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Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances

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ABSTRACT

Disturbance events vary in intensity, size, and frequency, but few opportunities exist to study those that are extreme on more than one of these gradients. This article characterizes successional processes that occur following infrequent disturbance events that are exceptional in their great intensity or large size. The spatial variability in disturbance intensity within large, infrequent disturbances (LIDs) often leads to a heterogeneous pattern of surviving organisms. These surviving organisms dictate much of the initial successional pattern on large disturbances where the opportunities for seeds to disperse into the middle of the disturbance are limited. The traditional distinction between primary and secondary succession is insufficient to capture the tremendous variability in succession following LIDs. Disturbance size influences succession where long-distance colonization by propagules is important. Observations from LIDs suggest the following interrelated hypotheses about trends in succession with increasing distance from seed sources when disturbance intensity is high: (a) initial densities of organisms will be lower; (b) nucleation processes, in which recovering patches serve as foci for additional colonization and expand spatially, will be more important; (c) competitive sorting will be less important relative to chance arrival in determination of community composition, and (d) community composition will be initially less predictable; and (e) the rate of recovery of community composition will be slower. Prediction of succession following LIDs without considering contingencies such as the abundance, types, and spatial distribution of residuals, and distance to seed sources is likely to be unsuccessful for large portions of the landscape. Abundance and spatial arrangement of survivors and arrival patterns of propagules may be the pivotal factors determining how succession differs between intense disturbances of large and small extent.

Key words: disturbance frequency; disturbance intensity; disturbance size; dispersal distance; landscape ecology; patch size; succession.

INTRODUCTION

Disturbance events vary in size, frequency, and intensity (see Table 1 for definitions), but few opportunities exist to study those that are extreme on more than one of these gradients. The growing accumulation of observations of extreme disturbances such as the 1980 eruption of Mount St. Helens, the 1988 fires in the Greater Yellowstone Ecosystem, and the 1993 floods in the upper Midwestern USA now enables comparative studies of succession following disturbances that were exceptional in their high intensity and large size. Early succession following these disturbances yielded a number of unexpected results. For example, succes-

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Table 1. Definitions Followed in This Report for Components of a Disturbance Regime: We Emphasize Disturbances That Are Large, Infrequent, and of High Intensity

Term	Definition
Frequency	Mean number of events occurring at an average point per time period, or decimal fraction of events per year; mean time between disturbances is obtained from the inverse of frequency.
Size	Area disturbed, which can be expressed as mean area per event.
Intensity	Physical energy of the event per area per time (for example, heat released per area per time period for fire, or wind speed for storms); characteristic of the disturbance rather than the ecological effect.
Severity	Effect of the disturbance event on the organism, community, or ecosystem; closely related to intensity, because more intense disturbances generally are more severe.
Residuals	Organisms or propagules that survive a disturbance event; also referred to as biotic legacies. Residuals are measure of severity, and thus (at least within one disturbance) an index of intensity.

Adapted from White and Pickett (1985).

sional sequences on Mount St. Helens were strongly influenced by local conditions, landscape context, and chance colonization events (del Moral and Bliss 1993; del Moral and Wood 1993). The spatial heterogeneity created by the 1988 Yellowstone fires was much greater than anticipated, even where fires were intense. The disturbance-created mosaic of burned patches of varying size and severity has strongly influenced the composition and structure of postfire vegetation (Turner and others 1997a, 1997b).

Succession following these large, infrequent disturbances [LIDs (see Turner and Dale 1998)] appeared much less consistent in space and time than the simple models of succession that prevail in the literature might lead one to expect. For example, predictions of successional dynamics from the "small-gap paradigm" do not generally apply well to LIDs. Despite widespread recognition of the pervasive importance of natural disturbance regimes in shaping communities [for example, see Watt (1947),] and appreciation that vegetation change can result from population interactions within fluctuating environmental conditions [for example, see Peet and Christensen (1980) and Glenn-Lewin and others (1992)], the extent of spatial variation in succession following large disturbances was unexpected. In this report, we consider factors that may be of particular importance in determining successional patterns following LIDs, and how successional concepts and models might be improved by incorporating the lessons learned from LIDs.

A thorough understanding of succession must include understanding of how successional processes vary with respect to disturbance intensity, size, and frequency (van der Maarel 1993). Large events are not necessarily infrequent or intense; grassland fires may span many square kilometers and recur every several years with little obvious change in community composition (Gleason 1913; Knapp and Seastedt 1986; Pianka 1992). Similarly, infrequent intense events need not be large; high-intensity windstorms may occur infrequently and affect only a few hectares in any 1 year (Canham and Loucks 1984; Patterson and Foster 1990). Past work on individual LIDs has typically suggested the events to be idiosyncratic, but this is probably a consequence of the paucity of observations of events in the extreme locations of the intensity–size–frequency state space. This report represents an attempt to compare varied examples of LIDs so as to identify commonalities in the recovery patterns and the processes that drive them. We begin by considering the implications for succession of disturbance intensity, size, and frequency, and then discuss the implications of these for successional concepts.

Variation in Succession with Disturbance Intensity, Size, and Frequency

Effects of Disturbance Intensity: Biological Legacies

LIDs can exhibit substantial spatial variability in intensity (Bellingham and others 1996; Harrington and others 1997; Turner and others 1997b; Foster and others 1998). Perhaps the most graphic example is provided by the 1980 eruption of Mount St. Helens in Washington: disturbance types included pyroclastic flows, mudslides/flows, blowdowns, heat scorch, and burial by varying amounts of tephra (Dale 1991; del Moral and Bliss 1993). When hurricanes strike mountainous landscapes, wind intensity, precipitation, and subsequent storm damage vary across the landscape, and landslides may occur in some areas (Lugo and Waide 1993; Boose and others 1994). Large fires in coniferous forest

landscapes vary spatially, containing light-to-severe surface burns as well as some areas affected by extreme crown fire (Johnson 1992; Turner and Romme 1994; Turner and others 1994). Complex spatial patterns of disturbance severity are also observed following severe floods. In mountain landscapes, for example, areas affected by large movements of soil, sediment, and wood following a large flood are interspersed with refuge sites that experience minor flood effects (Swanson and others 1998). In large river-floodplain landscapes, flood duration varies spatially across the floodplain with land elevation and is a critical influence on survival of biotic populations (Sparks and others 1998).

A consequence of the spatial variability in disturbance types and intensity is a heterogeneous pattern of surviving organisms and propagules. The abundance and spatial arrangement of such *biological legacies* or *residuals* can have substantial influences on successional dynamics after all types of disturbances (Franklin and others 1985; del Moral and Bliss 1993; Michener and others 1998). Residuals dictate much of the initial successional pattern following LIDs and influence the competitive environment encountered by colonizers (Timoney and others 1997; Zobel and Antos 1997). One reason why succession following LIDs has proved to be surprisingly variable is that the mosaics of disturbance type, intensity, and severity, and by implication the abundance of residuals, have seldom been characterized and are difficult to predict. Effects of disturbance intensities are especially conspicuous following LIDs because their spatial extent allows considerable variation in intensity, and thus residuals, to be observed within one disturbance area.

Life-history traits related to resistance or tolerance of the predisturbance populations to a particular type of LID interact with disturbance intensity to influence species composition of residuals. For example, mobility and degree of adaptation to flooding were critical in determining the effects of the 1993 floods on taxonomic and functional groups of organisms in the Midwestern United States (Sparks and others 1998). Virtually all individuals of tree species that could not tolerate the anoxic conditions that developed under extended soil saturation died (Sparks and others 1998). In contrast, some species of aquatic plants survived by growing upward into the lighted zone as the flood rose, and a rare species of false aster (*Boltonia decurrens*) that requires fresh mudflats for seed germination increased dramatically (Smith and others 1998). Some shrubs can survive even intense fires if they have high allocation to nutrient storage in roots and rapid postfire resprouting from root crowns and rhizome nodes. Such species can make up a disproportionate share of the living biomass after large, high-intensity fires. When such species are sclerophyllous and thus highly flammable, they also may be the key players in a positive feedback that changes fire from an infrequent to a frequent disturbance and shifts the species composition to an alternative, relatively stable assemblage (Latham and others 1996; Mack and D'Antonio 1998).

Residuals can affect early stages of succession following LIDs through several mechanisms. Seed dormancy and persistence may assure a supply of viable seed for some species. An especially notable example is the spectacular recruitment that can occur from buried seeds (the soil seed bank) after disturbances of certain forests [see Marks (1974)]. Similarly, seed storage in serotinous cones or fruits and their release following fire permits rapid reestablishment of these species (Clements 1910; Gill 1976; Muir and Lotan 1985; Wellington 1989). The Yellowstone fires of 1988 provide an example of how surviving organisms may produce propagules that then "fill in" the disturbed area. Scorching of soils generally affected only the upper 2 cm; roots and rhizomes of numerous herbaceous species resprouted in 1989 and flowered in 1990, leading to a substantial pulse of seedling recruitment in 1991 (Turner and others 1997a). Following the eruption of Mount St. Helens, species with dormant buds belowground were similarly able to resprout and set seed on the debris avalanche (Adams and others 1987; Dale 1991). However, in areas of pyroclastic flow, no residuals remained, and succession was initiated by species colonizing from off site (del Moral and Bliss 1993; del Moral and Wood 1993).

The presence or abundance of residuals also influences the ease of establishment of new colonizers. Residual plants that reestablish vegetatively following disturbance often grow larger more quickly than those that start from seed, and species with abundant or larger residual seeds have a head start on those that must disperse into the disturbed area from the surroundings. One example comes from the regeneration of a large forest windthrow. In 1985, a powerful tornado created a 400-ha area of windthrow in the old-growth hemlock–northern hardwood forest of the Tionesta Scenic Area in northwest Pennsylvania. During initial revegetation following the windthrow event, thickets of surviving advance regeneration of *Fagus grandifolia* and *Acer pensylvanicum* had a substantial size advantage over individuals that germinated after the disturbance, and that size advantage has been maintained (Peterson and Pickett 1995). These thickets of advance regeneration have severely inhibited local

colonization by *Betula alleghaniensis*, which is abundant in other areas of the blowdown having a lower density of residuals (Peterson 1992; Peterson and Pickett 1995).

Canopy closure or the co-opting of space by residuals may limit the time available for successful colonization by propagules, and a limited temporal window for recruitment can profoundly influence succession (Peterson and Carson 1996). In the successional development of northern hardwood forest following the 1938 New England hurricane, several tree species were unable to colonize after the first several years [Hibbs (1983), see also Peterson and Pickett (1995)]. The presence of a substantial seed bank of pioneer species in northeastern North America at the time of disturbance can reduce or even preclude establishment of slower-growing but not highly shade-tolerant species (Rankin and Pickett 1989). For example, abundant establishment of *Prunus pensylvanica* can inhibit several other midsuccessional species (*Acer rubrum*, *Fraxinus americana*, and *Pinus strobus*), but because of the short life span of *Prunus*, can actually shorten the time to dominance by late-successional species such as *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis*.

Similarly, forb and graminoid seedling recruitment following the Yellowstone fires peaked during year 3 after the fire, and the extensive herbaceous vegetation in some burned areas where conifer seedlings were scarce may lengthen the time required for forest development or preclude it entirely (Turner and others 1997a). The importance of residuals for speed of postfire recovery of Rocky Mountain forests is particularly evident when lodgepole pine forests with serotinous cone seed storage are contrasted with the Englemann spruce and subalpine fir forests, which lack seed storage and which grow at somewhat higher elevations. Lodgepole typically has sufficient postfire seedling establishment for the initial cohort of seedlings to form a new canopy. Reestablishment is slower in the spruce–fir zone (except near residual stands of living trees), and often a thick sward of sedges and grasses forms before the forest can reestablish, with the consequence that several centuries can be required for sufficient tree regeneration to again form a closed forest canopy (Stahelin 1943; Peet 1981). In short, forest structure and composition, and the ecosystem processes that ensue, may reflect for centuries the abundance of residuals present during the early postdisturbance period.

In contrast to the patterns obtained where density of residuals is high, where residuals are rare, their presence or that of early colonists may facilitate subsequent colonization by other species. On the pyroclastic flows of Mount St. Helens, patches of *Lupinus lepidus* trapped seed and moderated environmental conditions such that other species could subsequently establish (del Moral 1994). The nitrogen-fixing capability of *Lupinus* may also have facilitated subsequent colonization. Although this facilitation appears contradictory to the inhibitory effects of survivors on new colonizers described above, these differences represent ends of a continuum of residuals. At high survivor densities, residuals may negatively affect colonists due to competition whereas, at low survivor densities, residuals may enhance colonization by ameliorating harsh abiotic conditions (Bertness and Callaway 1994).

Disturbance intensity, which may vary independently of disturbance size and frequency, controls the presence and spatial locations of residuals. The traditional distinction between primary and secondary succession blurs in the face of such spatial heterogeneity and is not sufficient to capture the tremendous variability in succession following LIDs. Two quite different phenomena are frequently linked to the primary–secondary succession dichotomy, but both can be seen as continuous variables. In response to the overwhelming importance of the presence or absence of residuals for succession at Mount St. Helens, Franklin and colleagues (1985) and del Moral and Bliss (1993) suggested that primary succession differs from secondary succession in the absence of residuals. Clements (1915: 169) similarly appreciated the absence of residuals in primary succession, but his central concept of primary succession was vegetation development on newly formed soils or soils exposed for the first time. This concept is similar to that endorsed by many workers today [for example, see Gleeson and Tilman (1990) and Peet (1992)]. Our observations suggest that ecologists should move away from this simplistic dichotomy toward a recognition of a continuum of abundance of residuals left behind by a disturbance, and a separate, equally important continuum of soil development. Although problems with the application of primary and secondary succession are not unique to LIDs, they are particularly conspicuous.

Effects of Disturbance Size: Spatial Dynamics

Patterns and change in the physical environment. Because of their large size, LIDs encompass a wider range of environmental variation than smaller disturbances and create a diverse template of abiotic conditions. This variety of conditions results from preexisting site factors and spatial variation in intensity within the disturbance itself. In addition, the increased environmental variation encompassed in

large disturbed areas contributes to differential susceptibility to disturbance and variation in recovery dynamics between different landscape positions. For example, microsites on which trees established long ago in a Southeastern swamp forest determined their vulnerability to toppling by Hurricane Hugo in 1989 (Putz and Sharitz 1991), and levels of hurricane damage in Hawaii varied substantially along an elevational gradient (Harrington and others 1997). Forest stands of similar composition in Minnesota suffered different amounts of windstorm damage based on their location (Dyer and Baird 1997). After the eruption of Mount St. Helens, topographic positions where snow accumulated and protected the meristems of plants revegetated more quickly than other areas (Dale 1991; del Moral and Bliss 1993).

Disturbance-induced changes in the biophysical environment are subject to edge effects related to disturbance size. The centers of large, disturbed patches are likely to experience quite different physical conditions than small patches or disturbed areas near intact vegetation. In tropical moist forest, (relatively) larger gaps experienced higher air temperatures, lower humidity, higher wind speeds, and reduced soil moisture (Denslow 1987). However, changes in environmental factors with disturbance size have not been characterized across a wide range of sizes. Change in abiotic factors (for example, temperature) with distance from the edge of the disturbed area is likely to asymptote at some size considerably smaller than the areas affected by the LID (distances would vary for different abiotic parameters). Under extreme conditions, changes in the abiotic environment in the center of large disturbances can reduce or eliminate colonization by potential successional species. Nepstad and colleagues (1990) describe such harsh conditions in an abandoned Brazilian pasture that species from the surrounding rainforest were unable to colonize until exotic ruderal species had moderated the microclimate.

LIDs may be more likely to alter or to introduce new substrates via soil disturbance or physical movement, but existing data do not allow generalizations about this. Introduction or transformation of substrates is strongly influenced by disturbance intensity [for example, see Swanson and others (1998)]. One size-related distinction is clear: small gaps in tropical montane rainforests are not associated with landslides, whereas catastrophic windthrow from hurricanes often results in landslides (Romme and others 1998). The new substrate created by the landslide typically develops vegetation quite different from the surrounding forest [for example, tree fern communities that persist for decades (Walker 1994)]. In temperate forests, several studies have quantified the amount of newly exposed, disrupted soil after catastrophic wind disturbances—typically 5%–12% of the surface (Peterson and others 1990; Peterson and Rebertus 1997)—but the corresponding information for small gaps is not available.

Arrival and survival of propagules. The availability of propagules is a fundamental determinant of successional patterns (Clements 1915; Pickett and others 1987a) and one that can be especially sensitive to the combination of high intensity and large size. In small disturbed areas, the surrounding intact community is likely to provide sufficient propagules for succession, even if biotic residuals are few. However, the density of propagule inputs from the surrounding undisturbed area into a disturbed area decreases with distance (Aide and Cavelier 1994; da Silva and others 1996; Nepstad and others 1996), so the proportion of disturbed area beyond the zone of high propagule input decreases as disturbance size increases. Whether regeneration will depend on this external input of propagules depends largely on disturbance intensity. For at least some LIDs that contain large areas of high-intensity disturbance, a substantial proportion of potential establishment is contingent on the arrival of propagules from outside the disturbed area.

Dependence of succession on the arrival and survival or propagules is perhaps most evident in studies of succession on the pyroclastic flows following the eruption of Mount St. Helens (del Moral and Bliss 1993; del Moral and Wood 1993), where residuals were essentially absent. Similarly, large patches opened in intertidal mussel beds are colonized almost exclusively by recruitment from planktonic larvae rather than by leaning or lateral movement seen in smaller patches (Paine and Levin 1981). In sections of Yellowstone where pre-fire serotiny was low, large burned patches (500–3500 ha) have extremely low densities of tree seedlings, and colonization by conifers from the surrounding unburned landscape is likely to take many decades (Tinker and others 1994; Turner and others 1997a). In contrast, densities of tree seedlings in small patches (1–2 ha) of similar burn severity in the same locale (also with low pre-fire serotiny) are considerably higher, presumably because of greater seed input from nearby unburned areas. Disturbance size also contributed to qualitative differences in succession following the 1993 flood in the Midwest compared with shorter-duration floods. Trees and shrubs were killed from the roots upward, so they could not put out new leaves or resprout from belowground plant parts, as might occur during a less-

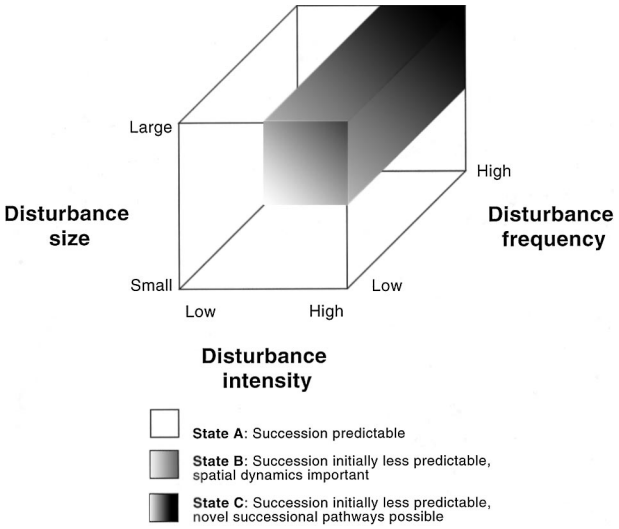

Figure 1. Conceptual state–space diagram for succession following disturbances varying in size, intensity, and frequency. Succession is more predictable and spatial attributes of the disturbance are less important whenever disturbance intensity is low (such that residuals are abundant) or disturbances are small (state A). Succession is initially less predictable and determined by disturbance size, shape, and configuration when disturbance intensity is high (such that residuals are scarce) and disturbances are large (states B and C). Successional pathways may be qualitatively altered if high-intensity, large disturbances increase in frequency (state C).

severe flood (Sparks and others 1998). The entire understory was eliminated in substantial areas of the floodplains within approximately 150 km of St. Louis, Missouri, and no saplings were available to grow following the death of the overstory trees. The large size of the area in which residuals were eliminated or drastically reduced suggests that several species of native oaks (*Quercus* spp.) and pecans (*Carya illinoensis*) that are poor dispersers may not reestablish stands because surviving seed sources are few and far between (Sparks and others 1998).

If dispersal from outside the disturbed area is important, the size, shape, and configuration of disturbed patches will influence propagule availability and thus vegetation composition (Figure 1). Distance from the edge of the disturbed patch, which is controlled in part by patch size, has a particularly strong effect (McClanahan 1986; Bergeron and Dansereau 1993; Galipeau and others 1997). For example, the abundance of conifer recruitment following fire in some boreal forests may be strongly influenced by distance to seed sources (Bergeron and Dansereau 1993). The central areas of large clear-cuts in northern hardwood forests are readily colonized by wind-dispersed seeds from outside the disturbed area, but large, gravity- or mammal-dispersed seeds recruit primarily along the edge of the disturbance (Hughes and Fahey 1988). Patch size also interacts with patch shape in determining distance to propagule sources. For example, tornadoes disturb narrow, linear swaths with a high perimeter–area ratio. A smaller disturbed patch with a lower perimeter–area ratio could contain more area, requiring long-distance dispersal. Residual organisms also serve as perches and/or attractants to frugivorous birds that disperse seeds in terrestrial community, thus prompting another size × severity interaction (Wunderle 1997). Consequently, disturbance size alone is insufficient to determine whether portions of the disturbed areas are propagule limited due to distance from intact habitat.

Disturbance size interacts with the life-history traits of potential colonizing species. Widely dispersed, ruderal species are often ubiquitous within disturbed areas—for example, *Epilobium angustifolium* colonizes even large burned areas very quickly. Late-successional species often are less readily dispersed, and this can result in arrested succession near the center of large disturbed areas (Stahelin 1943; McClanahan 1986). The rate of migration of species from intact regions to a disturbed area is also important. Species migrate at different rates, depending on weather conditions, the variety of the physical environments available, and the vegetation types that must be crossed. Predicting when a given reinvading species will reach a particular location within a very large disturbed area is difficult.

Introduction of exotic species following an LID can also have profound influences on succession and on the subsequent disturbance regime (Mack and D'Antonio 1998). Seeding of exotic grasses on Mount St. Helens to stabilize mudflows and reduce erosion also precluded the establishment of native tree species (Dale 1991). Introduction into Hawaiian woodlands of *Schizachyrium condensatum*, an invasive grass from Central America resulted in increased fire frequency and size; the grass also resprouts rapidly following fire whereas the native species do not, thereby increasing dominance of the invader within the community (D'Antonio and Vitousek 1992). Disturbances may promote biological invasions, and invasive species can in turn cause changes in disturbance regimes that profoundly alter the successional pathway of a community (Mack and D'Antonio 1998; D'Antonio and others forthcoming).

Patch size may also influence biotic interactions such as herbivory, which can accelerate, change, or redirect succession (Lubchenco 1978; Mills 1986;

Bowers 1993; Davidson 1993). In some cases, the disturbance × herbivore interaction is likely to be complex, facilitating the activities of herbivores of certain species or sizes and inhibiting herbivory by others. In a catastrophic windthrow of an old-growth Pennsylvania northern hardwood forest, the deposition of abundant woody debris and formation of treefall root mounds created localized microsites in which *Acer rubrum* and *Tsuga canadensis* were protected from deer browsing with consequently greater regeneration (Grisez 1960; Z. T. Long and others unpublished). The reduced browsing under debris is probably a function of deer size and debris arrangement; debris piles may be no hindrance to smaller herbivores.

Effects of Disturbance Frequency: Temporal Scaling

The focus of this report is on large and infrequent disturbances, where infrequent refers to a return time equivalent to or longer than the life span of the dominant organisms. Disturbances that occur with substantially greater frequency over long periods are likely to cause relatively little disruption of ecosystems in as much as the dominant organisms would have experienced strong selective pressure to survive and perhaps even exploit these events. For example, relatively frequent fires occurred historically in many landscapes, including prairies of the North American Midwest (Curtis 1959), longleaf pine savannas of the Southeastern United States (Glitzenstein and others 1995), and boreal forests in northern Sweden (Linder and others 1997), and the component plant and animal species were well adapted to these events. For example, the timing of important life-history events such as flowering corresponded with the passage of fire and associated conditions such as increased soil cation availability and decreased soil shading by litter [see Curtis (1959) and Christensen (1981)]. Fire suppression during the past century has lengthened the fire return interval and altered successional pathways [for example, see Glitzenstein and others (1995) and Linder and others (1997)]. The unusual absence of frequent predictable events (for example, cold, fire, or drought) also can disrupt the stability of the ecosystem and lead to a shift in species composition. Indeed, the virtual elimination of fire from once fire-maintained ecosystems and the reduction or elimination of flooding from many river systems have altered successional pathways [for example, see Linder and others (1997)].

An increase in the frequency of an LID can shift in successional pathways if the abundance or composition of residuals changes as a result. For example, numerous species have adapted to the possible occurrence of large infrequent fires by production of fire-resistant residuals such serotinous cones and fire-tolerant seed banks. The unusual juxtaposition of two large, high-intensity fires can have the effect of eliminating a new, post-LID generation before there is an opportunity to restock the habitat with fire-resistant residuals. In New Zealand, for example, volcanism occurring every 300–600 years was associated with the occurrence of extensive forest fires (Ogden and others 1998). Most New Zealand tree species are killed by fire; they neither resprout nor benefit from a seed bank. Nonetheless, the burned forests achieved their former structure and composition following a prolonged succession extending over centuries, and the median return time for fire at any given point on the landscape was about 2000 years. A dramatic increase in fire frequency associated with colonization about 700 years ago prevented succession to forest and resulted in the conversion of forests to herbaceous communities over large areas (Ogden and others 1998); the more frequent fires precluded successful tree establishment. Another example can by drawn from the Midwestern United States, where a flood in 1995 killed extensive tracts of seedling trees that established after the severe 1993 floods (Sparks and others 1998). Forest regeneration along the upper Mississippi River may be continuously reset until a series of drought years and low river levels allow trees to grow sufficiently tall to survive subsequent flooding. More intriguing, however, is the possibility that existing floodplain prairies might expand if droughts dry the standing and downed timber left by the 1993 flood sufficiently to facilitate fires (Sparks and others 1998). Similar interactions have been described in other systems (Heinselman 1973; Noble and Slatyer 1980; Myers and van Lear 1998). Several studies have shown that fires occurring after hurricanes can drastically slow recovery of forests (Unwin and others 1988; Elmqvist and others 1994; Vandermeer and others 1995; Smith and others 1997). This would be consistent with the idea that alternative communities may be able to persist for long periods within similar abiotic environments, and that disturbance history or other stochastic factors may determine which state is present at any particular place and time (Lewontin 1969; McCune and Allen 1985b; Laycock 1991; Wilson and Agnew 1992).

Commonalities Among LIDs

What commonalities do we observe among LIDs with regard to the predictability of succession and the importance of disturbance size and frequency?

Observations to date suggest that size and frequency effects must first be considered within the context of disturbance intensity as it influences the abundance of residuals. We suggest that succession will be relatively predictable following disturbances of any size when residuals are abundant and the effects of local environmental attributes (for example, nutrient availability, soil texture, and soil moisture) are considered (Figure 1). Spatial effects of disturbance (disturbance size, shape, and arrangement) become increasingly important when residuals are few or sparse and the disturbance is large; under these conditions, colonization and hence succession become slower and more difficult to predict (Figure 1). Furthermore, if the frequency of large, high-intensity disturbances increases such that residuals decrease in abundance or change in composition with successive disturbance events, successional pathways may shift qualitatively (Figure 1). As is generally true for disturbances, successional pathways also may shift if the frequency of an LID is substantially reduced or the disturbance is eliminated from the system.

The effect of disturbance size is most conspicuous following high-intensity LIDs (where residuals are sparse or absent) because colonization depends on long-distance dispersal. Although the number of LIDs that have been carefully studied is small, observations to date suggest several interrelated hypotheses regarding succession as distance from seed sources increases: (a) initial densities of organisms will be lower; (b) nucleation processes, in which recovering patches serve as foci for additional colonization and expand spatially, will be more important; (c) competitive sorting [sensu Peet (1992)] will be less important relative to chance arrival in determination of community composition, and (d) initially, community composition will be less predictable; and (e) the rate of recovery of community composition, if not structure, will be slower. These hypotheses could be tested among a broad range of LID events.

Comparison of results from LID studies with the known or inferred consequences of the biggest LIDs in earth history—the mass extinction events of the Permian/Triassic and Cretaceous/Paleocene boundaries—provides reassuring consistency (Harries and others 1996; Erwin 1997, 1998). Those mass extinction events were followed by opportunistic invasion by a few species. The degree to which bloom taxa dominated following the K/T impact varied geographically, apparently in relation to geographic intensity of the disturbance. Recovery was slow, and many taxa did not reappear until long after the events, apparently having survived in isolated refugia from which spread was slow. Postbloom recovery was spatially variable and unpredictable, apparently reflecting chance aspects of survival and spread. In short, the giant LIDs showed some of the same patterns of slow recovery and spatial variation driven by chance establishment patterns as generated by other LIDs.

Successional Concepts and Models: Challenges and Directions

Prediction of succession requires an understanding of interactions among multiple mechanisms (Pickett and others 1987a, 1987b; Walker and Chapin 1987). Prediction of the rate and direction of succession following LIDs remains challenging because (a) the successional mosaic often spans a gradient between primary and secondary succession due to spatial variation in disturbance intensity (and hence residuals); (b) the template of abiotic conditions remaining after the disturbance is complex and exhibits size-dependent spatial variation in environmental conditions; and (c) when residuals are low, propagule availability—and hence community composition and structure—is influenced by disturbance size, shape, and configuration.

Models exist in vegetation science to produce reasonably good predictions of successional dynamics at the canopy-gap scale (0.1–10 ha) (Glenn-Lewin and others 1992). In temperate and tropical forests, a substantial body of observation and theory has developed around the role of small gaps [for example, see Runkle (1982, 1985), Brokaw (1982, 1985, 1987), and Lertzman (1992)]. In the *small-gap paradigm*, differences in vegetation dynamics are primarily attributed to gap size, whereas shade tolerance differentiates tree species into *pioneers* and *climax species* (Swaine and Whitmore 1988). A typical prediction is increasing dominance by pioneer species as disturbance size increases. However, this paradigm is insufficient for LIDs, because this prediction would suggest nearly exclusive dominance by pioneer species when extrapolated to large disturbed areas. Such expectations have not been fulfilled following several LIDs extensively studied [for example, in a large tornado windthrow in Pennsylvania (Peterson and Pickett 1995) and in the northern hardwood–hemlock forest of northern Michigan (Frelich and Reich 1995)]. The small-gap paradigm is quite successful within a certain range of conditions, that is, when disturbance events are small relative to the size of the landscape, and when disturbance frequency is greater than recovery time (Turner and others 1993). The challenge, then, is to expand our predictive models of vegetation dynam-

ics to encompass the biotic and abiotic conditions created by LIDs.

Observations of LIDs suggest that additional independent variables that reflect both spatial and temporal contingencies must be included in models used to predict succession; that is, deterministic influences alone are insufficient predictors. Spatial and temporal contingencies may include vegetation age or successional stage (Peterson and Carson 1996), abundance and types of residuals and other within-patch heterogeneity (Nunez-Farfan and Dirzo 1988; Peterson and others 1990; Vandermeer and others 1995), shape and configuration of disturbed areas (Poulson and Platt 1989; Turner and others 1994; da Silva and others 1996), and herbivore densities (Runkle 1985; Mills 1986; Long and others 1998). It may be necessary to include spatial location information such as distance to seed sources to understand and predict successional dynamics at particular locations in large disturbed areas. These spatial contingencies may assume greater importance for successional dynamics following LIDs compared with smaller disturbances, although the mechanisms of succession do not change. Prediction of succession following LIDs in the absence of the consideration of spatial contingencies is likely to be unsuccessful for large portions of the landscape.

LIDs create more uncertainty and variability in successional trajectories than do smaller disturbances. The concept of multiple successional pathways has been incorporated into treatments of community dynamics during the past 20 years (Glenn-Lewin and van der Maarel 1992; Knowlton 1992; Wilson and Agnew 1992). Very different successional trajectories may be initiated within similar abiotic environments because of local differences in disturbance intensity or availability of plant propagules; that is, positive feedback-driven alternative pathways may lead to different, relatively stable endpoints. However, the degree to which spatial variation in early succession following LIDs will eventually converge on similar end points or lead to divergent communities is not yet known [for example, see Christensen and Peet (1984) and Leps (1991), but also McCune and Allen (1985b)]. Olson (1958) and Matthews (1979) found that a relatively uniform early successional landscape diverged to produce a mosaic of late-successional types tuned to underlying environmental variation. This is consistent with Whittaker's (1953) model of a climax mosaic and work on convergence during succession (Christensen and Peet 1984; Peet 1992). Following this model, if LIDs contain a large number of microenvironments, there may be a large number of eventual late-successional variants. If the outcome of succession is closely tuned to microenvironmental variation, succession following a single LID may be quite similar to that of a series of smaller disturbances encompassing the same area.

If spatial configuration and chance play significant roles in modulating the tight relationship between succession and environment, alternative successional pathways are possible within similar environmental conditions. In the early stages of plant succession on Mount St. Helens, Washington, there is little correlation of recovering vegetation with environment; chance survival and recruitment are playing the leading roles (Halpern and others 1990; del Moral and others 1995). The role of chance is highlighted in the lottery model (Chesson and Warner 1981) where species-rich communities such as Australian kwongan and South African fynbos may be maintained by stochastic disturbance and recruitment (Laurie and Cowling 1994; van der Maarel and others 1995). Panamanian rainforest on Barro Colorado Island also exhibits such chance effects (Hubbell and Foster 1986).

Multiple stable states are alternative successional outcomes that persist in the same environment and resist convergence. Although multiple stable states appear theoretically possible, they have proven exceedingly difficult to demonstrate in unexploited natural systems (Connell and Sousa 1983; McCune and Allen 1985a, 1985b), even though exploitive human activities such as livestock grazing can clearly lead to new stable equilibria (Perry and others 1989; Weetman and others 1990; Laycock 1991). Following clear-cutting in Newfoundland, for example, extensive tracts of *Picea mariana* forest were converted to shrub heathlands dominated by *Kalmia angustifolia* (Mallik 1995). Exceptional natural floods may have produced multiple stable states in riparian vegetation in southwestern Colorado (Baker and Walford 1995). An expiring extratropical North Pacific cyclone dropped exceptional rainfall on the headwaters of the Animas River in October 1911, leading to a flood with an estimated recurrence interval of close to 1000 years. This flood mobilized and transported large boulders, creating swaths of boulder debris on which plant succession may be leading to a different outcome than on adjoining geomorphic surfaces that only slightly pre-date the 1911 flood. Baker and Walford hypothesized that multiple stable states in natural ecosystems may be favored when the intensity of a natural disturbance exceeds the range of intensities experienced over the typical life span of ecosystem dominants, as was the case with the 1911 flood. In another example of multiple stable states, the patchy distribution of hardwood, mixed, and hemlock communities in the

Sylvania Wilderness Area in Western Upper Michigan was explained primarily by pattern of invasion and competitive interactions among species (Frelich and others 1993; Davis and others 1994).

In summary, if succession is dominated by controls that are deterministic, for example, abiotic environmental features such as topography or soils, then disturbance size will have little or no influence on composition of late seral communities. However, if contingent or stochastic factors are important and have long-lasting effects, then these are more likely to control succession following LIDs.

Conclusions and Future Directions

Our analysis suggests that succession following LIDs will differ from smaller disturbances if biological legacies are minimal and colonization from surrounding undisturbed habitats is required (Figure 1); if new substrates are created, particularly if unique species assemblages can develop; or if biophysical conditions or biotic interactions such as herbivory vary with patch size. Predictive models of succession following LIDs must include independent variables that account for both spatial and temporal contingencies. LIDs create more uncertainty and variability in successional pathways than do smaller disturbances and may provide unusual opportunities for initiation of multiple stable states, thereby potentially enhancing diversity of communities across the landscape. The traditional distinction between primary and secondary succession also fails to capture adequately much of the tremendous variation in vegetation dynamics following LIDs. Related to the continuum of residual abundance is the potential shift from facilitative to inhibitory effects of survivors on new colonists that can occur as the density of residuals increases.

Several key questions remain regarding the outcome of succession following LIDs. The spatial and temporal patterns of recovery, the degree to which convergence or divergence occurs, and what controls these outcomes, need to be addressed. Ecologists understand much about succession when disturbance size is relatively small and when biotic residuals following disturbance are abundant. However, the observation set is still small for large disturbances in which biotic residuals are low and for large disturbances that occur infrequently. Spatial variability in types and intensities of disturbance within LIDs will be further complicated by interactions with geomorphology, invasive species, and projected climatic change. Developing detailed, long-term case studies is crucial to further our understanding of ecosystem recovery following LIDs (Zobel and Antos 1997) and to identify complex interactions that might otherwise be dismissed as stochastic processes (Michener and others 1997). Prediction of succession following LIDs without considering contingencies such as the abundance, types, and spatial distribution of residuals, and distance to seed sources is likely to be unsuccessful for large portions of the landscape. Abundance and spatial arrangement of survivors and arrival patterns of propagules may be the pivotal factors determining how succession differs between intense disturbances of large and small extent.

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