occurs when dry-season fire in Mediterranean-climate shrublands promotes flooding and debris flows during the ensuing wet season. Conversely, one disturbance mechanism may reduce the likelihood of another. For example, grazing reduces the likelihood of fires in grasslands and the likelihood of crown fires in some forest ecosystems. Nearshore communities that are heavily impacted by wave disturbance may also experience lowered rates of predation. It is not difficult to imagine many such interactions operating across a wide range of spatial and temporal scales.

Disturbances often play an important role in invasion and spread of exotic species. In Hawaii, for instance, invasion of the nitrogen-fixing shrub, *Myrica faya*, was facilitated when native vegetation was thinned by heavy ash deposition from a volcanic eruption. There is a growing list of examples in which disturbance promotes the spread of an invasive species and then that species initiates ecosystem changes that introduce new disturbance processes. For example, in the western United States cattle grazing in shrub steppe promoted the spread of the exotic grass, *Bromus tectorum*, and the presence of a dry grass layer then increased wildfire size and frequency in that system, in which fires were historically uncommon.

As mentioned in Section I, compounded disturbances, or disturbances of communities already stressed

by abiotic or biotic forces, can have large and persistent effects on ecological communities if they occur in such rapid succession that they disrupt normal recovery processes. Repeated burning over a series of 2 or more years is a common means of converting shrublands to grasslands in semi-arid ecosystems. In a particularly dramatic example, Hughes (1994) describes the decline of corals in Jamaica due to the combined effects of overfishing, two major hurricanes, and disease that caused mass mortality in sea urchins. These impacts appear to have collectively precipitated a massive phase shift from coral-dominated to algal-dominated reefs.

## VII. HUMANS AS AGENTS OF DISTURBANCE

For many millennia humans have been manipulating ecosystem processes with varying impacts on ecosystem function and species distribution. Human activities that create disturbances at spatiotemporal scales to which organisms are adapted generally do not effect long-term changes in community composition or structure. For example, shifting agriculture in the humid tropical forests, like hurricanes, creates small, temporary forest clearings and results in landscape mosaics within which most species can persist. In contrast, commercial forest cutting and cropland and pasture development are large and/or persistent disturbances that can produce regional extinction of species and require much longer periods for forest recovery (Attiwill, 1994).

Another widespread human impact has been to regulate or arrest disturbances such as fires, floods, or animal activities that create habitats on which some species depend. Even when human ecosystem manipulations are, by design, modeled after a particular disturbance, it is difficult to incorporate all disturbance-related changes in the environment. For example, forest harvesting can occur at the spatiotemporal scale of a natural fire regime, but the post-fire nutrient pulse and legacy of dead snags are no longer factors in the recovering ecosystem. Streams may be regulated to mimic periodic flooding, but dams often inhibit fish migrations that would happen at that time (and agencies will understandably stop short of re-initiating very high-magnitude flood events).

As humans fragment terrestrial habitats through land-use conversion and aquatic systems through impoundments, diversions, dredging, trawling, and construction, permanent fragmentation of habitats is superposed on dynamic disturbance mosaics, causing

changes in disturbance regimes. Such fragmentation can retard disturbance spread (e.g., the spread of fire or disease), alter disturbance regimes in remnant patches, and create edge environments with novel disturbance regimes. Local human activities can have large cumulative effects. For example, the building of roads alters the natural cycles of erosion and landslide initiation, whereas agricultural land use often leads to the concentrated nutrient inputs and changes storm flows in receiving water bodies. In fact, most human activities have the capacity for altering historical disturbance regimes in some way.

At the broadest scale, humans are changing global climate patterns, and nearly all mechanisms of disturbance and disturbance effects are ultimately tied to climate processes. Changes in disturbance regimes during global climate change are inextricably tied to other ecological responses to changing climate, affecting whether species can persist in their current ranges or can invade new areas of more suitable environmental conditions. The tight coupling between biotic processes and structures and most disturbance patterns and processes—a recurrent theme in this article—creates complex feedbacks that could amplify or moderate the effects of global climate change on disturbance regimes, species, and ecosystems.

### See Also the Following Articles

DISEASES, CONSERVATION AND • ECOSYSTEM FUNCTION, PRINCIPLES OF • FIRES, ECOLOGICAL EFFECTS OF • GRAZING, EFFECTS OF • HERBACEOUS VEGETATION, SPECIES RICHNESS IN • HUMAN EFFECTS ON ECOSYSTEMS, OVERVIEW

### Bibliography

- Attiwill, P. M. (1994). The disturbance of forest ecosystems: The ecological basis for conservative management. *Forest Ecol. Manage.* 63, 247–300.
- Christensen, N. L. (1988). Succession and natural disturbance: Paradigms, problems, and preservation of natural ecosystems. In *Ecosystem Management for Parks and Wilderness* (J. K. Agee and D. R. Johnson, Eds.). Univ. of Washington Press, Seattle.
- Connell, J. H. (1978). Diversity in tropical rainforests and coral reefs. *Science* 199, 1302–1310.
- Everham, E. M., and Brokaw, N. L. V. (1996). Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62(2), 113–185.
- Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, New York.
- Hobbs, N. T. (1996). Modification of ecosystems by ungulates. *J. Wildlife Manage.* 60, 695.
- Holling, C. S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hughes, T. P. (1994). Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.

- Johnson, E. A., and Gutsell, S. L. (1994). Fire frequency models, methods, and interpretations. *Adv. Ecol. Res.* 25, 239–287.
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*. 73, 1943.
- Moritz, M. A. (1999). Controls on disturbance regime dynamics: fire in the Los Padres National Forest. Ph.D. dissertation, Department of Geography, University of California, Santa Barbara. 163 pp.
- Paine, R. T., and Levin, S. A. (1981). Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecol. Monogr.* 51, 145–178.
- Paine, R. T., Tegner, M. J., and Johnson, E. A. (1998). Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545.
- Pickett, S. T. A., and White, P. S. (Eds.) (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Reiners, W. A. (1983). Disturbance and basic properties of ecosystem energetics. In *Disturbance and Ecosystems: Components of Response* (H. A. Mooney and M. Godron, Eds.). Springer-Verlag, New York.
- Romme, W. H., Everham, E. H., Frelich, L. E., Moritz, M. A., and Sparks, R. E. (1998). Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* 1, 524–534.
- Sousa, W. P. (1984). The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–391.