Volcano Ecology: State of the Field and Contributions of Mount St. Helens Research

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Frederick J. Swanson and Charles M. Crisafulli

16.1 Introduction

The effects of volcanic eruptions on ecosystems have long interested ecologists. Pioneering studies at Katmai (Griggs 1918, 1922), Krakatau (Dammerman 1922, 1948; Docters van Leeuwen 1936), several volcanoes in the western United States and Mexico (Eggler 1941, 1948; Brattstrom 1963), Hawaiian volcanoes (Eggler 1971; Smathers and Mueller-Dombois 1974), and Surtsey (Fridrikssen 1975) identify fascinating ecological responses to a variety of volcanic disturbance processes. Many important contributions to this field of science have emerged since these early works, among them studies triggered by the 1980 eruption of Mount St. Helens. This eruption and the emergence of disturbance ecology as an important subdiscipline of ecology have helped propel development of the field of volcano ecology-the study of immediate effects of volcanic processes on ecosystems and the response of those ecosystems through the course of *succession*¹. Volcano ecology investigations have led to syntheses of studies focused on individual sites (e.g., Griggs 1922; Fridriksson 1975; Dammerman 1948; Thornton 1996; Dale et al. 2005a; DeGange et al. 2010) and comparing multiple volcanoes (e.g., Fridriksen and Magnusson 1992; del Moral and Grishin 1999; Thornton 2000, 2007; Dale et al. 2005a; Edwards 2005; del Moral and Magnusson

F.J. Swanson (🖂)

U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331, USA e-mail: fred.swanson@oregonstate.edu

C.M. Crisafulli

2014; Ruggiero and Kitzberger 2014; Crisafulli et al. 2015; Veblen et al. 2016).

The current state of global knowledge regarding volcano ecology provides a basis for evaluating the contributions of ecological research conducted at Mount St. Helens following the 1980 eruption. The work and findings to date range from case studies of ecological responses to an individual eruption to synthesis publications, including journal articles, books, book chapters, and reports. This literature reveals the broad scope of volcano ecology research by several aspects of its contexts, including (1) the relation of volcano ecology to allied fields of science, such as volcanology and disturbance ecology, (2) the global distribution of volcanoes and types of volcanism, (3) the diversity of biogeographic and climatic settings, and (4) societal aspects of volcanoes in terms of opportunities for ecological study, science outreach to the public, and implications for land management. This overview reveals common themes of analysis among the hundreds of studies, such as mechanisms of survival, importance of *biological legacies* from the pre-disturbance ecosystem, physiological sensitivity of organisms, site amelioration, processes of community assembly and succession, and biotic interactions operating in ecosystems influenced by contingencies and stochastic factors. In this chapter, we mention many of these phenomena but do not attempt a critical analysis and synthesis.

This chapter presents salient features of the developing field of volcano ecology based largely on assessment of the published literature and the global distribution of volcanoes that have erupted since 1883, when the eruption of Krakatau marked the beginning of ecological studies of recent eruptions. We first characterize volcano ecology in terms of the types of scientific inquiry involved: the volcanic, biogeographic, and climatic systems where volcanoes have been studied; and social settings of the volcanoes. Next we review the record of volcano ecology studies, noting their distribution among types of volcanic and biogeographic systems, and how the pace of this research, as measured by publication

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C.M. Crisafulli, V.H. Dale (eds.), *Ecological Responses at Mount St. Helens: Revisited 35 years after the 1980 Eruption*, https://doi.org/10.1007/978-1-4939-7451-1_16

¹Terms in *bold italic face* are defined in the glossary at the end of the chapter.

U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Mount St. Helens National Volcanic Monument, 42218 NE Yale Bridge Rd., Amboy, WA 98601, USA e-mail: ccrisafulli@fs.fed.us

records, has varied since 1883. A brief review of findings from work at many volcanoes reveals common lessons, despite the great variety of eruption types and affected ecosystems. Comments on the state of the science provide a basis for assessing how the work at Mount St. Helens has contributed to the emergence of volcano ecology. We conclude with suggestions for capitalizing on learning opportunities presented by ongoing research as well as future eruptions.

16.2 Settings of Volcano Ecology: Science, Geology/Volcanic Systems, Biogeography/Climate, and Society

16.2.1 Science Setting

To understand its scope, it is helpful to view volcano ecology in the context of the wide variety of disciplines, topics, and time scales involved. Ecological research on ecosystems influenced by volcanism encompasses numerous taxa, system types, and ecological processes across nearly all of the major biomes on earth (Crisafulli et al. 2015). Terrestrial and freshwater ecologists have tended to study initial effects of disturbances on ecosystems within a few days to a few years of an eruption and to track succession over decades to a few centuries. Soil scientists and geomorphologists are concerned about initial effects of volcanism, but also stretch their time scales of interest over millennia and beyond, sometimes using approaches based on the study of chronosequences and a wide array of dating techniques. Oceanographers examine "extremophiles" associated with the lightless environments of deep-sea vents to address a broad range of questions, such as the potential to find life on other planets and hypotheses about the origin of life. Paleontologists, geophysicists, and geochemists consider the likelihood of flood-basalt eruptions versus bolide impacts in triggering global extinction events over the past half billion years. In this chapter, we address only the interactions of terrestrial and, to a lesser extent, freshwater ecosystems at the time scales relevant to documenting immediate ecosystem response and to ecological succession spanning years to a few centuries following disturbance.

The field of volcano ecology has prospered during recent decades with the recent surge of interest in disturbance ecology, which addresses the roles of diverse disturbance processes in ecological systems (Pickett and White 1985; Turner 1987; Turner et al. 1997; Turner and Dale 1998; Peters et al. 2011). Ecological science has long involved the study of succession following disturbance, leading to some general findings. Spatial variability in intensity and severity of large disturbance events often leads to heterogeneous patterns of surviving organisms (Turner et al. 1998). When disturbance intensity is high, (a) initial density of organisms is low; (b) recovering patches may serve as foci for additional

colonization and expand spatially; (c) competition is less important relative to chance arrival in determining community composition; (d) community composition is not initially predictable; and (e) the rate of recovery of community composition is slow (Turner et al. 1998). In many types of disturbance processes that have been examined in the ecological literature, such as flooding, wildfire, windstorms, and insect defoliation, single disturbance types are involved. However, explosive volcanism adds complexities of multiple types and mechanisms of disturbance, and our review of several hundred publications on volcano ecology reveals a generally poor characterization of the volcanic disturbance types and mechanisms that altered the ecosystem, information critical to robust interpretation, especially for comparative studies.

Ecosystem interactions with volcanism make some distinctive contributions to disturbance ecology, partially because a critical feature of explosive volcanism is the involvement of several geophysical processes with varied properties as disturbance agents. The resulting mix of disturbance types in a single eruption event is unlike more frequent, single-process, nonvolcanic types of disturbances, such as wildfire, ice storms, and insect defoliation events. This complexity of volcanic disturbances in a single eruption fosters general thinking about multiple disturbance types and the importance of recognizing the mechanisms of disturbance within each disturbance type (Table 16.1). Our comparison of a sample of volcanic and nonvolcanic disturbance processes reveals that it is actually common for a single disturbance type to involve more than one mechanism and that volcanic disturbance types are more likely to include three or four mechanisms (Adams and Dale 1987; Turner et al. 1997).

The most immediate scientific approach to volcano ecology is undertaken during and immediately following an eruption. This can best be accomplished where a record of pre-eruption ecological conditions exists from earlier monitoring or studies, but such a record is rarely available. Rapid post-eruption assessments can provide much critical information that would be difficult to ascertain at a later time, such as identity of initial survivors and roles of transient refugia like snowbanks, factors that may have important long-term ecological consequences for disturbed systems. One-time sampling years to decades after an eruption can give a snapshot of then-current biological conditions, but critical information on ecosystem development is revealed only by assessments shortly after an eruption. It may be possible to gain a sense of the pace of ecological change-the development of the ecological complexity and successional trajectory-using a chronosequence approach in which biotic conditions are observed on substrates of different age, commonly referred to as space-for-time substitutions (Pickett 1989). This approach requires the assumption that the sites were similar before the eruption, were disturbed in the same way, and experienced similar ecological processes since the

Process type	Impact force	Abrasion	Heat	Erosion	Deposition	Canopy loading ^a
Volcanic						
Tephrafall	х	х			х	Х
Lava flow	X		X		X	
Blast PDC	Х	х	х		х	
Debris avalanche	Х	х			Х	
Lahar	х	х		х	х	
Pyroclastic flow	Х	х	X		Х	
Nonvolcanic						
Ice, wet snow						X
Wildfire			х			
Wind	х	х				
Landslide	Х	х		Х	Х	
Flood	х	х		х	х	

Table 16.1 Natural disturbance process types and physical disturbance mechanisms for a sampling of volcanicand nonvolcanic events. Capitalized and bold X denotes the possibility of especially high-intensity disturbance.

a"Canopy loading" refers to accumulation of tephra and precipitation in tree canopies, leading to canopy collapse under the weight of the load.

time of disturbance-assumptions that may not be valid. Another approach taken at a handful of volcanoes has been to establish a network of plots shortly after an eruption (days to months) and follow-up measurements at annual or some other increments over decades. Any of these approaches to timing of sampling can be taken in studies that are either narrowly focused or broadly interdisciplinary. Remote places, such as some oceanic islands, favor expedition-style visits (such as Surtsey, Kasatochi), which may foster interdisciplinary work. On the other hand, readily accessible places make possible near-continuous observations by teams with varying degrees of disciplinary diversity and collaboration. Some sites have been subjected to a blend of some repeated, annual sampling plus single or repeated, multidisciplinary pulses of effort-for example, Mount St. Helens (Dale et al. 2005b), Chaiten (Pallister et al. 2010), and Kasatochi (DeGange et al. 2010).

16.2.2 Geologic Setting of Volcanic Systems

Geologic settings of volcanoes vary greatly. They may be volcanic arcs associated with subduction zones in either marine (Aleutian archipelago) or continental margin (Andes, Cascade Range) settings, linear chains of volcanoes associated with hot spots in marine (Hawaii) or continental (Snake River Plain–Yellowstone) settings, linear vent systems associated with spreading centers (East Pacific Rise), or complex archipelagos related to hot spots associated with spreading centers (Galapagos, Iceland) (Fig. 16.1). The tectonic setting of volcanic systems influences the dominant style (explosive versus effusive), products, and frequency of eruptions (Siebert et al. 2015). There are two general types of eruption styles, explosive and effusive. Explosive eruptions occur when magma and solid rock material are violently fragmented and expelled from a vent by the tremendous force of expanding gases, which is common in volcanic chains associated with subducting tectonic plates of oceanic origin. Effusive eruptions, involving a steady flow of lava from a vent, are characteristic of oceanic ridge systems, as in the cases of mid-ocean ridges. Hot-spot volcanism has been responsible for the formation of island chains; the Hawaiian archipelago is a type example dominated by effusive eruptions. Intracontinental volcanic systems occur in conjunction with both hot spots (Yellowstone) and rift systems (East African Rift) where thick, silica-rich, continental crust contributes to highly explosive eruptions. Flood basalts are extremely voluminous and infrequent (nine events in the past 300 million years) and have profoundly altered the world's biota through periodic mass extinction events (Wignall 2005).

Water plays a critical role in many volcanic processes and is therefore an important factor in interpreting volcanic events and disturbance to ecosystems. Phreatic eruptions, debris avalanches triggered by sector collapse, and lahars are all critically influenced by the presence of groundwater and/or surface water. The water content of mobilized material influences runout and, consequently, the distance that volcanic disturbance processes can extend outward from the source. Large volcanic edifices tend to be water-rich because the orographic effect of the mountain entrains moisture from the atmosphere, and that moisture may be retained in the form of ice and snow at high elevation where eruptions commonly occur. Explosive eruptions can deposit fragmental ejecta over vast areas, potentially altering water runoff, sediment transport, river networks, and even climate (Pierson and Major 2014). Sediment deposition in channels and across floodplain and terrace surfaces disturbs in-stream and riparian ecosystems. This volcanic sediment



Fig. 16.1 Volcanoes listed in the Smithsonian Institution/US Geological Survey Global Volcanism Programs catalog that were reported to have erupted subaerially since 1883 CE, plotted on the World Wildlife Fund's map of terrestrial biomes of the globe. Volcanoes that have been the subject of published ecological study are symbolized by *black triangles*, those with no published studies by *white triangles*. (From Crisafulli et al. 2015).

may be stored and later remobilized, creating chronic or episodic disturbance for downstream ecosystems and human communities that may persist for decades.

The extensive reach of tephrafall, lahars, and other consequences of explosive volcanism can result in diverse ecosystems—such as desert, grassland, steppe, meadow, forest, lake, river, and marine systems—being affected by a single eruption. Single explosive eruptions often involve a half dozen processes; for example, the 1980 eruption of Mount St. Helens involved a major *debris avalanche*, pyroclastic density current (here referred to as the *blast PDC*), *lahars*, *pyroclastic flows, tephrafall*, and lava-dome growth (Lipman and Mullineaux 1981). A common feature of most of these processes is deposition of fragmental volcanic rock debris across the surrounding landscape. The thickness, texture, and temperature of materials and the force with which they are emplaced vary greatly among processes. Ecological effects of explosive events can range from benign to total obliteration; they may occur in quick succession; and their effects may overlap in extent, compounding effects on ecosystems. In contrast, effusive eruptions result in relatively slow flow of lava across the land surface, and the heat and resulting solid-rock deposit can eliminate preexisting biota and slow establishment of invading organisms.

Initial interactions among volcanic processes and biota are best interpreted by considering properties of individual disturbance types in terms of the mechanisms of each geophysical process that act as ecosystem disturbance agents (Table 16.1). Principal mechanisms involved in volcanic processes include deposition of volcanic material on vegetation and on the ground (burial); erosion of soil; heat; impact force (e.g., leading to toppling of trees); abrasion by flying, flowing, or falling rock debris and organic matter; and chemical pollutants (in rainwater, as aerosols, or in gaseous form). Individual volcanic processes may damage, kill, or utterly obliterate biota by combinations of these mechanisms.

Across eruptions the frequency, extent, and severity of ecological disturbance vary greatly among volcanic processes. The intensity of each disturbance type commonly decreases along the flow path and laterally away from the axis of the flow path of the process. Tephrafall is by far the most extensive (sometimes circum-global) and common volcanic disturbance process. Deposit thickness may exceed several 10s of m close to the vent, but over most of the depositional area deposit thickness is less than 1 mm. Lava flows are also very common and range widely in spatial scale, though they are commonly constrained in area (a few km²) and strongly influenced by topography, but they consistently cause severe damage to ecosystems and the resulting raw, stony landscape is slow to revegetate. Lahars are very common and can lead to severe disturbance of rivers and riparian zones, potentially extending 10s of km from volcanoes. Debris avalanches, on the other hand, are rather rare, and proximal zones of impact generally measure 10s of km² in extent and 10s of m in thickness, completely resetting terrestrial ecosystems and also creating new aquatic environments. PDCs include several types of high-intensity flow processes that consist of highly turbulent mixtures of fragmented rock and hot gas. These events are commonly associated with plinian and subplinian eruptions and are generated by a variety of mechanisms, such as dome collapse, column collapse, dome explosion, and lateral phreatic blasts. Generally, the zones of substantial ecological disturbance by these processes cover a few 10s of km², but the PDC associated with the Mount St. Helens 1980 eruption extended over several 100s of km². PDCs typically leave deposits only a few m thick or less, thus creating a landscape rich in biological legacies. Pyroclastic flows, a specific form of PDC, create high-intensity, high-severity disturbance with high temperature (300 to >800 °C), high velocity (up to 700 km h^{-1}), and highly variable deposit thicknesses (<1 m to 10s of m), and consequently few or no biological legacies survive.

16.2.3 Biogeographic/Climatic Setting

The geography of volcanoes and their environmental context strongly influence the types and pace of ecosystem response to disturbance. Historically active, terrestrial/subaerial volcanoes occur from 77.5° south (Mt. Erebus, Antarctica) to 71.1° north (Beerenberg volcano, Jan Mayen Island, Norway), spanning a wide range of biogeographic and climatic settings. Moist temperate and tropical regions are likely to support more rapid biomass accumulation, species assembly, and soil development in response to volcanic disturbance than are more arid and colder regions. The preponderance of volcanoes known to have been historically active is located in temperate and tropical settings, including volcanic chains associated with subduction zones tracing nearly

the entire length of the Americas, and the Southeast and East Asian volcanic chains (Fig. 16.1). The stature of these volcanic mountains orographically entrains precipitation, potentially adding to the wetness of their local and regional environments. For example, the continental–interior location of the East African Rift places it in an arid setting, but moisture from summer monsoons entrained by the topographic relief supports savannah and some forest cover. High-latitude volcanic landscapes such as Iceland, the Aleutians, and Kamchatka support tundra. A general point is that biomes and environmental settings differ in their regimes of native disturbance by nonvolcanic processes, which may add uncertainty to predictions of ecosystem response to volcanic disturbance (Paine et al. 1998).

The biogeographic context of an eruption-affected landscape also influences the geographic reach of nutrient fluxes and the dispersal of organisms and propagules, both locally and over vast expanses of the globe. Terrestrial and oceanic systems provide a striking contrast in limitations and opportunities for species and nutrient accrual. Newly emergent oceanic volcanoes (e.g., Surtsey) or severely disturbed islands (e.g., Krakatau) may experience very limited immigration of most terrestrial species that have to traverse great distances of open ocean (Fridriksson 1975; Thornton 1996). On the other hand, highly vagile organisms, such as many spider species, are an exception and quickly arrive at such sites in great numbers (Edwards and Thornton 2001). New islands can experience intense, locally derived nutrient subsidies from the marine system via nesting seabirds and congregations of large marine mammals on land (Sigurdsson and Magnusson 2010). Disturbed terrestrial sites and newly formed lakes and ponds, on the other hand, may be populated from adjacent areas but also benefit from long-distance dispersal via wind or from biotic vectors such as migratory birds and anadromous fish.

16.2.4 Societal Setting

The geographic distribution of erupting volcanoes, their eruptive products, and nearby human settlements profoundly affects hazards for human lives, property, and infrastructure, and also prospects for the pursuit of volcano ecology research and public education. A wide array of societal perspectives is relevant to volcano ecology: public education, assessment of economic impacts of eruptions, tourism, archaeology, art, literature, and film (Sigurdsson et al. 2015). Ecologists benefit where physical infrastructure (e.g., roads and trails), landowners, and administrators provide easy access to volcanic study sites. Eruption sites that include highly humanmodified landscapes obviously limit options for studying relatively pristine systems and may also reduce options for research because of limited access to privately owned property and increased potential for vandalism to study infrastructure and equipment. Even on public lands, such as parks and reserves, research opportunities may be compromised as the land and waterways are modified for hazard mitigation, planned and unplanned development, recreation, and ecosystem restoration. Intentional or inadvertent introduction of non-native species may also be an issue.

The capacity to support long-term volcano ecology research and interpretive programs for the public are key intersections of society and science, which vary widely from country to country. By communicating key lessons from ecological research at eruption sites, societies gain an appreciation of the geological forces that shape their wild and human-manipulated environments, as well as the stunning resilience of nature. Inspired by these powerful geological and ecological forces, the arts and humanities have helped shape public perception (Goodrich et al. 2008; Sigurdsson 2015; Sigurdsson and Lopes 2015). Such lessons also have pragmatic value for both individuals and societies in understanding the consequences of eruptions for important resources that humans rely upon, such as potable water, livestock, food crops, and forest and range products. A critical feature of research capacity is embodied in academic institutions, national research organizations, and science-funding agencies in a societal context that values natural resources, the environment, and science. Inventory and monitoring of environmental conditions, such as vegetation surveys and long-term gaging of streamflow and measurement of sediment yield, provide extremely valuable background information for interpreting effects of new landscape disturbances, including volcanic processes. In an extreme case of social factors affecting opportunity for volcano ecology research, areas of civil unrest and military exclusion zones (e.g., Kamchatka during the Cold War) may preclude access to interesting research opportunities.

16.3 Characteristics of Volcano Ecology Studies: Volcanoes, Affected Biomes, Research Themes, and Findings

16.3.1 Historically Active Volcanoes

To place the progress and biogeographic coverage of volcano ecology research in context, we examine records of the volcanoes that have experienced recent eruptions, the affected proximal terrestrial biomes, and the geographic and temporal distributions of published volcano ecology studies, drawing on the compilation and initial analyses of published literature referenced in Crisafulli et al. (2015) (Figs. 16.1, 16.2, and Table 16.2). We consider only volcanoes with documented eruptions beginning in or after 1883, when the major eruption of Krakatau launched the first such studies; we refer to these volcanoes as "historically active." We consider only subaerial eruptions, because the locations and eruptive history of submarine volcanoes are poorly known and they have not been a focus for most ecologists. Historic eruptions have occurred at 404 (26%) of the 1551 volcanoes in the Smithsonian–US Geological Survey catalog of volcanoes of the world (http://www.volcano.si.edu/search_volcano.cfm, accessed 20 March 2014).

Only 44 (11%) of these 404 historically active volcanoes have been studied by ecologists, who report that work in a total of 423 papers (Crisafulli et al. 2015). Although this record of published volcano ecology studies is incomplete, particularly for vegetation, it is sufficient to draw some useful conclusions. The limited number of recent eruptions that have been studied reflects several types of decisions by ecologists. For example, the most intensively studied eruptions appear to be high-magnitude eruptions that attract global attention, stimulating commitment of individuals, institutions, and science communities to undertake research. The Volcano Explosivity Index (VEI), based on the volume of ejected material and eruption column height, is a useful index of eruption magnitude (Newhall and Self 1982). One unit of the 0-8 VEI ranking scheme represents approximately a tenfold difference in eruption frequency, so an event with a VEI of 3 is 100 times more frequent than one with a VEI of 5. Ecologists have given disproportionate attention to major, explosive eruptions: 12 of the 44 studied events have the relatively infrequent VEI ranks of 5 or 6, whereas 22 eruptions of VEI of 1-3 have been the subject of volcano ecology publications (VEI values for each volcano are from the Smithsonian Institution Global Volcanism Program webpage [Venzke 2013]).

Despite the nonrandom, nonsystematic sampling of volcanoes by ecologists, the studied eruptions have occurred at volcanoes that represent a great variety of geophysical settings. Magma types range from low-silica basalt, characterized by nonexplosive eruptions (lava flows), through andesite and dacite rock types of increasing silica content, to the most silica-rich volcanic rock type, rhyolite. The latter three rock types commonly produce explosive eruptions. The volcanic processes that acted as disturbance agents in the studied ecosystems are broadly representative of the suite of important processes, including both violent events (explosions, pyroclastic flows, debris avalanches, lahars) and quiescent ones (lava flows, tephrafall). The representation of processes in the volcano ecology literature roughly follows their occurrence and extent, with tephrafall and PDCs being most common, lava flows and lahars intermediate, and debris avalanches and chemical toxicity least common. Tectonic settings of the 44 studied sites include volcanic arcs associated with subduction





Table 16.2 Distribution and number of volcanoes by biome type, with biome area, and associated number of volcano ecology studies with three ranks of study intensity: H (high-intensity), continuous, intensive, multiple topics/taxa; M (medium-intensity), several samplings over time, multiple topics/taxa; L (low-intensity), single sampling, limited subject matter.

	No. active volcanoes	Area (10 ⁶ km²)	Volcanoes/biome area (no./10 ⁶ km ²)	Number of volcanoes with ecology studies, by study-intensity category			Volcanoes
Biome				Н	М	L	studied (%)
Tropical forest	175	24.08	7.27	1	5	9	8.6
Temperate forest	63	16.90	3.73	1	3	8	19.0
Boreal forest	49	15.13	3.24	1	0	2	6.1
Tundra	39	11.65	3.35	0	1	5	15.4
Grassland/shrubland	34	35.99	0.94	0	0	4	11.8
Desert	23	27.89	0.82	0	0	1	4.3
Mediterranean	10	3.22	3.11	0	0	3	30.0

The volcanoes tallied are reported in the Smithsonian Institution/US Geological Survey Global Volcanism Program catalog reported to have erupted since 1883, excluding those noted as "submarine." Locations of these volcanoes were plotted onto the World Wildlife Fund's (WWF) map of terrestrial biomes of the globe. We combined some of the 14 biome types in the WWF system (e.g., three types of tropical and subtropical forests are shown as one, and four types of grassland/shrubland are combined), and several involving very small numbers (<10) of volcanoes and/or small area are not reported (flooded grasslands, mangrove, lake, and rock/ice). The Mediterranean type refers to Mediterranean forest, woodland, and shrubland. For volcanoes designated as "ocean" biome, but not "submarine," we assigned a terrestrial biome type based on published ecological literature from the volcano or surrounding area, web-based searches on vegetation of the target area, and visual inspection of Google Earth imagery (From Table 73.2 in Crisafulli et al. 2015).

zones (33), oceanic rift zones (e.g., Surtsey) (7), and intraplate volcanoes in oceanic contexts (e.g., Hawaii) (4). Most of these volcanoes (26) are in continental settings, and the others are islands of single volcanoes that existed before the studied eruptions (10), part of islands composed of more than two volcanoes (5), and only three are on islands newly emerged from the sea (2) or a lake (1). Despite their rarity, these three cases of entirely new subaerial volcanic substrates have received a great deal of study (Anak Krakatau, 41 published papers; Surtsey, 27; and Long Island, 11), in part to explore the theory of island biogeography, which makes propositions about species diversity in relation to island size and isolation (MacArthur and Wilson 1967).

16.3.2 Affected Biomes

To provide a biogeographic perspective on the global distribution of volcanoes that have erupted since 1883 and also those that have received study by ecologists, we examine these volcanoes in the context of major terrestrial biomes of the world, as defined by the World Wildlife Fund (http://www.worldwildlife.org/publications/terrestrial-ecore-gions-of-the-world, accessed 2008). These biomes vary in extent by more than an order of magnitude, and a significant sample (at least 10) of the historically active volcanoes occurs in each biome (Fig. 16.1, Table 16.2). Both the abundance and density of volcano ecology studies vary among terrestrial biomes (Table 16.2) (Crisafulli et al.

2015). Biomes with the highest number of studied volcanoes are tropical (15) and temperate (12) forest biomes, and biomes with the greatest coverage (percent of recently erupted volcanoes studied) are Mediterranean (3 of 10, 30% of recently erupted volcanoes studied) and temperate forest (12 of 63, 19%) biomes. Two of the three most intensively studied volcanoes occur in forest biomes-Krakatau in tropical forest, Mount St. Helens in temperate forest. Although based on its latitude Surtsey, the third, is in the boreal forest biome, its potential natural vegetation is mesic grassland with herbs, presumably owing to its oceanic setting (Borgthor Magnusson, personal communication). On an area basis, the tropical forest biome is more than twice as densely populated with active volcanoes as any other biome, whereas temperate and boreal forest, Mediterranean, and tundra biomes have quite comparable densities of active volcanoes.

The types of volcanic processes involved in an eruption strongly influence the distance that disturbance effects can reach, hence types of biomes that can be affected. Eruptions interact with proximal ecosystems via flowage processes, such as lahars, lava flows, and PDCs, which can extend 10s of km from the source vent. Effects of tephrafall and aerosol deposition can be acute proximally but can also extend to much greater distances, even around the globe, affecting ecosystems dissimilar to the proximal biomes. For example, mid-latitude, explosive eruptions of volcanoes in the Americas deliver tephra to distant grassland/shrubland and desert biomes, arid ecosystems lying in the rain shadows of volcanic chains located in forest biomes. Many of the volcanoes in East Asia and the Aleutians deliver tephra to proximal marine environments; some tephrafall from eruptions elsewhere commonly reaches more distant marine environments. More generally, Ayris and Delmelle (2012, p. 1927) note that, "tephra fallout across the globe may primarily fall into the ocean and mostly into coastal waters."

16.3.3 Volcano Ecology Studies: Topics and Timing

The publication record varies greatly in frequency, continuity, and thematic breadth of ecological study at the 44 volcanoes. Following Crisafulli et al. (2015), we rank study intensity for each volcano in three categories: (1) high-sustained (although it may be episodic), intensive, multiple topics/taxa; (2) moderate-several samplings over time, multiple topics/taxa; (3) low-single sampling, limited subject matter. (Table 16.2). As Crisafulli et al. (2015) report, only three volcanoes have the highest study-intensity ranking: Krakatau (1883), Surtsey (1963), and Mount St. Helens (1980). Dates noted are the initial eruptions in the study period. Each of these volcanoes erupted in subsequent years. but not all eruptions received ecological study. Several sites of current, substantial study may shift from the moderate to the high-intensity category if studies are sustained beyond the initial flush of excitement, for example, Chaiten (2008), Kasatochi (2008), and Cordon Caulle (2011). Most of the studied, recently active volcanoes (32 of the 44 volcanoes), have been the subject of only low-intensity ecological investigation.

Volcano ecology studies have substantial similarity in terms of topics and taxa but also some instructive variation (Crisafulli et al. 2015). Among topics of inquiry, the assembly of biological communities and the factors influencing both the pace and compositional pattern of this process have been dominant themes of study. Volcanoes with published studies of animal response (30 of the 44 recent eruptions) exceed those with studies of plant response; only 24 of the studies and 11 of the volcanoes incorporated both plant and animal response. Of the 302 publications on animal response to eruptions, 47% concern invertebrates and 42% vertebrates, and only 10% of papers concern both vertebrates and invertebrates (Crisafulli et al. 2015). Terrestrial arthropods, birds, and mammals have been common post-eruption faunal taxa studied, perhaps because these organisms are broadly distributed across biomes, play numerous roles in ecosystem functioning, are generally well known, and serve as good barometers of ecological response to disturbance. Arachnids and aquatic arthropods are next-most-common subjects of study. Several other taxonomic groups, such as porifera, cnidaria, and zooplankton, have been subjects of only a handful of studies. Plant survival and subsequent successional processes have been common topics of study, perhaps in part because vegetation is at the base of most food webs, plants are rooted in place and thus are very tractable, and vegetation is well documented to exhibit succession, a process of great interest to many ecologists.

We examine the timing of eruptions of studied volcanoes and related ecology publications by creating a timeline beginning with Krakatau in 1883 and ending with Cordon Caulle in 2011 (Fig. 16.2). The pace of eruptions studied increased from one per 2.5 years in the period 1883–1920, to one per 2 years in 1942–1970, to about one per year for the periods 1988-1995 and 2008-2011. It is not clear to us why there appears to be a brief hiatus in 1996-2007, when no eruptions of volcanoes that had not previously erupted since 1883 triggered publication of volcano ecology studies. The case of periodic eruptions from a single volcano attracting volcano ecology research in the study period has been rather rare, although Mauna Loa and Kilauea in Hawaii, Arenal, and Long Island are good examples where this occurred. The timing of publications after eruptions includes several types: the quick response followed by persistent study, exemplified by the Surtsey and Mount St. Helens cases; single or small numbers of studies that lag the eruption by short or long periods of time, such as Irazu and Fernandina; or a pulse of activity that lags the eruption by many decades, as in the case of Krakatau. Overall, the number of published studies picks up greatly since 1980, with 112 (SE 22.8) publications per decade in 1980-2010 (only 30.3, SE 6.5, per decade excluding Mount St. Helens and Krakatau), compared with 8 (SE 2.0) publications per decade for 1910–1980. Note that all the publications in the period 1883-1950 came from Krakatau, Novarupta, and Paricutin alone.

Human intervention in post-eruption landscapes and waterways may affect ecosystem responses and, therefore, volcano ecology research; however, literature on this topic is scarce (but see Franklin et al. 1988; del Moral and Grishin 1999; Dale et al. 1998, 2005c; Titus and Householder 2007; del Moral and Magnusson 2014; Dale and Denton, Chap. 8, this volume; Karr et al., Chap. 9, this volume). Land management objectives of volcanically disturbed areas are wide ranging and may call for actions such as erosion control on hillslopes and along rivers; removal of damaged trees, with subsequent replanting and fertilization to promote plant growth; fish stocking; and cessation of hunting. Lakes and ponds created by eruption processes are sometimes modified to prevent catastrophic failure of natural dams formed by landslides or deposits of other origins that could result in loss of life and property. Such situations have warranted engineered outlets that can compromise ecological research opportunities. Similarly, rivers flowing through volcanic deposits may carry exceedingly high sediment loads, prompting construction of sediment-retention structures to reduce downstream flood hazards or sediment deposition that interferes with river navigation and associated commerce. These structures and others designed to divert lahars from developed areas downstream may limit post-eruption ecological processes and research opportunities. Arguments about these practices are commonly rooted in competing world viewsone holding that nature exists to serve humans, the other that sees the natural world as having intrinsic value independent of humans, in which it is often better to let natural processes take their course. Site manipulation for recreation, public education, and even research itself also alter the landscape, possibly precluding or inhibiting the progress of natural processes.

16.3.4 Volcano Ecology Research

Below we briefly describe key findings from work at volcanically disturbed sites. The topics are ordered to roughly follow the sequence of phenomena over time and their relative frequency in the literature. The first stage of inquiry concerns initial interactions of the primary disturbance processes and biota and between geological and ecological research approaches and objectives—for example, how geologists use damage to biota to interpret geophysical processes and how ecologists use understanding of geophysical processes to interpret biotic responses at site and landscape scales. Ecologists have focused on numerous, often interrelated, themes addressing longer-term plant succession, animal community assembly, nutrient accrual, and the much more protracted processes related to soil genesis.

16.3.4.1 Research Themes at the Geology– Ecology Interface: Immediate Interactions

Generally, ecologists have poorly described the specific types, intensity, and spatial extent of the volcanic disturbances that have affected the sites they studied. In some cases, geologists provide detailed descriptions of geophysical processes and deposits in terms that set a framework for subsequent ecological investigations (at Surtsey and Mount St. Helens, among others). The common disconnect between geologists and ecologists may be related in part to the complexity of volcanic disturbance processes and the arrival of ecologists at eruption sites after some time has elapsed. This limits communication between geologists and ecologists and also allows time for changes in the volcanic deposits and the biota, possibly obscuring some of the interactions. **Table 16.3** Observations of damage to organic matter used to interpret properties of geophysical processes that imposed one or more disturbance mechanisms on terrestrial ecosystems. All references concern the 18 May 1980 eruption of Mount St. Helens and were published in Lipman and Mullineaux (1981).

	Observation of		
Process/zone	organic matter	Mechanism	Reference
Scorch/ standing dead forest	Melting of cuticular waxes on conifer needles	Heat	Winner and Casadevall
PDC/ blowdown forest	Color, smell, flexibility	Heat	Banks and Hoblitt, Moore and Sisson
PDC/ blowdown forest	Tree-fall arrangement	Impact	Kieffer
PDC	Fragmentation, bark/wood removal	Impact, abrasion	Hoblitt et al., Waitt
Debris avalanche	Fragmentation, tree-fall arrangement	Impact, abrasion	Voight et al.
Lahar	Bark/wood removal, tree-fall arrangement	Impact, abrasion	Janda et al.

PDC: pyroclastic density current.

Volcanic and associated hydrologic processes damage vegetation, leaving evidence that geologists can read to help interpret properties of geophysical processes. Examples are widely scattered in the literature, and the 1980 eruption of Mount St. Helens offers a particularly important case where dozens of volcanologists conducted detailed studies, often drawing on evidence recorded by vegetation damage observed within days or weeks of the eruption. The US Geological Survey's initial synthesis of the eruption (Lipman and Mullineaux 1981) provides many examples that capitalize on the rich diversity of geophysical processes and the characteristics of vegetation on the land at the time of the eruption (Table 16.3). Observations of disturbance by mechanisms of abrasion, heat (e.g., charring), and impact force recorded in tree-fall arrangement informed analysis of the PDC (lateral blast), lahar, and debris-avalanche processes. Even before the 1980 eruption, vegetation was used in unraveling the earlier eruptive history detailed in part through radiocarbon dating of organic matter killed at the time of emplacement of deposits and observations of charred wood used to distinguish hot from cold flowage deposits (Mullineaux and Crandell 1981).

Interpretations of initial disturbance caused by eruptions need to be founded on understanding of interactions of properties of the affected biota with properties of the geophysical processes and eruptive products. Nuances in the characteristics of a disturbance type can yield surprisingly different degrees of severity to biota. The 2008 Chaiten and 2011 Cordon Caulle eruptions, for example, both deposited tephra



Fig. 16.3 (a) Canopy abrasion by lithic gravel tephra at Chaiten volcano; (b) canopy litter (foliage, twigs, ephiphytes) deposited in the basal layer of lithic gravel tephra deposit at Chaiten volcano—samples of tephra deposits on white sheets (left to right) are from 0-5, 5-10, and 10-15 cm above pre-eruption ground surface and dark material is organic matter; (c) lack of canopy abrasion or limbfall by 50 cm of pumiceous tephra deposition at Cordon Caulle volcano; (d) presence of the understory plants *Drimys andina* in growth position buried in 35 cm of pumiceous tephra at Cordon Caulle volcano; (e) high concentration of fallen limbs interpreted as resulting from deposition of fine tephra in the forest canopy, possibly soaked by rain, leading to sufficient weight to cause limbfall at Chaiten volcano; (f) bigleaf maple (*Acer macrophyllum*) with foliage amid killed conifers in the standing dead forest zone of Mount St. Helens in 1980 (USDA Forest Service) (Photos: **a** J. Jones; **b**–**f** F.J. Swanson).

in Chile's Valdivian rainforests, but with different effects depending on particle size and density as well as deposit thickness. A distinctive, single rain of lithic gravel tephra (bulk density >2.0 g cm⁻³) at Chaiten (the beta layer of Alfano et al. 2011) severely abraded the tree canopy (Fig. 16.3a), depositing foliage and canopy epiphytes in the basal 5-8 cm of tephra deposits (Fig. 16.3b) (Swanson et al. 2013). In contrast, several 10s of cm of low-bulk-density, pumiceous lapilli tephrafall at Cordon Caulle did not abrade the canopy (Fig. 16.3c), failed to produce a concentration of organic matter in the lower part of the tephra profile, and gently buried perennial, understory plants with green foliage in growth position (Fig. 16.3d) (Swanson et al. 2016). At Chaiten, >15 cm of fine tephra (ash) deposition, possibly combined with interception of rainfall, triggered canopy damage when excessive weight in the canopy caused extensive breakage and delivery of limbs to the forest floor

(Fig. 16.3e) (Swanson et al. 2013). Both tree phenology in relation to the season when an eruption occurred and the capacity of damaged trees to sprout new limbs and foliage can strongly influence survival after scorching disturbance. In the 110-km² standing dead forest zone at Mount St. Helens, for example, all conifers were killed, but a bigleaf maple (*Acer macrophyllum*) had not yet burst bud by the 18 May eruption, so it survived (Fig. 16.3f). Several common tree species in the Valdivian rainforest, in contrast, have the capacity to sprout after disturbance by scorching, but sprouting occurs mainly from major limbs and the bole where the bark is thick enough to protect buds from heat damage.

16.3.4.2 Role of Biophysical Legacies

Ecologists have long known that components of the predisturbance ecosystem that remain after a disturbance can greatly influence the pace, pattern, and direction of ecological response-the course of secondary succession. Because explosive volcanism involves many geophysical processes, and these processes occur as intensity gradients along flow and depositional paths, the type, amount, and spatial distribution of biophysical legacies are commonly present and readily identifiable in post-eruption landscapes. The 1980 eruption of Mount St. Helens galvanized the study of biophysical legacies, as findings from early research there formalized many ideas that were more loosely defined in previous decades. Chief among these ideas is the widespread importance of surviving organisms, propagules, and other organic matter, even at sites that at first appear to have complete mortality. Legacies occur in many circumstances, such as under snow and ice, and within soil, sediment, and decomposed logs. In some cases it may be years before processes such as erosion of new deposits liberate surviving organisms and make pre-eruption soil available to support new life. Biological legacies can profoundly influence the pattern and pace of succession, because they can provide local sources of propagules rather than relying solely on dispersal from distant source populations. Legacies may also provide suites of resources for recolonizing and newly colonizing species, such as food and cover for animals, and safe sites, higher moisture retention, shade, and nutrients that facilitate establishment under harsh environmental conditions (e.g., nutrient-impoverished substrates). However, in many cases organisms may survive the primary disturbance but then fail to persist on the site because of limiting resources, inhospitable environmental conditions, predation, or secondary disturbances, which commonly increase after severe site modification.

16.3.4.3 Plant Succession

A primary focus of ecologists across numerous volcanic settings has been tracking plant species accrual and changes in community structure (composition, richness, and abundance) through time at eruption sites. This work has included classic vegetation science as well as novel experimental work aimed at teasing out the underlying mechanisms causing the observed patterns. Most volcano ecology succession work has adopted a plot-based approach at relatively fine spatial scales $(0.25-500 \text{ m}^2)$, and these plots are revisited through time to depict the sequence of ecological change. Some of these studies stand as excellent examples of plant responses to disturbance and are widely cited throughout the broader successional literature. Successional development on disturbed sites requires dispersal of seeds and spores from source populations and the amelioration of environmental conditions by many mechanisms, including weathering of inorganic substrates, accumulation of organic matter, and development of biotic structures that serve as habitat for animals. Under primary-successional scenarios, plant community development

may be slow and strongly influenced by stochastic processes and contingencies, such as arrival sequence. In contrast, when surviving vegetation is abundant and widespread, vegetation development may proceed quickly and be more deterministic. Del Moral and Magnusson (2014), for example, found that plant species richness in cases of primary succession at Mount St. Helens plateaued in the second decade post-disturbance but cover continued to gradually increase at many sites over longer periods. The more remote, insular, and higher-latitude Surtsey volcano had rather stable richness by the fourth decade at many plots.

16.3.4.4 Animal Community Assembly

Animal ecologists have a long and rich history of describing arrival and accrual of animals, both vertebrates and invertebrates, at eruption sites. In some cases, such as at Krakatau, this work has been accomplished by periodic expeditions to sites where animal taxa are cataloged and compared to assemblages from earlier post-eruption trips. Such investigations appear to have rarely used plot- or transect-based sampling design. In contrast, at a few eruption sites, most notably Mount St. Helens and Surtsey, ecologists arrived shortly after the site was created (Surtsey) or disturbed (Mount St. Helens) and established networks of plots and transects where a diverse array of animals has received detailed and repeated measurements (annually) for decades. Community assembly proceeds at a pace set by extent of survivors and proximity of source populations. In a review of findings from eruptions at seven volcanoes, Edwards (2005) notes rapid accrual of the "aerial plankton" of arthropods adrift on the winds, birds, and other highly mobile organisms. He comments on "pioneers gaining early entry, transients establishing an early beachhead, and permanent colonization proceeding from these sites" (Edwards 2005, p. 268). Across a volcanic disturbance gradient at Mount St. Helens, the pace of small-mammal community assembly was strongly influenced by residual mammals and the amount of living and dead vegetation present in the posteruption landscape (Crisafulli et al. 2005). For highly mobile taxa, like birds and bats, development of suitable habitat appears to be the single most important factor determining both the rate and pattern of species establishment. Number of bird species climbed through three decades post eruption at Mount St. Helens and at a higher rate than at Surtsey, which appears to have plateaued in the fifth decade (Crisafulli et al. 2015). These two cases also reveal complexities of trajectories of species assembly, such as (1) the role of canopy closure in abruptly reducing plant species diversity after 15 years in some environments at Mount St. Helens; (2) the abrupt increase in bird species at Mount St. Helens in response to habitat structure provided by shrubs and tree saplings; and (3) after 20 years at Surtsey, the effects of nesting seabird colonies in increasing nutrient supply and, thereby, plant accrual and spread (Sigurdsson and Magnusson 2010).

16.3.4.5 Biotic Interactions

Because biological populations are typically reduced or more rarely extirpated during eruptions, in the first years after a volcanic event, ecosystems are rendered relatively simple. Biotic interactions are likely to be more apparent, be unusually strong, and become important in allowing affected systems to initiate biotic assembly, as by mutualism. These mutual interactions are important because of the poor nutrient status and water-holding capacity of volcanic deposits and are therefore of particular interest to ecologists. Examples of mutualistic relationships include those between nitrogenfixing bacteria and plants, and certain fungi associated with the root systems of plants, called mycorrhizae (see Allen et al., Chap. 11, this volume) in which the plant provides carbon to the fungus, and the fungus supplies the plant with otherwise-limited nutrients, such as phosphorus, along with water. Plant and animal interactions, both positive and negative from a plant perspective, have been reported to be important in volcanic landscapes (Andersen and MacMahon 1985; Che-Castaldo 2014). Herbivory by both ungulates and insects has strongly influenced plant populations and community structure, and seed and spore dispersal by animals has been important for the arrival at eruption sites of plants with poor dispersal mechanisms. Animals influence plant communities by trampling and burrowing (bioturbation), as well as depositing nutrients in the form of urine and feces.

16.3.4.6 Nutrient Inputs and Soil Genesis

Ecologists have been quick to note that volcanic deposits are nutrient impoverished, typically devoid of plant-available nitrogen as well as carbon. The source, accumulation rates, and concentrations of these essential building blocks for ecosystem development have been studied in the context of both oceanic volcanic islands (e.g., Surtsey, Krakatau, San Bernardino) and in continental settings, such as Mount St. Helens. The vectors leading to nutrient enrichment of volcanic deposits can be as varied as aerial fallout of arthropods, plants and their nitrogen-fixing bacterial symbionts, and development of seabird colonies on islands with associated marine-derived guano. In areas with high mortality of trees, remaining boles and branch systems provide nest and perch sites that draw birds and mammals that enrich the site through uric acid/urine and fecal inputs. These animals also deposit seeds and spores that initiate new plant growth. Eventually dead trees decompose, providing a "time-release" source of carbon and increasing the water-holding capacity of the volcanic deposit. Surviving

vegetation provides nutrient inputs through litterfall and by snaring wind-blown particles. Longer-term soil genesis processes have been investigated on the Hawaiian Archipelago, among other locations.

16.4 Discussion and Conclusions

16.4.1 Status of Volcano Ecology: A Global Perspective

The pace of volcano ecology research has accelerated over recent decades as the growing body of work calls attention to its value and provides concepts to be tested with study of new eruptions. The pace of study of new volcanic eruptions has increased from one published study per 2.5 years in 1883–1920 to one per year in recent decades. A wide array of biomes, taxa, and ecological processes has been studied around the globe. The studied volcanoes represent a wide range of tectonic settings, biogeographic contexts, volcanic processes, magma composition, and properties of deposits.

The field of volcano ecology is still in an early stage of development. Much of the work has been opportunistic, incomplete in coverage of eruptions, spotty in terms of taxonomic coverage, and lacking in standardized protocols for research approaches. Sustained commitment to study at individual locations has been rare, and, where it has occurred, it is a mix of personal and institutional commitments. However, there have been some notable exceptions, such as the use of common sampling protocols at Mount St. Helens and several Chilean eruption sites; the use of systematic, multidisciplinary planning of campaigns at Krakatau and Kasatochi; and the sustained commitment to sampling at Surtsey and Mount St. Helens. The high incidence of studies in Mediterranean and temperate forest biomes suggests that research potential is influenced by proximity of academic and governmental researchers to recently active volcanoes and, thereby, proximity for governmental investment in research and infrastructure. On the other hand, researchers have conducted studies at very remote volcanoes, but this work has been largely implemented and financed by wealthy nations (Iceland, Japan, the Netherlands, the United Kingdom, and the USA). The tendency for studies to occur at sites of major (high-VEI) eruptions reflects the interesting questions that can be addressed after large, complex eruptions, such as those producing conditions for primary succession, and also the greater public interest and economic and social effects, which may make it easier to secure funding for studies.

Efforts to provide a spatial or geographic framing for volcano ecology studies have taken several forms across the published record of research. Some studies and whole research programs have adopted useful "disturbancegradient" designs using at least two approaches: (1) study sites located along a gradient of disturbance severity (proportion of organisms killed by the primary disturbance event), regardless of the disturbance type; and (2) study sites on a gradient of disturbance intensity (physical force exerted on an ecosystem by a single disturbance type or mechanism, such as thickness of tephrafall deposits). A set of core studies at Mount St. Helens, for example, has been arrayed along a gradient of primary disturbance severity ranging from thick, initially sterile, pumiceous pyroclastic-flow deposits to thin tephrafall deposits (several chapters in Dale et al. 2005b). Examples of studies along a gradient of disturbance for a single disturbance type include effects of tephrafall depth on forest understory vegetation (Antos and Zobel 2005), tephra effects on boreal forests (Grishin et al. 1996), and variation in abrasion of vegetation and depth of deposits along lahar flow paths (Frenzen et al. 2005). However, many of the volcano ecology studies we have reviewed do not clearly describe the volcanic disturbance processes that affected study sites and do not place the sites in the larger pattern of the disturbances, which limits interpretation of findings.

We note, however, a near absence of landscape-scale studies that move beyond plot systems and gradients to address large-scale vegetation patterns and the interplay with secondary disturbances (e.g., erosion and deposition during major floods). This work would occur at a scale embracing multiple disturbance types and a sampling of ecosystem types. Such an approach is necessary to test hypotheses about the relative importance of movement into a disturbed area from the edge of the disturbance zone or outward from hot spots of biological legacies within the disturbance zone. Relevant observations (Adams et al. 1987; Lawrence 2005) offer some starting points for this work at Mount St. Helens.

Unlike the field of volcanology, which has established dozens of volcano observatories in many countries since the 1980 eruption of Mount St. Helens, no counterpart ecological observatories focus on volcanoes. The major motivation for volcano observatories is the great risk to public safety posed by eruptions, which justifies the expense. However, volcano ecology studies also serve society by providing information that can be used to anticipate effects of eruptions on the landscape around them, near and far, and what the prognoses are once an eruption occurs, including the potential consequences for a suite of factors of societal importance such as natural resources, agriculture, water, and infrastructure (e.g., transportation systems). Furthermore, volcanoes provide one endpoint in the continuum of large, infrequent disturbances from natural to wholly anthropogenic, and thus can inform ways to formulate and address management goals in the face of disturbances (Dale et al. 1998; Turner and Dale 1998).

In some respects Mount St. Helens and Surtsey have become volcano ecology observatories, with sustained, dedicated staff, an ecological monitoring program, complex portfolios of research activities, and in the case of Mount St. Helens, intensive public outreach.

16.4.2 Mount St. Helens in the Global Context of Volcano Ecology Research

Mount St. Helens has been an important contributor to the field of volcano ecology, as a result of a special combination of circumstances. The major eruption involved diverse processes, which offer a wide array of study opportunities. Precursor studies provided in-depth understanding and knowledge of volcanic and ecological historical settings, giving a strong frame of reference for assessing disturbance effects on ecosystems. Several months of precursor volcanic activity drew the attention of a large, interdisciplinary, regional and national science community that stood ready to take on the opportunity provided by the eruption. Immediate, intensive geological investigations led by the US Geological Survey gave the ecological science community a thorough interpretation of the complex eruption, which formed the template for ecological investigations that followed. Access to the disturbed area was constrained at first because of the destruction of roads, and relied heavily on helicopters, but within a year many roads were repaired and vehicle access was possible. Most importantly, the US Congress created the (44 515-ha) Mount St. Helens National Volcanic Monument, with the goal of allowing geological forces and ecological processes to "proceed substantially unimpeded" and to foster science, education, interpretation, and recreation to the public's benefit. This legislation ensured that research would be a primary focus of the post-eruption landscape and that adequate protection would be in place to safeguard research infrastructure from loss or damage. The federal agency responsible for the new Monument, the US Forest Service, has made a concerted effort to protect research sites and opportunities. Strong institutional support for science has come from the US Forest Service and National Science Foundation; funding for quick response was especially important. Vegetation and aquatic studies completed before the eruption were extremely valuable in assessing system response. Eager, attentive public and media organizations have sustained interest in the area and thereby reinforced agency support.

The contribution of Mount St. Helens to advancement of volcano ecology has taken many forms. The science program has contributed 177 (42%) of 423 publications in the Crisafulli et al. (2015) database. Mount St. Helens scientists have coauthored a large share of the multi-volcano synthesis publications, which has been a rather recent phenomenon

(e.g., del Moral and Grishin 1999; Dale et al. 2005a; Edwards 2005; del Moral and Magnusson 2014; Crisafulli et al. 2015). Scientists in the large Mount St. Helens community have frequently consulted with foreign government agencies and academics concerning research opportunities and ecosystem effects associated with new eruptions, co-convened international symposia and field tours on volcano ecology, and been integral players in the emerging global network of scientists working in the field of volcano ecology. Another dimension of advancing volcano ecology has been partnering with colleagues to initiate studies following eruptions elsewhere, using protocols in common with those used at Mount St. Helens: research underway, for example, with Chilean colleagues working at Chaiten, Cordon Caulle, and Calbuco volcanoes. The vibrancy of the Mount St. Helens research program, community of scientists, and outreach specialists signals that these roles are likely to continue.

The 1980 eruption and the setting of Mount St. Helens make it a representative case for study of eruption-ecosystem interactions in some respects and an unusual case in others. The tectonic setting of Mount St. Helens in a volcanic chain associated with a subduction zone is very common, and the highly energetic, explosive 1980 eruption (VEI = 5) in a mountainous landscape with moist, maritime climate involved a wide variety of volcanic and associated hydrologic processes. However, the suite of volcanic processes in the 1980 eruption of Mount St. Helens does not provide examples of several important types of eruptions and settings of volcano ecology studies, such as basaltic lava flows. The pyroclastic flows of the 1980 eruption did not have opportunity to interact with pristine terrestrial or several types of aquatic ecosystems, because those existing just before the eruption had been obliterated by the huge debris avalanche and then by a powerful blast PDC (lateral blast) before the pyroclastic flows occurred. In terms of its ecological setting, Mount St. Helens resides in the temperate forest biome, which is intermediate in extent among the seven types of terrestrial biomes considered (Table 16.2).

Public communications about volcanoes and volcano ecology have been a hallmark of the Mount St. Helens program and a model for other locations around the world. Outreach infrastructure and networking include several visitor centers, dozens of Ranger Naturalists who provide presentations to hundreds of thousands of people annually, sustained relationships with national and international media, a nonprofit organization focused on science education and stewardship at the volcano (the Mount St. Helens Institute), and museums that curate tens of thousands of Mount St. Helens' biological specimens and make them available to researchers around the world. A distinctive feature has been use of the volcanic venue to explore the intersection of arts, humanities, and science, which is a growing phenomenon nationally at sites of long-term ecological research (Swanson 2015). Since 2000, creative writers and scientists have gathered at Mount St. Helens on 5-year eruption anniversaries to share their learning with one another and with the public in performances and written works (Snyder 2004; Goodrich et al. 2008; Buntin 2010; terrain. org 2013).

Highly collaborative, interdisciplinary research and broader inquiry requires a strong, interactive community. Volcano ecology research at Mount St. Helens is unusual in terms of the diversity of disciplines and intensity and duration of studies, which make it one of only three sites in our highest class of study intensity (Table 16.2) and the only one in a continental setting; the other two (Krakatau and Surtsey) are in marine settings. This history highlights the importance of an open, diverse scientific community for dealing with the social and ecological complexity of major volcanic disturbance events. At Mount St. Helens, the Forest Service has made concerted efforts to sustain and enlarge the research community through mechanisms such as week-long field gatherings every 5 years, termed "pulses," which attract more than 100 members of the science community and actively recruit new, early-to-midcareer scientists to maintain long-term studies and to initiate new research. The pulses also host groups of creative writers and involve participation by high-school students and undergraduates. The overall effect is to encourage and sustain interpersonal and interinstitutional collaborations, facilitate group publications, and assist in the intergenerational handoff of research projects.

16.4.3 Future Volcano Ecology Research

This review of the state of global volcano ecology research and the experience of volcano ecology at Mount St. Helens prompts several recommendations for further study:

- Ongoing research at eruption sites should continue, and at those sites where there has been a lapse in measurements, work should be reinitiated to document long-term patterns of ecosystem responses to volcanic disturbance. This sustained effort is particularly important for ecosystems with long seres following disturbance, such as forests or cold regions that may require centuries to develop following high-intensity eruptions.
- 2. At sites with multidecadal research, investigators or other responsible parties (e.g., agencies) need to recruit new members into the research community as aging scientists approach retirement, thus allowing for intergenerational transfer of long-term data and plot systems, and stewardship of studies well into the future.
- 3. In the case of future eruptions, it is important to initiate work as soon as access is possible and conditions are safe,

because early interpretation of the physical disturbance effects across the landscape and initial responses of biota is a key to understanding longer-term processes of biotic assembly. Evidence of ephemeral phenomena (e.g., influence of snow) may quickly vanish yet may be important to explaining organism survival and other phenomena.

- 4. An integrated multidisciplinary science approach at eruption sites should investigate numerous taxa, ecological interactions, and ecosystem processes, as well as human responses to eruptions at scales of individuals, communities, and nations.
- 5. Volcano ecology studies should be founded on investigation at the geology–ecology interface to place the work in a clear geographic context by sampling along disturbance gradients and other aspects of landscape context.
- 6. It is essential to thoroughly document research efforts and data, so they are available to future researchers. Such efforts should include plots that are georeferenced, publically accessible data sets, monumented photopoints, and physical voucher-specimen collections that are deposited in safe, curated repositories.
- 7. Despite the wealth and diversity of volcano ecology research efforts to date, several areas of inquiry remain unexplored or only sparsely explored. Understudied subject areas that deserve attention include
 - (a) Evolutionary processes in sites with limited population size and concomitant isolation in post-eruption landscapes may lead to shifts in genetic structure through genetic drift and bottlenecks. Similarly, immigrants to eruption sites may be subject to founder effects associated with small population size, absence of or low gene flow, and suites of novel selective pressures in the post-eruption landscape. Although tantalizing, such evolutionary processes have only occasionally been assessed at eruption sites, and the results have been variable across taxa.
 - (b) Landscape ecology perspectives addressing broadscale (100–1000 km²) vegetation change and associated animal community assembly to assess influences on landscape pattern development and consequences for ecological processes. Such approaches would provide a template for follow-up studies of patch dynamics and metapopulations.
 - (c) Studies of biogeochemical cycling and soil genesis.
 - (d) Development and change in food-web structure during the course of succession.
 - (e) Aquatic–land interactions in post-eruption landscapes, such as the flows of energy, matter, and organisms.
 - (f) Comparisons of the patterns and rates of change in key ecosystem parameters (e.g., net primary production) and processes among different system types, such as terrestrial, lake, and stream environments that were disturbed by the same eruption.

(g) Attention to emerging phenomena, such as climate change and invasive non-native species that may alter the course of ecosystem response.

Acknowledgments We greatly appreciate the assistance of E. Schyling in assembly of the bibliographic database, K. Christiansen in creation of the Fig. 16.1, and K. Ronnenberg for creation of timeline, photo plate, and additional editorial assistance. Reviews of the manuscript by V. Dale, J. Franklin, C. Millar, and R. Parmenter were especially helpful. Funding for our research activities at Mount St. Helens and abroad has been provided by the USDA Forest Service, Pacific Northwest Research Station and the National Science Foundation (LTREB Program DEB-0614538). Collaborations with colleagues at Mount St. Helens and in Alaska, Chile, Argentina, China, and Iceland have strengthened our volcano ecology perspectives. We acknowledge and thank the ecologists who since the 1883 eruption of Krakatau have provided important foundational work in the field of volcano ecology.

Glossary

- **Biological legacy** Live and dead organisms and organic matter that survive an ecological disturbance and may affect the pace and pattern of post-disturbance ecosystem development.
- Blast PDC (blast pyroclastic density current) A form of pyroclastic density current initiated by rapid decompression of lava domes or cryptodomes (magma bodies cooled high within a volcanic edifice) owing to sudden collapse. Rapid decompression results in a directed explosion that initially impels the current laterally before it becomes a gravity-driven flow. [Sources: a generalized definition based on definitions of PDCs provided in Pierson and Major (2014) and Sigurdsson et al. (2015)]. In the case of the Mount St. Helens 1980 eruption, failure of the volcano's north flank unroofed pressurized magma and superheated groundwater. Rapid exsolution of magmatic gases and conversion of superheated groundwater to steam produced a laterally directed blast, which formed a density current that flowed across rugged topography. The current contained fragmented rock debris as well as shattered forest material (Lipman and Mullineaux 1981).
- **Debris avalanche** A rapid granular flow of an unsaturated or partly saturated mixture of volcanic rock particles (\pm ice) and water, initiated by the gravitational collapse and disintegration of part of a volcanic edifice. Debris avalanches differ from debris flows in that they are not watersaturated. Although debris avalanches commonly occur in association with eruptions, they can also occur during periods when a volcano is dormant. (Sources: Pierson and Major 2014; Sigurdsson et al. 2015).
- **Lahar** An Indonesian term for a rapid granular flow of a fully saturated mixture of volcanic rock particles (\pm ice), water, and commonly woody debris. A lahar that has \geq 50% solids by volume is termed a *debris flow*; one that has roughly

10–50% solids by volume is termed a *hyperconcentrated flow*. Flow type can evolve with time and distance along a flow path as sediment is entrained or deposited. (Sources: Pierson and Major 2014; Sigurdsson et al. 2015).

- **Pyroclastic flow** Rapid flow of a dry mixture of hot (commonly >700 °C) solid particles, gases, and air, with a ground-hugging flow that is often directed by topography. Flows are generally gravity driven but may be accelerated initially by impulsive lateral forces of directed volcanic explosions. Flows typically move at high velocity (up to several hundred km h^{-1}).
- **Refuge (refugia)** Localized sites where organisms survive a disturbance event at a level greater than the surrounding, disturbance-affected area.
- **Succession** Development of an ecosystem following disturbance, including processes such as species assembly by immigration and establishment, species interactions (e.g., herbivory), and site amelioration (e.g., weathering of inorganic substrates). Primary succession refers to cases with no legacies of the pre-disturbance ecosystem; secondary succession refers to cases where some biota from the pre-disturbance ecosystem persists.
- **Tephrafall** A rain of volcanic particles to the ground following ejection into the atmosphere by an explosive eruption. Tephra is a collective term for particles of any size, shape, or composition ejected in an explosive eruption. (Sources: Pierson and Major 2014; Sigurdsson et al. 2015).

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