

Disturbance, Survival, and Succession: Understanding Ecological Responses to the 1980 Eruption of Mount St. Helens

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1.1 Introduction

The ecological and geological responses following the May 18, 1980, eruption of Mount St. Helens are all about change: the abrupt changes instigated by geophysical disturbance processes and the rapid and gradual changes of ecological response. The explosive eruption involved an impressive variety of volcanic and hydrologic processes: a massive debris avalanche, a laterally directed blast, mudflows, pyroclastic flows, and extensive tephra deposition (Lipman and Mullineaux 1981; Swanson and Major, Chapter 3, this volume). Subsequent, minor eruptions triggered additional mudflows, pyroclastic flows, tephra-fall events, and growth of a lava dome in the newly formed volcanic crater. These geological processes profoundly affected forests, ranging from recent clear-cuts to well-established tree plantations to natural stands, as well as meadows, streams, and lakes. This book focuses on responses of these ecological systems to the cataclysmic eruption on May 18, 1980.

Initial ecological response to the 1980 eruption was dramatic both in the appearance of devastation (Figure 1.1) and in subsequent findings that life actually survived by several mechanisms in many locations (del Moral 1983; Halpern and Harmon 1983; Andersen and MacMahon 1985a and 1985b; Franklin et al. 1985; Crawford 1986; Adams et al. 1987; Zobel and Antos 1986, 1992). Ecological change occurred as a result of survival, immigration, growth of organisms, and community development. The pace of these biological responses ranged from slow to remarkably rapid. In addition, subsequent physical changes to the environment influenced biological response through weathering of substrates and by secondary disturbances, such as erosion, that either retarded or accelerated plant establishment and growth, depending on local circumstances. The net result of secondary physical disturbances was increased heterogeneity of developing biological communities and landscapes.

The sensational volcanic eruption of Mount St. Helens initially dwarfed the ecological story in the eyes of the public and the science community; but as the volcanic processes quieted,

ecological change gained attention. The variety of disturbance effects and numerous interactions between ecological and geological processes make Mount St. Helens an extremely rich environment for learning about the ecology of volcanic areas and, more generally, about ecological and geophysical responses to major disturbances. More than two decades after the primary eruption, geophysical and ecological changes to the Mount St. Helens landscape have become so intertwined that understanding of one cannot be achieved without considering the other.

The 1980 eruption of Mount St. Helens and its ecological aftermath are the most studied case of volcanic impacts on ecological systems in history (Table 1.1). Ecological research at other volcanoes has often considered ecological responses based on observations made several years, decades, or even centuries after the eruption. In contrast to eruptions of some other volcanoes, lava surfaced only in the crater of Mount St. Helens; and most of the disturbance processes left deposits of fragmented volcanic rocks through which plants can easily root and animals can readily burrow. Furthermore, studies at other volcanoes typically investigated only one group of organisms (e.g., plants) and one type of volcanic process or deposit, which contrasts to the diversity of terrestrial and aquatic life and volcanic processes and deposits considered in this book.

Since the 1980 eruption of Mount St. Helens, analyses of ecological response to eruptions of other volcanoes and to ecological disturbance, in general, have made important advances. Ecological responses to other volcanic eruptions have been the subject of retrospective investigations of historic eruptions [e.g., Krakatau in Indonesia (Thornton 1996)] and analyses of responses to recent eruptive activity [e.g., Hudson volcano in Argentina (Inbar et al. 1995)]. More broadly, the field of disturbance ecology has blossomed through development of theory (Pickett and White 1985; White and Jentsch 2001; Franklin et al. 2002); intensive study of recent events, such as the Yellowstone fires of 1988 (Turner et al. 1998) and Hurricane Hugo (Covich and Crowl 1990; Covich et al. 1991; Covich and McDowell 1996); and consideration of effects of climate change on disturbance regimes (Dale et al. 2001). Lessons

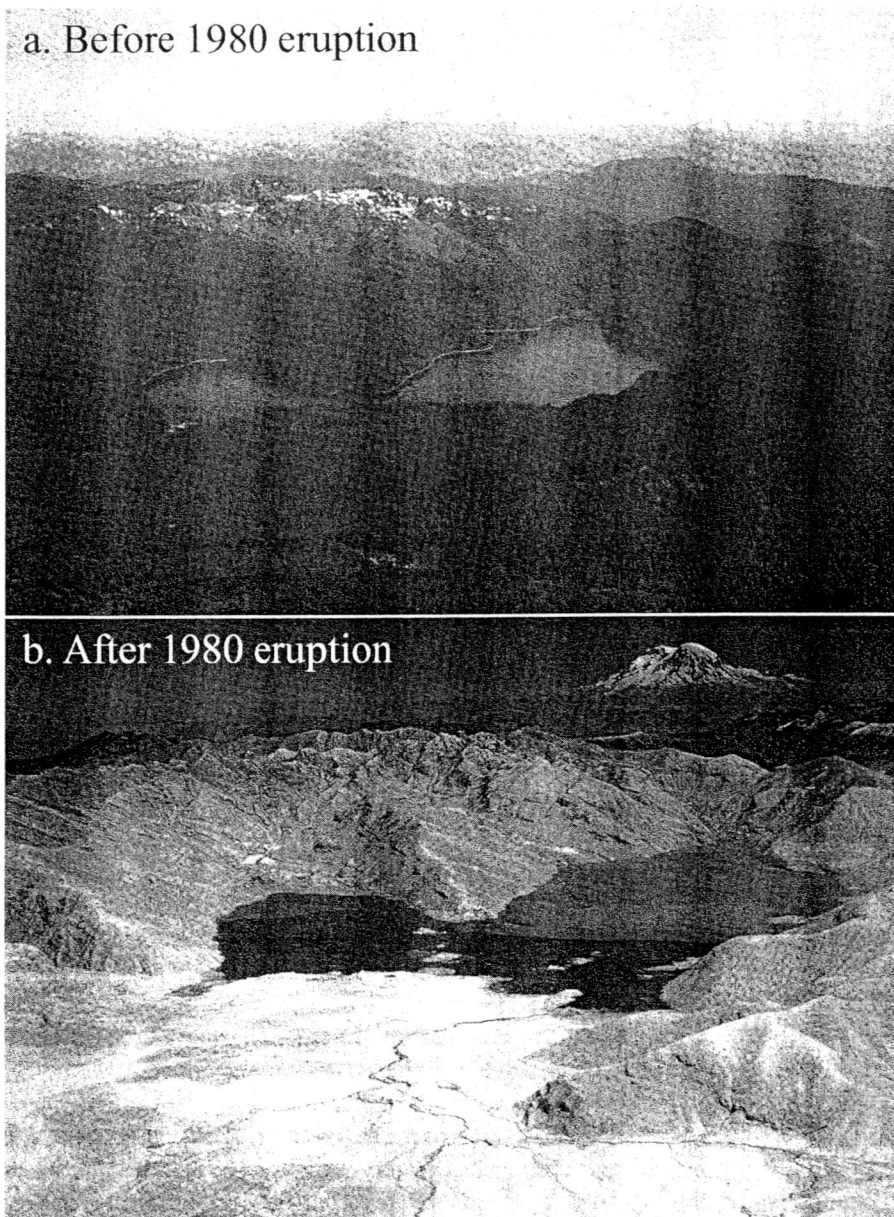


FIGURE 1.1. Before and after photographs of the Mount St. Helens landscape: (a) view north from top of Mount St. Helens toward Mount Rainier across Spirit Lake before 1980; (b) same view in summer 1980. (Source: USDA Forest Service photos.)

about ecological response at Mount St. Helens are shaping understanding of succession (Turner et al. 1998; Walker and del Moral 2003), disturbance ecology (Turner et al. 1997; Turner and Dale 1998; del Moral and Grishin 1999), ecosystem management (Swanson and Franklin 1992; Dale et al. 1998, 2000; Franklin et al. 2002), evolution and the origin of life (Baross and Hoffman 1985), trophic interactions (Fagan and Bishop 2000; Bishop 2002), and landscape ecology (Foster et al. 1998; Lawrence and Ripple 2000).

In the context of this progress in disturbance ecology in general and ecological studies at Mount St. Helens more specifically, it is timely to synthesize knowledge of ecological response to the 1980 eruption of Mount St. Helens. In the first 7 years after the eruption, several compilations documented the numerous, intensive studies of ecological response (Keller 1982, 1986; Bilderback 1987); however, since 1987,

the scientific community has not prepared a book-length synthesis of the scores of ecological studies under way in the area. Yet, more than half of the world's published studies on plant and animal responses to volcanic eruptions have taken place at Mount St. Helens (see Table 1.1) (Dale et al. 2005; Edwards 2005). The 25-year synthesis presented in this volume makes it possible to more thoroughly analyze the initial stages of response, to assess the validity of early interpretations, to examine the duration of early phenomena in a broader temporal context, and to consider landscape processes and patterns that were not evident in the early years. These studies provide an understanding of ecological change in a complex, continually changing environment. Hence, the Mount St. Helens volcano has come to hold a special place in the study of volcanic eruptions not only in the Pacific Northwest of the United States but also throughout the world.

TABLE 1.1. Summary of research on effects of volcanic activity on vegetation organized by types of physical impact.

Type of physical impact and volcano	Location	Dates of eruption	Reference
<i>Lava</i>			
Mount Wellington	New Zealand	9000 years before present (YBP)	Newnham and Lowe 1991
Mt. Fuji	Japan	1000	Hirose and Tateno 1984; Ohsawa 1984; Masuzawa 1985; Nakamura 1985
Rangitoto	New Zealand	1300, 1500, 1800	Clarkson 1990
Mt. Ngauruhoe and Mt. Tongariro	New Zealand	1550+	Clarkson 1990
Snake River Plains	Idaho, USA	~1720	Eggler 1971
Jorullo	Mexico	1759	Eggler 1959
Ksudach	Kamchatka, Russia	1907	Grishin et al. 1996
Waiowa	New Guinea	1943	Taylor 1957
Kilauea Iki and Mauna Loa	Hawaii, USA	1959	Fosberg 1959; Smathers and Mueller-Dombois 1974; Matson 1990; Kitayama et al. 1995; Aplet et al. 1998; Baruch and Goldstein 1999; Huebert et al. 1999
Surtsey	Iceland	1963	Fridriksson and Magnusson 1992; Fridriksson 1987
Isla Fernandina	Galapagos, Ecuador	1968	Hendrix 1981
Hudson	Argentina	1991	Inbar et al. 1995
Krakatau	Indonesia	1883, 1927	Whittaker et al. 1989, 1992, 1998, 1999; Partomihardjo et al. 1992; Thornton 1996
<i>Pyroclastic flow</i>			
Vesuvius	Italy	79	Mazzoleni and Ricciardi 1993
Kilauea Iki	Hawaii, USA	1750, 1840, 1955	Atkinson 1970
Miyake-Jima	Japan	1874, 1962, 1983	Kamijo et al. 2002
El Paracutin	Mexico	1943	Eggler 1948, 1959, 1963; Rejmanek et al. 1982
Mount St. Helens	Washington, USA	1980	Wood and del Moral 1988; Morris and Wood 1989; Wood and Morris 1990; Halvorson et al. 1991b, 1992; del Moral and Wood 1988a,b, 1993a,b; del Moral et al. 1995; Chapin 1995; Halvorson and Smith 1995; Tsuyuzaki and Titus 1996; Tsuyuzaki et al. 1997; Titus and del Moral 1998a,b,c; Bishop and Schemske 1998; Tu et al. 1998; del Moral 1998, 1999a; Fagan and Bishop 2000; Bishop 2002; del Moral and Jones 2002; Fuller and del Moral 2003
<i>Avalanche</i>			
Mt. Taranaki	New Zealand	1550	Clarkson 1990
Ksudach	Kamchatka, Russia	1907	Grishin 1994; Grishin et al. 1996
Mt. Katmai	Alaska, USA	1912	Griggs 1918a,b,c, 1919, 1933
Mount St. Helens	Washington, USA	1980	Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003
Ontake	Japan	1984	Nakashizuka et al. 1993
<i>Mudflow</i>			
Krakatau	Indonesia	1883	Tagawa et al. 1985
Mt. Lassen	California, USA	1914–1915	Heath 1967; Kroh et al. 2000
Mount Rainier	Washington, USA	1947	Frehner 1957; Frenzen et al. 1988
Mount Lamington	New Guinea	1951	Taylor 1957
Mount St. Helens	Washington, USA	1980	Halpern and Harmon 1983
Mount Pinatubo	Philippines	1991	Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003
<i>Tephra and ash deposition</i>			
Auckland Isthmus	New Zealand	~9,500 YBP	Newnham and Lowe 1991
Krakatau	Indonesia	~1880	Whittaker et al. 1998
Laacher Volcano	Germany	~12,900 YBP	Schmincke et al. 1999
Laguna Miranda	Chile	~4,800 YBP	Haberle et al. 2000
Mount Usu	Japan	1977–1978	Tsuyuzaki 1991, 1995; Tsuyuzaki and del Moral 1995; Tsuyuzaki 1997; Tsuyuzaki and Haruki 1996; Haruki and Tsuyuzaki 2001
Lascar Volcano	Chile	1993	Risacher and Alonso 2001
Mount Mazama	Oregon, USA	~6,000 YBP	Horn 1968; Jackson and Faller 1973
Craters of the Moon	Idaho, USA	~2,200 YBP	Eggler 1941; Day and Wright 1989
Vesuvius	Italy	79	Dobran et al. 1994

(continued)

TABLE 1.1 (continued)

Type of physical impact and volcano	Location	Dates of eruption	Reference
Mt. Taranaki	New Zealand	1655	Clarkson 1990
Jorullo	Mexico	1759	Eggler 1959
Mt. Victory	New Guinea	1870	Taylor 1957
Krakatau	Indonesia	1883	Bush et al. 1992; Thornton 1996
Mt. Tarawera	New Zealand	1886	Clarkson and Clarkson 1983; Clarkson 1990; Clarkson et al. 2002; Walker et al. 2003
Soufriere	St. Vincent, BWI	1902	Beard 1976
Katmai	Alaska, USA	1912	Griggs 1917
Popocatepetl	Mexico	1920	Beaman 1962
Mount Lamington	New Guinea	1951	Taylor 1957
Kilauea Iki	Hawaii, USA	1959	Smathers and Mueller-Dombois 1974; Winner and Mooney 1980
Isla Fumandina	Galapagos, Ecuador	1968	Hendrix 1981
Usu	Japan	1977–1978	Riviere 1982, Tsuyuzaki 1987, 1989, 1991, 1994, 1995, 1996; Lamberti et al. 1992; Tsuyuzaki and del Moral 1994
Mount St. Helens	Washington, USA	1980	Mack 1981; Cook et al. 1981; Antos and Zobel 1982, 1984, 1985a,b,c, 1986; del Moral 1983, 1993; Seymour et al. 1983; Cochran et al. 1983; Hinckley et al. 1984; del Moral and Clappitt 1985; Frenzen and Franklin 1985; Zobel and Antos 1986, 1987a, 1991a, 1992, 1997; Adams et al. 1987; Harris et al. 1987; Wood and del Moral 1987; Pfisch and Bliss 1988; Chapin and Bliss 1988, 1989; del Moral and Bliss 1993; Tsuyuzaki and del Moral 1995; Foster et al. 1998
El Chichón	Mexico	1982	Burnham 1994
Hudson	Argentina	1991	Inbar et al. 1994
Mount Koma	Hokkaido, Japan	1929	Tsuyuzaki 2002; Titus and Tsuyuzaki 2003a,b; Nishi and Tsuyuzaki 2004
Santorini	Greece	~9,000 YBP	Bottema and Sarpaki 2003
Mijake-Jima	Japan	~9,000 YBP	Kamijo et al. 2002
Kula	Turkey	~9,000 YBP	Oner and Oflas 1977
<i>Blowdown</i>			
Mount Lamington	New Guinea	1951	Taylor 1957
Mount St. Helens	Washington, USA	1980	Franklin et al. 1985, 1988; Frenzen and Crisafulli 1990; Halpern et al. 1990

Source: Updated from Dale et al. (2005).

This chapter provides background on concepts of disturbance, succession, and the integration of ecological and geophysical perspectives that are explored further in this book. First, it defines disturbance, survival, and succession, and then briefly examines the major components of ecological response: survival, immigration, site amelioration, and community development. Next, the chapter addresses linkages among biotic and physical factors influencing succession. Finally, it considers the relation of events at Mount St. Helens to succession and disturbance ecology concepts. The chapter closes with an overview of what follows in subsequent chapters.

1.2 Ecological Change: Definitions and Descriptions of Disturbance, Survival, and Succession

1.2.1 Disturbance

Ecological disturbance has been defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate

availability, or the physical environment” (White and Pickett 1985). Rather than being catastrophic agents of destruction, many disturbances are normal, even integral, parts of long-term ecological dynamics. The composition, structure, and function of ecological systems are partially products of disturbances. In fact, some species and ecosystems are well adapted to frequent disturbances, so in some cases the absence of disturbance constitutes a disruption that can lead to changes in species, structures, or processes (White and Jentsch 2001; Dodds et al. 2004). To better understand any particular disturbance event, it should be considered in the context of the typical disturbance regime of the area.

Important characteristics of disturbance include their intensity (i.e., force exerted, such as heat release per unit length of fire front), severity (i.e., ecological effect, such as change in live plant cover), frequency, predictability, size, and spatial distribution (White and Pickett 1985). Severity and intensity are related but commonly differ because of differential species response to disturbance. Disturbance regimes span a broad range of frequency and predictability of occurrence. Disturbance size may be simply delineated when the area affected is uniform or may be quite complex where disturbance-impacted areas are

patchy or the disturbance is variable in intensity and severity. Small, more frequent disturbances include individual tree falls; small fires; and small, patchy insect outbreaks. Large, infrequent disturbances include volcanic eruptions, crown fires, and hurricanes. Areas affected by large disturbance events commonly encompass complex patterns of disturbance intensity and severity, reflecting heterogeneity in the predisturbance landscape as well as complexity of the disturbance process itself (Turner et al. 1997). Timing of a disturbance can influence its effect on an ecological system. For example, ice storms can have more severe consequences in a deciduous forest if they are late enough in the spring that trees have leafed out (Irland 1998).

It is useful to distinguish between disturbance type and mechanism. Disturbance type refers to the geophysical or ecological phenomenon that has a disturbance effect, such as wind-storm, fire, glacier advance or retreat, volcanic eruption, flood, wave action, insect or pathogen outbreak, or human activity. Mechanisms of disturbance are the specific stressors sensed by organisms, such as heat, impact force, and erosion or deposition. Both volcanic and nonvolcanic disturbance processes involve combinations of disturbance mechanisms. Intense forest fires, for example, can include high temperature and strong wind; and mudflows of volcanic or nonvolcanic origin involve impact force, scour, and deposition. Different disturbance types may have similar mechanisms of disturbance, such as occurs with both wildfire and volcanic processes that involve mechanisms of heating. Initial biological response to disturbance is reaction to the *mechanism* rather than the *type* of disturbance. Hence, understanding both the mechanisms involved in a particular disturbance process and the biotic response to individual mechanisms is critical to interpreting and predicting disturbance effects. There are several implications of this perspective. First, if the mechanism and intensity of disturbance by two different processes are similar, similar biological response would be expected, despite the difference in disturbance type (e.g., spores of some fungal species germinate when exposed to heat of wildfire or of volcanic eruption). Thus, some species may be adapted to mechanisms imposed by rare disturbance types (e.g., volcanic blast) because of adaptations to a more common disturbance type (e.g., fire). Second, where several mechanisms are involved in a particular disturbance type, the mechanism with the greatest severity overrides effects of the others.

1.2.2 Survival

Survival is a critical ecological process involving the interaction of organisms and disturbance processes, and survivors potentially play important roles in succession. Ecological effects of disturbances are determined, in part, by both living entities and nonliving biological and physical structures from the predisturbance system that remain after the disturbance (North and Franklin 1990; Foster et al. 1998; White and Jentsch 2001). The potential importance of residual plants and animals was noted by Clements (1916) and Griggs (1918a)

but did not gain much prominence in early work on succession because of a focus on primary succession and old-field succession, where agricultural practices had erased any vestiges of previous forest. More recently, the term *biological legacy* has been defined as the types, quantities, and patterns of biotic structures that persist from the predisturbance ecological system. Living legacies can include surviving individuals, vegetative tissue that can regenerate, seeds, organisms in resting stages (particularly important for zooplankton), and spores. Dead biological legacies include standing dead trees, wood on the ground, litter, and animal carcasses. *Physical legacies* can strongly influence plant and animal survival, colonization, and growth. Important physical legacies after many disturbances are remnant soil, talus, rock outcrops, and aquatic habitats (e.g., seeps and springs).

1.2.3 Succession

The interplay of disturbance and response is an essential part of ecological change in landscapes. The process of gradual ecological change after disturbance, termed *succession* by Thoreau (1993), refers to changes that occur over time in biological and physical conditions after a site has been disturbed (Figure 1.2). Succession is the suite of progressive changes that occur to an ecological system and not the regular, seasonal, or interannual change in biological systems. In forests, succession can proceed over decades or centuries; whereas in microbial systems, succession occurs over days or months. Succession has intrigued ecologists since the first studies of ecology (McIntosh 1999). Early views of gradual ecological change were drawn, in part, from observations of sets of sites thought to represent different stages along a sequence of biotic development following some common initiating event, such as abandonment of farm fields, sand-dune formation, or deposits left by retreating glaciers (Cowles 1899; Clements 1916; Gleason 1917; Olson 1958). After a long period of debate about the processes and consequences of succession (Whittaker 1953; Odum 1969; Drury and Nisbet 1973; Bazzaz 1979; Odum 1983; McIntosh 1999), in recent decades ecologists have increasingly turned their attention to the study of disturbances and their ecological effects (Pickett and White 1985; White and Jentsch 2001).

Historically, ecologists distinguished *primary succession*, which follows formation of entirely new substrates and areas cleansed of biota, from *secondary succession*, which follows disturbances that leave substantial legacies of earlier ecological systems. Primary succession was thought to take place on entirely denuded sites, such as in the aftermath of a lava flow or glacier retreat, and in newly created habitats, such as lakes and streams on fresh landslide deposits. Primary succession is now commonly considered an endpoint along a continuum of abundance of residual organisms and biological structures left by a disturbance.

Following disturbance, succession does not follow an orderly path to a single endpoint. Instead, succession is commonly complex, having different beginning points, stages

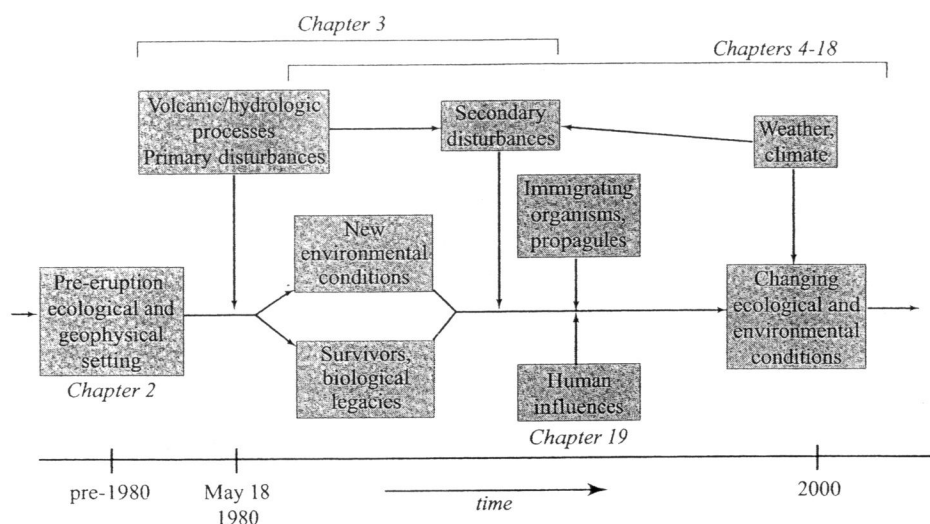


FIGURE 1.2. Sequential interactions of disturbance and succession processes over time and the relation of these topics to chapters in this book.

with different mixes of species and dominance patterns, and interruptions of successional trajectories by subsequent disturbances or other factors. Consequently, multiple pathways of succession may occur (Baker and Walford 1995). Ecosystems may undergo succession toward prior ecological conditions if the prevailing climate, species pools, and substrates have not been altered significantly. Yet, when one or more of these or other factors change, such as preemption of a site by a particular species or a profound change in soil conditions, a new stable state may be achieved (Paine et al. 1998).

1.3 Response to Disturbance: Processes of Change

Succession includes influences of biological and physical legacies, if any are present; immigration of organisms; establishment of some of these migrants; accrual of species and biomass; replacement of some species by others; and amelioration of site physical conditions. The replacement concept can be extended to include (1) replacement of one kind of community by another and (2) progressive changes in microbes, fungi, plants, and animal life, which may culminate in a community that changes little until the next disturbance.

1.3.1 Processes Affecting Survival

Survival depends on interactions between properties of the disturbance events and traits of organisms that allow them to avoid, resist, or respond neutrally or positively to disturbance impacts. Organisms may withstand disturbance by being in a protected location within the disturbed area (e.g., subterranean or under cover of lake ice) (Andersen and MacMahon 1985a) or being well adapted to withstand disturbance (Gignoux et al. 1997). Organism size can also foster survival; small macroalgae, for example, can better withstand the thrashing of intense wave action than can large algae (Blanchette 1997).

Some species may persist in a disturbed landscape by having either all or part of their populations away at the time of disturbance. For example, migratory birds and anadromous fish may be away from sites during disturbance and, upon their return, reoccupy the area if suitable habitat and food are present.

Despite apparently tight coupling of species-disturbance interactions, survival of individual organisms and populations is frequently a matter of chance. Nuances of site conditions, organism vigor, disturbance intensity at the site, timing of disturbance relative to the life history of the organism, and other factors can tip the balance of life versus death in ways that are difficult to anticipate.

1.3.2 Immigration, Establishment, and Site Amelioration

The early stages of succession are strongly influenced by persistence and growth of survivors; immigration, establishment, and growth of colonists; and interactions among these colonists. Mobility of organisms and propagules, as well as the conditions of the environment through which they move, affect dispersal patterns. Highly vagile organisms, such as those capable of flight and passive movement by wind, typically are first to reach disturbed areas distant from source populations. In contrast, low-mobility organisms, such as seed plants that lack structures for wind dispersal and animals which travel through soil, would be expected to slowly reach distant, disturbed sites. Many species with poor dispersal mechanisms can be transported great distances by hitchhiking in or on animals, moving in flowing water, or capitalizing on the influence of gravity. Dispersal is commonly thought to be determined by the distance to source populations, but complexities of disturbance processes and patterns and the state of the affected ecological system make such simplistic, distance-related interpretations unrealistic.

Once an organism disperses to a new location, its ability to establish, grow, and reproduce is determined by prevail-

ing climate, site conditions, previously established organisms, and the organism's own requirements and tolerances. For animals, the requirements for successful establishment are often expressed as adequate cover and food. Cover provides protection from physical stresses as well as a place to hide from potential predators. Plant establishment requires appropriate light, moisture, and nutrient levels for germination and growth.

Site amelioration is an important process that can involve changes to soil conditions, microclimate, and microtopography. Soil development is often an essential factor in succession, especially in the case of primary succession, where soil is initially of poor quality. Soil formation involves physical and chemical weathering of rocks and minerals, accumulation and decay of biotic material, establishment of a microbial fauna, and marshalling of any legacies of earlier soil on the site. The death or stress of biota in response to the disturbance may deliver a pulse of litter to the soil surface or within the soil via root death. As a site ameliorates, plants establish and spread, species interact, and a community develops. Animals are tightly coupled to plant composition or physiognomy, so their colonization frequently tracks the development of vegetation.

Humans can profoundly influence the course of succession in many ways, both intentionally and unintentionally. A common influence is the introduction of invasive, nonnative species, which can have far-reaching ecological and management repercussions. Disturbance commonly favors establishment of invasive species, but predicting the vulnerability of a system to invasion is still a challenge (Mack et al. 2000). Planting of native trees and stocking with native fish can profoundly alter community structure and function.

1.3.3 Concepts of Change in Ecological and Environmental Factors During Succession

Changes in ecological and environmental conditions are both consequences and determinants of the path of succession. Today, concepts of succession and disturbance ecology have reached the point where they are examined and modified through experimental and modeling approaches as well as by studies of ecological change imposed by major disturbance events.

1.3.3.1 Community Development Through Succession

Species richness, biomass, and structural complexity of communities increase during succession. Various types of interactions among species drive community development, and these processes may change in their relative importance over the course of succession. In some cases, one species is replaced by another over time in what is called the process of relay succession. In these cases, the change in species is as abrupt as the handing over of a baton from one runner to another (building

on the concepts of Egler 1954). Yet, such predictable and unidirectional transitions do not always occur.

In an attempt to advance understanding of succession, Connell and Slatyer (1977) proposed three models of mechanisms of succession, termed: facilitation, tolerance, and inhibition. These models describe the way in which species interact with their environment and with later-arriving species to either promote, hinder, or have minimal effects on the establishment and/or growth of some species and thus to shorten or lengthen the time to dominance by another species (Connell and Slatyer 1977). However, succession is highly variable; and in most cases, these three mechanisms, plus others, occur simultaneously during a successional sequence (McIntosh 1999). In addition to these models of succession, numerous species–species interactions, such as mutualism, predation, parasitism, and herbivory, help shape the pace and direction of succession.

Facilitation was first interpreted as the process of early successional species altering conditions or the availability of resources in a habitat in a way that benefits later successional species (Clements 1916; Connell and Slatyer 1977). For example, the first species to become established create shade, alter soil moisture, and ameliorate soil texture and nutrient conditions via decomposition of their parts and other processes. Commonly, nitrogen is a limiting factor in early successional stages, and the presence of plants with the ability to infuse the soil with nitrogen through association with nitrogen-fixing bacteria enhances soil development. Facilitation is now more broadly interpreted as positive interactions between species (Bruno et al. 2003) and as processes that improve a site's physical conditions (e.g., soil development) (Pugnaire et al. 2004). These beneficial interactions appear to be common under stressful environmental conditions (Callaway and Walker 1997).

In contrast to facilitation, the process of *inhibition* may slow or temporally arrest successional development (Grime 1977; Connell and Slatyer 1977). This process occurs when a resource, such as space, water, or nutrients, is so intensely used by one or more species that it is not available in life-sustaining quantities to other species. For example, following a mudslide along Kautz Creek on the flanks of Mount Rainier in Washington State, the depositional area was quickly colonized by an almost continuous mat of mosses and lichens. Germinating tree seedlings could not penetrate the mat and reach mineral soil, and thus tree establishment was inhibited for decades (Frehner 1957; Frenzen et al. 1988).

Tolerance refers to the situation where organisms best able to tolerate prevailing conditions are favored, but recognizes that prevailing conditions change with time. Under this model, later successional species are unable to become established without site amelioration by pioneer species that do not inhibit the later colonists (Connell and Slatyer 1977). A primary premise of the tolerance model is that later successional species can grow with lower resource levels than can earlier species and are better at exploiting limited resources. As later

successional species grow and produce progeny, they replace the earlier, less-tolerant species and become dominant. Thus, life-history characteristics are critical in determining the sequence of species replacements.

1.3.3.2 Biotic and Geophysical Forces of Succession

Drivers of disturbance and succession can be viewed as falling on a continuum of relative influence of geophysical forces (*allogenic* succession) versus biological factors (*autogenic* succession) (White and Pickett 1985). Where allogenic succession dominates, physical forces (such as chronic, secondary geophysical disturbances) override biological causes of succession. Autogenic succession is driven by intrinsic properties of a community and the ability of organisms to affect their environment, such as when certain species preempt sites, create shade, and alter soil structure and chemistry.

Patterns of water runoff, sediment transport, and other geophysical processes can change dramatically after severe landscape disturbance. Some processes alter site conditions in ways that prepare a site to experience other processes. Analyses of drainage basin evolution (Koss et al. 1994) and sediment routing following wildfire and forest cutting (Swanson 1981; Swanson et al. 1982b; Benda and Dunne 1997), for example, reveal sequential interactions among geomorphic processes in ways that are akin to facilitation in biotic succession.

Often, biotic and geophysical patterns of succession occur in parallel following severe disturbance and involve both positive and negative feedbacks:

- Episodic disturbances, such as landslides, can erase a decade or more of ecological response following the primary disturbance event.
- Development of vegetation and its associated litter layers and root systems can suppress erosion processes.
- In some instances, erosion of new deposits exposes buried plant parts in the predisturbance soil, thus favoring plant and animal survival and development of ecological interactions.

Recognition of the succession of ecological and geophysical processes in severely disturbed landscapes can be useful in interpreting the direction, rate, and cause of ecological responses to disturbance. Ecological response to severe disturbance is, in part, a function of the pace at which the landscape stabilizes geophysically to a point where biological response can proceed with vigor. For example, fish reproduction may not occur in a disturbed site because of physical instability that degrades spawning habitat or conditions required for egg development.

Secondary disturbance processes (i.e., those that are influenced by a primary disturbance) often play important roles in ecological change. Examples of secondary disturbances include the increased pace of lateral channel migration as a result of increased sediment load and precipitation runoff. This chronic disturbance repeatedly removes developing riparian vegetation.

1.4 Linking General Concepts and the Mount St. Helens Experience

The wealth of knowledge about disturbance, survival, and succession briefly summarized above and elsewhere (Pickett and White 1985; McIntosh 1999; White and Jentsch 2001; Walker and del Moral 2003) provides useful concepts for examining the initial effects and subsequent ecological and geophysical change at Mount St. Helens during and following the 1980 eruption. These science concepts are in continuing states of development and searches for generality (McIntosh 1999; White and Jentsch 2001). No single concept or theory is adequate to structure the scientific analysis or the telling of the highly multifaceted Mount St. Helens story. On the other hand, lessons from studies at Mount St. Helens have influenced the development of these topics.

The Mount St. Helens landscape and the lessons drawn from research conducted there have changed substantially during the quarter of a century since the 1980 eruption. Initial observations emphasized the nearly desolate character of the landscape, the importance of surviving organisms, factors influencing patterns of species dispersal and colonization, and community development. Some of these initial ecological responses have had lasting effects, but others of them proved to be transient. After 25 years, much of the landscape has filled with plants, and the once stark gray area has been transformed to mostly green. Extensive tracts of the most severely disturbed areas remain in early seral stages dominated by herbs and shrubs and will require several more decades before becoming closed-canopy forest, if they ever do. Numerous conifer saplings are present in all disturbance zones, and the development of forest cover is accelerating in many locations. By 2005, the ash-choked lakes and streams of 1980 glisten with clear, cold, well-oxygenated water and support biota typical of the region. The growth and spread of surviving and colonizing species during the first 25 years after the 1980 eruption have provided many new opportunities to address questions about succession, patterns of landscape response, and consequences of secondary geophysical processes. Even so, many questions regarding ecological responses to the 1980 eruption remain unanswered. Continuing change of the Mount St. Helens landscape may bring new answers and certainly will bring new questions about ecological responses to major disturbances.

1.5 Overview of Book

This book presents much of the existing research that explores succession, disturbance ecology, and the interface between geophysical and ecological systems at Mount St. Helens (see Figure 1.2). Chapters 2 and 3 review the geological and ecological setting before the 1980 eruption and the geophysical environments created by the May 18, 1980, eruption. Chapters 4 to 8 focus on the survival and establishment of plant communities across diverse volcanic disturbance zones. Chapters 9

to 14 consider responses of animal communities, in particular, arthropods, fish, amphibians, and small mammals. Chapters 15 to 18 discuss responses of four sets of ecosystem processes: the symbiotic relationship between mycorrhizal fungi and plants in soils, animal decomposition in terrestrial environments, effects of a nitrogen-fixing plant on soil quality and function, and the complex biophysical processes of lake responses. Chapters 19 and 20 synthesize changes that have occurred across land-management issues, species, ecological systems, and disturbance zones during the first quarter century after the 1980 eruption.

Together, these chapters provide an in-depth analysis of ecological patterns of response after the 1980 eruption of Mount St. Helens. Conventional terminology is used throughout the book (see the Glossary at the end of the volume), and throughout the book locations of the various research studies are shown

on a common reference map. A single bibliography for all chapters is at the end of the book. The major taxonomic source for species mentioned in the book is the Integrated Taxonomic Information System (<http://www.itis.usda.gov>). Additional information about the area and the research results is available at <http://www.fsl.orst.edu/msh/>.

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