

CHAPTER 10

How Mount St. Helens Changed Our Understanding of Succession



Frontispiece: Prairie lupines dominate the lower slopes of Studebaker Ridge during its second population explosion (July 18, 2001). Population fluctuations and multiple biotic interactions involving lupines led to many advances in our understanding of succession

Introduction

Each research trip produced new questions, offered unique opportunities and generated remarkable challenges. That is why I could continue to explore vegetation development for over 30 years...it just never got boring. The recurring challenge was to find emerging patterns amidst the myriad details and the greater challenge was to explain them. I believe that I met these challenges successfully through the years and in this book. However, for this long-term exploration of one tiny patch of the planet to be meaningful, it must have provided answers to broad questions. I believe that it has.

Since 1980, the study of succession has made enormous progress, and we have discarded much of the failed legacy that required unequivocal deterministic processes. Spurred by the work on Mount St. Helens, a new generation of ecologists (including Annette Baasch, John Bishop, Nick Cutler, Chris Fastie,

John Lichter, Karel Prach, Kristin Svavarsdottir and Shiro Tsuyuzaki) explored primary succession from a perspective informed by ecosystem sensibilities, understanding of interactions between trophic levels, powerful statistical methods and landscape ecology. The paradigm of succession has shifted from prescriptive to stochastic and from descriptive to explanatory. Dearly held beliefs have been revised, modified and, finally, surrendered.

Studies by a diverse battalion of scientists on Mount St. Helens highlighted many ecological processes and provided insight into how communities assembly. Understanding these processes created a new way to visualize primary succession. The lessons derived from this understanding are now applied to restoration of landscapes devastated by human activities. Restoring habitats is one essential part of the struggle to arrest ecosystem degradation and the loss of biodiversity. Below I provide a summary of lessons learned

from studies on Mount St. Helens. Many were revealed by scrutiny of the developing Mount St. Helens landscape. They have been confirmed in such diverse locations as the young volcanic island of Surtsey (Magnússon et al. 2009), lava fields in Iceland (Cutler 2010), volcanoes on Hokkaido (Tsuyuzaki 2009), sand dunes (Ujhazy et al. 2011) and flood plains in Alaska (Fastie 1995).

Landscape factors affect species composition

The landscape position of a recovering site may be the one most important factor governing its recovery. Because the dispersal ability of most species is limited, even short distances selectively filter colonists. On Mount St. Helens, colonists were species with buoyant, light seeds produced in massive quantities. Barriers such as ridges or canyons also heighten the isolation experienced by a particular site.

Sites isolated from donor populations are initially heterogeneous because the meager seed rain essentially falls at random. Different species pioneer similar sites, weakening any bond between environment and plants. On Mount St. Helens, the distance beyond which all sites look equally isolated was remarkably short, well under 100 m. Sites next to intact vegetation demonstrated steep invasion gradients. Species common in mature, stable forests may invade along these margins, but because their dispersal abilities are limited, the extent of the invasion must be restricted. Attempts to restore landscapes must actively introduce desirable species because under most conditions, they simply will not appear spontaneously.

Because the blast was directed across the landscape, there was a gradient of destruction; similar habitats received different degrees of damage. Monitoring these sites demonstrated that succession does not follow any prescribed path to recovery. I concluded that the mosaic of vegetation types found on most landscapes is normal, not an aberration.

Serendipity has enduring effects

The luck of the draw has never been as evident in ecology as on Mount St. Helens. Significant random events started with the timing of the eruption itself...much earlier and the devastating lahars would have been far worse. Much later, and the searing lateral blast would have consumed vegetation that was protected by snow in May. Even the time of day affected survival of animal species. Nocturnal mammals like deer mice were safe within burrows while large animals like elk and bear were fully exposed, and

suffered accordingly. The summer of 1981 was an extremely hot one, retarding seedling establishment. Any cooler and succession may have accelerated in many places. Chance and singular events have long-term ramifications that persist. These unpredictable factors combine to explain why ecologists rarely find snug relationships between vegetation and environmental factors.

Dispersal is overrated

Isolation puts a premium on long-distant dispersal, so remote sites are dominated by plumed seeds from the sunflower family and by fireweed and its relatives. These species are often poor competitors. Over time, increasingly more competitive, persistent species with less effective dispersal reach the site. New arrivals often diffuse gradually from intact vegetation along a broad front. Animal dispersed species often hurdle barriers and travel substantial distances, like paratroopers; they then expand from their footholds. The combination of multiple dispersal traits combined with uncertain animal vectors creates heterogeneous establishment and development patterns. As a result, adjacent sites may be at different successions stages. Superimposed on the chaotic nature of long-distance dispersal is the uneven dispersal by diffusion that produces strong floristic gradients demonstrated along lahar margins. The unpredictable nature of dispersal and its effects on early succession were not well understood prior to the work of Mount St. Helens.

That distance alone can be a dispersal barrier increases concerns that many species will become locally, or even globally extinct in the face of climate change resulting from global warming. The dispersal rates of most species, even without barriers, are slow, and may be exceeded by rates of habitat change. This suggests that the need for rescue colonization, in which species with limited mobility are transported into new suitable habitats, is even greater than has been anticipated.

Trajectories are intricate

The pattern of development, trajectories, was more complex than would have been predicted. Early studies of European dunes and flood plains suggested patterns at odds with the deterministic, progressive pattern predicted by the founding fathers of succession ecology. Mount St. Helens revealed convergence in some cases, but as often, divergence was the rule. Divergence occurred when a few pioneer species were supplemented by species more attuned to the

local conditions and when priority effects altered the trajectory.

Trajectories develop at different rates that are related to the effective growing season of the site. Traditional views measure stages of succession in years. My studies on Mount St. Helens demonstrated that succession should be measured by the rate of biomass accumulation. On Mount St. Helens, initial stages may endure for only a short time if the site is at low elevation, on fertile soil or near donors. This stage can be prolonged by stress and by isolation. The studies of Mount St. Helens revealed that successional rates are controlled by stress, and suggested how to accelerate succession under managed conditions.

Amelioration is crucial

The late John Edwards demonstrated the importance of “aeolian effects” in the alpine zone of mountains (Edwards 1987) and on volcanoes. The introduction of organic matter onto sterile sites by the wind is crucial when there is no carbon or nitrogen in the substrate. Pollen, spores, insects and spiders combine to provide the first wave of fertility. Other well-known forms of amelioration were also observed on Mount St. Helens. The positive effects of erosion were revealed in several studies. Surface wind and water erosion removed thick deposits of silt to allow survival of buried materials. Channels cut by mild erosion created safe-sites, a previously unappreciated phenomenon. Even minor surface movements proved to be important to facilitate seedling establishment. These subtle effects of erosion can now be taken into account in planning for the restoration of barren sites.

Safe-sites are indispensable

While the concept of safe-sites was well established, the work on Mount St. Helens was among the first to demonstrate how crucial very favorable microsites were to seedling establishment on barren sites. Initially, safe-sites are created by physical processes, but established plants also can create conditions less hostile for seedling establishment. Mature individuals become “nurse plants.” Studies on Mount St. Helens also demonstrated that safe-sites can be ephemeral. Either erosion eliminates the habitat or, more commonly, established plants create adverse conditions for new seedlings.

Biotic effects are complex

Legacies. Sites where vegetation survived are called relicts or refugia because they contain legacies (Franklin et al. 1985). The term legacy is apt since it conjures the quite proper image of a bequest, in this case the potential to enhance surroundings or the next generation. Legacies can accelerate recovery. They are important when most of the habitat persists because survivors will be adapted to the developing conditions. In contrast, remnant snippets in otherwise barren habitats have limited value for recovery because survivors are ill adapted to colonizing stressful habitats. Unexpectedly, legacy habitats did provide sites that could support invading pioneer plants which thrived, reproduced copiously and deposited a dense seed rain into the surroundings. Even so, in primary succession sites, this effect is spatially limited.

Nurse plants. The nurse plant concept was developed in desert ecosystems and is commonly invoked in hostile environments. The most important nurse plant on Mount St. Helens is prairie lupine, which enhances soil nitrogen and adds carbon to the soil. Delayed nurse plant effects were documented for the first time. This phenomenon revealed the delicate balance between positive and negative effects of nurse plants. Some species benefit from amelioration, others suffer from competition. My studies on Mount St. Helens documented selective nurse plant effects and showed how they altered trajectories. They suggested that the application of nurse plant concepts in restoration must be measured and carefully considered.

Competition. Competitive effects during succession favor species that benefit from improved soil fertility and which are persistent. Thus far, strong competition has been demonstrated only in a few cases. Invading conifers create dramatically different environments that eliminate species adapted to the dry, exposed conditions typically found on lahars and pumice. This is hardly unexpected. That shrubs such as pinemat manzanita and juniper create local patches lacking other species shows that some species are strong competitors. Mosses, contrary to expectation, became dominant in two situations. Rock moss is dominant in stable, dry lahar situations and appears to resist further invasion. Haircap moss, facilitated by prairie lupine, is dominant in old lupine patches, where it seems to resist the invasion of species adapted to barren conditions. Thus, we learn that seemingly inferior species (according to conventional accounts of primary succession) can persist due to

their competitive abilities.

Herbivory. Animals can eliminate potentially successful species by eating them or their seeds. Elk browse on aster flowers and have reduced its abundance. They forage widely and intensively, but much remains to be learned about their overall impact. It may be that the most interaction is that of the introduced willow stem-boring beetle that appears to inhibit struggling willows in the uplands and may retard succession.

Determinism increases over time

The entire discipline of succession ecology was built on the premise that trajectories were predictable because there were sturdy links between the environment and species composition. Early studies of this link on Mount St. Helens found it to be weak and dominated by landscape factors, not environmental ones. However, over time, several of my studies discovered links that, while still weak, were strengthening. These findings suggested that there were assembly rules. Because patterns remained weak, it is likely that assembly rules operate more on functional types than on species. Thus, vegetation in a particular habitat will be assembled from species that first pass through the dispersal filter, can tolerate the local conditions and possess traits that allow them to pass through an environmental filter. Rules rarely appear to be so stringent that only one combination of species can occur.

Alternative states are possible

In several situations, it appears that two or more species assemblages may occur in similar environments. This demonstration, rare in terrestrial environments, suggests that multiple restoration results should be expected and welcomed. Alternative states are a predictable result of priority effects, gradients of disturbance and limited competitive abilities in stressful environments. Priority effects were suggested by comparisons between dense and sparse lupine patches. In restoration, heterogeneity and variable combinations of species confer advantages rarely appreciated. Heterogeneity permits greater biotic diversity, which tends to confer greater stability on the system. It also helps to ensure that there is an appropriate mix of soil organisms usually necessary for high survival.

Alternative states may result because one site develops along predictable trajectories, while another site, having been colonized by a species new to the

area, follows a different path. As invasive species become increasingly common, novel communities will become more common. In the blown-down zone, communities in which such species as Scot's broom and tansy ragwort have become increasingly common.

Long-term studies are priceless

My experience on Mount St. Helens strongly suggests that long-term studies are invaluable when trying to untangle complex interactions. I was often asked questions such as "Why do you need another grant for more research?" This is a fair question because we are used to thinking that any project, event, game, etc. has a natural progression and a conclusion. In this case, however, something new kept emerging. The sudden explosion of lupines across the landscape could not have been predicted from its nearly stagnant behavior until 1999. The emergence of deterministic interactions had only barely begun after 25 years. Everyone who has studied the biota of Mount St. Helens for any length of time will have his or her own examples. Long-term studies demonstrate that serendipity is an essential part, not only of succession, but also of any human enterprise.

Coda

The landscapes and biota of Mount St. Helens will continue to change and mature. Without a doubt, more surprises are in the offing for those who continue to study this development. As for me, I just consider myself fortunate to have been able to study this most interesting and dynamic landscape.

Directly or indirectly, this research has allowed me to travel globally and to meet many fine people. Sometimes, I was able to collaborate with ecologists who share my interests on volcanoes and to learn that most of what I learned on Mount St. Helens can be applied to other volcanoes and to other systems. Emilia Poli Marchesse guided my studies on Mt. Etna and was a most gracious host during my time in Sicily. Sergei Grishin and Sasha Krestov guided me through the wilds of Kamchatka to visit two remote regions rarely seen by Westerners. At other times, I was able to explore succession in different systems with distinguished colleagues. A. D. Bradshaw was my kind host in Liverpool, and helped to foster my interest in the application of succession theory to restoration. Joe Walker organized my early studies in Queensland, Australia, and later showed me how primary succession on dunes did not follow the rules.

My work on Mount St. Helens gained considerable international notice, which resulted in invitations to deliver papers on succession and restoration and to conduct research. These included talks in Iceland to ecologists interested in succession on volcanoes and to an international group of experts in lupines. While in Iceland, I became friends with several ecologists, notably Borgþór Magnússon, who made it possible for me to study on Surtsey. I was invited to Japan on several occasions. In Hokkaido, I met Shiro Tsuyuzaki, who has studied Mt. Usu to provide a unique perspective on succession. I also met Hideo Tagawa, who led the Japanese studies of Krakatau and who explained the history of Sakurajima to me.

My studies on Mount St. Helens also brought me many students and field collaborators over the years. Each contributed in their special way to enrich the experience for all concerned. Several students continued to achieve their Ph. D. or to work professionally in ecology. Notable contributions were made to my Mount St. Helens project by many people. Andrew Eckert, Erin Ellis, Michael Fleming, Chad Jones, Tara Fletcher Ramsey, Jon Titus and David

Wood received their Ph. D. at the University of Washington. Suzanne Bard, Arlene Cook, Katrina Dlugosch, Iara Lacher, Marko Spasojevic and Mandy Tu graduated and received their doctorates elsewhere. Chris Clampitt, Roger Fuller and Nancy Weidman received master's degrees and now work with NGOs. Lara Rozzell and Shiro Tsuyuzaki were research associates; Lara works for the National Parks Service, Shiro is a professor at Hokkaido University, Japan. Elli Jenkins Theobald, Jeremy Sandler and Claire Muerdter are in graduate school. Several recent students, including Jennifer Emenegger, Natasha Lozano, Jason Saura, Lindsay Thomason and Anthony Wenke, are pursuing careers in conservation or remain in school.

Most importantly, my work on Mount St. Helens led me to form a lasting friendship with Lars Walker, with whom I share many interests, ecological and otherwise. We co-authored two books on succession and disturbance ecology, experiences that led me to this book and Lars to write several others.

I thank all of these people.