

# Disturbance, Scale, and Boundary in Wilderness Management

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**Abstract**—Natural disturbances are critical to wilderness management. This paper reviews recent research on natural disturbance and addresses the problem of managing for disturbances in a world of human-imposed scales and boundaries. The dominant scale issue in disturbance management is the question of patch dynamic equilibrium. The dominant boundary issue in disturbance management is the effect of boundary conditions on disturbance frequency and magnitude. Human property and attitudes outside wilderness areas influence management decisions on disturbances within natural areas.

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The preservation of wilderness involves two paradoxes: First, we seek to preserve ecosystems that must change and, second, we must often apply human management to ecosystems where we ultimately want minimal human influence (White and Bratton 1980). Natural disturbances are among the most important sources of ecosystem change. If our goal in wilderness management is to promote such natural processes, we must understand the spatial and temporal scales at which they occur. The role of disturbance in wilderness leads directly to issues of scale and boundary: All of conservation is a sampling problem, in that our protected areas are a bounded subset of the original whole. Furthermore, it is the very nature of administrative units to be fixed in space, with management plans that prescribe actions that are fixed in time. This contradicts an important historic quality of natural areas which experienced considerable stochastic dynamics and directional changes in the past. In addition, nature had a certain resilience at large spatial scales. This resilience was the ability to change without loss of parts. Despite fluctuations in species abundance and distribution, extinction was relatively rare. Managers of wilderness areas should understand and provide for this resilience—that is, for persistence of species and habitats despite local fluctuations in abundance.

During the past 15 years, scale and boundary issues have produced a large literature in conservation biology (Angelstam

1992; Forman 1990; Hansen and di Castri 1992; Janzen 1986; Knight and Landres 1998; Newmark 1985, 1987; Schoenwald-Cox 1983; Schoenwald-Cox and Balylliss 1986; Schoenwald-Cox and Buechner 1993; Schoenwald-Cox and others 1992; Shafer 1994; Theberge 1989). This work has often focused on the effect of park size on population persistence and on negative impacts along natural area edges. For example, Schoenwald-Cox (1983) investigated the relationship between reserve size and persistence for three groups of mammals. Using a population size of 1,000 individuals as a correlate of long-term persistence, she concluded that small herbivores required at least  $10^3$  hectares, large herbivores required at least  $10^5$  hectares, and large carnivores required at least  $10^6$  hectares. Populations were present on smaller preserves initially, but would be subject to higher extinction risks. An empirical study found that park size was correlated with the number of mammal species extirpated from the western United States (Newmark 1987).

Managing wilderness is also challenging because the species and ecosystems we observe at a particular time are manifestations of processes difficult to observe and to document. As the poet W. B. Yeats wrote:

Oh chestnut-tree, great rooted-blossomer,  
Are you the leaf, the blossom or the bole?  
O body swayed to music, O brightening glance,  
How can we know the dancer from the dance?

In our case, the dancers—the species and ecosystems—are both the products and the producers of the dance. It is easier to observe and write management plans for the dancers; it is much harder to understand and protect the dance, though it is the dance that has produced the very wilderness we seek to perpetuate. In the extreme, we may perpetuate the dancers in ways that prevent future change. Some conservationists have argued that we will not be able to sustain the continued evolution of large mammals, but can only retain the species by managing for diverse but unchanging gene pools. Similarly, some management options would freeze ecosystems in historic states or restore them to a historic state and let them resume natural dynamics in an otherwise changed environment (for example, Bonnicksen and Stone 1985). Managing nature so that it can continue to change represents a difficult challenge, one that requires a paradigm shift in our view of wilderness. We will return to this dilemma at the end of this review.

This paper discusses the problem of managing natural disturbances in a world of human-imposed scales and boundaries. Our essay is aimed at generality across different wilderness areas; as a preamble, we make a brief statement

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In: McCool, Stephen F.; Cole, David N.; Borrie, William T.; O'Loughlin, Jennifer, comps. 2000. Wilderness science in a time of change conference—Volume 2: Wilderness within the context of larger systems; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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of the ecological and evolutionary context that makes finding generality difficult. After reviewing recent findings about disturbance, we address the question, How are today's bounded wilderness areas different from the original state in which natural disturbances prevailed? We address two topics in seeking to answer this question. First, we consider the size of wilderness areas relative to the scale of their dynamics and the question of long-term dynamic equilibrium, a phenomenon recently redefined in the context of the historic range of variation and the natural range of variability (Morgan and others 1994). In terms of disturbance, the historic range of variation, and the potential for dynamic equilibrium, large wilderness areas have made fundamental and irreplaceable contributions to our basic understanding of the way nature works. Our second topic in the analysis of bounded wilderness is to consider the influence of boundaries themselves. Wilderness areas adjoin non-wilderness areas. Boundary problems virtually guarantee that wilderness managers will have to be concerned with external, as well as internal, processes. Boundaries also signal the changed spatial context of wilderness areas—the changed context can affect disturbance regime and recovery. Edges will require management if we are to avoid progressively losing what remains of landscape function. In a final section, we discuss prospects for the future of wilderness management.

## The Search for Generality in an Ecological and Evolutionary Context

We propose that the search for generality in understanding ecosystems must take into account five principles that are rooted in past events and produce characteristics that change very slowly relative to disturbance, succession and management action (Table 1). In essence, these five principles produce the factors that are the “givens” of wilderness management.

First, the absolute rates of ecosystem processes like growth, establishment, mortality, productivity and succession vary among ecosystems because of differences in the physical environment. Some ecosystems change quickly, others

slowly, in the face of particular disturbances, fragmentation, or boundary conditions. Since the physical environment and resource levels vary among ecosystems, the effect of disturbance—which often removes dominant competitors and transfers material from living to detrital pools, thus promoting mineralization—on resource levels will vary among ecosystems. While disturbances usually increase resources, the relative increase depends on the predisturbance condition. Thus, disturbance effects should be interpreted relative to predisturbance conditions in any search for generality. We should search for repeated patterns of system response to disturbance that change along gradients, thus resulting in general hypotheses about ecosystem dynamics that will help us formulate recommendations for wilderness management under given circumstances.

Second, the species of a particular landscape have different life history traits, responses to environmental gradients and disturbance, and dispersal and gene flow characteristics. Different disturbances promote different species. This makes simple labels—for example, with regard to successional role—difficult to apply. For example, Vogl (1974), when abandoning early vs. late successional terminology for grassland species, classified them as increasers, decreasers, invaders, retreaters and neutrals relative to a particular fire event. A straightforward corollary of species differences is that a given disturbance will be good for some, but not all species. Furthermore, a given disturbance may occur at different times relative to species life history, resulting in a range of effects on a particular species (Pavlovic 1994). Clearly, a mix of conditions and processes is required for all species to reproduce and persist. The question then arises, whether a given wilderness area is large enough for such dynamics to occur, or whether management needs to influence the intensity and return interval of disturbances within the given boundaries in order to allow for regeneration.

Third, given the first two principles, we deduce the following: Species differences span a different range of absolute values in different ecosystems. For example, all forests have trees with differences in height growth rates after disturbance; the maximum height growth rates of disturbance-responding trees varies systematically from the tropics (up to 2-3 m per year) to the temperate zone (up to 1 m per year),

**Table 1**—The five “givens” of disturbance management. These factors cause variation in ecosystem response to disturbance and make generalization difficult across ecosystems.

Factor	Comments
Absolute rates vary	While disturbance dependent plants often grow more quickly than other species, absolute values (the range of expected maximum and minimum rates) vary systematically and geographically with physical factors and resources
Species vary	The species living in any landscape vary in their response to disturbance; individual species respond to a given disturbance differently depending on life stage or season and often have plastic responses to environment.
Absolute response varies	Given the first two factors, responses to disturbance vary across ecosystems and there will be considerable variation, at least locally, in how a particular ecosystem responds to a particular disturbance.
Two-fold preconditioning	Ecosystems are the result of past events; disturbance response varies with the history of prior disturbances in ecosystems. Species have been exposed historically to disturbances; they have traits that reflect survival over those past conditions.
The spatial template	The configuration of habitats in landscapes determines critical parameters like area and isolation which influence the propagation of disturbances regardless of physical environmental factors and species present.

to the boreal forest (up to 0.3 m per year). These values are 5-10 times greater than the height growth rates of shade tolerant species in the same ecosystems. Species richness also varies along the latitudinal gradient. The consequence is that while all three areas have disturbance-dependent "fast" growing species, the number of such species and their absolute rates of growth vary with the physical environment. Similar comments could be made about other life history traits and the patterns of succession derived from them. We believe nonetheless that the ranges of absolute values and the patterns of system responses vary systematically; thus, it will be possible to work towards generality in understanding the effects of disturbances across ecosystems.

Fourth, the characteristics of species and ecosystems are themselves the products of past events on evolutionary and ecological time scales. This produces a two-fold preconditioning in ecosystem response to disturbance. Species responses are preconditioned, in the sense that their physiological abilities and life history traits are the result of evolutionary exposure to past conditions. The history of an ecosystem also influences its range of possible responses to present events because it controls species presence and resource levels. McCune (1984) showed, for example, that differences in present vegetation of three neighboring valleys with identical environmental conditions were due to historic factors: the different past influences of fire and settlement within these three valleys. The evolutionary and historic context of species and ecosystems means that managers, in some sense, will always need to investigate the nature of past conditions, in order to understand the range of current options.

Finally, the surface of the earth forms a unique template for each wilderness we manage. The physical template sets the pattern of environmental gradients and the size and position of habitat patches. These, in turn, affect disturbance regime and responses to other changes (such as, climate variation). Even if we had abstract rules for species traits, ecosystem characteristics, disturbance, scale and boundary, how these play out in a given situation is contingent on the underlying geophysical template.

The differences among species and ecosystems mean that generality of response to variation in disturbance, scale and boundary must be developed as a function of variation in absolute properties, such as the shape of the physical template, dispersal distances, seasonal migrations, birth rates, death rates, regeneration patterns and productivity. A corollary is that there will always be a need to understand the history, characteristic dimensions and rates of change of the ecosystems we manage. The significance of disturbance, size and boundary will vary among ecosystems, depending on these characteristics. If we are interested in generality about disturbance (or scale or boundary), we should examine variation in disturbance along a continuum of environmental conditions and ecosystem properties. This would point the way to the development of general principles that could be adapted to particular wilderness areas.

## **Disturbance and Disturbance Regime**

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Natural ecosystems are dynamic. Changes can be gradual (succession, climate change, geomorphologic evolution, soil

development), annual (seasonality), interannual and semiperiodic (hydrologic flux, the ecological consequences of the Southern Oscillation in Pacific Ocean surface temperatures that produces El Nino/La Nina climate variation) or abrupt and destructive (disturbance) (DeAngelis and White 1994). These processes of change interact and, with topography and geology, they create the spatial variation we observe at any one time. Whether we look at the relatively recent past or at evolutionary time scales, historical patterns and processes have shaped modern ecosystems and their biota.

Disturbances are relatively discrete events in time that disrupt ecosystem, community or population structure and change resources, substrate availability or the physical environment (White and Harrod 1997; White and Pickett 1985; White and others 1999). A subset of this definition is that proposed by Grime (1979): disturbance as the destruction of biomass. Although these definitions are absolute (as opposed to definitions that suggest that disturbance is a departure from normalcy), the magnitude of disturbance in a particular ecosystem must be expressed in relative terms (White and Pickett 1985)—that is, by the change in biomass in relation to predisturbance biomass or the change in resources in relation to predisturbance resource levels. Responses to disturbance will vary with the magnitude of change relative to the predisturbance conditions.

Disturbances are described in terms of their spatial characteristics (area, shape, spatial distribution), temporal characteristics (frequency, return interval, rotation period), specificity (to species, size class, successional state), magnitude (force, intensity, severity) and synergisms (interactions among disturbances) (White and others 1999). Disturbance occurrence and characteristics vary with climate, topography, substrate, and history. Together, the disturbances that occur within a particular landscape or ecosystem define its disturbance regime. Documenting historic and modern disturbance regimes has been a major focus of wilderness science over the past three decades, and the restoration of historic disturbances, particularly fire (Baker 1994) and flooding (Dahm and others 1995), is one of the most common restoration goals.

Some 15 kinds of natural disturbances occur in North America (Table 2; White and others 1999). Under some circumstances, almost all of these present problems of boundary and scale in the sense that they disturbance can move across boundaries and the scale of their dynamics can exceed the size of wilderness. However, five kinds of disturbance are particularly important because they routinely impinge upon or move across boundaries and because they are, at least potentially, under management control: fires, hydrologic flux (floods, associated alluvial erosion and deposition and water level fluctuation in basins), coastal erosion and deposition, episodic outbreaks of heterotrophs (insects, pests and diseases and grazing animals) and animals that routinely alter ecosystem structure (burrowing animals, beavers). Three other disturbances may move across wilderness boundaries but are restricted to particular topographic and geological circumstances: wind-caused substrate movements (dune migration), gravity-caused substrate movements (avalanches, debris flows) and volcanic eruption. Several other disturbances (drought, salinity changes and shoreline battering by ice and waves) become boundary issues when land uses surrounding a natural area affect their occurrence. Conservation design might help with some

**Table 2**—Boundary and scale issues associated with natural disturbances in North American wilderness. “Design principles” indicate those disturbances for which preserve design can play a strong role in the occurrence of boundary and scale issues. “Management” indicates those disturbances that are directly managed as disturbance forces (“Dist.”) or are indirectly managed through influence on ecosystem structure (“Struct.”). “Surrounding land use” indicates those disturbances whose occurrence in wilderness is influenced by surrounding land use.

Disturbance	Boundary issues	Scale issues	Design principles	Management		Surrounding land use
				Dist.	Struct.	
Wind	Rarely	Rarely	Rarely	No	No	Yes (edges only)
Fire	Yes	Yes	Yes	Yes	Yes	Yes
Hydrologic flux	Yes	Yes	Sometimes	Yes	No	Yes
Pest outbreaks	Yes	Yes	Yes	Yes	Rarely	Yes
Animals/structure	Yes	Yes	Yes	Yes	Rarely	Yes
Dune movement	Rarely	Rarely	Rarely	No	Rarely	Rarely
Substrate movement	Rarely	Rarely	Rarely	No	Rarely	Rarely
Coastal erosion/dep.	Yes	Rarely	No	No	Rarely	Yes
Drought	Rarely	Rarely	No	No	Rarely	Yes
Freezes	No	Rarely	No	No	No	No
Cryogenesis	No	Rarely	No	No	No	No
Ice storm	No	Rarely	No	No	No	No
Salinity changes	Rarely	Rarely	Rarely	No	No	Yes
Shore battering	Rarely	Rarely	Rarely	No	No	Yes
Volcanic eruption	No	Rarely	No	No	No	No

disturbances—in the sense of maintaining dynamics within the conservation area and preventing conflicts with surrounding lands—but many occur at such large scales and involve such large forces that they can rarely be designed away as management issues (Table 2).

The five disturbances that frequently raise boundary issues often pose scale issues—issues based on area and dynamic pattern (Table 2). Significantly, the frequency and magnitude of disturbances that pose the most frequent scale and boundary issues are also strongly influenced by climate and can become regional phenomena because of the scale of atmospheric processes, as discussed below.

It is not just the disturbance force that we should consider in scale and boundary issues. Disturbance in natural areas sometimes threatens property or economies outside these tracts. The perception and values of people outside the natural area will influence management options for disturbances within it—an important kind of boundary issue in itself.

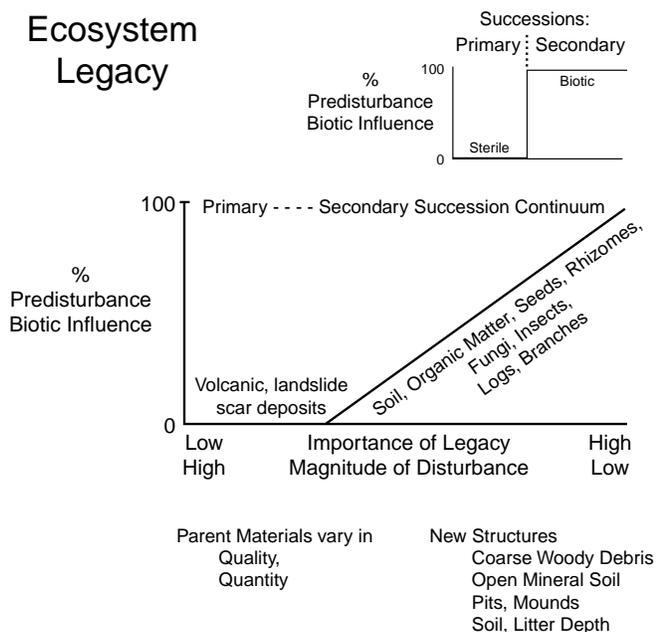
During the past 20 years, research on the role of natural disturbances in ecosystem dynamics has expanded the kinds of disturbances studied, the geographical distribution of places studied and the spatial and temporal scales of study. The process of disturbance, called nudation by Clements (1916), has been a rich area of study and has been found to be a source of variability in ecosystems. In the following paragraphs, we summarize five findings of the past two decades of research about the process of disturbance (see White 1979, White and Pickett 1985, and White and others 1999 for reviews of the disturbance literature more generally): (1) disturbances produce a continuum of conditions between extremes termed primary and secondary succession and leave behind a wide range of legacies from the predisturbance ecosystem; (2) there are feedbacks and interactions between disturbances; (3) disturbance probability varies with climate; (4) disturbance regime is influenced by landscape pattern; and (5) disturbance regime can be altered by exotic species invasions.

## The Continuum From Primary to Secondary Succession and Ecosystem Legacies

Text books have commonly defined primary and secondary successions as discrete: Primary successions occurred on sterile sites without the imprint of previous occupation by living things, whereas secondary successions occurred on sites previously occupied and affected by living things. Recent studies of the effects of disturbance, however, show that there is a continuum between these extremes (Swanson and Franklin 1992) and considerable variation within each (Figure 1). Disturbances create a variety of primary successions that vary in the quality and depth of the parent material. They also produce a variety of secondary successions, which differ in the amount and distribution of organic matter after disturbance and vary also in other legacies left by the previous ecosystem.

The residual material from the previous ecosystem—including organic matter, seeds, rhizomes, plants, fungi, insects and other animal populations—has been termed biological or ecosystem legacy (Franklin 1989; Swanson and Franklin 1992). This legacy influences site environment, the location of organisms that affect disturbance recovery, and recruitment. The magnitude of disturbance and the legacy after disturbance also affect the success of various plant colonization strategies. After fire in the Swedish boreal forest, for example, Schimmel and Granstrom (1994) found that depth of burn controlled the dominant colonization strategy: Shallow burns were followed by resprouting and regeneration from perennial rhizomes, medium burns were followed by regeneration from the seed bank, and deep burns were followed by colonization of wind dispersed species. Nakishizuka and others (1993) showed that as the amount of residual material decreased, the importance of wind-dispersed species increased on Japanese avalanche scars.

## Ecosystem Legacy



**Figure 1**—The continuum from primary to secondary succession based on ecosystem legacy and the effects of disturbance. The x-axis is a gradient of increasing ecosystem legacy and decreasing disturbance magnitude and the y-axis represents the influence of the pre-disturbance ecosystem on recover from low (0%) to high (100%). The smaller diagram in the upper right presents the historic and overly simplified definition of primary (no influence of the pre-disturbance ecosystem) and secondary (100% influence) succession.

Ecosystem legacies also influence the likelihood of further disturbance and thereby the length of recovery interval and the amount of successional change. For example, the amount of organic detritus after a disturbance event determines fuel levels and the occurrence of fire.

Disturbance also creates new structures—new arrangements of the substrates and organic matter in an ecosystem—compared with the pre-disturbance stand. The tangled branches of a windfall have been shown to provide a refuge for seedlings against deer browsing in U.S. deciduous forests (Peterson and Pickett 1995). Snapping of tree boles increases light to the intact forest floor; uprooting of trees, by contrast, increases light, but also creates pit and mound microtopography and exposed mineral soil. Similarly, spring and summer fires vary in impacts on canopy and forest floor. Whereas some species respond to the increased light alone, others depend on the new microsites and particularly on soils with no covering of leaf litter and low competition for space (Forcier 1975; Harmon 1982). Such sites often have high germination rates.

In short, disturbances are not equal, and the pattern of recovery is a function of the kind and intensity of disturbance and the legacy of the pre-disturbance stand. The legacies created by disturbance often create internal heterogeneity within the ecosystem, with different species favored in different kinds of patches. For example, fires do not burn at uniform intensity but have patches of relatively high and low intensity. These patches are left with different amounts of organic matter and have different mortality levels of the plants from the pre-fire stand. Such patches present a diverse

array of postdisturbance microsites for plant recovery. Heterogeneity of disturbance effects may also be important in recovery because less disturbed areas may act as sources of colonists for more disturbed patches.

One of the ways that some human disturbances differ from natural disturbances is in the different ecological legacies that remain after disturbance. For example, Hansen and others (1991) described the differences in coarse woody debris of managed and unmanaged forests in the northwestern U.S. They found that logged stands lie outside the bounds of naturally disturbed stands in terms of several measures of ecosystem structure, including the sizes and amounts of coarse woody debris.

## Disturbance Interactions and Feedbacks

Interactions among disturbances are reported for all ecosystem types (see review in White and others 1999). The feedbacks between disturbances can be positive; that is, one disturbance promotes the next, so repeat disturbances are likely. For example, gaps expand over time as gap edge trees are exposed to wind (Runkle and Yetter 1987). Fire-damaged trees are vulnerable to fungal infections, making the trees more vulnerable to future wind disturbance (Matlack and others 1993). Disturbance feedbacks can also be negative, as when one disturbance delays another. Romme (1982; see also Romme and Despain 1989; Romme and Knight 1981) showed that hot fires burn fuels that take centuries to reaccumulate in Wyoming; hot fires are thus spaced by centuries. However, those hot fires, once they start, can burn across stands with varying fuel levels (Johnson and Wowchuk 1993). In Colorado, Veblen and others (1994) showed that avalanche scars restrict fire spread, thus limiting fire size and increasing recurrence intervals. Veblen and others also showed that spruce trees become vulnerable to spruce bark beetles only after 70 years of postfire succession. Fire and beetle outbreaks thus tend to be nonoverlapping in space as well.

Land use history and the history of past natural disturbances can alter the frequency and magnitude of current disturbances (Baker 1995). In central New England, Foster (1988; Foster and Boose 1992) showed that hurricane damage increased with stand age, but at a different rate for old field pine compared to hardwood forests. Tyrell and Crow (1994) showed that gap sizes increase with stand age as tree size increases in mesic deciduous forest, making older stands more patchy in light regime than younger stands. In the Great Smoky Mountains, Harmon (1984) found that fire-caused mortality at a given fire intensity decreases with time since last fire as trees age into fire-resistant size classes (bark grows proportionally faster than diameter in fire-adapted species). If fires are too far apart, trees survive into fire-resistant size classes, changing the effects of future fires. In general, stands can be preconditioned to current disturbance by their history of past disturbance.

## Disturbance and Climate Variation

The past decade has seen demonstrations of strong links between disturbance and climate (Clark 1988; Johnson and Larsen 1991; Johnson and Wowchuk 1993; Nash and Johnson 1996; Swetnam 1993; Webb and Betancourt 1992). Human-induced climate change will influence disturbance regimes,

as well as other ecosystem processes (Romme and Turner 1991). Swetnam and Betancourt (1990) demonstrated that the area burned in the American Southwest from 1905-1990 varied with an index of the intensity of the Southern Oscillation. They also showed that climate can synchronize vegetation dynamics over large areas. Over a 300-year sequence, an average of 5-10 sites experienced fire each year, but there were 20 unusually dry years in which fire events were many times more frequent than this average.

Johnson and Wowchuk (1993) produced similar findings for central Canadian boreal forest, reporting that years with persistent high-pressure systems had more lightning strikes, more ignitions, larger fires and higher fire intensities and rates of spread than other years. Fire size was particularly important: 2% of the fires burned 99% of the area. During persistent highs, temperature was warmer than normal and precipitation lower for days to weeks. Fuel moisture was low, which resulted in more fires, but fires burned across different fuel conditions. As a result, fires were strongly correlated with weather but weakly correlated with fuel conditions—fuel loading varied less than weather—hence successional age and fire suppression were relatively unimportant in fire occurrence. Johnson and others (1995) have shown that there was a shift in fire regime in their study area ca. 1730. Warmer and drier conditions before 1730 produced a fire rotation of 50 years, but this increased to 90 years after 1730.

Regional synchronization by climate variation has important consequences for human societies because it means that fire years for one place are correlated, at regional spatial scales, with fire years for all places (the scale of such synchronization will vary with the scale of climate effects). Regional synchronization stretches management resources thin. There are also consequences for conservation: Regional synchronization invalidates metapopulation models that describe persistence of species as a function of the independent dynamics of local populations. More generally, all populations, even those not connected by migration and gene flow, would experience parallel fluctuations under regional synchronization. Age structures of populations would be similar across space, and extinction risks would not be independent in a given year. Such a situation would create problems for a “put your eggs in different baskets” strategy of allocating more resources to separate populations, rather than lowering extinction risk within a single population (see discussion in White 1996).

Climate variation is also directly tied to estimates of flood regimes. Webb and Betancourt (1992) showed that the calculation of the 100-year flood event in Tucson, Arizona, was highly dependent on the period of time used in the models. Using data from 1930-1960, the 100-year flood discharge was 300 cubic meters per second and was dominated by the pattern of monsoonal storm floods. After 1960, the 100-year flood discharge was over 1,000 cubic meters per second, an increase due to increased tropical cyclone floods, as well as increased monsoonal storm floods. A change in atmospheric flow altered the sources and amounts of precipitation to the Santa Cruz River.

## **Disturbance and Landscape Configuration**

The probability of disturbance at one point is influenced by the structure and composition of the vegetation surrounding

that point and the occurrence of disturbances within the surrounding area (Knight 1987; Rykiel and others 1988; Turner 1989; Turner and others 1989). Some disturbances, such as fire and insect outbreak, spread contagiously through a landscape. Such disturbances may affect sites that otherwise have a low probability of disturbance. Humans alter disturbance regimes not only by affecting the agents of disturbance (for example, in fire suppression, Baker 1992a), but by altering the pattern of vegetation on the landscape and enhancing or reducing heterogeneity of patches. This can both increase and decrease disturbance frequency (Franklin and Forman 1987). It has been hypothesized that large-scale logging in northeastern Maine has created large areas of even-aged stands of balsam fir through which insect outbreaks spread quickly. It has been argued that forest fragmentation has reduced fire size in the longleaf pine stands of the southeastern U.S. (Frost 1993). Bergeron and Brisson (1990) have shown that lake islands in the Canadian boreal forest have different fire regimes than the nearby mainland. Many investigators have shown that fire size plays a larger role than the number of fire ignitions in the boreal forest—five percent of the fires have been said to burn 95 percent of the area (Johnson and others 1995). Fire size is affected by human activities and land use patterns.

In a comparative example with implications for understanding the interaction of disturbance regime and landscape configuration, Minnich (1989) showed strong differences in fire size and frequency between areas with natural fire-regimes in Baja California and those with fire suppression management in Southern California despite overall similarity in the amount of land burned per century in the two areas. Without fire suppression, vegetation heterogeneity and ignition rate was high, but the size of burned patches was low, while under fire control, vegetation was more homogeneous, ignition rate was low, but size of burned patches was high because of rapid fire spread through homogeneous fuels.

## **Disturbance Regime and Exotic Species Invasions**

Exotic species invasions are now one of the major human influences in natural areas. Among invaders, some cause particularly drastic effects because they alter fundamental processes within ecosystems, including disturbance regime. Billings (1990) showed that brome grass invasion alters fire regimes in the western U.S. Bodle and others (1994) proposed that exotic tree species in the Everglades transpire more water than native species, thereby lowering the water table and altering fire regimes. Disturbance can also foster exotic invasions by removing established competitors (R. White and P. S. White, unpublished data).

## **Scale, Disturbance, and Wilderness Management**

Since the earliest disturbance studies, investigators have asked whether small-scale dynamics can lead to a dynamic equilibrium at larger scales (see reviews in White 1979; White and Pickett 1985; White and others 1999). An early discussion of the consequences of disturbance dynamics concluded that the minimum area for reserves should be

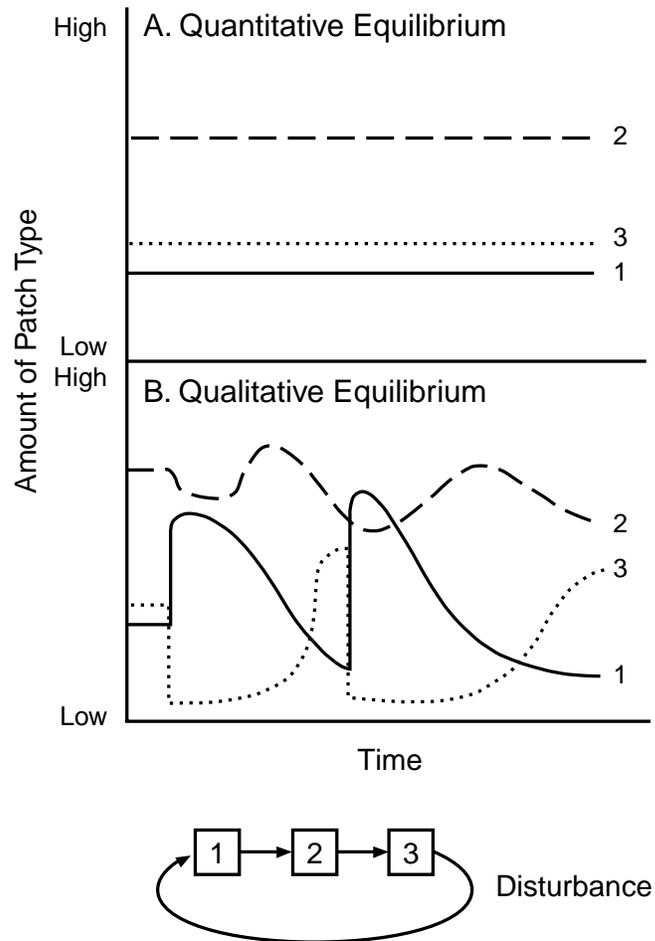
based on the area required for successional states and implied the idea of the dynamic equilibrium (Pickett and Thompson 1978; White 1979).

If the creation of newly disturbed patches of low biomass and early successional species is balanced by succession to higher biomass and older aged vegetation elsewhere in the same landscape, a dynamic equilibrium is possible (Shugart 1984). The distribution of land into various patch states would remain the same, even though the location of the various patch types would shift in space. At any one time, the landscape would have a characteristic patchiness in age and structure—and it would exhibit constant and predictable structure at large spatial scales, despite high variance at smaller scales (Busing and White 1993; Smith and Urban 1988; Urban and others 1987). Species both dependent on and sensitive to disturbance would persist. If a mix of species with different successional strategies is always present, the rate and pattern of succession will also be stable—no species will be missing from succession because of extirpation or dispersal limitation. Such a landscape would be robust in retaining its biodiversity over time and would be relatively easy to manage: Natural processes would maintain the dynamic equilibrium of species and patch types. It is one of the major challenges for conservation management to understand the spatial and temporal scales at which natural processes and disturbance regimes operate, and whether a particular conservation area is large enough for the processes to result in dynamic equilibrium. Often, boundaries of wilderness areas are administrative rather than functional, so that processes outside nature conservation areas affect internal dynamics and internal dynamics affect outside areas.

Questions about equilibrium, scale and process have been asked specifically at the population level. Zedler and Goff (1973) showed that sugar maple (*Acer saccharum*), a shade-tolerant tree, had a reverse-J, all-aged population structure at relatively small scales, but quaking aspen (*Populus tremuloides*), a shade-intolerant tree, attained this stable distribution only at scales large enough to include many independent patches of different successional ages. Reproduction is absent within populations of adults and age structures are unbalanced if observed at small scales of time and space. Shifting sites of reproduction are one sort of metapopulation dynamics (see discussion in White 1996). In such cases, the absence of reproduction within adult populations is to be expected; persistence depends on new sites becoming available for establishment within the years of reproductive maturity and within the dispersal distance of the adults.

Given the potential importance of patch dynamic equilibrium to wilderness management, we should ask what conditions would tend to produce equilibrium, whether such conditions are common in nature and whether human influences have affected the likelihood of a dynamic equilibrium. We start with a more detailed discussion of the nature of dynamic equilibria.

Four kinds of patch dynamic equilibrium are described in the literature (White and others 1999): (1) persistence or qualitative equilibrium; (2) the shifting mosaic, steady state or quantitative equilibrium; (3) the stable trajectory or stationary dynamic equilibrium; and (4) the statistical equilibrium. These are briefly described below (see also Figure 2).



**Figure 2**—Quantitative and qualitative equilibrium. The relative importances of three successional states (1, 2 and 3) across a hypothetical landscape are shown through time. A. Quantitative equilibrium in which the three states occupy a constant proportion of the landscape through time. B. Qualitative equilibrium in which the three states fluctuate in abundance but all persist.

**Persistence or Qualitative Equilibrium (DeAngelis and Waterhouse 1987)**—This is the least stringent of the definitions. Species, successional states and patch types all persist through time, but they may fluctuate widely in abundance. The key criterion is that the species and patch states are never lost from the landscape.

**The Shifting Mosaic, Steady State, or Quantitative Equilibrium (Bormann and Likens 1979; Cooper 1913, 1926; Heinselman 1973; Sprugel 1976)**—This definition of equilibrium is more narrow, in that it requires that the species abundances and the fraction of the landscape in each patch type remain constant through time despite, shifts in spatial location.

**The Stable Trajectory or Stationary Dynamic Equilibrium (Loucks 1970)**—This is an equilibrium in which the same successional sequence repeatedly occurs, despite fluctuation in the abundance of species or the frequency of patch states. The stable trajectory equilibrium requires that

all species important to successional changes have access to a site through continual reproduction, dispersal or seed banks, but not that the species be constant in abundance or present as adults.

**Statistical Equilibrium (Johnson and Gutsell 1994)**— Like quantitative equilibrium, this is equilibrium with a stringent definition. Annual rates of disturbances are not required to remain constant, but may vary considerably from year to year. If the annual proportion of the landscape disturbed, examined over many years, conforms to a statistical distribution such as a negative exponential or Weibull function, mean disturbance rates and landscape conditions will remain stable through time.

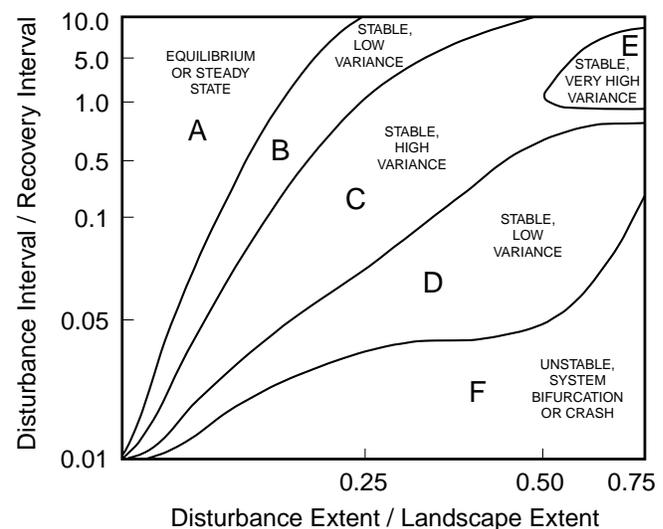
Whether equilibrium is likely to occur and, more particularly, which kind of equilibrium is to be expected, will vary with the size of the disturbance patch, relative to the landscape in which it occurs, and the rate of recovery of the patch, relative to length of the return interval between disturbances (Turner and others 1993). For example, when patches are small relative to the landscape where disturbance interval is long enough to allow recovery to the original condition (that is, biomass levels), and where dynamics on adjacent patches are independent, each patch will exhibit the full range of patch state values over time (biomass levels, successional states) and the average of a large collection of patches will be a constant (White 1979; White and Pickett 1985). Using simulation models, Shugart (1984) suggested the 1:50 rule: When independent patches that are smaller than  $1/50^{\text{th}}$  of the size of the landscape in which they occur, and when each patch recovers to the undisturbed biomass level before becoming vulnerable to disturbance again, biomass averaged across all patches is constant. This is one formulation (based on biomass) for shifting mosaic or quantitative equilibrium. In Shugart's model, disturbance intervals were set by successional time because patches became vulnerable to disturbance only as patch age reached a maximum. As a general principle, White and Pickett (1985) suggested that a feedback between disturbance risk and time since disturbance would make an equilibrium patch dynamics more likely, given independent dynamics of small patches in a large landscape and lack of contagious spread among patches. However, when disturbances can spread contagiously from patch to patch, increases in disturbance susceptibility with stand age may contribute to the synchronization of disturbance across large areas. Such appears to be the case with the Yellowstone fires of 1988. These fires resulted in large fluctuations rather than less: Hot fires spread to less susceptible patches, leading to very large patch sizes (Turner and others 1993). White and Pickett's (1985) condition that risk of disturbance increases through successional time is also violated when one disturbance increases the likelihood of subsequent disturbance.

Turner and others (1993) further clarified the expectation by expressing the spatial and temporal scale issues on two axes and by adding variance to the idea of dynamic stability (Figure 3). The first axis was the amount of disturbed area relative to landscape area. As this ratio decreases, they predicted the chance for a dynamic equilibrium increased. The second axis was the length of the interval between disturbances, relative to the time required for complete recovery to undisturbed conditions. As this ratio increases (as more time is available for full recovery), the chance for a dynamic

equilibrium increases. By creating a two dimensional graph of these two ratios, they defined a range of conditions from stable (species and successional patches persist) to unstable (species and successional patches do not persist) and further showed that stable landscapes could nonetheless exhibit a range of behaviors from low variance to high variance. A stable landscape with variance fits the definition of qualitative equilibrium—persistence of species and patch states despite fluctuation in abundance. They suggested that the ecosystems of Yellowstone National Park, which are characterized by infrequent but very large and intense fires, would fit the definition of a stable landscape with high variance.

In situations in which patches are small relative to landscape area, the patches have independent dynamics, disturbance regime is constant, and the patches recover fully between disturbances, patch dynamic equilibrium can occur in both a qualitative and quantitative (low variance in abundance) sense. If the rate of disturbance is controlled in part by the community itself (for example, vulnerability to disturbance increases with successional time or plant size or age), disturbances will have a relatively constant return interval, and statistical equilibrium of disturbance regime may also occur. These conditions may hold for small-scale gap dynamics in some forests, patch-wise mortality in heathland communities (Watt 1947), and the dynamics of inland dunes (Jentsch, unpublished data). A classic example is the fir wave phenomenon in montane fir forests (Sprugel 1976).

In contrast, where patches are large, where disturbance in one patch affects the probability of disturbance in neighboring patches regardless of patch conditions there, where disturbance regime is strongly linked to climate variation, and where disturbance intervals are at best loosely correlated with the time between disturbances, landscapes are either nonequilibrium or, perhaps, in qualitative equilibrium.



**Figure 3**—Stability and variance as a function of two ratios: the relation of disturbance patch size to landscape area (x-axis) and disturbance interval to recovery interval (y-axis) (redrawn from Turner and others 1993). When disturbance extent is small relative to landscape area, stability is promoted. When disturbance interval (the time between disturbances) is long relative to recovery interval (the time needed for recovery to the pre-disturbance state), stability is promoted.

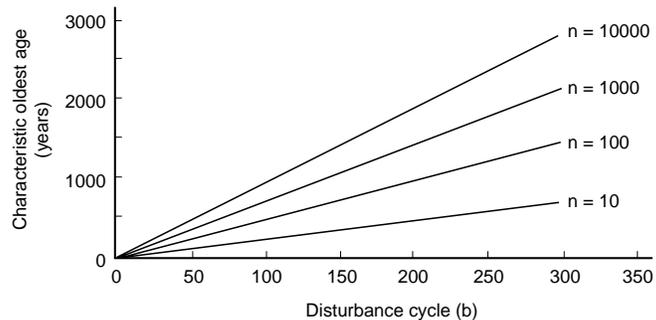
Indeed, E. A. Johnson (Johnson and Gutsell 1994; Johnson and Larsen 1991; Johnson and Wowchuk 1993; Johnson and others 1995; Nash and Johnson 1996) has argued that fire regime in the boreal forest is characterizable but not fixed, that infrequent but very large fires dominate forest dynamics, and that fuel buildup with time since fire is unimportant to fire occurrence because of the overriding influence of climate.

The question of dynamic equilibrium is a fundamental one in wilderness management (Baker 1989a, 1992b, 1994; Pickett and Thompson 1978; Sprugel 1991; Turner and others 1993). It is one aspect of the questions about the “balance of nature”. Conservation managers often have the goal of a situation in which species and habitat types persist even if they fluctuate in abundance—the less stringent equilibrium known as persistence or qualitative equilibrium. In essence, we have to ask: How closely do we have to replicate disturbance processes to get persistence of all biota and patch types? Because human use of the landscape has reduced the size of protected landscapes, the ratio between disturbance area and landscape area has mostly increased, which would tend to make landscapes less stable and higher in variance. In nature, persistence occurred despite high variance because of large size and juxtaposition of unlike conditions. Disturbances create patchiness across landscapes that, historically, allowed both disturbance-dependent species and disturbance-sensitive species to persist. The mix of newly disturbed conditions and refuges from disturbance is critical to nature’s resilience.

Management for persistence may be particularly challenging in small protected areas in which fragmentation has increased the ratio between disturbance size and landscape size, decreasing stability and increasing variance relative to unfragmented landscapes. One consequence of increased temporal fluctuations in these small landscapes may be the loss of species that require either early- or late-successional conditions.

The relationship of wilderness size to the area needed for a patch dynamic equilibrium is therefore an important question. While larger is always better, is wilderness size ever large enough to encompass equilibrium dynamics? As early as 1963, Leopold and others wrote that few of the world’s parks were large enough to be self-regulating ecological units. While they considered seasonal animal migrations and the source areas of park waters, subsequent research on landscapes with large fire sizes (such as, Baker 1989a; Johnson and Gutsell 1994; Turner and others 1993) has also indicated that quantitative equilibrium is rare except for the smallest disturbance patches in the largest areas. The result is that wilderness managers are likely to have to take a role in monitoring and maintaining patch variability, particularly in smaller wilderness blocks or where natural fires cannot be permitted to burn uncontrolled. A related question concerns the time necessary for recovery after disturbance. If wilderness size in relation to disturbance patch size is too small to allow for dynamic equilibrium, then temporal parameters like return intervals or frequency of disturbance might have to be controlled by wilderness managers if all species are to reproduce.

The interaction of disturbance regime with landscape area has implications for our understanding and management of old growth (Figure 4; Johnson and others 1995). In natural landscapes, the occurrence of disturbance has a



**Figure 4**—Implications of disturbance rate and landscape area for the age of the oldest aged patch (redrawn from Johnson and others 1995). Under a given disturbance regime (disturbance cycle), the larger the landscape (the higher the number of patches,  $n$ ), the greater the maximum age expected in the landscape for individual patches (these are the patches escape disturbances for longer than the average for the landscape as a whole). For a particular landscape size (as represented by  $n$ ), the longer the disturbance cycle, the greater the characteristic oldest aged patch.

stochastic component; by chance, some patches will experience at intervals shorter than the mean, while others will escape disturbance for much longer periods. These rare, old patches will represent the tail of the statistical distribution. The larger the wilderness relative to disturbance patch size, the longer the tail, and the older the maximum expected age. Wilderness area thus has implications for how old patches can become—for a given disturbance cycle and without management intervention. The spatial variation in ecosystem structure is predicted to be a function of disturbance rate and landscape area.

Bergeron and others (1998) applied this idea in a comparison of two landscapes, one managed on a 100-year logging rotation and the other with a 100-year natural fire rotation. Despite similar mean disturbance return intervals, the two boreal forests would have very different stand age distributions. The managed forest would have equal numbers of stands in all age classes up to 100 years, but nothing older. The distribution of patch ages in the wilderness landscape would follow a negative exponential or Weibull distribution of time since fire; this landscape would thus have both a higher proportion of young stands and a larger portion (~1/3) of stands older than 100 years.

## Historic Range of Variation and Natural Range of Variability

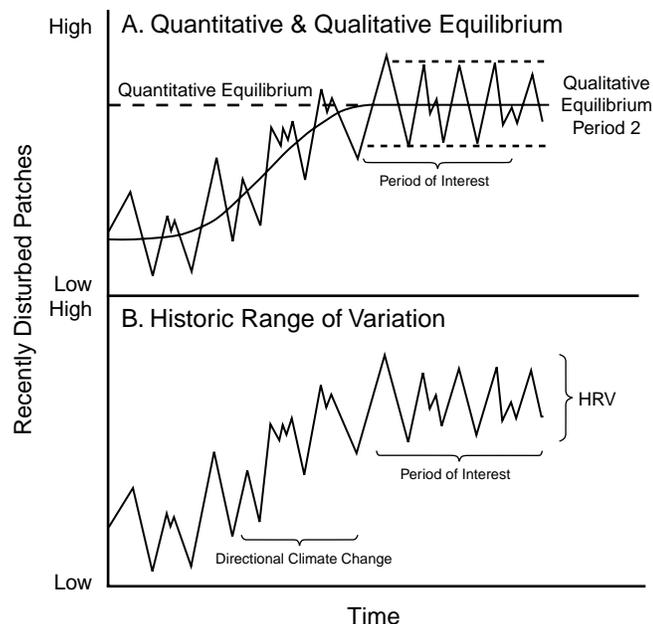
Whether we look at the relatively recent past or at evolutionary time scales, historical patterns and processes have shaped modern ecosystems and their biota. Documenting the history of ecosystems is thus a key to understanding and managing their current dynamics. It is also natural to ask whether current conditions and dynamics have historical precedence. The historical range of variation approach (Figure 5; Landres 1992; Landres and others 1998c; Morgan and others 1994; Swanson and others 1994; Swetnam 1993; Wright and others 1995) goes beyond a general recognition of the importance of history to ask a more specific question: Are current dynamics within the range of values that characterized the

ecosystem in the past? The concept of the natural range of variability is similar; here we suggest that this concept be applied to the variation in space and time for an ecosystem without the constraint of an arbitrary historic record.

Wilderness exhibits neither static and predictable conditions nor totally random or unpredictable ones. Nature has variation—but variation within bounds. This is presumably why extinction is rare, despite great fluctuation in local abundances. However, the historic range of variation poses several difficult questions: What ecological parameters should be considered and at what spatial and temporal scales should these be evaluated? Over what historical period should variability be assessed? Can past conditions be reconstructed with acceptable accuracy and resolution? Do parameters of interest remain within well-defined bounds around a stable long-term mean, or does the amount of variation or the mean change through time? Will novel conditions such as exotic species invasions or a changing global climate render past conditions irrelevant? Regardless of the answers to these questions, documenting the history of the ecosystems is an essential step in understanding their dynamics and trajectories.

## Boundary, Disturbance and Wilderness Management

Disturbances occur at particular places and either have indirect effects on nearby areas or spread contagiously to them. Because of this inherent importance of spatial



**Figure 5**—Quantitative equilibrium, qualitative equilibrium and the historic range of variation (HRV) illustrated by trends in the number of recently disturbed patches in a hypothetical landscape undergoing two periods of relative stability and a period of directional climate change. A major challenge in this approach is the development of data of sufficient spatial and temporal resolution, the available time periods of record and the inherent rarity of extreme, but nonetheless important, events.

location, wilderness boundaries raise issues for disturbance management (Angelstam 1992; Forman 1990; Schoenwald-Cox and others 1992; Shafer 1994). This section describes boundary characteristics and examples of cross-boundary problems.

Natural boundaries are rare, relatively gradual, old or all three. By contrast, administrative boundaries are ubiquitous, relatively sharp (or become so through time) and relatively recent. The effects of boundaries vary with the amount and rate of ecological change across them and their influence on natural processes like individual movement, the physical environment and disturbance spread (Landres and others 1998a, 1998b).

Whether or not boundaries affect natural processes, they can affect management in other ways. Boundaries often separate public from private ownership or conservation management from other land uses. Even public lands managed by a single agency may have internal zones for different purposes (such as, natural area protection, historic scene management and recreation) and with different management plans. Just as with the ecological contrast that exists or develops on either side of administrative boundaries, the contrast in land use and management goals can affect management practices and their ecological outcomes. For example, a natural fire may be perceived as a threat to development outside a wilderness—a situation exacerbated if wilderness attracts residential or other development—to the tourism industry that develops around the wilderness or to the safety of traffic in areas affected by smoke.

Single agency lands may also be compartmentalized by division into management units, even when the overall management goals are the same for these subunits. Managing disturbances within these units may impose constraints similar to the management of individually small wilderness areas.

## Boundary Placement: Natural, Artificial and Historic Boundaries

Some administrative boundaries follow natural features, such as rivers, bodies of water or watershed divides, while others are made up of arbitrary survey segments (Newmark 1985; Theberge 1989). Those that follow natural features usually are derived from topography which, in turn, affects environmental gradients, the flow of water and the position of land relative to water bodies. However, even topographically determined boundaries are unlikely to be arrayed with regard to natural processes, such as migration of animals or the spread of disturbances. In some sense, no ecosystems have natural boundaries unless these are set by the natural process with the furthest spatial extent. Boundaries therefore range from arbitrary to natural. Most boundaries only partially encompass natural processes.

Boundaries may also be determined by previous human land use (for example, old-growth forest vs. farmed land). These historical boundaries can also be correlated with natural features—productive and flat valleys were taken by agriculture, with steep and rocky land left in forests. In any case, historical land use boundaries used to determine administrative boundaries are also unlikely to be defined with regard to natural processes.

## Boundary Width, Dynamics and Edge Effect

Management and administrative units are usually delineated by a line on a map with no definable width, although units are sometimes separated by transition or buffer zones of defined width (Figure 6). By increasing the width of a boundary, buffers reduce the rate of change across the boundary (Landres and others 1998a, 1998b). The quantitative description of boundaries and edges is still in its formative stages (Fortin and Drapeau 1995).

Administrative boundaries may begin as boundaries through contiguous natural areas and then develop as ecological boundaries through time. Landres and others (1998a) call these induced or generated edges and note the importance of three characteristics: width (buffers increase the width and reduce the rate of change across the edge), the amount of change (ecological contrast) between ecosystems on either side of the edge, and the rate of change of ecosystem structure across the edge.

If land use sharpens ecological boundaries, edge effects develop. These are not constant, but develop through time. For example, increased wind exposure on an induced edge may result in higher rates of treefall, so that, over time, the edge is transformed as tree density decreases and the density of shrubs and saplings increases. That change causes a change from increased sunlight and reduced humidity at the forest floor on the edge to dense shade and increased humidity later. The age and stability of the edges on an administrative boundary are thus important to its ecological effects.

Edges also vary as a function of position on the landscape. For example, in the north temperate zone, north-facing forest edges receive little direct sunlight, while south-facing edges receive the most direct sun; west-facing edges receive

direct sun during hotter hours of the day than east-facing edges. The penetration of edge effects will also vary as a function of topographic characteristics (steepness, slope position and slope shape) or environmental factors (such as prevailing wind direction).

Edges affect ecological fluxes (Hansen and di Castri 1992; Landres and others 1998a, 1998b; Schoenwald-Cox and Bayliss 1986; Schoenwald-Cox and others 1992): the movement of individuals, propagules, genes, water, soil nutrients, leaf litter, woody debris, and wind. Edges become the semipermeable membranes of natural areas and can act as filters that change both the quantity and quality of the fluxes. Edges may be resistant to flux (for example, fire breaks) or may direct fluxes parallel to the edge (for example, animal movements along, rather than across the edge). Permeability of the edge is a key to understanding boundary effects. Edges can be absolute barriers or barriers with “pores” that are neutral or conducent to movement of individuals, environmental influences and disturbances (Landres and others 1998a).

## Examples of Disturbances that Cross Boundaries

Disturbances that are affected by boundaries include fires, hydrologic flux (flood-caused alluvial erosion and deposition), wind-caused substrate movements (dune migration), gravity-caused substrate movements (avalanches, debris flows), coastal erosion and deposition and episodic outbreaks of heterotrophs that can cause elevated plant mortality (insects, pests and diseases, grazing and burrowing animals). Boundaries can both increase and decrease these disturbances within wilderness. Even when the boundary itself plays no ecological role, the proximity of other land uses and human life and property near wilderness boundaries often brings political pressure to reduce fire, flood and pest outbreaks. We briefly review the three most common disturbances affected by boundaries (Figure 6, Table 3): fires, floods and insect, pest and disease outbreaks.

**Fires**—Forest fragmentation and the permeation of fire breaks, such as roads and land conversion, are widely blamed for the reduction in fire frequency in the longleaf pine forests of the Southeastern coastal plain (Frost 1993). Compartmentalizing this ecosystem has greatly reduced fire sizes and nearby tracts must be ignited by independent lightning strikes. Research in Sequoia-Kings Canyon National Park suggests that ignitions in low-elevation chaparral created fires that burned into montane sequoia groves. These sites of ignition were largely excluded when the park boundary was created (Kilgore and Heinselman 1990; McKelvey and others 1996).

Boundary effects can also increase fire incidence. For example, Habeck (1985) suggested that fire suppression on the edge of the Selway-Bitterroot Wilderness increased fuel loads and increased fire frequency and intensity in western red cedar forests within the Wilderness. Arson fires in Great Smoky Mountains National Park are mainly set on roadsides and park boundaries, increasing fire frequencies on lower slope positions (Harmon 1982).

In addition to fires that move across wilderness boundaries, the smoke produced by fires is a significant management

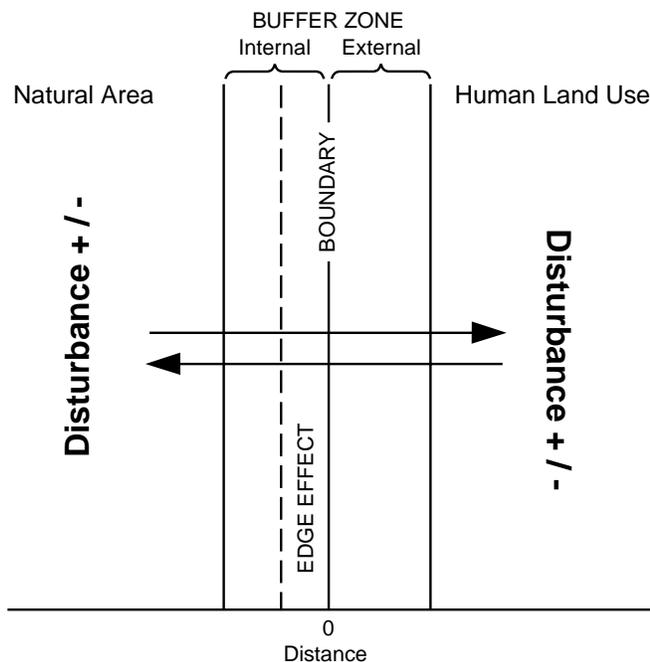


Figure 6—Boundary effects on disturbance (see text and Table 3).

**Table 3**—Disturbances that are frequently influenced by wilderness boundaries.

Disturbance	Increased rate	Decreased rate
<b>A. Effects of surroundings on wilderness:</b>		
Fire	Human set fires in surrounding areas	Suppression in surroundings
	High fuel loads in surrounding areas	Fragmentation, isolation Fewer ignitions Smoke impacts Risk to life and property
Flood	Increased runoff	Impoundments
Insects, pests	Homogeneous vulnerable vegetation	Fragmentation, isolation
<b>B. Effects of wilderness on surroundings:</b>		
Fire	Management fires that escape	Construction of fire breaks
	Management for intense fire	Reduced fuel loads at boundaries
Flood	Unregulated flow	Protection of wetlands, soils
Insect, pests	Native species allowed to outbreak	Heterogeneous vegetation

concern and may constrain the seasons and intensities of fires possible in wilderness landscapes. Changes after fire can also influence downstream water quality. For example, fire can increase nitrate levels in streams, and these may influence aquatic productivity.

**Hydrologic Flux**—Many wilderness areas do not control the headwaters or other parts of their watersheds. The control of water flow by activities outside Everglades National Park (Kushlan 1987), Grand Canyon National Park (Johnson and Carothers 1987; Stevens and others 1995) and many other areas often decreases water flow to these areas, removes the peak floods and creates a higher frequency of droughts. Reduction in flooding reduces scouring and alters succession on riparian bars and banks, leading to regeneration failures in some species (Johnson 1994; Kaufman and others 1997). The artificial stabilization of riverside habitats can cause successional changes and exotic species invasions. Restoration of natural water flows is a major issue for these areas. In Everglades National Park, the problem is made worse in some areas by the invasion of exotic trees able to transpire water at greater rates than the native ecosystems (Bodle and others 1994). As a result, water levels drop, exacerbating lowered levels caused by water impoundments upstream and perhaps leading to more severe fires. Boundary influences can also increase water flow and change water quality within a wilderness. For example, higher runoff from developed areas can increase downward erosion and increase siltation in natural areas.

**Diseases and Pests**—The dispersal of pest organisms can be influenced by landscape characteristics. The control of the southern pine beetle outside Great Smoky Mountains National Park may affect outbreaks inside the Park; in addition, neighbors campaign for control of the beetle within the wilderness areas of the Park itself. Surrounding land use can also increase pest outbreaks in wilderness. For example, it is hypothesized that large scale logging in Canada has led to the development of large, contiguous tracts of second-growth balsam fir and thus has increased the areal extent and severity of outbreaks of spruce budworm.

**Other Boundary Problems**—Preserved wilderness may attract development along its edges. That development brings both property vulnerable to disturbance (by fire) and people in proximity with the edge. Increased populations can also result in higher taking of plants, animals, and fungi, whether legally or by poaching. Increased populations also bring roads (Schoenwald-Cox and Buechner 1992), other disturbances and such activities as horticulture and animal farming that both create corridors for invasion by exotic species and increase the availability of these species for invasion. If wilderness attracts development on its edges, boundaries can sharpen.

Habitat loss and fragmentation around wilderness can also reduce immigration into and out of the wilderness area. Changes in species presence can be random but are often differential: Area-sensitive and poorly dispersing species (whether because of inherent lack of dispersal ability or reaction to the disturbed matrix around the wilderness area) are lost. Some species with important ecological roles, like large mammalian predators, are among those most affected, leading to increases in other populations, such as large herbivores.

## The Importance of Boundary as a Function of Shape and Area

The shape (perimeter to area ratio) of a wilderness tract will influence the relative importance of boundary and scale issues. A large wilderness of more-or-less round shape will have less edge relative to interior habitat and, if its dynamics are characterized by relatively small patch size (relative to its total area), managers may more readily treat the edge and boundary as buffering lands. In the extreme, the boundary would be considered a barrier to the outside, and the wilderness would then become fortress-like (Hales 1989). By contrast, a wilderness with large-scale dynamics or impinging forces along the boundary cannot simply buffer itself from the surrounding world. Yellowstone National Park is an example of the need to integrate management across very large areas (Christensen and others 1989). The

Park is one of the largest in the world and yet has experienced the full range of boundary and size problems.

## Conclusions: Prospects for the Future of Wilderness

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Content is what lies within wilderness, but the future of that wilderness is also dependent on context (Landres and others 1998a). Parks have been considered as islands, in the sense that they may be surrounded by very different land uses. However, Janzen (1986) wrote “no park is an island” in an essay entitled “the eternal external threat” to draw attention specifically to this context. Not only are parks surrounded by different land uses, those land uses may impinge on the values of the natural area itself, in both negative and positive ways. In that sense, the “sea” surrounding a park is not simply a neutral expanse that can be represented merely by the distance of isolation. Rather, the surroundings have a host of influences on the wilderness tract itself.

The relationship of disturbance regime to the size of wilderness will influence management options. Small-scale disturbances in large areas may result in steady state landscapes. Disturbances characterized by large patch sizes are of greater concern. Some large disturbances (fire, hydrologic flux and pests and diseases) can be influenced by management and may be influenced both positively and negatively by wilderness boundaries. Even disturbances like hurricanes that are not under direct management control have consequences subject to management action and political pressure, such as influences on fuel loading, loss of native species in affected areas, pest species and water quality.

Disturbances can traverse wilderness boundaries in either direction, and land use surrounding wilderness can both decrease and increase the rate of disturbance within the wilderness. Boundaries can influence both ecological processes and management policies—for example, when the wilderness is perceived as creating danger to surrounding lands and property. Wilderness managers will have to form partnerships with neighbors to be able to manage their areas for natural processes and wilderness values.

Nature’s dynamics are both cause and effect: The dynamics are responsible for the diversity of species and ecosystems that are present, but these species and ecosystems then contribute to the responses to future dynamics. Various sources of historical and contemporary data will help us understand these dynamics (White and Walker 1997). However, the future is unlikely to duplicate the past in all details. Because of our evolving understanding and the likelihood of continued environmental change, we must employ both monitoring and adaptive management. We will have to determine the actions needed for qualitative or persistence equilibrium; this will force us to ask how sensitive that persistence is to the details of management. Particularly troubling for wilderness managers will be the forces that act across large distances, that have influenced even large and remote wilderness areas, that may introduce novel conditions and that reset the basic properties and geographies of ecosystems: exotic species invasions, climate change and air pollution.

These occur in even the largest wilderness areas, easily traverse boundaries and affect disturbance regimes.

Because of our ambivalence about managing areas where we want natural forces to reign, we are now faced with a series of choices that collectively reflect the paradigm shift forced upon us by expanding human use of land and dwindling wilderness areas. At one extreme with regard to natural process management (vs. managing for species), we can leave wilderness unmanaged. This treats wilderness as the “canaries in cages,” its fate determined by a host of ecological changes, including the change in scale and boundary that causes a loss of natural dynamics. At the other extreme, we can manage for historic state and essentially attempt to “freeze” ecosystems through a management regime that may incorporate disturbance, but does so in a way that allows no deviation from a particular, historically determined conditions. Such management ignores changing climates, although the historic disturbance regime may be contingent on climate conditions that no longer exist.

In between these two extremes lies many options among which is another course of action: Introducing those disturbances missing because of scale and boundary problems but allowing prescriptions to vary, as natural disturbances did, by coupling them to a climate signal or even allowing stochastic inputs. For example, because variation in hydrology through the Everglades was historically correlated with precipitation, precipitation measured at a monitoring station could be used to determine water releases from the water management districts upstream from the Park. The variation in rainfall would then drive the variation in a major ecosystem variable, as it did before impoundments were created. Whether this approach can be used in other cases is unknown. Such approaches would, however, still raise scale and boundary issues. For example, there would still likely be political pressure to eliminate the most extreme events from the prescription if they threatened human life and economic value.

## References

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- Angelstam, P. 1992. Conservation of communities—the importance of edges, surroundings, and landscape mosaic structure. In: Hansson, L., ed., *Ecological principles of nature conservation*. New York: Elsevier Applied Science: 9-70.
- Baker, W. L. 1989a. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology* 70:23-35.
- Baker, W. L. 1989b. Effects of scale and spatial heterogeneity on fire-interval distributions. *Canadian Journal of Forest Research* 19:700-706.
- Baker, W. L. 1992a. Effects of settlement and fire suppression on landscape structure. *Ecology* 73:1879-1887.
- Baker, W. L. 1992b. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7:181-194.
- Baker, W. L. 1994. Restoration of landscape structure altered by fire suppression. *Conservation Biology* 8:763-769.
- Baker, W. L. 1995. Longterm response of disturbance landscapes to human intervention and global change. *Landscape Ecology* 10:143-159.
- Bergeron, Y., P.J.H. Richard, C. Carcaillet, S. Gauthier, M. Flannigan, and Y.T. Prairie. 1998. Variability in fire frequency and forest composition in Canada’s southeastern boreal forest: a challenge for sustainable forest management. *Conservation Ecology* [online] 2(2).
- Bergeron, Y.; Brisson, J. 1990. Fire regime in red pine stands at the northern limit of the species’ range. *Ecology* 71:1352-1364.

- Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301-322 in G. M. Woodwell (ed.), *The earth in transition*. Cambridge: Cambridge University Press.
- Bodde, M. J.; Ferriter, A. P.; Thayer, D. D. 1994. The biology, distribution, and ecological consequences of *Melaleuca quinquenervia* in the Everglades. Pages 341-355 in S. Davis and J. Ogden (eds.), *Everglades: the ecosystem and its restoration*. St. Lucia Press.
- Bonnicksen, T. M.; Stone, E. C. 1985. Restoring naturalness to national parks. *Environmental Management* 9:479-486.
- Bormann, F. H.; Likens, G. E. 1979. Catastrophic disturbance and the steady-state in northern hardwood forests. *American Scientist* 67:660-669.
- Busing, R. T.; White, P. S. 1993. Effects of area on old-growth forest attributes: implications for the equilibrium landscape concept. *Landscape Ecology* 8:119-126.
- Christensen, N.L.; Agee, J. K.; Brussard, P. F.; Hughes, J.; Knight, D. H.; Minshall, G. W.; Peek, J. M.; Pyne, S. J.; Swanson, F. J.; Thomas, J. W.; Wells, S.; Williams, S. E.; Wright, H. A. 1989. Interpreting the Yellowstone Fires of 1988. *Bioscience* 39:678-685.
- Clark, J. S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334:233-235.
- Clements, F. E. 1916. *Plant Succession: an Analysis of the Development of Vegetation*. Washington, D. C.: Carnegie Institute of Washington. 512 pp.
- Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. *Botanical Gazette* 55:1-44.
- Cooper, W. S. 1926. The fundamentals of vegetation change. *Ecology* 7:391-413.
- Dahm, C. N.; Cummins, K.; Valett, H. M.; Coleman, R. L. 1995. An ecosystem view of the restoration of the Kissimmee River. *Restoration Ecology* 3:225-238.
- DeAngelis, D. L.; Waterhouse, J. C. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57:1-21.
- DeAngelis, D. L.; White, P. S. 1994. Ecosystems as products of spatially and temporally varying driving forces, ecological processes, and landscapes--a theoretical perspective. Chapter 2, pages 9-28, in S. Davis and J. Ogden (eds.), *Everglades: the ecosystem and its restoration*. St. Lucia Press.
- Forcier, L. K. 1975. Reproductive strategies and the co-occurrence of climax tree species. *Science* 189:808-810.
- Forman, R. T. T. 1990. Ecologically sustainable landscapes: the role of spatial configuration. Pages 261-278 in: Zonneveld, I. S., and R. T. T. Forman (eds.), *Changing landscapes: an ecological perspective*. New York: Springer-Verlag.
- Fortin, M.-J.; Drapeau, P. 1995. Delineation of ecological boundaries: comparison of approaches and significance tests. *Oikos* 72:323-332.
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, U.S.A. *Journal of Ecology* 76:135-151.
- Foster, D. R.; Boose, E. 1992. Patterns of forest damage from catastrophic wind in central New England. *Journal of Ecology* 80:79-98.
- Franklin, J. F. 1989. Towards a new forestry. *American Forests* November/December:37-44.
- Franklin, J. F.; Forman, R. T. T. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecology* 1:5-16.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. *Proceedings of the Tall Timbers Fire Ecology Conference* 18:17-43.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Chichester: Wiley.
- Habeck, J. R. 1985. Impact of fire suppression on forest succession and fuel accumulations in long-fire-interval wilderness habitat types. In: Lotan, J. E.; Kilgore, B. M.; Fishcer, W. C.; Mutch, R. W., eds., *Proceedings, Symposium and workshop on wilderness fire*. Ogden, UT: USDA Forest Service, Gen. Tech. Rept. INT-182: 110-118.
- Hales, D. 1989. Changing concepts of national parks. In: Western, D.; Pearl, M., eds., *Conservation for the twenty-first century*. New York: Oxford Univ. Press: 139-144.
- Hansen, A. J.; di Castri, F. 1992. Landscape boundaries: consequences for biotic diversity and ecological flows. New York: Springer-Verlag.
- Hansen, A. J.; Spies, T. A.; Swanson, F. J.; Ohman, J. L. 1991. Conserving biodiversity in managed forests: lessons from natural forests. *Bioscience* 41:382-392.
- Harmon, M. E. 1982. The fire history of the westernmost portion of Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Club* 109:74-79.
- Harmon, M. E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65:796-802.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-382.
- Janzen, D. H. 1986. The eternal external threat. In: Soule, M. E., ed., *Conservation Biology: the science of scarcity and diversity*. Sunderland, MA: Sinauer: 286-303.
- Johnson, E.A.; Larsen, C. P. S. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. *Ecology* 72:194-201.
- Johnson, E. A.; Miyanski, K.; Weir, J. M. H. 1995. Old-growth, disturbance, and ecosystem management. *Can. J. Bot.* 73:918-926.
- Johnson, E. A.; Wowchuk, D. R. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. *Can. J. For. Res.* 23:1213-1222.
- Johnson, E. A.; Gutsell, S. L. 1994. Fire frequency models, methods and interpretations. *Advances in Ecological Research* 25:239-287.
- Johnson, R. R.; Carothers, S. W. 1987. External threats: the dilemma of resource management on the Colorado River in Grand Canyon National Park, U.S.A. *Environmental Management* 11:99-107.
- Johnson, W. Carter. 1994. Woodland expansions in the Platte River, Nebraska: patterns and causes. *Ecological Monographs* 64:45-84.
- Kaufmann, M. R.; Graham, R. T.; Boyce, Jr., D. A.; Moir, W. H.; Perry, L.; Scott, M. L.; Auble, G. T.; Fridman, J. M. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* 7:677-690.
- Kilgore, B. M.; Heinselman, M. L. 1990. Fire in wilderness ecosystems. Pages 297-335 in *Wilderness Management*, 2<sup>nd</sup> edition (J. C. Hendee, G. H. Stankey, and R. C. Lucas, eds.) North American Press, Golden, Colorado.
- Knight, D. H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. pp. 61-80 in M.G. Turner, ed., *Landscape Heterogeneity and Disturbance*. New York: Springer-Verlag.
- Knight, R. L.; Landres, P. B. 1998. Stewardship across boundaries. Washington, D.C.: Island Press. 371 p.
- Kushlan, J. A. 1987. External threats and internal management: the hydrologic regulation of the Everglades, Florida, U.S.A. *Environmental Management* 11:109-119.
- Landres, P. B. 1992. Temporal scale perspectives in managing biological diversity. *Transactions of the North American Wildlife and Natural Resources Conference* 57:292-307.
- Landres, P. B.; Knight, R. L.; Pickett, S. T. A.; Cadenasso, M. L. 1998a. Ecological effects of administrative boundaries. In: Knight, R. L.; Landres, P. B., ed. *Stewardship across boundaries*. Washington, D.C.: Island Press: 39-64.
- Landres, P. B.; Marsh, S.; Merigliano, L.; Ritter, D.; Norman, A. 1998b. Boundary effects on wilderness and other natural areas. In: Knight, R. L.; Landres, P. B., ed. *Stewardship across boundaries*. Washington, D.C.: Island Press: 117-139.
- Landres, P. B.; White, P. S.; Aplet, G.; Zimmerman, A. 1998c. Naturalness and natural variability: definitions, concepts, and strategies for wilderness management. *Proceedings of the Eastern Wilderness Conference*, June, 1996, Gatlinburg, TN.
- Leopold, A.; Cain, S. A.; Cottam, C. M.; Gabrielson, J.N.; Kimball, T. L. 1963. Wildlife management in national parks. *American Forests* 69:32-35, 61-63.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* 10:17-25.
- Lynch and Clark 1996xx
- Matlack, G. R.; Gleeson, S. K.; Good, R. E. 1993. Treefall in a mixed oak-pine coastal plain forest: Immediate and historical causation. *Ecology* 74:1559-1566.
- McCune, B. (1982): *Site, History and Forest Dynamics in the Bitterroot Canyons, Montana*. Dissertation, University of Wisconsin-Madison, pp. 166.
- McKelvey, K. S.; Skinner, C. N.; Chang, C.; Erman, D. C.; Husari, S. J.; Parsons, D. J., van Wagendonk, J. W.; Weatherspoon, C. P. 1996. An overview of fire in the Sierra Nevada. In: *Sierra Nevada*

- Ecosystem Project*, Final Report to Congress, Volume II. Davis, CA: Centers for Water and Wildland Resources, University of California, Davis: 1033-1040.
- Minnich, R.A. (1989): Chaparral fire history in San Diego County and adjacent northern Baja California: an evaluation of natural fire regimes and effects of suppression management. In: S.E. Keeley (ed.). *The California Chaparral: Paradigms reexamined*. Science Series No. 34. Natural History Museum of Los Angeles. 171 p.
- Morgan, P.; Aplet, G. H.; Haufler, J. B.; Humfries, H. C.; Moore, M. M.; Wilson, W. D. 1994. Historical range of variability: A useful tool for evaluating ecosystem change. In: Sampson, R. N.; Adams, D. L., eds., *Assessing Forest Ecosystem Health in the Inland West*. The Haworth Press: 87-111.
- Nakashizuka, T.; Iida, S.; Suzuki, W.; Tanimoto, T. 1993. Seed dispersal and vegetation development on a debris avalanche on the Ontake volcano, central Japan. *J. Vegetation Science* 4:537-542.
- Nash, C. H.; Johnson, E. A. 1996. Synoptic climatology of lightning-caused forest fires in subalpine and boreal forests. *Can. J. For. Res.* 26:1859-1874.
- Newmark, W. D. 1985. Legal and biotic boundaries of western North American national parks: a problem of congruence. *Biological Conservation* 33:197-208.
- Newmark, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325:430-432.
- Pavlovic, N.B. (1994): Disturbance-dependent persistence of rare plants: anthropogenic impacts and restoration implications. In: M.L. Boeles & C. Whelan (eds): *Recovery and restoration of endangered species*. Cambridge University Press, Cambridge, pp. 159-193.
- Peterson, C. J.; Pickett, S. T. A. 1995. Forest reorganization: a case study of an old-growth forest catastrophic blowdown. *Ecology* 76:763-774.
- Pickett, S. T. A.; Thompson, J. N. 1978. Patch dynamics and the design of nature reserves. *Biological Conservationist* 13:27-37.
- Pickett, S. T. A.; White, P. S. (eds.). 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press. New York. 496 p.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52:199-221.
- Romme, W. H.; Despain, D. G. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* 39:695-699.
- Romme, W. H.; Knight, D. H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62:319-326.
- Romme, W. H.; Turner, M. G. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone ecosystem. *Conservation Biology* 5:373-386.
- Runkle, J. R.; Yetter, T. C. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology* 68:417-424.
- Rykiel, E. J. Jr.; Coulson, R. N.; Sharpe, P. J. H.; Allen, T. H. F.; Flamm, R. O. 1988. Disturbance propagation by beetles as an episodic landscape phenomenon. *Landscape Ecology* 1:129-139.
- Schimmel, J.; Granstrom, A. 1994. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77:1436-1450.
- Schoenwald-Cox, C. 1983. Guidelines to management: a beginning attempt. Pages 414-446 in C. Schoenwald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas (editors),
- Schoenwald-Cox, C.; Bayliss, J. W. 1986. The boundary model: a geographical analysis of design and conservation in nature reserves. *Biological Conservation* 38:305-322.
- Schoenwald-Cox, C.; Buechner, M. 1992. Park protection and public roads. Pages 373-395 in P. L. Fiedler and S. K. Jain (eds.), *Conservation biology*. New York: Chapman and Hall.
- Schoenwald-Cox, C.; Buechner, M.; Sauvajot, R.; Wilcox, B. 1992. Cross-boundary management between national parks and surrounding lands: a review and discussion. *Environmental Management* 16:273-282.
- Shafer, C. 1994. Beyond park boundaries. In: Cook, E. A.; Vanlier, H. N., eds. *Landscape planning and ecological networks*. England: Elsevier Publishers: 201-223.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer, New York.
- Smith, T. and D.L. Urban, 1988. Scale and resolution of forest structural pattern. *Vegetatio* 74:143-150.
- Sprugel, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *Journal of Ecology* 64:889-911.
- Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: what is "natural" vegetation in a changing environment? *Biological Conservation* 58:1-18.
- Stevens, L. E.; Schmidt, J. C.; Ayers, T. J.; Brown, B. T. 1995. Flow regulation, geomorphology, and Colorado River marsh development in the Grand Canyon, Arizona. *Ecological Applications* 5:1025-1039.
- Swanson, F. J.; Franklin, J. F. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* 2:262-274.
- Swanson, F. J.; Jones, J. A.; Wallin, D. O.; Cissel, J. H. 1994. Natural variability—implications for ecosystem management. In: Jensen, M. E.; Bourgeron, P. S., eds. *Volume II: Ecosystem management: principles and applications*. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-318:80-93.
- Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. *Science* 262:885-889.
- Swetnam, T. W.; Betancourt, J. L. 1990. Fire-southern oscillation relations in the southwestern United States. *Science* 249:1017-1020.
- Theberge, J. B. 1989. Guidelines to drawing ecologically sound boundaries for national parks and nature reserves. *Environmental Management* 13:695-702.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197.
- Turner, M. G.; Gardner, R. H.; Dale, V. H.; O'Neill, R. V. 1989. Predicting the spread of disturbance across heterogeneous landscapes. *Oikos* 55:121-129.
- Turner, M. G.; Romme, W. H.; Gardner, R. H.; O'Neill, R. V.; Kratz, T. K. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* 8:213-227.
- Tyrell, L. E.; Crow, T. R. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75:370-386.
- Urban, D.L.; O'Neill, R.V.; Shugart, H. H., Jr., 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. *BioScience* 37:119-127.
- Veblen, T. T.; Hadley, K. S.; Nel, E. M.; Kitzenberger, T.; Reid, M.; Villalba, R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82:125-135.
- Vogl, R. J. 1974. Effects of fire on grasslands. Pp. 139-194. In T. T. Kozłowski and C. E. Ahlgren (eds.), *Fire and ecosystems*. Academic Press. New York.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.
- Webb, R.H.; Betancourt, J. L. 1992. Climatic variability and flood frequency of the Santa Cruz River, Pima County, Arizona: U.S. Geological Survey Water-Supply Paper 2379.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Reviews* 45:229-299.
- White, P. S. 1996. Spatial and biological scales in reintroduction. Pages 49-86. In D. A. Falk, C. Millar, and M. Olwell (editors), *Restoring diversity*. Island Press, New York.
- White, P. S.; Bratton, S. P. 1980. After preservation: the philosophical and practical problems of change. *Biol. Conserv.* 18:241-255.
- White, P. S.; Harrod, J. 1997. Disturbance and diversity in a landscape context. Pages 128-159. In J. A. Bissonette (ed.), *A primer in landscape ecology*. New York: Springer-Verlag.
- White, P. S., J. Harrod, W. Romme, and J. Betancourt. 1999. The role of disturbance and temporal dynamics. In: *Ecological Stewardship: a common reference for ecosystem management*. Johnson, N.C., A. J. Malk, W. T. Sexton, and R.Szaro (eds.) Oxford, England: Elsevier Science Ltd. Volume 2:281-312.
- White, P. S.; Pickett, S. T. A. 1985. Natural disturbance and patch dynamics, an introduction. Pp. 3-13. In S. T. A. Pickett and P. S. White (eds.), *The ecology of natural disturbance and patch dynamics*. Academic Press. New York.

White, P. S.; Walker, J. L. 1997. Approximating nature's variation: selecting and using reference sites and reference information in restoration ecology. *Restoration Ecology* 5:338-249.

Wright, K. A.; Chapman, L. M.; Jimerson, T. M. 1995. Using historic range of vegetation variability to develop desired conditions and model forest plant alternatives. Pp. 258-266. In *Analysis in*

*support of ecosystem management: analysis workshop III*. USDA Forest Service, Ecosystem Management Analysis Center, Washington, D.C.

Zedler, P.; Goff, F. G. 1973. Size-association analysis of forest successional trends in Wisconsin. *Ecological Monogr.* 43:79-94.