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Fires, Hurricanes, and Volcanoes: Comparing Large Disturbances

Large disturbances are heterogeneous spatially and not as catastrophic as they may initially appear

Monica G. Turner, Virginia H. Dale, and Edwin H. Everham III

The importance of natural disturbances in shaping landscapes and influencing ecosystems is now well recognized in ecology (e.g., Pickett and White 1985, Turner 1987, White 1979). Disturbance can be defined generally as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource or substrate availability or the physical environment (White and Pickett 1985). In recent years, ecologists have learned a great deal about the dynamics and effects of relatively small, frequent disturbances. Extensive studies addressing patch dynamics and gap-phase replacement (where a canopy tree has died, initiating active recruitment of new individuals into the canopy), especially in temperate deciduous and tropical forests, have led to good understanding of and predictive capability in these systems (e.g., Runkle 1985). By contrast, natural disturbances that affect large areas but occur infrequently have not been well studied. Whether large disturbances are qualitatively different from numerous small disturbances remains an unresolved issue in ecology, in part because of a paucity of long-term data on the effects of large-scale disturbances and the impossibility of replicating such events.

Whether large disturbances are qualitatively different from numerous small disturbances remains an unresolved issue in ecology

During the past two decades, several large natural disturbances—the eruption of Mount St. Helens in 1980, the Yellowstone fires of 1988, and Hurricane Hugo in 1989—captured the attention of the public and received considerable postdisturbance ecological research. In this article, we compare these three natural disturbances to determine whether general trends in the ecological effects of large-scale disturbance can be detected. For example, do large disturbances create similar kinds of heterogeneity across the affected landscape? Are the spatial patterns of disturbance predictable based on landscape position? Are recovery mechanisms similar? We focus on similarities and differences in the characteristics of the disturbances, in the effects of the disturbances on vegetation, and in the postdisturbance recovery of vegetation. Our analysis takes advantage of existing data for each disturbance and draws on our individual experiences in each ecological system. Because the independent studies were not designed comparatively, data for quantitative comparisons are not always available. Nevertheless, we believe that these contrasts may provide a foundation for a detailed comparative, synthetic analysis.

The three large disturbances

We begin by providing a brief introduction to the three disturbances to be compared. These events were high in intensity and large in spatial extent.

Mount St. Helens. Mount St. Helens is an active volcano in southwest Washington. Before 1980, the mountain was surrounded by a patchwork of forested and clear-cut land in varying stages of reforestation. The 18 May 1980 eruption affected more than 700 km^2 and created a variety of disturbances in the immediate vi-

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cinity of Mount St. Helens: a 0.25 km² pyroclastic flow; a 550 km² area of trees that had been blown down bordered by 96 km² of scorched trees; a 60 km² debris avalanche; and massive mudflows (Figure 1). The interaction of disturbance characteristics and the life forms of species present at the time of the eruption resulted in different patterns of surviving plants in these areas (Adams et al. 1987, Franklin et al. 1985).

The pyroclastic flow consisted of hot gases, rock fragments, and superheated steam, which poured forth from the crater at temperatures of 350–850 °C. No plants survived on these flows, and the slow recovery is characterized by diverse herbaceous and forb species whose seeds were transported by wind (del Moral and Bliss 1993). The blowdown zone included areas where the eruption force was strong enough to knock over trees, although herbaceous and understory vegetation survived, particularly in sites buried under snow (Franklin et al. 1985, Halpern et al. 1990). Temperatures of materials deposited in the blowdown zone ranged from 100 to 350 °C. Encircling the blowdown zone was the scorch perimeter, where temperatures were hot enough to burn leaves, but winds were not strong enough to down the trees. Coniferous trees—which do not have the ability to releaf after defoliation—died, but some deciduous trees survived (Adams et al. 1987).

The debris avalanche deposits, or landslides, were a relatively cool 95 °C but were deep, averaging 45 m but reaching depths of 150 m in some locations (Fairchild 1985). No viable seeds survived the landslide; most of the early successional species that colonized the avalanche have plumed seeds that can disperse long distances (Dale 1989). The very few surviving plants developed from rootstocks or stems that were transported by the landslide and came to rest near the surface (Adams et al. 1987). Vegetation cover on the debris avalanche gradually increased from 0 to 35% by 1994. A few conifers have established, but red alder (*Alnus rubra*) now has the greatest cover. Even so, the distribution of red alder is patchy, and it is absent from large areas.

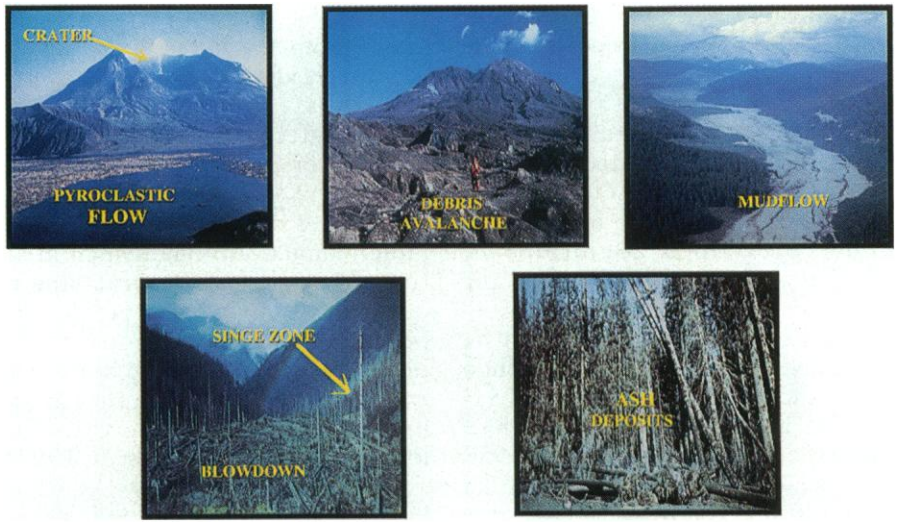

Figure 1. Disturbance effects created by the 1980 eruption of Mount St. Helens. This volcanic eruption created several distinct disturbances, including the crater itself, pyroclastic flow, the debris avalanche, mudflows, blowdown, and singe perimeter and ash deposits.

Figure 2. The 1988 Yellowstone fires created a striking mosaic of burn severities across the landscape. Blackened areas indicate areas of crown fire, brown sections show areas of severe surface burns, and green forest indicates either light surface burns or unburned forest.

Mudflows occurred on the major rivers draining the Mount St. Helens area, induced either by earthquake-generated liquefaction (i.e., numerous earthquakes shook the water-laden debris avalanche so severely that water rose to the surface) or by the rapid melting of glaciers on the mountain. Although much of the understory vegetation and small trees were washed away by the mudflows, large trees that were taller than the surface of the flow survived. The proximity of surviving vegetation and seeding by humans (often involving exotic graminoids) have resulted in close to 100% cover on the mudflows today (Halpern and Harmon 1983).[1]

The eruption also deposited tephra (i.e., solid material ejected during the eruption and transported through the air) over thousands of square kilometers. Trees survived in these areas, but herbaceous plants were buried under deep layers of tephra. Some plants were able to grow through as much as 15 cm of material (Antos and Zobel 1985). Where tephra was less than 25 cm deep, both survival of buried herbaceous vegetation and establishment of seedlings were enhanced by the burrowing of pocket gophers (*Thomomys talpoides*; Anderson and MacMahon 1985).

The 1988 Yellowstone fires. Yellowstone National Park encompasses 9000 km² in the northwest corner of Wyoming and is primarily a high, forested plateau. Fire has long been an important component of this landscape (Romme 1982, Romme and Despain 1989), and, as in most other parts of the Rocky Mountains, fire

[1]V. H. Dale, unpublished observation.

has profoundly influenced the fauna, flora, and ecological processes of the Yellowstone area (e.g., Despain 1991, Houston 1973, Taylor 1973).

A natural fire program that was initiated in 1972 permitted lightning-caused fires in Yellowstone National Park to burn without interference under prescribed conditions of weather and location. Most of the 235 fires observed in the park between 1972 and 1987 went out by themselves before burning more than 1 ha, and the largest fire (in 1981) burned approximately 3100 ha.[2] Thus, the size and severity of the 1988 fires, which burned over 250,000 ha in the Greater Yellowstone region due to prolonged drought and high winds (Renkin and Despain 1992), surprised many managers and researchers. The 1988 fires also spread rapidly through all forest successional stages and were influenced more by wind speed and direction than by subtle patterns in fuels or topography. Reconstructions of fire history suggest that the last time a fire of this magnitude occurred in Yellowstone was in the early 1700s, so the 1988 fires may represent a major disturbance event that occurs at intervals of 100–300 years in this landscape (Romme and Despain 1989).

The Yellowstone fires created a strikingly heterogeneous mosaic of burn severity (Figure 2) across the landscape (Turner et al. 1994). In the most severely burned areas, where crown fires (fires that consume and spread through the tree crowns) occurred, needles of the canopy trees were completely consumed by fire, and tree mortality was essentially 100%. The soil organic layer was almost entirely burned, leaving the soil bare, with no litter. However, because the depth to which soil was charred averaged only 13.6 mm in crown fires, resprouting of herbaceous plants and shrubs was significant (Turner et al. 1997). Other areas were affected by severe surface burns, in which canopy tree mortality was extensive but the conifer needles were not consumed by the fire. In such areas, the soil organic layer that existed before the fire was largely burned, but the soil was soon covered by dead needles that had fallen from the canopy. Still other areas were affected only by light surface burns, in which the canopy trees retained green needles and generally did not die, although their stems often were scorched. The soil organic layer of these areas remained largely intact, although small areas (on the order of several square meters) were patchily burned. The percent cover of herbaceous vegetation in these light surface burns was not distinguishable from that in unburned forest within two years following the fires (Turner et al. 1997).

Hurricane Hugo. Hurricanes are an important force influencing forest composition and structure on numerous islands and coastal regions (Waide and Lugo 1992, Weaver 1986). During the past 300 years, 15 hurricanes have passed over the island of Puerto Rico (Scatena and Larsen 1991). Hurricane Hugo passed over the northeast corner of Puerto Rico on 18 September 1989 as a category 4 hurricane with sustained winds of over 166 kph (Boose et al. 1994, Scatena and Larsen 1991). Although Hugo continued to the northwest and struck the coast of South Carolina, where it affected over 3 million hectares of timberland (Sheffield and Thompson 1992), we focus here only on the impact of the hurricane in Puerto Rico, particularly the 11,000 ha Luquillo Experimental Forest in the northeast corner of Puerto Rico. Hurricane Hugo passed to the northeast of the Luquillo Experimental Forest on a northward track, generating winds that came first from the northeast and then, with the passage of the storm, shifted to the north and northwest (Scatena and Larson 1991). Prior to Hurricane Hugo, the last hurricane to have a direct impact on the Luquillo Experimental Forest was San Ciprano in 1932, although San Felipe (in 1928), San Nicolas (in 1931), and Santa Clara (also known as Betsy, in 1956) had tracks near the Luquillo Experimental Forest and may have had some localized effects on it (Weaver 1986).

Hurricanes are an important and possibly the dominant influence on forest composition and structure in the Luquillo Experimental Forest (Waide and Lugo 1992, Weaver 1986). The forest canopy consists of small-crowned trees and fewer emergents than continental tropical forests (Weaver 1986). Simulation studies indicate that patterns of diversity and dominance in this forest are maintained by regular hurricane disturbance. In the absence of hurricanes, the forest becomes increasingly dominated by late-successional species, and diversity begins to decline after 60 years (Doyle 1981); these trends are supported by long-term studies of posthurricane forest dynamics earlier this century (Weaver 1986).

Hurricane disturbance includes both wind and rainfall effects. Wind intensity may be quantified by maximum gusts, sustained wind speed, duration of wind, and distance from the center of the storm system (Everham and Brokaw 1996). Scatena and Larsen (1991) developed three indices of storm intensity: maximum sustained wind and storm duration, maximum sustained wind and proximity to the storm center, and rainfall totals (as a percentage of annual rainfall). Hugo, with a four-hour duration over the island and a maximum rainfall of 339 mm (15% of the annual total), was classified as a moderate-intensity event (Scatena and Larsen 1991). As with the eruption of Mount St. Helens and the Yellowstone fires, disturbance intensity varied over the landscape (Scatena and Larsen 1991), leading to a mosaic of effects (Figure 3). However, detailed information on the spatial variation of wind and on the rain intensity is not usually available after a hurricane because of the impact of wind on remote weather stations.

Hurricane wind alters the structure of the forest canopy, reducing canopy height by an average of 50% (Brokaw and Grear 1991). The severity of wind damage to vegetation ranges from defoliation to debranching, stem breakage, and uprooting. Mortality of trees following hurricanes tends to be low, rarely exceeding 40% (Everham and Brokaw 1996). The severity of hurricane-related wind damage in the Luquillo Experimental Forest decreased from the northeast to the southwest. This pattern of wind damage was related to proximity to the storm's center and was modified by the Luquillo

[2]D. Despain, 1990, personal communication. National Biological Service, Bozeman, MT.

Table 1. Comparison of characteristics of three broad-scale disturbances.

Characteristic	Crown fires	Hurricanes	Volcanoes
Disturbance-generated heterogeneity	Coarse-grained mosaic with some fine-grained variation	Fine-grained mosaic	Very coarse grained landscape mosaic
Endogenous versus exogenous	Both: quality and quantity of fuel plus synoptic weather	Exogenous	Exogenous
Spatial predictability of disturbance pattern	Unpredictable because topography has little effect under severe burning conditions	Predictable based on terrain at broad (tens to hundreds of hectares), but not fine, (less than 1 ha) scales	Predictable based on direction of blast and topography
Return time of disturbance in the landscape	100–500 yr, depending on latitude and elevation	60–200 yr in Puerto Rico, depending on intensity of storm; varies geographically	100–1000 yr for "ring of fire" volcanoes around the Pacific Ocean; Mount St. Helens last erupted in 1857
Seasonality of disturbance	Summer	Summer and fall	None, although timing of eruption will influence recovery

Mountains. Trees on the southwest slopes of the mountains suffered fewer broken or uprooted stems, with canopy damage limited mainly to defoliation and debranching. In addition, there were fewer broken or uprooted stems on the northwest side of the mountains (4–20% of stems in study plots) than on the northeast side (11–49% of stems in study plots). Gaps created by damage to the canopy varied from smaller than 0.0025 ha (associated with branch damage) to multiple treefall gaps, which can exceed 0.04 ha (Everham 1996).

The rainfall associated with hurricanes often triggers landslides. Landslides ranging in size from 0.002 to 0.482 ha occurred in 9.1 ha of the 6474 ha of Luquillo Experimental Forest surveyed with aerial photography after Hurricane Hugo (Scatena and Larsen 1991). These landslides were associated with steep concave slopes and with the heavier rainfall that occurred closer to the center of the storm. Recovery of vegetation on landslides was faster in the lower zone of accumulation than in the upper area of the slide, but even these areas may return to predisturbance forest conditions within 50 years (Guariguata 1990).

Characteristics of the disturbances

Disturbances and disturbance regimes can be described with a variety of parameters (e.g., White and Pickett 1985). We focus on five: the landscape heterogeneity created by the disturbance; whether the disturbance is exclusively exogenous to the system or incorporates some endogenous factors; whether the spatial pattern of disturbance was predictable based on landscape position; anticipated return time; and any regular seasonality in the disturbance events.

All three disturbances exhibited substantial heterogeneity in their severities across the landscape, and the spatial scale of the disturbance mosaic varied (Table 1). In Yellowstone, the mosaic was of differential fire severity, and islands of unburned forest remained within the overall burn perimeters (Christensen et al. 1989, Turner et al. 1994). Although some areas of crown fire extended for several kilometers, 75% of the most severely burned areas were located within 200 m of unburned or lightly burned forest (Turner et al. 1994). Hurricane Hugo created a mosaic of disturbance effects (wind-driven defoliation, blowdowns, and landslides) that varied in type more than effects observed in Yellowstone; each type could, in turn, be characterized by levels of severity (e.g., percentage of individuals or area affected). The spatial pattern of disturbance effects in the landscape was not quantified as was done for the Yellowstone fires, but the mosaic resulting from Hurricane Hugo appeared to be more fine grained than that resulting from the Yellowstone fires—that is, it varied over tens of meters rather than thousands of meters. Estimates of the spacing of hurricane-created gaps ranged from 10 to 35 m and varied with the method of quantifying damage; regardless of how damage was measured, the mode of patch size was 0.0025 ha (Everham 1996).

The volcanic eruption of Mount St. Helens also led to substantial landscape heterogeneity. As was the case with Hurricane Hugo, disturbance effects varied qualitatively across the landscape (i.e., debris avalanche, mudflows, pyroclastic flows, blowdown, crater formation, and ash deposit). Of all three disturbances, the Mount St. Helens eruption probably had the greatest diversity of types of disturbance effects. Again, severity varied within each type of effect. The mosaic that was created, however, was coarse grained, with large, isolated patches and linear mudflows. Thus, among the three disturbances, the effects at Mount St. Helens exhibited the most diversity and those at Yellowstone the least, and the disturbance-created mosaic was most coarse grained at Mount St. Helens and most fine grained in Puerto Rico following Hurricane Hugo (Table 1).

The predictability of the spatial pattern of disturbance varied among the three disturbances (Table 1). For the Yellowstone fires, the spatial pattern of disturbance was generally not predictable based on landscape position: Analyses based on slope, aspect, and vegetation pattern did not explain variability in fire pattern

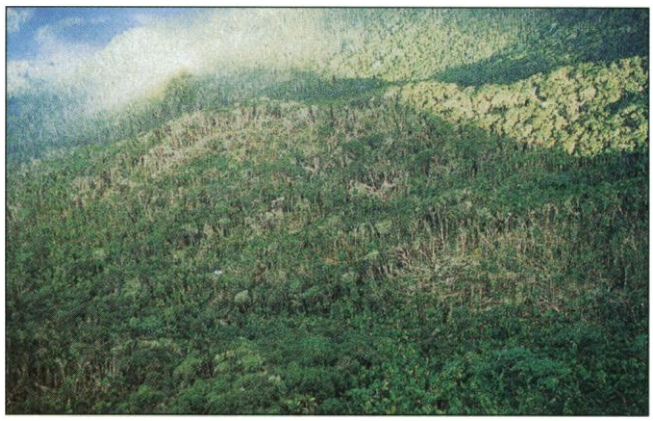

Figure 3. Spatial heterogeneity of hurricane disturbance effects in Puerto Rico, as shown from the top of the Mt. Britton tower in the Luquillo Experimental Forest, six months after Hurricane Hugo struck. Multiple treefalls created large patches of severe damage within stands that were defoliated but already leafing out. Photo: Allan Drew.

Figure 4. Recovery of the hurricane-damaged canopy showed rapid refoliation and restructuring of the canopy, as illustrated in this view of the Rio Mamayes, a river in the Luquillo Experimental Forest (top) six months, (middle) 18 months, and (bottom) 30 months after Hurricane Hugo. Photos: Allan Drew.

(Turner et al. 1994), and the addition of topographic effects in a spatial model of fire spread (Gardner et al. 1996) did not substantially alter simulated fire patterns. Under burning conditions as severe as those of the Yellowstone fires, fire spread is controlled almost wholly by wind direction and speed rather than by landscape variation (Bessie and Johnson 1995). Even large geographic features, such as the Grand Canyon of the Yellowstone, were not effective as fire breaks.

By contrast, a combination of topographic position (i.e., slope, elevation, and aspect) and knowledge of the direction of the storm or blast could be used to predict regions of maximum or minimum exposure for both Hurricane Hugo and the Mount St. Helens eruption (Table 1). The disturbances created by the eruption of Mount St. Helens were due more to characteristics of the volcanic eruption than to topography. Because of a weakness in the layer of rock on the north side of the mountain, the eruption was a northward-directed blast that left the south side of the mountain virtually untouched. However, the pyroclastic flow and blast were forceful enough to overcome topographic features in the vicinity of the mountain. The mudflows followed the river valleys but defined new channels. For Hurricane Hugo, the Luquillo Mountains provided some protection at the landscape scale from the predominantly north and northwest winds (Boose et al. 1994). Southwest slopes of the mountains were least affected by the wind. Valleys also provide protection if they are oriented away from the wind; in valleys oriented parallel to the wind, by contrast, the increased velocity of the channeled wind may cause severe damage (Everham 1996, Everham and Brokaw 1996).

Hurricanes and volcanoes are largely exogenous disturbances, in which the existing vegetation has little or no influence on disturbance intensity and pattern. However, local wind gusts during hurricanes can be affected by canopy structure; moreover, stand age, density, and successional class may influence severity of damage (Everham and Brokaw 1996, Zimmerman et al. 1994). Both exogenous (synoptic weather conditions; e.g., Bessie and Johnson 1995, Johnson and Wowchuk 1993) and endogenous (fuel availability) components affect fire intensity and pattern. Provided that fuel is available, however, large crown fires are not greatly influenced by variations in fuel structure that are associated with successional stage. Thus, each of the three disturbances is primarily exogenous.

Return times for each disturbance—that is, the interval between recurrent disturbances at a given location—are relatively long, ranging from decades to centuries for large hurricanes and from one to several centuries for crown fires and for volcanoes (Table 1). Fires and hurricanes both tend to occur seasonally from summer through early fall, whereas volcanic eruptions occur without any seasonal regularity. However, the timing of an eruption will strongly influence the effects on vegetation. An eruption during the growing season, for example, would have different effects than one during a season when plants are dormant. Even in the wet tropical forests of the Luquillo Experimental Forest, seasonal patterns of flowering and fruiting (Lugo and Frangi 1993) can influence the effects of a specific hurricane.

Table 2. Effects of large-scale disturbances on vegetation.

Effect on vegetation	Crown fires	Hurricanes	Volcanoes
Differential direct mortality among species or life forms?	Generally not, at least among trees in Yellowstone; mortality often 100% in stand-replacing burn	Greater mortality of early successional species; exposure to wind increases with stem size	Differential mortality related to the position of the dormant buds, but mortality is often more than 99%
Is there extensive delayed mortality? If so, at what time lag?	No; however, some scorched trees may die or be more susceptible to other disturbance	Yes; mortality increased up to 50% from years 1 to 3; delayed mortality may last for more than five years	No
Preconditioning of vegetation response by other disturbance types?	No; however, previous fire events may have an influence	Yes; chronic wind stress can precondition, although its impacts differ with direction of chronic wind (e.g., trade winds) and of a hurricane	Yes; adaptations to fire, snowslides, and recurrent floods may reduce effects of volcano

Effects of disturbance on the plant community

One effect of a large disturbance is that it can directly kill individual plants. All three disturbances did so, but the patterns and timing of mortality varied (Table 2). In Yellowstone, data on direct mortality are available only for tree species. The coniferous forests of Yellowstone are dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), although subalpine fire (*Abies lasiocarpa*), Engelman spruce (*Picea engelmannii*), aspen (*Populus tremuloides*), and Douglas fir (*Pseudotsuga menziesii*) may be locally abundant. Differential mortality among species was not observed,[3] and tree mortality was 100% in crown fires and severe surface burns. However, in less severe surface burns tree mortality was related to tree size, with larger trees (e.g., 15–20 cm diameter at breast height [dbh]) being less likely to die than small trees.

Tree mortality following Hurricane Hugo was related to successional stage and to height within the canopy. Early successional species (e.g., *Cecropia schreberiana*) tended to undergo stem snap (21.3% of stems) and death (52.9%). Late successional species (e.g., *Dacryodes excelsa*) tended to lose branches (29.9% of stems); both stem snap (3.6% of stems) and mortality (1.6%) were low in these species (Zimmerman et al. 1994).

Species-specific differences in damage and mortality obscured relationships to size or height within species. Whereas Frangi and Lugo (1991) found greater structural damage to intermediate-sized stems (12–14 m in height) in the Luquillo Experimental Forest, Basnet et al. (1992) reported that intermediate-sized stems (20–25 m in height, 50–60 cm dbh) were the least damaged. A positive correlation between stem size and damage has been suggested from studies of other hurricanes in New England (Foster and Boose 1992), Puerto Rico (Wadsworth and Englerth 1959), the Solomon Islands (Whitmore 1974), and Mauritius (King 1945). However, survival was highest among the largest trees following a hurricane in Nicaragua (Boucher 1990). A thorough review of impacts of intense wind disturbances suggests a more complex relationship between stem size and damage (Everham and Brokaw 1996). The smallest stems are sheltered from the wind but are subject to indirect damage from other falling stems. Exposure to wind increases as stem size increases, but the largest stems may be preconditioned by previous wind and survive subsequent disturbance.

On Mount St. Helens, plant mortality often exceeded 99% of individuals in severely affected areas, with few differences in mortality among species. Patterns of survival were related to the position of dormant buds (Adams et. al. 1987). Plants with subterranean dormant buds (geophytes) and those that could generate from fragments best survived the blast, scorch, and landslide. Survival on the mudflow was higher for large trees.

Most disturbance-induced plant mortality was immediate for the crown fire and volcano, but hurricane-caused plant mortality showed a time lag of several years (Table 2). In Yellowstone, although most mortality was immediate, some scorched trees near the perimeter of the burned area likely died the following year or could have been stressed sufficiently to be more susceptible to other disturbances (Knight 1987). At Mount St. Helens, some trees on the mudflow died later (depending on the depth of the mud), but again, most mortality was immediate. Following Hurricane Hugo, by contrast, mortality increased by as much as 50% between years one and three, indicating time lags of several years (Everham 1996, Walker 1995). Mortality following a hurricane may be delayed for as long as five years, as has been observed in Jamaica (Bellingham 1991), Florida (Craighead and Gilbert 1962), and Sri Lanka (Dittus 1985).

We also investigated whether prior exposure to different stresses or disturbances might "precondition" vegetation such that it can better recover from a large disturbance. For crown fires, other types of disturbance do not appear to influence responsiveness to fire, although fire history may be important. For example, lodgepole pine (*Pinus contorta* var. *latifolia*) is well known for having serotinous cones that release their seed when heated. Prefire serotiny levels strongly influence postfire succession, and Muir and Lotan (1985) found that the time and severity of the most recent fire at a site was the best predictor of percent serotiny in

[3]M. G. Turner, unpublished data.

Table 3. Postdisturbance recovery of the vegetation.

Recovery property	Crown fires	Hurricanes	Volcanoes
Primary modes of recovery	Dispersal and seedling establishment (for dominant trees); resprouting (for herbs and shrubs)	Resprout, seedling establishment, or release from suppressed stage (for dominant trees; not quantified for herbs and shrubs)	Dispersal and seedling establishment (after the crater, pyroclastic flow, and debris avalanche disturbances)
Seedling dynamics	Early pulse (1–3 yr postfire)	Early pulse (1.5–2.5 yr after hurricane)	No pulse; establishment gradual
Reestablishment rate	Percent cover reestablished rapidly	Very rapid	Slow, although spatially variable
Plant species dominance	Shifts in herbaceous species but not trees; landscape diversity likely to increase	Shifts with large pulse of early successional species; landscape diversity may increase	Shifts with succession; landscape diversity may increase
Plant species richness	Maintained at landscape scale, increasing locally	Maintained at landscape and local scales	Increasing at landscape and local scales; exotics increase but cause native species to decline

lodgepole pine. Thus, stands that have burned more frequently in the past may be reforested more rapidly following a crown fire.

For hurricanes and volcanoes, however, some preconditioning may occur from other disturbances. Chronic wind stress may strengthen limbs and alter vegetation architecture such that effects of a hurricane are less severe (Webb 1958). However, the actual impact of a given hurricane will depend on whether the direction of the chronic wind (e.g., trade winds) and of the hurricane coincide. In addition to morphological changes that mitigate severity of damage, response to hurricane disturbance may be facilitated by adaptations of species to the frequent treefalls associated with background tree mortality. Similarly, for Mount St. Helens, adaptations to fires, snowslides, and floods appear to have reduced the effect of the volcano (Adams et al. 1987). Periodic fires and storms (in particular, heavy precipitation, mainly in the form of snow) may explain the high proportion of geophytes in the Pacific Northwest flora. Montane forest and subalpine meadows of Washington have recurrent fires and snowslides, which remove aboveground plant biomass in a manner similar to that of the 1980 lateral blast of Mount St. Helens. Species with the ability to regenerate from meristematic tissue located several centimeters below the surface have the greatest survival rate during fires (Flinn and Wein 1977). The species that regenerated from underground buds in the blast zone and scorch areas of Mount St. Helens also regenerate after fires and snowslides (Cushman 1981).

Postdisturbance vegetation recovery

What is the legacy of a large-scale disturbance? Disturbance effects are mitigated by the ability of the system to recover, and the mechanisms of vegetation recovery are quite varied. We focus on modes of recovery in trees, shrubs, and herbaceous species; whether seedling establishment was gradual or pulsed; and how cover and species richness has changed through time (Table 3).

The mechanisms leading to vegetation reestablishment in Yellowstone and Mount St. Helens appeared to be similar; those in Puerto Rico were more varied. For Yellowstone and Mount St. Helens, reestablishment of the dominant trees, which in both cases are conifers, occurred only through seed. By contrast, the tree species of Puerto Rico exhibited varied recovery mechanisms, including resprouting, seeding, or rapid growth following hurricane-induced opening of the canopy (Figure 4). Although it is possible that the differences in recovery mechanisms reflect the fact that Puerto Rico is a tropical system, whereas the other two systems are temperate, both temperate and tropical forests show a similar complexity of responses following intense wind disturbance (Everham and Brokaw 1996). Reestablishment of herbaceous species in areas of Mount St. Helens where ash deposition was less than 25 cm deep was similar to herbaceous reestablishment in areas of stand-replacing burn (i.e., crown fire or severe surface burn) in Yellowstone. In both systems, perennial grasses, sedges, and forbs often resprouted and began filling the disturbed area (Antos and Zobel 1985) in a manner similar to that observed following the 1912 eruption of Mount Katmai (Griggs 1919). Where ash deposition on Mount St. Helens exceeded 25 cm, resprouting did not occur, and colonization by seed was needed for plant reestablishment (Dale 1989, Franklin et al. 1985). The dynamics of herbaceous species were not quantified following Hurricane Hugo.

Postdisturbance seedling establishment occurred in a pulse following the Yellowstone fires and Hurricane Hugo. In Yellowstone, new conifer seedlings were abundant during the first two years following the fires, and new aspen seedlings were present only during the first postfire year (Romme et al. 1997). Herbaceous species flowered profusely in the burned forests in 1990 (Figure 5). Seedlings of herbaceous plants peaked during 1991, three years after the fires, and then returned to low levels (Turner et al. 1997). In Puerto Rico, seedlings were most abundant 1.5–2.5 years following the hurricane, and seedfall was two to three times greater than prehurricane levels (Walker and Neris 1993). By contrast, a seedling pulse was not

observed on Mount St. Helens during the first 15 years following the eruption, although average plant cover throughout the area has gradually increased (Figure 6). The area affected by the volcano was so large that dispersal distances exceeding several kilometers were often needed for vegetation establishment, and establishment has been gradual rather than pulsed. On the mudflows, deciduous trees that established as seedlings provided 100% cover by 1994. On the debris avalanche, cover approached 34% by 1994 but was extremely variable across the deposit. Vegetation recovery on the pyroclastic flows is still minimal and consists of isolated individuals or groups of plants in favorable microsites (del Moral and Bliss 1993).

Patterns of species richness varied among the three disturbances. Plant species richness was still increasing at the scale of sampling plots (less than 10 m^2) five years after the Yellowstone fires, but overall species richness of the landscape was unaffected by fire. That is, species richness varied locally and increased as species "filled in," but cumulative species richness across all sampling points seemed insensitive to the fires. However, dominance among the herbaceous species has shifted following fire, as many species recovered but varied in relative abundance. Fireweed (*Epilobium angustifolium*), for example, became much more abundant after the fire than it was before. Landscape diversity—the number and relative abundance of different community types—may increase if areas previously dominated by conifer forests shift to other community types, such as meadows or aspen groves.

Following Hurricane Hugo, plant species richness increased at some sites at an intermediate spatial scale (i.e., hectares) but was maintained at both larger and smaller scales. As in Yellowstone, however, species dominance shifted substantially because early successional species thrive in the hurricane-created gaps. The addition of these early successional patches also may lead to a short-term increase in landscape diversity. Over the next three decades, self-thinning and the short life span of the early successional species should result in reduced dominance and landscape diversity (Everham 1996, Weaver 1986).

On Mount St. Helens, species richness was still increasing at the plot level 15 years after the eruption. Of 296 species reported for the area prior to the eruption (St. John 1976), 156 species occurred on the debris avalanche by 1994,[4] and 16 occurred on the pyroclastic flows by 1990 (del Moral and Bliss 1993). Species dominance is likely to shift as succession proceeds, and new community types may be introduced within the landscape. A complicating factor at Mount St. Helens was colonization by exotic species (sometimes resulting from intentional seeding of exotics), which resulted in local increases in cover but decreased richness of native species and increased mortality of tree seedlings (Dale 1991).

Finally, given our current conceptual understanding of postdisturbance succession at each site, how well can we explain vegetation recovery? Although the important factors controlling recovery vary among the sites, two important similarities were observed. First, at all three locations a hierarchy of factors appears to control succession, with different factors being more important at different spatial scales. In Yellowstone, postfire succession is controlled by broad-scale gradients in serotiny, by meso-scale variability in fire severity and patterning, and by microscale variability in soil conditions, slope, and aspect. Following Hurricane Hugo, pathways of vegetation response were first related to broad-scale patterns of severity of canopy damage (Everham 1996). If mortality and structural damage were minimal, recovery occurred through resprouting. Greater structural damage or mortality led to increased establishment of early successional species. With either response, succession was also influenced by landscape patterns of light and moisture availability. At Mount St. Helens, disturbance type (especially depth of volcanic material) determined the degree of vegetation survival over broad scales. Recovery was influenced largely by prevalence of seeds being dispersed, which was a function of both distance to surviving vegetation and wind patterns (Dale 1991). Microtopography, local disturbances, and herbivory were important on a local scale (Dale 1989, del Moral and Bliss 1993).

The second similarity was evidence for multiple successional pathways at each site and for the early development of certain communities that inhibit subsequent vegetation reestablishment. In some of Yellowstone's burned forests, those in which the percentage of serotinous trees was low before the 1988 fires, the rapid development of herbaceous vegetation may preclude tree establishment for decades. In Puerto Rico, the development of fern meadows following the hurricane is also likely to inhibit forest development. On Mount St. Helens, extensive lichen development may inhibit tree establishment and forest development for decades, as it has at the Kautz Creek Mudflow on Mount Rainier (Frehner 1957, Frenzen et al. 1988). Thus, a positive feedback process may occur in which the lack of rapid plant establishment permits lichen establishment, a relatively slow process, and the lichens then inhibit plant growth.

Synthesis: legacies of large disturbances

Ecologists still have relatively few observations and long-term studies of disturbance events that are large, severe, and infrequent. The three large-scale disturbances that we have compared here shared several characteristics. Each was relatively infrequent (returning at intervals of decades to centuries) and had strong exogenous forcing. The spatial patterns of a disturbance could be predicted based on topography if it had a known directionality (e.g., prevailing wind direction) and a sheltering effect. Although these large disturbances were spatially extensive, in all of them the effects across the landscape were heterogeneous. The complex disturbance-initiated mosaic created a legacy that will influence the ecosystem well into the future, regardless of whether primary or secondary succession was initiated. Indeed, although their effects on plants were not as catastrophic as suggested by first impressions, these disturbances may be the dominant

[4] V. H. Dale, unpublished data.

forces influencing the structure of these systems.

Considering all modes of reestablishment of vegetation, recovery rates were highest following Hurricane Hugo and slowest following the eruption of Mount St. Helens. Mortality induced by the disturbances was generally immediate and substantial for the crown fire and volcano, whereas hurricane-induced mortality was less and lagged in time for as much as five years. Recovery mechanisms appeared to be related more to disturbance severity than to disturbance size per se. The greater survival of dominant trees following Hurricane Hugo likely was a major factor contributing to the more rapid recovery after this disturbance. Propagule availability was generally not a factor controlling response to hurricane disturbance in Puerto Rico because of the fine-grained heterogeneity of damage, low mortality, rapid flowering and fruiting, and an adequate soil seed bank. Recovery rates were slowest for the most severely disturbed areas of Mount St. Helens. When recovery was relatively rapid (as for the crown fire and hurricane), the window of opportunity for seedling establishment was short and pulsed. By contrast, when recovery was slow (as for the volcano), seedling establishment seemed to be a protracted, gradual process.

The effect of disturbance size appears to be strongly influenced by the abundance and spatial distribution of survivors and propagules—that is, by disturbance severity. If survival is high or the seed bank is sufficient, disturbance size may be relatively unimportant for succession. By contrast, if survival and propagule availability are both low, then disturbance size becomes important for colonization and for establishment, and chance colonization events may send succession in different directions.

Given the importance of large-scale disturbances in structuring ecosystems, changes in these disturbance regimes—for example, as a result of global climate change—could have substantial ecological implications. Global climate change would not affect the frequency of volcanic activity, but higher ocean surface temperatures would increase both the frequency and intensity of hurricanes. Past climate changes have altered fire regimes (e.g., Clark 1990), and simulations suggest that the Yellowstone landscape would be substantially altered by the more frequent fires associated with a warmer, drier climate or by the less frequent but even larger fires associated with a cooler, wetter climate (Gardner et al. 1996). Understanding the response of disturbance regimes characterized by large, infrequent events to climatic change remains an important challenge.

Our comparison of the effects of the eruption of Mount St. Helens, the Yellowstone fires, and Hurricane Hugo suggests intriguing similarities and differences among these large disturbances. Our understanding of the effects of large disturbances would benefit from comparisons with other types of disturbance. For example, large, infrequent flooding events in river systems (e.g., Baker and Walford 1995) and in near-coastal communities, such as coral reefs and kelp forests, are influenced by infrequent, severe storm events (e.g., Dayton et al. 1992). Our analysis highlights the extremely heterogeneous nature of large-scale disturbances. Further study of these and other large disturbances would enhance our understanding of how large-scale disturbances restructure landscapes and influence succession.

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Figure 5. Postfire seedling recruitment in Yellowstone was pulsed. Profuse flowering in burned areas was observed in 1990 (left), but not in 1991 (right), when seedlings reached peak density.

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Figure 6. Vegetation recovery on the debris avalanche created by the 1980 eruption of Mount St. Helens. By 1994, when this photograph was taken, recovery of vegetation was still sparse.

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