

# Are Large, Infrequent Disturbances Qualitatively Different from Small, Frequent Disturbances?

William H. Romme,<sup>1\*</sup> Edwin H. Everham,<sup>2</sup> Lee E. Frelich,<sup>3</sup> Max A. Moritz,<sup>4</sup> and Richard E. Sparks<sup>5</sup>

<sup>1</sup>Department of Biology, Fort Lewis College, Durango, Colorado 81301; <sup>2</sup>Florida Gulf Coast University,

Fort Myers, Florida 33908–4500; <sup>3</sup>Department of Forest Resources, University of Minnesota, St. Paul, Minnesota 55108;

<sup>4</sup>Department of Geography, University of California, Santa Barbara, California 93106; and <sup>5</sup>Water Resources Center, University of Illinois, Urbana, Illinois 61801, USA

## ABSTRACT

In this article, we develop a heuristic model of ecosystem-disturbance dynamics that illustrates a range of responses of disturbance impact to gradients of increasing disturbance extent, intensity, or duration. Three general kinds of response are identified and illustrated: (a) threshold response, (b) scale-independent response, and (c) continuous response. *Threshold responses* are those in which the response curve shows a discontinuity or a sudden change in slope along the axis of increasing disturbance extent, intensity, or duration. The response threshold occurs at a point where the force of the disturbance exceeds the capacity of internal mechanisms to resist disturbance, or where new mechanisms of recovery become involved. Within this conceptual framework, we find that some unusually large or intense disturbances, but not all, produce qualitatively different responses compared with similar disturbances of lesser magnitude. If disturbance impact does not increase with increasing disturbance extent, intensity, or duration, or if the response curve changes monotonically, then large disturbances are *not* qualitatively different from small ones. For example, jack pine tends to become reestablished after stand-replacing fire in boreal forests, regardless of fire size, because its serotinous

cones provide an adequate seed source throughout the burned area. Thus, large fires are not qualitatively different from small fires in terms of jack pine reproduction. However, if disturbance impact does increase abruptly at some point with increasing disturbance extent, intensity, or duration, often because of thresholds in the capacity of internal mechanisms to resist or respond to disturbance impact, then large disturbances *are* qualitatively different from small ones, at least for some parameters of ecological response. For example, balsam fir and white cedar can recolonize a small burned patch of boreal forest in close proximity to surviving individuals of these species, but they will be eliminated from a large burn because of their susceptibility to fire-caused mortality and their inability to disperse their seeds over long distances. The conceptual framework presented here permits some new insights into the dynamics of natural systems and may provide a useful tool with which managers can assess the potential for catastrophic damages resulting from large, infrequent disturbances.

**Key words:** disturbance size; disturbance impact; thresholds; large, infrequent disturbances; extreme ecological events; fire in boreal forests; fire in temperate forests; windstorms in temperate forests; hurricanes in tropical forests; floods in floodplain ecosystems; kelp forests; mussel communities; intertidal communities; ecosystem management

Coauthors are listed in alphabetical order; all authors contributed equally to development of this report.

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\*Corresponding author; e-mail: romme\_w@fortlewis.edu

## INTRODUCTION

A recent spate of large, rare natural “disasters” (for example, the Yellowstone fires in 1988, Hurricane Hugo in 1989, and the upper Mississippi River floods of 1993) has caught the public’s attention and raised fundamental questions about the nature and consequences of these kinds of events (Flavin 1996; Turner and others 1997). Can we predict the ecological effects of large disturbances (for example, hurricanes), about which we know relatively little due to their rarity and unpredictability, based on our knowledge of similar-appearing and better-studied small disturbances (for example, treefall gaps)? Can we substitute smaller, more controllable disturbances (for instance, prescribed fires) for dangerous, uncontrollable large natural disturbances and still achieve the same management objectives (fuel reduction and desirable vegetation mosaics, for example)?

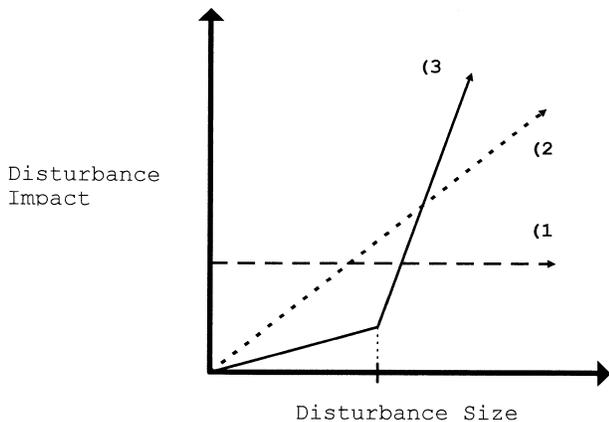
To answer these questions, it is necessary to know whether large, infrequent disturbances (LIDs) differ from small, frequent disturbances only in amount of effect, for example, the number of organisms killed or number of hectares of bare substrate exposed (quantitative differences)—or whether they also differ in kinds of effects, for example, initiation of alternative successional trajectories or evolutionary responses (qualitative differences). If the differences are merely quantitative, then prediction and management are conceptually straightforward (though not necessarily easy in practice!): we can extrapolate from known effects of similar small disturbances, and we can implement controlled, small disturbances at an appropriate frequency and extent to disturb the same amount of area cumulatively as would occur naturally in a single large disturbance during a time period comparable to the natural return interval of the large disturbance. However, if LIDs introduce fundamentally new kinds of phenomena into ecological systems, then we must be prepared for some ecological surprises in the aftermath of large events, and we may need to devise strategies for incorporating the large disturbances into our management framework.

A conceptual challenge in answering the question posed in the title of this report is to define what constitutes “large” or “infrequent” relative to disturbances. One can take a statistical approach to this definition, assemble an empirical distribution of sizes, intensities, or frequencies of disturbances, and determine which represent the extreme tail of the distribution. [For example, see Gaines and Denny (1993), Grissino-Mayer (1995), and Moritz (1997)]. However, it still is an arbitrary decision where to

draw the line between “large” and “small,” or “infrequent” and “frequent,” for example, whether to focus on the largest or rarest, say, 10% or 1% of the distribution. Moreover, because of the rarity, we may not have an adequate empirical base for describing the extreme end of the distribution for many kinds of disturbances. For example, the largest fires observed by managers in Yellowstone National Park prior to 1988 had burned less than 15,000 ha. It is understandable, therefore, that many people were surprised when over 300,000 ha burned in 1988 (Christensen and others 1989). However, once long-term fire-history studies were completed, based on tree rings and lake sediments (Romme and Despain 1989; Millspaugh and Whitlock 1995), it appeared that the 1988 fires actually were within the normal range of prehistoric fire sizes and ecological effects in the Yellowstone ecosystem. As an alternative approach to this definition, LIDs could be viewed in the context of the spatial and temporal scales of the system of interest (O’Neal and others 1986). For example, a single treefall would be a massive, rare disturbance from the perspective of ants living in the trunk, but small and common within the forest landscape. In this context, the spatial and temporal perceptions of the researchers are critical, and a purely objective definition of large disturbances is not possible (or even necessary).

In this article, we have adopted a heuristic definition of large disturbances that incorporates both of the concepts just described. We define *large* disturbances as those that lie toward the far end of a statistical frequency distribution and are of a magnitude that humans perceive to be large. Thus, the aforementioned single treefall is not considered a large disturbance, despite the ants’ perception, but the 1988 Yellowstone fires and the 1993 Mississippi River floods are large disturbances. We also are interested not only in disturbances of great spatial extent but also those of unusual intensity, duration, or frequency.

A second challenge in this report is to define what is meant by a “qualitative” change in impact or effect. As the areal extent, intensity, duration, or frequency of a disturbance event changes, we can imagine a corresponding change in any impact or effect on the system disturbed. A graph of any impact or effect versus disturbance size, intensity, or frequency may exhibit a curve either with a relatively uniform slope or with a discontinuity or severe change in slope. We refer to this latter pattern—a sudden change in impact or effect along a disturbance gradient—as a *threshold*. Further, we define *qualitatively different* impacts as those that



**Figure 1.** Graphical model of ecosystem-disturbance dynamics showing three general kinds of response of disturbance impact to increasing “size” (extent, intensity, duration, or frequency) of disturbance: (1) scale-independent response, (2) continuous response, and (3) threshold response. See the text for further explanation and clarification of terms and for examples of each kind of response.

exhibit a threshold response. Finally, we explore the idea that thresholds of this kind are predictable, that is, that sudden changes in the shape of the response curve occur when some physical limit in the system is reached (for instance, wind force exceeds the ability of a tree stem to resist breakage) or when some shift in functional response to disturbance occurs (for example, from resprouting of damaged individuals to recruitment of new individuals from seed).

## A GENERAL CONCEPTUAL FRAMEWORK

We developed a general conceptual framework for examining ecosystem-disturbance dynamics and for exploring the question whether LIDs are qualitatively different from small, frequent disturbances. We employ Sousa’s (1984: 356) definition of *disturbance* as “a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.” Our model (Figure 1) is a representation of ecological effects or impacts (the dependent variable) caused by disturbances of progressively greater “size” (the independent variable). An analysis must be bounded by a specific study area, and we will assume that to be the total area of the ecosystem of interest.

The  $x$ -axis in Figure 1 represents a gradient in disturbance size, which may be represented by extent, intensity, duration, or frequency [sensu

Sousa (1984: 357)]. By disturbance *extent* we mean spatial extent, for example, number of hectares disturbed. *Intensity* refers to the strength or physical force of the disruptive event being applied to the system during the disturbance, for instance,  $\text{kWm}^{-1}$  in a fire (Johnson 1992), wind speed/duration in a hurricane (Lugo and others 1983; Everham and Brokaw 1996). *Duration* is the length of time that a stress is applied, for example, the duration of high water in a flood. Disturbance *frequency* is expressed as number of disturbance events during a specified period, or as the time interval between successive disturbances. (Although this report focuses mainly on large disturbances that are infrequent, we also examine some interesting cases in which the special feature of the disturbance is its unusual frequency of occurrence.)

Within this basic framework (Figure 1), we propose that there are three general patterns of response of disturbance impact to increasing disturbance extent, intensity, duration, or frequency: (1) no change in impact (*scale-independent response*), (2) gradual change in impact (*continuous response*), and (3) more-or-less abrupt and dramatic change in impact at some point along the size gradient (*threshold response*) [cf. Allen and Hoekstra (1992: 4)]. It is important to recognize that various parameters or measures of disturbance size and impact may exhibit different kinds of relationships within the conceptual space defined by Figure 1—even for the same kind of disturbance and in the same ecological system (examples follow). In the following sections, we illustrate these three kinds of responses in more detail, though we make no attempt to cover all possible examples or combinations. Table 1 contains a summary of the examples discussed below.

### Threshold Responses

Because this type of response has the most relevance to the question posed in this article, we develop it in greatest detail and with the most examples. First consider an individual tree that is subjected to increasingly strong winds. The impacts on the tree can be viewed as a series of thresholds that are exceeded as the force of the wind steadily increases. The wind must first reach a speed where the tree will lose leaves. If this is the maximum force of the disturbance, the impact will be limited to defoliation, and the long-term consequences for the tree will be minimal. With increasing wind speed, thresholds for the loss of twigs and larger branches will be exceeded, and finally the tree itself will snap

**Table 1.** Types of Response of Disturbance Impact to Increasing Disturbance “Size” (Extent, Intensity, Duration, or Frequency) as Illustrated by the Examples in This Report

System and Disturbance Type	Parameter of Disturbance Size	Parameter of Disturbance Impact	Type of Response	Mechanism(s) Controlling Response
Fire in boreal forests	Spatial extent of burned area (2–180,000 ha)	Postfire establishment of jack pine and black spruce	Scale independent	Serotinous or semiserotinous cones provide adequate seed supply throughout burned area
		Postfire establishment of aspen	Scale independent	Production of abundant, wind-dispersed seeds by surviving adults along lakeshores and in other protected locations
		Postfire establishment of balsam fir, red pine, white pine, white cedar	Threshold response: abrupt decrease in density with increasing distance from survivors	Seeds with poor dispersal mechanisms produced only infrequently by survivors in restricted locations
Wind and fire in temperate forests	Spatial extent of blowdown	Postdisturbance change in tree species composition	Scale independent	Surviving advanced regeneration reestablishes original canopy composition
	Spatial extent of blowdown	Mechanism of biotic response	Threshold response: seedling recruitment in larger gaps only	Threshold in light availability with increasing gap size
	Intensity (windstorm versus fire)	Postdisturbance change in tree species composition	Threshold response: replacement of sugar maple and hemlock by aspen and paper birch only after fire	Death of advanced regeneration and creation of open spaces where new species can colonize only after fire
Hurricanes in tropical forests	Recurrence interval between hurricanes	Persistence of forest species and forest structure	Threshold response: shift to nonforest vegetation at very short recurrence intervals	Trees eliminated when recurrence interval becomes less than minimum age of seed production
Floods in riverine floodplains	Depth and spatial extent of short-term flooding	Tree mortality	Scale independent	Floodplain species are physiologically adapted to annual, short-term flooding
	Duration of flooding (1–120 days)	Tree mortality	Threshold response: extensive tree death only after a certain duration of flooding	Prolonged anoxia in soils; exceeds tolerance of most trees
		Change in species composition	Threshold response: loss of <i>Quercus</i> spp. and <i>Carya</i> spp. and possible shift to nonforest after a certain duration	Poor dispersal capability and fragmented surviving populations of <i>Quercus</i> and <i>Carya</i> ; possible fires in fuels created by dead trees
Wave disturbance in mussel beds	Intensity (wave force and exposure)	Size of bare patches produced by dislodging of mussels	Threshold response: none dislodged up to a point, then extensive loss of mussels with increasing wave force	Interconnected mat of mussels provides resistance to dislodging, up to a point, but once a few are lost, the others are more vulnerable
Wave disturbance in kelp forests	Wave height and frequency, and drag force of moving water	Mortality of the dominant <i>Macrocystis</i> canopy	Threshold response: little or no mortality with ordinary wave action, but substantial mortality after a certain point	Holdfasts and stipes can resist breakage up to a level of drag; once individuals begin to break, they entangle others and accelerate mortality
	Spatial extent and magnitude of <i>Macrocystis</i> mortality	Probability of change in patch structure and species composition	Threshold response: no change below a certain level, but possibility of change after more intense disturbance	Rapid regeneration from surviving individuals in small patches; scramble competition in large openings of the <i>Macrocystis</i> canopy; other factors involved also

or uproot, with the severe consequence that the tree dies or loses its canopy position. The points at which the physical limits of this system (leaf retention, branch strengths, and bole or root or substrate strength) have been exceeded are the levels of force that constitute thresholds for this "system." Regardless of the measure of disturbance size or intensity (for example, wind speed or storm intensity classification) and disturbance impact (for instance, loss of biomass or photosynthetic capacity), there has been a sharp increase in the impact to the system beyond a certain threshold. Before each threshold, recovery of the system involved different mechanisms (refoliation, branch growth, and bole regrowth, for example). Each new threshold requires the expenditure of additional energy and the utilization of additional nutrients, and an increasing possibility of mortality. The tree may be adapted to the stress of winds and have mechanisms, such as buttresses, to resist this disturbance (Mattheck 1991), but these mechanisms break down rapidly when the force of the wind reaches a specific magnitude.

Scaling up from the individual tree to a larger system, consider an even-aged, single-species forest stand subjected to the same strong winds. As the strength of disturbance increases, there will be increasing ecological impact in the form of defoliation and possibly a small percentage of trees that snap or uproot, usually those that are weakened or dead. Although cumulative damage to the system may be substantial and increasing, no threshold appears to have been crossed. The disturbance might not be considered "catastrophic" yet, because healthy trees have not been destroyed (Attiwill 1994). As disturbance force continues to increase, either in terms of wind strength or duration, a point is reached at which healthy trees begin to fall and create large gaps in a "domino" effect [for example, see Van der Meer and Bongers (1996)]. In this case, a threshold appears to have been crossed when the force of the storm and the dynamics of gap creation become stronger than the ability of the system to resist these destabilizing forces. Certain forest systems may have internal mechanisms that resist the disruptive force of wind disturbances, such as the "tree unions" of tropical forests (Basnet and others 1993), but this resistance quickly breaks down once the threshold has been reached. Stand age and structure also may influence the points along the gradient of wind speed or duration at which various thresholds are crossed. For example, vulnerability to extensive windthrow in some Andean *Nothofagus pumilio* forests increases sharply when stands reach 100–125 years of age (Rebertus and others 1997). Similarly, Foster and Boose (1992) describe relation-

ships between stand age, tree architecture, and susceptibility to wind damage in New England.

#### *Examples of threshold responses to disturbance extent.*

Several studies in temperate deciduous forests of eastern North America, and in broadleaf tropical forests around the world, have demonstrated a qualitatively different biological response to small versus large treefall gaps (but also see the discussion of scale-independent responses below). Small gaps, such as those caused by a single tree, generally are filled by expansion of branches on surrounding canopy trees and by accelerated growth of understory trees that were already present before the disturbance. Larger gaps, usually caused by multiple treefalls, also stimulate accelerated lateral growth of surviving canopy trees and vertical growth of understory trees, but in addition provide adequate light to allow recruitment of new individuals from seed (Oliver and Stephens 1977; Dunn and others 1983; Brokaw and Scheiner 1989; Lorimer 1989; Poulson and Platt 1989; Whitmore 1989). Trees that become established from seed within large gaps include shade-intolerant species, for example, black cherry (*Prunus serotina*), yellow poplar (*Liriodendron tulipifera*), and white ash (*Fraxinus americana*), that generally do not regenerate under an undisturbed forest canopy (Poulson and Platt 1989). Thus, there is a threshold in gap extent beyond which there occurs a qualitatively different kind of biological response to disturbance, viz., recruitment of new individuals from seeds, including a new suite of shade-intolerant species. This threshold in biotic response occurs because light availability on the forest floor increases gradually with increasing gap size until it reaches a point where tree seedlings can survive. Multiple treefalls also tend to create special kinds of habitats, such as tip-up mounds, which further enhance seedling establishment of some species such as yellow birch (*Betula alleghaniensis*) (Dunn and others 1983). The threshold extent of canopy opening needed to stimulate recruitment of tree seedlings has rarely been documented quantitatively, though Brokaw and Scheiner's (1989) work on Barro Colorado Island in Panama suggests that the threshold is at about 150 m<sup>2</sup>.

Some fire-sensitive boreal species exhibit a threshold response to fire extent. Frelich and Reich (1995b) studied an extensive unlogged area in the Boundary Waters Canoe Area of northern Minnesota that was characterized by a historic fire regime of large intense fires with a rotation period of about 50 years (Heinselman 1973; Van Wagner 1978; Johnson 1992). Balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), and white cedar (*Thuja occidentalis*) were confined to unburned or

lightly burned lakeshores. Interior portions of the landscape (more than 30 m from lakeshore refugia) apparently were too far from seed sources for effective colonization between successive fires in the past. For example, white cedar seeds only travel about 20 m (Cornett 1996) in numbers large enough to regenerate a stand of the species. Less than a quarter of the landscape is accessible from the lakeshore at this distance. In addition, several good seed years (coming at 5-year intervals) are required to stock a stand, and then another 30–40 years are needed for the new recruitment to attain seed-bearing age in the forest so that the species could spread even farther inland. Given a 50-year fire rotation period, however, they will not be able to advance very far inland. Thus, these fire-sensitive species with limited dispersal capabilities show a threshold response to fire size (but see below for an example of scale-independent responses by other species in this boreal landscape).

*Examples of threshold responses to disturbance intensity.* Mesic forests of sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*) may exhibit a striking threshold response to disturbance intensity as measured by wind versus fire disturbance. Fires are very rare in this vegetation type, occurring with rotation periods of several thousand years (Frelich and Lorimer 1991). When fires do occur, however, even though usually small in spatial extent, they kill the overstory and advanced regeneration, and result in replacement of the former canopy dominants by aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*).

Another example of a threshold response to increasing disturbance intensity is seen in kelp forests off the coast of southern California (Tegner and Dayton 1987). A major cause of mortality in the dominant canopy of giant kelp (*Macrocystis pyrifera*) is physical damage due to wave action (Seymour and others 1989). Some wave damage occurs every year, but in the 1980s there were two extraordinary storm events in the kelp forests off Point Loma, California: a series of powerful storms during the 1982–83 ENSO (El Niño–Southern Oscillation) winter, and a single storm in 1988 that apparently was the most intense storm in the area in 200 years (Dayton and Tegner 1984; Dayton and others 1992). Giant kelp is well adapted to ordinary wave action and can remain attached to the substratum in all but the strongest waves (Seymour and others 1989). However, as wave force and the resulting drag of moving water on the plants increases beyond a certain point, holdfasts begin to fail, and stipe bundles part. The dislodged plants then become entangled with other individuals, increasing the

drag further and breaking off these individuals as well (Seymour and others 1989). Thus, there is a threshold response in mortality of canopy plants to increasing intensity of wave action. The threshold results primarily from the mechanical limits of physical attachment mechanisms to wave-induced drag as well as the “domino effect” of entanglement by plants already broken off.

Disruption of the *Macrocystis* canopy over a small spatial extent, for example, a few square meters, is almost always followed by rapid recovery to pre-disturbance composition and structure (Dayton and Tegner 1984; M. J. Tegner personal communication 1996). However, large-scale disturbance, as occurred with the 1980s’ storms, results in scramble competition among several species of kelp to colonize the open space. Hence there is the potential for changes in patch structure and composition; that is, a *threshold* in biological response to increasing storm intensity (Tegner personal communication 1996). The outcome of this competition may depend on the interaction of other variables. For instance, the storms of the early 1980s were followed by poor growing conditions for *Macrocystis* (warm, nutrient-poor waters), and several understory kelp species established new cohorts that persisted for several years. In contrast, growing conditions after the 1988 storm were excellent for *Macrocystis* (cool, nutrient-rich waters), and the post-storm cohorts of *Macrocystis* were able to exclude understory kelp species competitively in many locations [see Tegner and others (1997) and Tegner personal communication (1997); also see Paine and others (1998)].

A final example of a threshold response to disturbance intensity comes from mussel beds dominated by *Mytilus californicus* within rocky intertidal areas [for example, see Dayton (1971) and Paine and Levin (1981)]. Due to the harshness of this environment during intense storms, patch creation has not been directly observed and quantified, but the degree of wave exposure has been used as a surrogate for actual measurements of wave forces (Denny 1994a, 1995). Similar to what occurs in forests subjected to wind disturbances, dead or weakened individual mussels are probably the first to be dislodged (Paine and Levin 1981). As the strength of waves increases, the probability of dislodgment for a given individual also increases, due to the lift component of hydrodynamic force and other factors (Denny 1987). The interconnected mat-like structure of mussel beds may provide support for neighboring individuals, but may also increase the likelihood that groups of individuals are removed once the patch initiation process has begun [see Dayton (1971), Paine and Levin (1981), Denny (1987), and

Denny and others (1985), but also Denny (1995) for a somewhat different interpretation]. Despite uncertainties about the physical mechanisms involved, it appears that as wave strength reaches the point where entire clumps of mussels are being dislodged, a threshold in disturbance impact has been crossed. Denny (1994b, 1995) notes that organisms will be most sensitive to variations in disturbance force where the cumulative probability distribution for breaking force is steepest, meaning that small increases in force can result in an amplified response for disturbances in this region. The resistance of this system against disturbance is a structural one, namely, the physical continuity of the mussel beds themselves.

*Examples of threshold responses to disturbance duration.* The effects of the unusual Mississippi River floods of 1993 on riverine and floodplain ecosystems were dramatically different from the effects of the frequent but less severe floods that characterize this system (Sparks 1995, 1996). The key feature of the 1993 floods was not volume of water or spatial extent of flooding, but the extreme duration and seasonal timing of the flood. The 1993 flood began in April, during the normal flood season, but multiple peaks continued through the entire growing season (normally the low flow season), and the river did not drop below flood stage at St. Louis until 30 September (Southard 1995). The ordinary, short-duration floods that occur nearly every year may injure some small trees and shrubs, but mature trees are usually unaffected and most of the injured small individuals can resprout from surviving roots. In 1993, however, low-lying soils were saturated long enough for anoxic conditions to develop, so even roots of mature trees eventually died and water was no longer transported upward to stems and leaves. One startling sight in August 1993 was the number of trees that had brown, drying leaves, even though they were standing in water—as though a drought, rather than a flood, was occurring! The entire understory and much of the canopy was eliminated in substantial portions of the floodplain in 1993 (R. E. Sparks personal observations). Within a year, the areas of most severe tree mortality were dominated by opportunistic herbaceous species (for example, *Bidens aritosa*, *Polygonum* spp., and *Ipomoea pandurata*) and vines (for instance, *Vitis* spp., *Sicyos angulatus*, *Campsis radicans*, and *Convolvulus* spp.). Some tree species with abundant, aerially dispersed seeds and rapidly growing seedlings (*Populus deltoides* and *Acer saccharinum*, for example) may become reestablished quickly in these areas. However, other tree species having more limited dispersal capability and slower-growing seedlings (for example, *Quercus pal-*

*ustris*, *Q. macrocarpa*, *Q. lyrata*, and *Carya* spp.) may be unable to reestablish themselves within the dense stands of opportunistic herbs and vines.

The post-1993 successional trajectories on the Mississippi River floodplain also will be sensitive to effects of subsequent disturbances [see Sparks (1996); see also Paine and others (1998)]. Where tree seedlings do become established, they will be vulnerable for many years to injury even by lower-intensity floods. Spring floods in 1995 killed extensive tracts of seedling trees developing after the 1993 floods (Sparks personal observations). A prolonged drought could dry the standing and downed timber left by the 1993 flood sufficiently to fuel fires, which could burn seedlings and saplings and favor expansion of remnant prairies (Nelson and others 1994).

*Examples of threshold responses to disturbance frequency.* In snow avalanche tracks of the Canadian Rocky Mountains, where average interval between avalanches is less than 15–20 years, forests are absent and vegetation is dominated by small shrubs that can survive avalanches without stem breakage. However, locations where intervals exceed 20 years support forests or shrublands with interspersed trees (Johnson 1987). In tropical forests, threshold responses to hurricane frequency are suggested by simulation studies. Doyle (1981) predicted species richness associated with changing hurricane recurrence intervals for the Luquillo Forest, Puerto Rico, by using the forest-gap model FORICO. He found greatest richness near an intermediate level of disturbance, and loss of species in a discontinuous fashion when he either increased or decreased disturbance frequency. These findings for the Luquillo Forest were supported by another simulation study using the same model in a spatially explicit context (O'Brien and others 1992). This study included simulations with extremely frequent (once per year) and intense (100% mortality) hurricanes. In these simulations, the forest system ceased to exist at the extreme end of the intensity and frequency scales. Another threshold response exists where the interval between successive hurricanes is shorter than the time required for tree species to mature and bear fruit.

### Scale-Independent Responses

Widespread survival of biological legacies (Foster and others 1998) within a disturbed area may enable the previous community to recover with little or no change in composition, regardless of disturbance extent, intensity, duration, or frequency. For example, some of the dominant species of boreal forests exhibit scale-independent re-

sponses to fire extent and intensity. Portions of the Boundary Waters Canoe Area in northern Minnesota have never been logged and still exhibit the natural pattern of stands of different ages created by the historic fire regime of large intense fires on a 50-year rotation period (Heinselman 1973; Van Wagner 1978; Johnson 1992). What is striking is that the dominant species composition of regenerating forests does not vary much over a large range of fire sizes (Frelich and Reich 1995b). Forests on upland sites were dominated by the same set of species—jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and aspen—after fires of 180,000 ha in 1864, of 91,000 ha in 1875, of 21,000 ha in 1910, and of 1000 ha in 1976 (Heinselman 1973, 1981; Ohmann and Grigal 1981; Frelich and Reich 1995b). A major reason for this lack of variability is that a high proportion of jack pine have serotinous cones and many black spruce have semiserotinous cones that open after a fire so that a seed source for these species is readily available throughout a burned area regardless of its extent or intensity. Aspen seeds are short-lived and fire sensitive, but the seeds are carried by wind into nearly all of the burned areas from refugia along lakeshores where patches of adult aspen trees generally survive the fires (Frelich and Friedman unpublished data).

Temperate deciduous forests were described above in the context of threshold responses to disturbance extent. However, recent research within a remnant of unlogged forest in the Porcupine Mountains Wilderness State Park, Michigan, reveals that scale-independent responses also may occur in these systems (Frelich and Lorimer 1991). In mesic forests dominated by two extremely shade-tolerant species—eastern hemlock and sugar maple—the common disturbance regime consists of severe thunderstorm winds that blow down scattered trees or small groups of trees every 10–50 years. Rare, intense downbursts also may level areas as large as nearly 4000 ha (Canham and Loucks 1984). However, little difference was found in species composition over a large range of gap sizes. Even the less shade-tolerant species, such as yellow birch, green ash (*Fraxinus pensylvanica*), and basswood (*Tilia americana*), showed no higher probability of capturing a canopy position within a 1400-ha blowdown that occurred in 1953, than in gaps 0.01–0.05 ha in area in old-growth stands (Frelich and Lorimer 1991). This forest survives the common disturbance type in the form of advanced regeneration, which is little affected by wind and insures good regeneration of the dominants at any location within a blown-down area of forest. Patches of differing species composition exist, but are apparently formed

by biotic interactions between tree species at the neighborhood level (Frelich and others 1993; Frelich and Graumlich 1994; Frelich and Reich 1995a); spatial extent of wind disturbance has little influence on composition.

### Continuous Responses

Disturbance impact, measured as the total quantity of some ecological entity, conceivably may exhibit a continuous response to disturbance size. However, good examples of continuous responses are difficult to find. A somewhat trivial example might be increasing spatial extent of fire in a grassland or forest that is associated with a continuous increase in the total number of dead culms or stems. Another example might be an old-growth mixed-species forest containing many species of trees having different wood strengths, a wide range of tree sizes, and varying degrees of decay. Here we could hypothesize that the number of trees that break off during a storm increases in a continuous fashion as wind speed increases. However, this pattern actually would result from integration of the many thresholds of the individual trees and species in the community. The continuous response to increasing disturbance extent, intensity, or duration may be in fact a relatively rare phenomenon.

## DISCUSSION

We have developed a heuristic model of ecosystem-disturbance dynamics that provides some new insights into the role of LIDs. The model demonstrates that in at least some ecosystems, and for at least some ecological parameters, there is a qualitative change in disturbance impact with increasing disturbance extent, intensity, duration, or frequency; that is, there is a *threshold* in the response curve. Interestingly, however, not all systems or all parameters of disturbance size and impact exhibit threshold patterns: some apparently are not influenced by disturbance size (*scale-independent response*), and others may change continuously with increasing disturbance size (*continuous response*). The systems that do display threshold responses appear to have well-developed internal mechanisms for resisting the disruptive force of a disturbance or responding quickly to it; a threshold or discontinuity in impact occurs when the disturbance becomes so large, intense, long-lasting, or frequent that these mechanisms break down or different mechanisms of recovery are activated.

Persistent systems must have endogenous mechanisms to limit the disruption caused by an exogenous force. The conceptual framework we present

here is consistent with the classic concepts of ecosystem stability, resistance, and resilience [for example, see Holling (1973), Whittaker (1975), and Westman (1978)]. For example, the degree to which a system is resistant to disturbance through endogenous mechanisms is probably related to the slope of the line in Figure 1. A highly resistant system might experience only small increases in impact with increasing disturbance size, intensity, or frequency (that is, a relatively flat line in Figure 1)—up to the point where a threshold is crossed, the curve changes dramatically, and resistance is lost. Most of the classic stability theories place great emphasis on species diversity. Although species diversity can be an important component in our conceptualization, we have also drawn attention to the role of endogenous structural mechanisms, often in a physical sense, and how they relate to stability in ecosystem-disturbance dynamics. This framework also fits recent theories of self-organized systems, which emphasize positive feedback mechanisms for stability and potential destabilization after threshold transitions [for example, see Kauffman (1993) and Perry (1995)].

So, we now return to the question posed in the title of this article: are LIDs qualitatively different from small, frequent disturbances? The answer appears to be yes for some systems and some parameters, but not for all (Table 1). If disturbance impact shows a threshold response to increasing disturbance extent, intensity, or duration, as conceptualized in Figure 1, then LIDs are qualitatively different from small, frequent ones. Some LIDs, such as stand-killing fires in jack pine forests and stand blowdowns in hemlock–hardwood forests, are necessary or at least compatible with perpetuation of the same species composition. Others, such as stand-killing fires in the hemlock–hardwood forest or floods of unusually long duration along major rivers, cause profound and long-lasting changes in community structure and composition [also see Turner and others (1998)].

Do we need to be concerned about possible qualitative differences between large and small disturbances? Given the altered state of many of the world's natural ecosystems, we believe that these differences are becoming increasingly important. Some systems appear to persist largely through internal mechanisms of resistance to the disruptive effects of disturbances and thus display threshold responses to disturbances whose sizes exceed the capacity of these mechanisms. Human activities often damage these internal resistance mechanisms; for example, fire exclusion may homogenize the fuel mosaic in forests. Ecosystem fragmentation also

may increase the probability of qualitatively different successional responses to large-scale disturbance events. Finally, human activities may bring about multiple disturbances, or those that are “pulsed” (Paine and others 1998) and push a system across a threshold in response to disturbance intensity.

As ecosystem managers, we generally cannot prevent or control LIDs. However, we can affect the state of the system before the disturbance and its recovery afterward (Dale and others 1998). Whether the impacts of these LIDs are viewed as positive or negative in relation to specific management goals, we must understand the mechanisms that influence their impact. This may involve adjusting management treatments to capitalize on these threshold responses or acting to maintain or restore the internal mechanisms of resistance and resilience against disturbances. Our challenge is to gain deeper insight into ecosystem-disturbance dynamics and to understand the role of large disturbances and the mechanisms by which ecosystems survive them. We hope that the heuristic model and analysis presented here is a step in this direction.

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