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# Disturbance Ecology and Forest Management: a Review of the Literature

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## Research Summary

Land managers are incorporating ecosystem perspectives into their local and regional management decisions. This review of the disturbance ecology literature, and how it pertains to forest management, is a resource for forest managers and researchers interested in disturbance theory, specific disturbance agents, their interactions, and appropriate methods of inquiry for specific geographic regions. The approach is broadly interdisciplinary and includes efforts from ecologists, biologists, geographers, historians, wildlife scientists, foresters, entomologists, pathologists, hydrologists, and modelers. The author broadly defines disturbance ecology as the study of any distinct events that disrupt the function of ecosystems. These disruptions may occur over widely varying scales of time and space. Greater understanding of multiple disturbance mechanisms, and how they interact within forests, will contribute significantly to land managers' ability to work with natural systems, rather than battling against individual disturbance agents. Implications for the future of disturbance ecology based management are discussed.

Additionally, this paper introduces land managers to a wide body of literature pertaining to disturbance ecology and forest management. The References section is recommended as a resource.

## Contents

	Page
Introduction .....	1
Defining disturbance ecology .....	1
Equilibrium and nonequilibrium .....	2
Forest dynamics and disturbance agents .....	3
Abiotic disturbance agents .....	3
Biotic disturbance agents .....	7
Disturbance interactions on the landscape:	
two case studies .....	10
Established methods in disturbance ecology .....	10
Historical sources .....	11
Field ecological methods .....	11
Modeling .....	12
Toward management with disturbance ecology .....	13
References .....	14

## Foreword

Land managers in the National Forest System are currently faced with some of the most serious challenges in the history of the Forest Service, U.S. Department of Agriculture. No longer does a career in the Forest Service result in an idyllic life of a free roving ranger. Increasingly it has become a life spent in front of a word processor working on public law documents or in courtrooms facing litigation. The land management decisions on our National Forests are subjected to excruciating scrutiny, not only from traditional resource-based industries, but also from citizen groups representing broadly based interests in the multifaceted values of our forested lands. In response to these societal pressures, the

Forest Service has adopted a policy of ecosystem management that emphasizes maintaining the values of sustainability, biodiversity, productivity, and forest health rather than focusing on particular deliverable products.

In the attempt to implement ecosystem management, land managers are asking basic scientific questions that go far beyond the scope of historical Forest Service research. Concurrent with this demand are budgets being slashed and research positions being eliminated. Land managers are being asked to implement new knowledge-intensive programs at a time when resources are being dramatically reduced. To address this significant dilemma, we need to re-evaluate how research is conducted within the Forest Service and how more effectively to involve partners from the research community.

As a part of this effort, we have established an Intermountain Center for research on Disturbance Ecology at the Logan Forestry Sciences Laboratory, Intermountain Research Station. Although the objectives of the center are more fully described in the memorandum of understanding that created it, the defining objectives of the center are:

- Create an environment that is more responsive to the research needs of the National Forest System
- More effectively utilize information from ongoing Forest Service research projects to address disturbance issues
- Facilitate effective collaborations with universities and other extramural research partners.

An important way in which the Intermountain Center for Research on Disturbance Ecology hopes to encourage collaborative research, both within the Forest Service community and the research community at large, is through visiting collaborator positions. Working a few months to perhaps a few years in the center, visiting collaborators will reap the intellectual and practical benefits from interaction between scientists and land managers with diverse work experiences and professional backgrounds. We anticipate that the resulting insights will be difficult to gain in any other way. We anticipate additional material benefits (products) that will advance the objectives of the center and facilitate the practical application of disturbance ecology principles to management practices on public lands.

Paul Rogers was the first collaborator at the center. Paul is an ecologist with the Interior West Inventory Project, Intermountain Station, Ogden, UT. He received his B.S. degree in geography from Utah State University and an M.S. degree in geography from the University of Wisconsin-Madison. He has wide ranging interests in landscape and disturbance ecology. Paul spent 2 months on detail as a visiting collaborator, and given his relatively short tenure, we decided that a review of the disturbance ecology literature pertaining to forest management issues would provide for both accomplishing his goals and furthering the interests of the center. This review is the final product of Paul's efforts.

Rather than providing an exhaustive listing of every reference on disturbance ecology, the objectives were to focus specifically on the aspects of disturbance ecology that most directly impinge on management of public lands and to identify key references that provide an entry into the literature on these important issues. As such, this publication is similar in scope and objectives of an Annual Review journal article. Paul also initiated creation of a computer data base on disturbance ecology. References in this review are a subset of that data base.

The intention of the center is to continue developing the disturbance ecology data base for providing an information resource for the research community at large.

Jesse A. Logan  
Acting Director, Intermountain Center for  
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# Disturbance Ecology and Forest Management: a Review of the Literature

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*Then there are insects—moths, weevils, caterpillars, worms, beetles, sawflies, termites, and borers. They march, dig, fly, bore, crawl, reproduce within trees, and nourish themselves and their young. Some, like the bark beetles, are the mortal foe of conifers.*

*Insects are the worst of all enemies of trees. They cause twice as much damage as disease, and seven times more damage than fire.—Frome (1962, p. 240).*

*Natural disturbances are quite common in all regions of North America and the world when viewed from a long-term perspective. Each area has characteristic frequencies and types of disturbances based on its climate, soils, vegetation, animals, and other factors. Fires, windstorms, and other disturbances have specific behaviors and leave certain conditions for growth.—Oliver and Larson (1990, p. 92-93).*

*Previous to settlement of the country, fires started by lightning and Indians kept the brush thin, kept the juniper and other woodland species decimated, and gave the grass the upper hand with respect to possession of the soil. In spite of periodic fires, the grass prevented erosion.... The removal of the grass [by settlers] relieved the brush species of root competition and of fire damage and thereby caused them to spread and "take the country."—Leopold (1924, p. 2-3).*

## Introduction

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How land stewards view ecological disturbance in an ecosystem is an indicator of how a given landscape will be managed. The first two quotes above typify different philosophies in different eras of forest management. The third quote is an exceptional view of management by an early forest ranger. Further scrutiny reveals a paradigmatic shift from that of humans having an antagonistic relationship with nature, to one of acceptance of nature as a regulator with which humans must work in tandem. Leopold illustrated that our capacity to work with natural systems, including disturbance, is only limited by our ability to

understand their role at larger temporal and spatial scales.

If natural disturbance is fundamental to the development of forest ecosystems, then our management of natural areas should be based on an understanding of disturbance processes (Attiwill 1994; Gordon 1993; Grumbine 1994; Lorimer and Frelich 1994; Malanson and Butler 1984; Pfister 1993). Now, as Federal land management agencies adopt ecosystem management philosophies, it becomes critical that disturbance is viewed as complementary, rather than solely deleterious, to human and forest functions (Grumbine 1994; Monnig and Byler 1992; Pfister 1993).

This review highlights recent work in a broad array of studies related to disturbance ecology. This publication is a resource for managers and researchers interested in disturbance theory, specific disturbance agents, their interactions, and appropriate methods of inquiry for specific geographic regions.

## Defining Disturbance Ecology

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Disturbance ecology encompasses the study of interrelationships between biotic and abiotic components of an environment. White and Pickett (1985) give the most widely quoted definition of disturbance: "Any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment." No definition of disturbance will satisfy all ecologists, but White and Pickett speak to the critical elements of disruption and changed resource allocation. A more thorough discussion of alternative definitions may be found in a recent publication by Glenn-Lewin and van der Maarel (1992). Though both "disturbance" and "ecology" are defined somewhat loosely, together they focus primarily on distinct events that disrupt the function of ecosystems. That broad statement will be used as a working definition of disturbance ecology for the purposes of this review.

A further consideration is scale. Definitions of disturbance cannot be limited by size or timing, as these factors are relative to the systems being evaluated. For example, disturbance in a fungal community may

take place several times a year and at a scale measured in square feet, while other disruptions, such as tropical cyclones, may cover hundreds of square miles and occur, in the same place, on a temporal scale of centuries.

White and Pickett (1985) also clarify the use of “perturbation” and “catastrophe” as covering the rare small and large events, respectively. Perturbation refers primarily to specific alteration of systems that are clearly and narrowly defined. Most often perturbations are purposeful human manipulations that can be measured in totality. Catastrophes, on the other hand, are rare events, especially destructive ones, and are unlikely to be repeated with regularity. Though many have used these terms interchangeably (such as Foster 1988; Odum 1985), for this review I will use White and Pickett’s narrower definitions, which rely predominantly on the term “disturbance” to describe all but the rarest events.

Discussion of scale often centers around the median area and timing of disturbances for specific landscapes, otherwise known as disturbance regimes. Understanding disturbance regimes for a particular landscape is fundamental to the study of disturbance ecology. In North America, the scale of the dominant force of vegetation change for a given landscape defines study parameters (Glenn-Lewin and van der Maarel 1992; O’Neill and others 1986; Shugart and West 1981; Sprugel 1991). Single plant mortality forms “gaps,” groups of plants affected by disturbance form “patches,” and whole landscapes are discussed in terms of “community” or “stand replacement.” Generally, in studies of forest disturbance in the Eastern United States and Eastern Canada where mortality occurs most frequently at the single tree or small-group scale, the focus is on gap-phase dynamics. Though large-scale events such as fire and hurricanes do occur in this region (Henry and Swan 1974), it is the tree-by-tree replacement over time that controls the overall structure and function of these systems (Bormann and Likens 1979; Busing and White 1993; Canham and others 1990; Lorimer and Frelich 1994; Payette and others 1990). These gap disturbances often result in an uneven-aged vegetation structure that is largely dependent upon maximum attainable age of the dominant species being shorter than the stand-replacing disturbance interval (Oliver 1980-1981).

In the Western United States and Western Canada where long-lived species and mostly dry conditions prevail, disturbance regimes are almost universally studied at the stand or landscape level (Covington and Moore 1994; Johnson and Larsen 1991; Keane and others 1990). When disturbance intensity is high, for example severe wildfires in portions of Yellowstone National Park in 1988, even-age stand establishment follows (Romme and Despain 1989). Even lower intensity events in the West, such as insect or disease

outbreaks, which tend to kill more selectively, are spoken of in terms of patch disturbance, rather than gaps (Amman 1978; Castello and others 1995).

A possible exception is a study (Canham and others 1990) that compared light falling through “tree-fall gaps” in forest types of the East to the relatively moist Pacific Northwest. The conclusion was that the gap-to-height ratio of the Western forest precluded significant resource availability from gap occurrence. In this particular Douglas-fir/hemlock forest type, one might conclude that other environmental factors, most likely large-scale disturbance or nutrient availability, take precedence over light allocation from single tree-gap formation. The Eastern forests, on the other hand, immediately took advantage of the light resulting from gap formation by filling in the space with new tree growth. Still, it appears likely that Pacific Northwestern forests do take advantage of gaps by releasing other resources to shade-tolerant tree species, thereby promoting an overall patchiness in the absence of large-scale disturbance.

These examples illustrate a basic dichotomy in the scale of prevailing disturbance mechanisms. Further discussion of disturbance processes and scale often centers on the question of system stability, or equilibrium (Botkin 1993; Glenn-Lewin and van der Maarel 1992; Veblen 1992).

## Equilibrium and Nonequilibrium

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Spatial and temporal scale are pivotal to any dialogue regarding equilibrium versus nonequilibrium systems. At issue is whether systems are maintained in some equilibrium by disturbance, or whether the ubiquity of disturbance prevents systems from ever reaching “steady state.” If one makes the case for nonequilibrium at one scale, then critics may charge that at a larger scale ecological “balance” can be reached. In other words, if things appear unbalanced, just expand the scale of interest until equilibrium is reached. For example, Botkin (1993) describes recent usage of the term “landscape-level” stability as a condition where small disturbances occurring continuously across a landscape “average” each other out at a chosen scale. This argument can effectively be made to encompass several eco-regions, or even up to a global scale (Prentice 1992).

On a temporal scale, Vale (1988) presents arguments for employment of various equilibrium viewpoints to justify or vilify clearcut logging simply by adopting an appropriate time frame. For example, if we look at logging (as a disturbance) as it affects a forest on a 100-year scale, we can imagine a clearcut, and then a developmental path toward an equilibrium composed of vegetation similar to the original site.

From a 1,000-year view, several logging events may take place at regular intervals never allowing the forest to reach a balance. Or at an even longer scale, vegetation cover may move completely away from the concept of balance due to climatic changes toward a totally new landscape dynamic.

In general, as we expand spatial or temporal scale, explanations of equilibrium become either more complex—for example, “quasi-equilibrium,” “shifting-mosaic steady state,” “near-equilibrium,”—or in other cases, nonfunctional, nonequilibrium, “non-linear,” or even “chaotic.”

Current thought appears to favor an overall nonequilibrium perspective, although significant exceptions do exist (Botkin 1993; Peet 1992; Veblen 1992). Similar to the earlier discussion of the East-West dichotomy in North America exhibited by scale of disturbance, a roughly parallel argument could be made for equilibrium and nonequilibrium ecosystems. As Sprugel (1991, p. 6) points out: “Whenever individual disturbances are so large that a single disturbance event can affect a relatively large proportion of the landscape, achievement of an equilibrium becomes unlikely.”

Where large-scale fire, windstorms, disease, or insect infestations occur regularly, forests are unlikely to reach steady-state (Bergeron and Dansereau 1993; Botkin 1993; Foster 1988; Prentice 1992; Romme 1982; Romme and others 1986). Many western forests are dominated by such large-scale disturbance dynamics. In the North, boreal landscapes burn at large scales (Hunter 1993), and in the East, near-coastal forests often experience large cyclonic winds (Foster 1988; Henry and Swan 1974; Wyant and others 1991). Inland deciduous forests of the Eastern United States seem to be the major exception to the trend, exhibiting infrequent or almost no large disturbances, and thus, near equilibrium conditions (Bormann and Likens 1979; Busing and White 1993; Lorimer and Frelich 1994; Payette and others 1990; Prentice 1992; Runkle 1985). Busing and White (1993) conclude, however, that equilibrium may be based on a variety of factors, such as biomass or composition, and that by changing such factors, not unlike changing scales, different conclusions about equilibrium may result.

In a broader context, we should all critically evaluate the use of equilibrium and nonequilibrium labels. If these terms are so dependent on scale (Botkin 1993; Vale 1988; Veblen 1992) and other select factors (Busing and White 1993), can they be manipulated to fit whatever needs an author intends? Or does the exercise of demonstrated equilibrium (or nonequilibrium) further our understanding of disturbance and landscape processes? Are these concepts merely human constructs that, for whatever reason, become psychologically attractive in their effort to impose order on

systems in states of continual change (Sprugel 1991)? In any event, it seems prudent to use caution when applying the equilibrium and nonequilibrium labels.

## Forest Dynamics and Disturbance Agents

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Most land managers are aware of the variety of disturbance agents but have less knowledge of how they interact on a landscape to mold past, present, or future ecological systems. This section focuses on forms of disturbance and the dynamics that bind them.

Disturbances can be both endogenous (internal) or exogenous (external) to the ecosystem; they can be biotic (such as insects, disease, animal damage) or abiotic (such as wind, flood, fire). They can be large (measured in hectares) or small (measured in meters). They can be intense (such as crown fires) or weak (such as creeping ground fires). One thing most disturbance agents have in common, however, is that they rarely act alone. Agents such as drought and fire or disease and insects most often act in concert across both time and space in shaping the landscape. While it is true that a discrete event, for instance a landslide, drastically alters a successional course, recent heavy precipitation and possibly previous loss of vegetation cover from road building, fire, or grazing, all contribute significantly to that event. So most disturbance events are an interaction of many disturbance agents.

### Abiotic Disturbance Agents

**Drought**—Concerns about drought are closely linked to discussions of global warming and climate change in general (Ojima and others 1991; Overpeck and others 1990; Prentice 1992). However, not all climate change is toward drought. Witness, for instance, the “little ice age” of the mid-1400’s to early 1800’s. When drought does occur, a host of disturbance processes are likely to act together. It may be helpful to view drought as an indirect, or secondary, disturbance agent as opposed to discretely affecting successional development alone. A narrow distinction exists between agents that have the potential to directly kill perennial plants and those, such as drought, that often do not lead to mortality. Drought overall is clearly a significant factor in vegetation change over time.

Several authors have linked drought to incidents of insect infestations (Hadley and Veblen 1993; Mitchell and others 1983), disease (Baker 1988; Castello and others 1995), and fire (Arno 1980; Callaway and Davis 1993; Johnson and Larsen 1991; Romme and Despain 1989; Weaver 1951). Moreover, George and others (1992) describe the effects that severe drought has on wildlife, in their case grassland birds of the



Fires that burn at high intensity leave forests that recover more slowly than after less severe burns. This charred landscape is a result of a severe portion of the Yellowstone fires of 1988. Less intense burns were visible from the same vantage point. Some were evenly burned ground fires, while others seemed to burn more intensely in small patches of tree crowns.

northern plains, in terms of short- and long-term population dynamics. Currently, many disturbance agents are experiencing near epidemic levels in the Western United States because of prolonged drought in combination with other human-induced factors such as fire suppression, historic forest cutting practices, and urban encroachment. Furthermore, Overpeck and others (1990) predict that these conditions will be amplified in the coming decades as result of human-induced global warming.

**Fire**—Fire is probably the most widely known and extensively studied disturbance, possibly due to its spectacular appearance or innate human attraction.

Views of wildland fire on this continent have evolved from Native Americans’ purposeful use of fire, to European immigrants’ fear of, disdain for, and control of fire, to the appreciation for fire in its varied ecological guises. Rather than tracking the entire history, and the myriad of papers on this subject, I will focus on the current understanding of fire in disturbance ecology.

While fire is commonly correlated with drought, many authors have highlighted other environmental stressors which promote ignition conditions, such as insect infestations (Amman 1978; Baker and Veblen 1990; Gara and others 1984; Knight 1987; Schowalter and others 1981), disease outbreaks (Baker 1988; Castello and others 1995), windthrow (Lorimer and Frelich 1994), and global climate change (Overpeck and others 1990). Many studies have focused on establishing historical fire regimes to gain some understanding of how fire shapes vegetation development. Examples can be found for nearly every ecological region across North America and internationally (see table 1).

Studies document changes in fire regimes that are attributed to specific human actions, such as fire suppression, land clearing, logging, or grazing. If human disruptions of “natural” fire regimes can be gleaned from the historical data, then, presumably, a better understanding of the role of fire in determining forest structure and function can be achieved. Problems arise, however, when we attempt to distinguish between how much human intervention is “natural” and how much is not “natural.” Determining that might lead to management practices that emulate the disturbance regimes before humans changed their course. Unfortunately, separating out “the human factor” is

**Table 1**—Examples of fire regime studies by region.

Region	Authors	Year
Pacific Northwest, U.S.A.	Gara and others	1984
	Swanson and others	1992
Pacific Southwest, U.S.A.	Callaway and Davis	1993
	Weaver	1951
Southwest, U.S.A.	Covington and Moore	1992, 1994
	Romme	1982
Intermountain, U.S.A.	Arno	1980
	Johnson and Larsen	1991
Rockies, Canada	Reed	1994
	Bergeron and Dansereau	1993
Boreal, Canada	Hunter	1993
	Lorimer and Frelich	1994
Upper Midwest, U.S.A.	Baker	1992
	Bormann and Likens	1979
Northeast, U.S.A.	Henry and Swan	1974
	Bradshaw and Hannon	1992
Sweden	Attiwell	1994
Australia	Veblen and others	1992
Argentina		

not so easy. As a related question, should fire suppression, or the prevention of any natural disturbance, be considered a disturbance process in itself? The act of prevention certainly “disrupts ecosystem, community, or population structure,” as White and Pickett (1985, p. 7) have defined it. This places the focus of the question on the “discreteness” of the disturbance. Other disturbance types, such as livestock grazing, affect landscapes over long periods in a similar fashion to fire suppression. If viewed from a longer time scale, disruptions in natural processes that occur over decades may appear very discrete.

Aboriginal use of fire and their settlement practices had some effect on nature’s own fire regimes (Attiwell 1994; Bradshaw and Hannon 1992; Denevan 1992; Hammett 1992). Evidently Native American populations were at 500-year lows during the 19th century (Denevan 1992; Sprugel 1991), a time commonly referred to by ecologists as “presettlement.” Does that mean this period was characterized by “unnaturally” low levels of human-caused fires, and therefore, historically unusual vegetation patterns?

One approach to finding answers might be to separate, by an order of magnitude, the scale of human intervention between, say, agricultural and industrial-level societies. If we could define some average level of intervention at the “agricultural scale” and the

“industrial scale” then possibly some comparisons could be made, and consequently, “values” of “naturalness” might be assigned. This loose approach shows that human intervention in fire regimes is probably as much a philosophical dilemma as it is a scientific one. Are human actions part of nature? If so, at what level do they become “unnatural?” However, managers and scientists must address these difficult questions or risk aiming at constantly moving ecosystem targets in their management objectives.

**Wind**—Intense wind storms, often of cyclonic origin, may destroy healthy vegetation without employing other disturbance agents from within a system. In the Teton Wilderness in Wyoming, an unusual high elevation cyclonically driven storm flattened a strip of trees 15 miles long and up to 1 mile wide (see photo). The bulk of these trees were vigorous, large diameter conifers without any obvious sign of previous damage.

Other researchers have documented long-term “wind regimes” resulting from occasional hurricanes along the East Coast (Bormann and Likens 1979; Foster 1988; Henry and Swan 1974; Wyant and others 1991).

Both intense storms and smaller wind events are important disturbance agents. The smaller blowdowns usually thin forests of trees already damaged by fire, insects, or disease, creating gaps in the canopy (Castello



An unusual, high elevation windstorm in northwestern Wyoming caused large-scale damage in 1987. Damage to apparently healthy trees came in two forms: either whole trees uprooted, or trees snapped off at the main bole about 15 feet from the ground. In the following year portions of this 15-mile swath were burned in the Yellowstone fires.

and others 1995; Lorimer and Frelich 1994; Payette and others 1990; Runkle 1985).

Wind may increase the severity of fire at several scales. At its minimum, wind acts as a drying agent, increasing the combustibility of forest fuels. Moderate winds push a fire steadily from one flammable plant to the next. High winds, in combination with severe conditions, can drive fire at a furious pace, jumping any human-constructed barriers. These events, known as “fire storms,” can consume huge acreages of forest in a single day (Romme and Despain 1989).

**Geomorphology and Gravity**—Included in this category are earth-shaping processes such as volcanism, subduction, earthquakes, and glacial movement. Also included are disturbance mechanisms governed by gravity, such as mass wasting (landslides and mudflows), fluvial processes, and avalanches, both snow and rock. In general, these disturbances tend to have long lasting effects because they often involve removal or destruction of the upper soil horizons. As a result, it may take many years before any plants can become established, thereby beginning the successional process. Swanson and others (1992) looked at a variety of geomorphic disturbances in two differing forest types in New Mexico and Oregon. In both areas topography was a key factor influencing “potential disturbance energy.” When steep areas were combined with human impacts, such as logging or road building, debris flows were common (see also, Olsen 1996).

Veblen and others (1992) measured the effects of a geomorphic agent in the Argentine Andes, including tree mortality from earthquakes, fire, and windthrow. Apparently, some trees died and others showed signs of reduced growth from the “intense shaking.” In this same region, but on the Chilean slope of the Andes, one large earthquake triggered several thousand landslides (Veblen and others 1992).

Unlike the above processes, snow avalanches normally do not remove soil layers. Snow avalanches act as thinning agents within forests and along forest margins. Trees affected by avalanches are typically at least 4 to 5 inches diameter at breast height and found on slopes of greater than 25 degrees (Johnson 1987; Potter 1969). Areas meeting these conditions, with open snow accumulation zones above them, may have average avalanche frequencies of 3 to 10 years (Carrara 1979; Johnson 1987). Areas in mountainous terrain with heavy snow cover may be affected by unusually large avalanches even if they don’t meet the slope and tree size requirements mentioned above. A large avalanche may have a runout zone on flat terrain, or even up opposing slopes.

In areas where avalanches run frequently, non-forest conditions will persist in “avalanche tracks.” Younger trees, or more flexible species (such as aspen), will survive in these tracks, but more commonly they are dominated by shrub or forb layers. Avalanches in mountainous zones create a patchy or striped mosaic running parallel to steeper slopes (Patten and



Avalanche paths and scree slides fragment high elevation forests in linear patterns. This disturbance pattern may limit the spread of fire or forest pathogens.



Trees that appear lighter in this landscape were killed by mountain pine beetle. This photo illustrates the patchy nature of some insect infestations.

Knight 1994; Veblen and others 1994). Malanson and Butler (1984) suggest that this linear pattern of avalanche tracks acts as an effective barrier to fire spread, and in some cases may be used as a fire suppression tool for that reason.

### Biotic Disturbance Agents

**Insects**—Large-scale insect infestations can severely alter successional development. These infestations may be associated with drought for wood borers such as the mountain pine beetle (*Dendroctonus ponderosae*) (Amman 1978; Mitchell and others 1983), or moist seasonal weather for the spruce budworm (*Choristoneura occidentalis*) (Hadley and Veblen 1993; Swetnam and Lynch 1993), or fire scarring (Amman and Ryan 1991; Gara and others 1984; Knight 1987), or any weakening that reduces a tree's ability to combat insects (Mattson and Addy 1975; Romme and others 1986). In the Southeastern United States, Rykiel and others (1988) noted that many southern pine beetle (*Dendroctonus frontalis*) outbreaks originated on trees that had recently been struck by lightning but not killed. These damaged trees act as "host trees" in which adult beetles lay eggs. Once larvae have matured, beetles begin to disperse to surrounding healthy trees. This symbiotic, or even cybernetic, relationship between lightning and insect may be crucial to the survival of beetles and host species.

Whether beetles are a regulating factor of primary productivity has been debated (Mattson and Addy 1975; Romme and others 1986; Rykiel and others 1988). However, native insect populations do play an integral role, in conjunction with other forest disturbances, in shaping local and regional vegetative patterns (Amman 1978; Amman and Ryan 1991; Baker and Veblen 1990; Gara and others 1984; Harvey 1994; Martin 1988; Schowalter and others 1981; Veblen and others 1994). Removal of native insects from a system through the application of chemical or biological controls can directly affect ecosystem health by inhibiting nontarget species (Miller 1990; Sample and others 1993) and long-term successional development through the loss of a critical ecosystem component.

Introduction of exotic insects, for instance the gypsy moth (*Lymantria dispar*) or the larch sawfly (*Pristiphora erichsonii*), can have devastating effects on forests without defense mechanisms to combat them. This situation can be exacerbated where human management practices have favored single species retention. Similar to agricultural systems, exotic insects or diseases can overrun entire forested landscapes without respite.

The larch sawfly presents a more interesting scenario. This insect was previously thought to have been introduced from Europe around 1880. But Jardon and others (1994) make a case using tree ring chronologies

that the sawfly had established a disturbance regime at least 150 years prior to that date. If the early 1700's date is accurate, then perhaps these forests have developed some "natural" defenses to larch sawfly.

**Disease**—Pathogens are major agents of forest diversity. Unfortunately, the study of disease (and insects) often takes on negative connotations. But "damage" occurs only when "some purpose of management has been frustrated. Diseases which reduce timber production are certainly damaging in commercial forests.... The same disease, however, may be of little or no consequence in parks or watershed protection areas" (van der Kamp 1991, p. 353). In fact, human management may act as a means of spreading disease, for example, through logging and road building (Schowalter and Means 1989). As with insects, areas of monoculture may cause diseases to spread faster (Baker 1988). Given this, it is probably wise to maintain as much diversity in forest stands as possible over age classes and species.

Changes in disturbance regimes can sometimes have far reaching effects. Where regeneration of certain species is not present, a single epidemic can wipe out the entire population of that species in a stand. McCune and Cottam (1985) noted just such an incident with oak wilt (*Ceratocystis fagacearum*) on large oaks (*Quercus alba* and *Quercus velutina*). This former oak savanna was maintained by fire, which probably kept the disease at bay. In the absence of fire, the disease seems to flourish and the older oaks are slowly dying off, while regeneration is unlikely given the dense undergrowth.

Castello and others (1995) characterize most diseases as "selectively eliminating less vigorous" trees, rather than killing large tracts of forest as abiotic disturbances do. Although there is some similarity between insects and disease, diseases seem to leave more distinct patches, most likely due to their method of dispersal. Interestingly, van der Kamp (1991) noted the extreme longevity of disease centers, up to 1,000 years, in an old growth forest of the Pacific Northwest where "root disease climax" maintained a relative equilibrium of structure and composition over an extended period. van der Kamp believes that root diseases act as primary regulators of these small forest patches. Finally, pathologists seem to agree that fire suppression has increased disease outbreaks significantly, where once this agent kept them at relatively moderate levels (Castello and others 1995; Gara and others 1984; Harvey 1994; Martin 1988; van der Kamp 1991).

Exotic pathogens can also have devastating consequences. In the first half of this century, white pine blister rust (*Cronartium ribicola*) nearly decimated western white pine (*Pinus monticola*) in the Inland Northwest. The chestnut blight (*Endothia parasitica*)

nearly wiped out the American chestnut tree (*Castanea dentata*) in the East.

**Grazing**—Herding or grazing of livestock has a long history in wooded and semiwooded areas around the world. Anthropologists, cultural geographers, and historical ecologists have documented civilizations in varying forest types who maintained sparse forests with little understory through grazing and burning over several centuries (Bradshaw and Hannon 1992; Denevan 1992; Hammett 1992). This strategy appears to favor fast-growing, shade-intolerant species. Bradshaw and Hannon (1992) note that once these disturbance agents were removed from a southern Swedish forest, a completely new forest type of conifers took over a site previously dominated by hardwoods. In the American Southwest, decades of overgrazing have produced landscapes dominated by shrubs and woodlands in which grass was previously the prevailing cover (Leopold 1924; Swanson and others 1992).

Where fire has been kept out, this situation is exacerbated. In coastal California, Callaway and Davis (1993) measured rates of change between shrublands and grasslands with and without fire and grazing. Where these disturbances were excluded, rates of change to coastal scrub, shrub, and oak woodlands were much faster than when fire or grazing were included. The authors caution that these trends may be largely modified depending on specific soil and topographic considerations. A myriad of conspiring factors, most notably human decisions on where and how much to graze, can also strongly influence these potential effects.

**Direct Human Impacts**—This section will focus on only those disturbances in which human actions directly affect natural communities. For example, road building is a direct human impact, whereas the slope failure that occurs because of a road cut is a secondary disturbance, or indirectly related to the human impact. Similarly, people breed cattle and largely determine their grazing movements, but the cattle are the primary, or direct, disturbers of forest, rangeland, and riparian zones. Because nearly everything we humans produce and consume has a direct effect on our environment (such as agricultural produce, petroleum products, fibers, metals), I will limit this discussion to a few examples.

In the case of logging, Ripple and others (1991) describe the resulting patchwork landscape as a secondary mosaic of disturbance overlaying nature's disturbance regimes. In their attempts to describe and conserve critical habitat for the northern spotted owl (*Strix occidentalis caurina*) these authors and others (Murphy and Noon 1992; Spies and others 1994) have focused on forest fragmentation resulting from logging. As with other threatened species, the strategy is



Logging, a direct human impact on the landscape, leaves a distinct pattern. One may easily discern the natural opening in the left foreground from those of the clearcuts in the middle of the photo. What landscape-level impacts may occur when human caused fragmentation is superimposed upon natural disturbance regimes?

to conserve enough of the old-growth matrix, including viable corridors between population centers, to ensure sustainable reproduction of these species.

In addition to wildlife concerns, logging and related road building have direct impacts on slope stability. Most recently heavy rains in northern Idaho appear to have led to road and slope failures in logged areas, while adjacent unlogged watersheds exhibited notably less severe damage (Olsen 1996). Both Sidle (1992) and Swanson and others (1992) have studied the relationship between repeated logging and landslide occurrence. Sidle's model calculates the effects of different logging treatments on slope stability. Long-term consequences of intensive logging on vegetation dynamics, regardless of soil stability, are also pertinent. A justification for logging practices for most of this century has been that the number of times we cut a forest is inconsequential as long as we allow the vegetation to go back to its prelogging condition (Trefethen 1976). This "traditional" forestry approach sees forests as "renewable resources," which, if managed properly will look much like the original cover once the forest reaches a mature state again (Hirt 1994, p. 17-24). Or, as Veblen (1992, p. 157) states, "Since vegetation managers have traditionally accepted the idea of climax both in theory and practice,

the recognition of the climax state is of considerable practical importance." He goes on to explain how that recognition is difficult to find in nature. However advocates of this traditional approach have adopted scientific theories that support a climax endpoint, such as Clements (1916) or Daubenmire and Daubenmire (1968), to validate logging practices (clearcutting, rotation periods, industrial forestry, or trees as crops). But more recently, Vale (1988) asserted that this approach should be taken with caution given the many unknowns of nonequilibrium pathways.

Veblen and Lorenz (1986) examined vegetation development on severely disturbed sites along Colorado's Front Range near Boulder. The combined effects of logging, burning, and mining devastated the natural vegetation of this area soon after pioneer settlement late in the 19th century. Since that time some stands have grown back similar to their forest cover before the disturbance, while others have developed along new successional pathways. Modern efforts to revegetate mining sites have taken a more aggressive approach of seeding, and in some cases replacing soil, with native materials in an attempt to re-establish natural successional processes at an early seral state. These efforts have met with mixed success, depending mostly on the severity of soil disruption from the

original mining activity (Brown in press; Brown and others in press; Chambers and Wade 1992).

Recently, scientists have begun to acknowledge air pollution as another human-caused disturbance affecting forests. In addition to gaseous pollutants that contribute to global warming, other pollutants, such as ozone, can directly affect plant growth and vigor (Miller 1980; Smith and others 1994). Reduced vigor in areas of high ozone damage may lead to the types of secondary infection already discussed under insect and disease disturbances. Bormann's (1985) argument for more stringent clean air laws, before whole ecosystems suffer irreversibly, reinforces the notion of unnatural scales of human vegetation manipulation. Some levels of direct human alteration of forests are apparently "natural" or within sustainable limits, maybe at the "agricultural scale" of societies. However, human alteration of global ecosystems in this postindustrial age is difficult to defend as a "natural" system process.

## Disturbance Interactions on the Landscape: Two Case Studies

Two studies have examined the interactions of disturbance regimes over long periods. Using these studies as examples, resource managers and scientists may begin to understand how disturbance agents interact to shape landscape patterns.

**Case Study 1**—On the western slope of the Colorado Rockies, Veblen and others (1994) mapped the forest types and their disturbance histories across the upper end of a wilderness watershed. Predominant stand altering disturbances in this subalpine forest are fire, spruce beetle (*Dendroctonus rufipennis*), snow avalanche, and rockfall. Dating of each disturbance was conducted by using dendrochronology methods and field observations for more recent events. Finally, stands were outlined on aerial photographs, entered into a geographic information system, and georegistered using map checks and a global positioning system. The geographic information system allowed the researchers to calculate actual areas affected by each disturbance type within the total mosaic over multiculturies. Results from this study suggest, for example, that in Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) forests, fire frequencies are much greater than those of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). These spruce-fir dominated types are more frequently affected by spruce beetle infestations between longer fire intervals of 300 years or more. Additionally, a small percentage of the total area (estimated about 9 percent) is affected by nearly annual snow or rock avalanches.

These avalanche-defined forests tend to remain sparse and be dominated by trees of relatively small stature and young age (mostly less than 100 years). As trees become too large they are broken off by avalanches, while younger trees remain protected under snowpack. In sum, this study has uniquely combined methodological techniques (geographic information system, global positioning system, dendrochronology, photo interpretation, and even historical photographs) across a landscape to attain a much broader temporal and spatial understanding of forest dynamics. In this part of the Rocky Mountain West, fire, spruce beetles, and avalanches appear to play a key role in determining historical, large-scale, vegetation patterns.

**Case Study 2**—Gara and others (1984), describe the ecological relationships between fire, fungi, and mountain pine beetle in lodgepole pine forests of south-central Oregon. Their basic tenant is that these disturbances work in a complementary fashion over long periods to maintain lodgepole forests in various successional states across a landscape. This landscape level diversity, in turn, serves to limit the extent of any one disturbance event. The authors describe two disturbance-driven successional pathways—one highly dependent on fire and the second acting in fire's absence. After fires, basal scars result from intense heat and flames from adjacent burning logs. Basal scars are infected by several possible fungi (Gara and others 1984, p. 155), which eventually weaken trees. These trees are subsequently colonized by mountain pine beetle and Ips bark beetle (*Ips pini*), initiating more widespread insect attacks. Dead and fallen trees resulting from the beetle kill prime the forest for another fire. One component that seems key to this cycle is the proliferation of large downed woody debris.

When fire is absent, disturbance processes tend to act more selectively, promoting a more diverse forest landscape. In these nonfire patches, frequent but minor fungi and insect disturbances prevail. (Amman [1978] found similar patterns of mountain pine beetle driven diversity when fire was absent from old growth lodgepole stands.) As with the first case study, ecological experimentation and knowledge of long-term disturbance interactions proved to be an effective method of discerning two distinct landscape patterns.

## Established Methods in Disturbance Ecology

Research designs and sampling procedures derived from a number of disciplines can be fruitful in studies of disturbance ecology. Basic study methods fall into three categories: historical sources, ecological field methods, and modeling. Combining methods can often produce the most interesting and scientifically

credible results. This section will briefly explain the various methods and give examples of their successful implementation.

## Historical Sources

Historical sources include survey records, written accounts, historical photographs, and archaeological evidence (Denevan 1992; Hammett 1992; Vale 1982). Written accounts should be scrutinized the most thoroughly. Forman and Russell (1983) caution that strict protocol should be followed when examining written accounts. Reliable sources would be first-hand accounts, free of individual or societal bias (to the extent possible). The authors should have some knowledge of the species in question. The researcher should take into account the historic context of the statements. Survey records tend to be more accurate, but they too could incorporate individual, and especially societal, bias. Additional checking should be done to establish the context for the original need for survey records.

Historical photographs provide an excellent record of general trends in vegetation cover. But photography is unavailable for many areas and, where it is available, the record is only as old as the technology. Nevertheless, a few studies have successfully employed historic photographs in their assessment of disturbance related changes over time (Baker 1987; Baker and Veblen 1990; Gruell 1983; Veblen and others 1994), although all included field observations and ecological data to augment the photography.

As with any technology, researchers should be keenly aware of the limits of historical photos. For instance, conclusive identification of species, or causes of tree mortality, will likely be beyond the resolution of most historical photos. However, at a broader scale accurate estimates of cover type and amount could be made.

Aerial photographs and remote sensing data may also be considered "historical" in the sense that time series sets of the same site provide records of change over time. Several examples using this technology to monitor change detection are given in Hobbs (1990) and Howarth and Wickware (1981).

Archaeologic records may include specific sources, from wall or animal skin paintings depicting cultural activities, to acquisition of preserved plant materials used by previous inhabitants, to evidence of broader scale impacts, such as mound digging, road construction, or city building. Both Hammett (1992) and Denevan (1992) employ these and other sources to back the notion that native cultures throughout the western hemisphere made significant impacts on ecological communities. These impacts seem to have been especially pronounced prior to severe declines in aboriginal populations when Europeans introduced small pox and other diseases (Denevan 1992; Sprugel

1991). The use of fire for hunting, land clearing, and other uses was apparently a widespread phenomenon.

## Field Ecological Methods

Field ecological methods are any strategies where direct field data or samples are collected to make further statements about disturbance processes. This may encompass any number of empirical approaches. This discussion will be limited to a small list of methods.

Probably the most commonly used sampling method for dating past disturbance is dendrochronology, which involves the reconstruction of time series data based on tree ring observations. The great strength of this method lies in crossdating, which was formalized by Douglas (1941). Crossdating is the synchrony of precisely matched tree ring patterns that allows assignment of a calendar year to each ring. In this way, one may "build" a chronology of forest history by matching overlapping segments of rings of varying ages, even from dead trees or wood fragments. Ideally, this crossdating effort will result in a verified set of data representing a decadal to multicentury record of climate and disturbance regimes. An outline of this procedure and its application to ecological research has been compiled by Fritts and Swetnam (1989). Dendrochronological studies related to specific disturbance types include: for insects (Hadley and Veblen 1993; Jardon and others 1994; Stuart and others 1983; Swetnam and Lynch 1993), for fire (Arno and others 1993; Barrett and Arno 1988; Johnson and Larsen 1991; Romme 1982), for avalanches (Carrara 1979; Potter 1969), and for climate fluctuations (Douglas 1941; Fritts and others 1965; LaMarche 1982). Some authors suggest less intensive, and presumably less destructive, dendrochronologically based methods be employed in wilderness or other reserved forests (Barrett and Arno 1988; Lorimer 1985).

Another approach to long-time series dating has been analysis of pollen deposits preserved in bogs, lake sediments, or sometimes soil (MacDonald 1993; MacDonald and Cwynar 1985; Prentice 1992). Species in strata of pollen indicate what plants or animals were present on a site over time. Additionally, certain plant parts may be preserved in the pollen layers, adding evidence to plant-climate associations (Vale 1982). Similar procedures were used to date insect presence over time (Elias 1985, 1991). This technique appears particularly useful for dating century to millennium-scale climate and disturbance patterns (Prentice 1992). Bradshaw and Hannon (1992) successfully employed a pollen dating method to construct a 4,000-year record of forest cover change in southern Sweden. While they did detect climate changes during this period, they attribute most of the vegetation change to human land-use practices.

Overpeck and others (1990) constructed a multi-century pollen record of two sites in Wisconsin and Quebec, then entered that data into a climate and disturbance simulation to project future conditions. Based on their pollen data of past forest and climate dynamics, they forecast a future of greater disturbance frequencies brought on by continued warming and drying conditions.

Gradient analysis is an ecological tool for assessing environmental and community structure and function over a given space. It is applied to disturbance ecology to check disturbance interactions and spread. Fritts and others (1965) tracked the fluctuation of forest types along an elevation and precipitation gradient over time using dendrochronological methods. They found that climate changes had the greatest effect on the growth patterns of trees found at the lower forest margin. Gosz (1992) also highlights the importance of measuring disturbance effects at vegetation ecotones (transition zones) in his regional demonstration of gradient analysis. He maintains that ecotones form critical barriers to the spread of disturbance. Gosz further states that by focusing on these transition areas, scientists may track the movement of disturbance-maintained boundaries over time. Explanations for changes in spatial disturbance regimes may be found by isolating possible causes at similar sites across a region.

A related method is the ecological risk assessment approach commonly used by the U.S. Environmental Protection Agency. Risk assessment is most often applied to direct human-caused disturbance. Graham and others (1991) demonstrate this approach at the regional scale by evaluating the possible effects of ozone in the Adirondack region. They also emphasize the importance of monitoring forest ecotones for early warning signs of ozone-caused disturbance. The basic procedure for ecological risk assessment is to collect data and monitor field sites over time, while simultaneously building a model of "critical risk" for specific ecological indicators based on field inputs. When field sites approach "critical levels," further mitigating action will be warranted to reduce the disturbance, if possible. Although risk assessments are being widely used, the scientific community is concerned with basic methodology, including the projection of small data sets over much larger scales, both spatially and temporally (National Research Council 1993). Misunderstanding of basic assessment purposes also affects final product meanings. Lackey (1994-1995) points to at least six commonly used approaches to assessing ecological risk. These wide and varied approaches have often served to confuse policymakers and the general public.

A final example of field ecological methods is the intensive site study. Field teams intensively measure

a large number of site attributes in a small area to project conclusions to a much broader scale. One such classic study is that of Henry and Swan (1974). On their 0.1-acre plot in New Hampshire they mapped, identified, and aged all living, dead, and buried trees and fragments. Through exhaustive field and laboratory analysis they were able to create a thorough record of vegetative change resulting from disturbances over the past 300 years.

In Quebec, Payette and others (1990) constructed a chronology of gap formations and closures over the past two centuries. Although these authors focused on above-ground material only, they too, mapped and aged every live and dead tree on a slightly larger area than Henry and Swan. From dendrochronological evidence and examination of tree fall patterns they concluded that small-scale, gap-phase dynamics have been the dominant disturbance pattern in their area for at least two centuries.

## Modeling

Modeling techniques have been widely applied to disturbance ecology. Although some people, have little understanding or perceived need for the abstractions of modeling, it does allow scientists to explore spatial and temporal variability in an artificial medium, where similar studies on the ground would be logistically impossible (Botkin 1993; Turner and others 1994). Nevertheless, good models must build upon defensible empirical data. The main weakness of modeling is being able to bring findings back from abstraction to some real world understanding.

An example of a successful model is Keane and others (1990) model of forest succession, accounting for five disturbance regimes and three tree species, to simulate fire effects and vegetation development over a 200-year period. Their FIRESUM model is built on decades of ecological research for specific forests, habitat types, and fire regimes, plus information from other studies of climate, soil properties, moisture retention, fire spread rates, fuel loading, and other factors. These authors compared fire regimes from actual study sites using dendrochronologies with their modeling results as a means of "grounding" their model. Results showed similar forest development patterns to those of actual sites from the years 1600 to 1900.

The two basic modeling approaches are theoretical and simulation modeling. Theoretical models build upon the idea of taking sound mathematical principles and applying them to natural systems in the most economic manner, adding complexity only when absolutely necessary (for example, Clark 1991; DeAngelis and Waterhouse 1987). Simulation models incorporate as much complexity as is needed to accurately

describe natural processes (Keane and others 1990; Overpeck and others 1990). Simulations models may be monstrous in form, but they more closely reflect actual ecological systems. While modeling applications often employ one approach or the other, a continuum exists between the purely theoretical and the purely simulation approaches, and at least one author has advocated a synthesis of the two as a means of employing the strengths of both (Logan 1994).

Because of technological advances, many modelers are beginning to take this approach, but are doing so with space as a focal point. An example is the use of epidemiology theory to project rates of spread over a landscape (O'Neill and others 1992). In theory, disturbances, such as fire, spread across a landscape much as diseases spread through human or other populations. With a basic mathematical model borrowed from the medical discipline, "real world" modifications were made based on landscape criteria, and spatial applications relevant to rates of disturbance spread were projected. From this model, the authors concluded that vegetation patterns in conjunction with topography are at least as important as disturbance dynamics in determining the extent of disturbance regimes. Other authors have used spatial models at a variety of scales to simulate disturbance dynamics (Fahrig 1992; Frelich and Lorimer 1991; Urban and Shugart 1992; Urban and others 1991).

Taking synthesis further, let us consider a modeling track in which spatial information is projected over time in a mapped format. To do this, a great deal of information and data need to be included in the model, necessitating use of geographic information systems because of their analytical power and flexibility (Johnson 1990). Baker (1992) used this approach in analyzing settlement and fire suppression effects on the fire regime of the Boundary Waters Canoe Area. He focused on fire regime interactions—or patch "births" and "deaths"—as a key element of landscape dynamics. A new patch occurs when a fire event defines a new polygon on the landscape. Patches die when larger, or newer, fires override previously defined polygons. In this way, a 1,000-year simulation was run using actual fire regime data both prior to, and after, settlement. After the simulation midpoint of 1868, data were split to compare the effects of settlement and suppression with those of the natural fire regime for the next 500 years. The researcher concluded that frequent human-caused fires for land clearing during the pioneer period, combined with subsequent fire suppression, resulted in a much different landscape than would have occurred without these factors. The management implications of this study become more apparent as Baker further hypothesizes the effects of current human alterations to that landscape; namely, prescribed burning and global climate change.

## Toward Management with Disturbance Ecology

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Current scientific knowledge of disturbance ecology suggests we take a broader approach to management. This philosophical viewpoint may aptly be called a paradigm shift. In the past, managers viewed disturbance as having mostly negative impacts, whereas currently, evidence suggests nearly the opposite: preservation of natural disturbance regimes is essential to promote healthy, dynamic ecosystems. Many attempts to suppress disturbance are now proving deleterious to the long-term healthy functioning of forest ecosystems (for example, fire suppression and insecticide application). Further aggressive tactics in forest management seem certain to compound previous disturbance mismanagement. Where fire suppression has reigned, further suppression will increase density and change composition drastically. Where widespread clearcutting is dominant, more clearcutting and subsequent planting of single species will reduce diversity and increase the chances of epidemic levels of insects and disease. And where overgrazing prevails, furthering this practice may lead to soil loss, reduced regeneration, exotic species invasion, and riparian damage. Rather than continue this antagonistic approach to nature, perhaps now is the time to work with natural processes if our overall goal is to maintain ecological integrity.

Just being aware of these trends will not be enough. To implement disturbance ecology into management plans, specific ecosystem understanding of dominant processes is essential. Noss (1990) suggests a hierarchical approach to monitoring systems for critical components, functions, and processes. Though his objective was to develop indicators for monitoring biodiversity, he also outlines a course for inquiry into critical functions, such as disturbance interactions. Both community and regional level events should be tracked for aerial extent, frequency, rotation period, predictability, intensity, severity, and seasonality (Noss 1990, p. 359).

Much of the needed information can be gathered from previous studies, or modified from regional data. When information on disturbance is not available, some preliminary background research is recommended to increase knowledge, to save time, and to standardize methods with similar studies where practicable. The value of standardized procedures will become more critical as data are increasingly exchanged across agency and political boundaries in pursuit of greater regional understanding.

Once reliable data are obtained, the difficult decisions of management begin. Humans will continue to need products from the land, but with knowledge about ecosystems, limits of extraction and use can

and should be defined (Gordon 1993; Grumbine 1994). Management decisions will ultimately involve more than purely ecological, or even scientific, reasoning (for example, Franklin 1995). Or, as Pfister (1993, p. 231) has put it: "Ecology may provide many of the answers—but only if it is holistic enough to incorporate the human element as part and parcel of the ecosystem." Zimmerer (1994), in a critical attempt to integrate the previously disparate realms of ecology and human geography, strongly advocates the recognition of natural disturbance regimes in management practices in tandem with human considerations. In realizing the uncertainty this will incorporate, he further states: "Managing for uncertainty includes evaluating the limits within which natural processes and human interventions are likely to produce a certain result (as opposed to asserting the certainty of single values and ironclad outcomes)" (p. 118). The former objective acknowledges a variability inherent in both natural and human systems, while the latter assumes a false confidence in human ideals.

Just as ecologists and managers should strive to incorporate human values into management decisions, humans in general will need to gain a better understanding of ecology so that they can better participate in public land management and thus become part of a solution that strives to work with nature. With this in mind, adoption of disturbance ecology-based management should emphasize education at all levels to ensure effective and productive public participation.

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This review of the disturbance ecology literature, and how it pertains to forest management, is a resource for forest managers and researchers interested in disturbance theory, specific disturbance agents, their interactions, and appropriate methods of inquiry for specific geographic regions. Implications for the future of disturbance ecology-based management are discussed.

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Keywords: equilibrium, forest dynamics, human disturbance, landscapes, regions, modeling

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