Primary succession on Mount St. Helens, with reference to Surtsey

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ABSTRACT

Vegetation development on Surtsey and Mount St. Helens has been influenced by remarkably similar processes. Both are isolated, so colonizers are filtered. In each case, species accumulation and vegetation development were initiated by a few species, with a lag phase before biomass accumulated rapidly. On both, establishment was first concentrated in favorable microsites and facilitated by nutrient inputs. Established plants often fostered other species in both cases. That such contrasting systems exhibit similar mechanisms of community assembly offers important restoration lessons.

INTRODUCTION

Surtsey is a unique, new volcanic island. Mount St. Helens volcano (Washington State) erupted violently in 1980. Each provides a matchless opportunity to explore how ecosystems develop (Walker & del Moral 2003). Here I summarize plant primary succession mechanisms found on Mount St. Helens and compare them to those determining succession on Surtsey.

STUDY AREA

The 18 May 1980 eruptions of Mount St. Helens formed a complex pattern of new and denuded land (Dale *et al.* 2005). This extraordinary landscape beckoned irresistibly to ecologists to study reassembly (Fig. 1). This report draws on studies conducted by myself and colleagues since 1980. Methods are in the references. Vegetation structure was monitored in transects of permanent plots: 12 on Pumice (from 1989), 10 on a lower Ridge (from 1984) and 10 from upper sites on this ridge (from 1989; del Moral 2007).

RESULTS

Species richness and cover

Species assembly was slow. Pumice richness stabilized by 1998, and after 2003 it declined due to an explosion of *Lupinus lepidus* (del Moral & Rozzell 2005). Ridge richness declined after 1998 (Fig. 2). In each case, there was a core of species (stable) and several species with sporadic occurrences. Sporadic species absent for at least the last three years are deemed "extinct" (Table 1). More species persisted at higher elevations where cover was lower.

After a lag, cover on Pumice began to accrue (Fig. 3). Cover in lower plots peaked in 2000, then declined. Cover developed slowly in upper plots. Despite pulses of *L. lepidus* (1999, 2004, 2007), cover was 50% of the lower plots. The rate of development on the Ridge was related to elevation (del Moral 2007). *Lupinus* cover exploded in the lowest plots (1989, 1994, 1999), then declined. By 2008, there was a steady decline of cover with elevation.

Dispersal

Primary succession requires colonization, establishment, development and biotic interactions. In terrestrial systems, colonization is significantly less of a problem than on islands, but dispersal remains a significant constraint (del Moral & Eckert 2005). Seeds dispersed by animals are poorly adapted for establishment in stressful sites (Wood & del Moral 1987). Wind dispersed species continue to dominate the flora, but shifts in the dispersal spectrum occurred. Wind dispersed species include Parachute (e.g. *Hieracium*, *Chamerion*), Parasail (e.g. *Abies*, *Carex*), Tumbler (e.g. several grasses, *Eriogonum*, *Polygonum*) or spore bearing (ferns, mosses). The Other category consists primarily of *Lupinus* (explosive dehiscence and ants) but includes a few animal-dispersed species (e.g. *Arctostaphylos*, *Fragaria*).

I summarized the transect data by the first and last four years to characterize the changing spectra. Species were grouped by dispersal types and the spectra compared (Fig. 4). Pioneers were dominated by parachute species, but mosses and ferns were sparse; these species need facilitation to establish. Over time, dominance by less nimble species increased as they invaded, persisted and expanded. The temporal pattern is also revealed in spatial patterns. The dispersal spectrum changed over short distances. Isolated sites were initially dominated by parachutists, while sites near donors were dominated by other types (del Moral & Ellis 2004).

Establishment

Initial establishment was facilitated by safe sites (del Moral & Wood 1993). Seedling survival was strongly favored by surface cracks, large rocks and erosion features. As conditions generally improved, seedling establishment became dispersed, and establishment of most species was no longer confined to special habitats.

Facilitation

Facilitation, processes that improve establishment, occurred in two ways. Nutrient inputs in the form of pollen, seeds and spores, insects, spiders, feces from birds (and later elk) and rainfall produced physical amelioration. Once plants established, they produce more organic matter. Thus, development was initially slow, but accelerated with the establishment of nurse plants, notably *Lupinus*. Young *Lupinus* colonies promoted grasses compared to adjacent sites with sparse lupines (del Moral & Rozzell 2005) while old *Lupinus* colonies promoted mosses.

Inhibition

A grid of 100-m^2 plots was sampled in 2008. Dense conifer (*Pinus* and *Abies*) plots (> 35% cover) were compared to sparse conifer plots (< 20% cover). Dense conifer plots had fewer species, lower ground layer cover and were less diverse (Table 2) than plots with sparse conifers. Conifers changed the understory composition and reduced the ground layer vegetation.

COMPARISONS WITH SURTSEY

Dispersal

Both volcanoes illustrate that isolation alone can structure vegetation. On Mount St. Helens, nearly all pioneers were wind dispersed, in contrast to the surroundings. On Surtsey, the sea provided the first few colonists, which still dominate beaches. Once seabird colonies became established, species common to Iceland's shores were introduced. Later, wind dispersed species became established in several habitats. The vegetation on Surtsey and on Mount St. Helens remains impoverished relative to their sources.

Species accumulation

The colonization patterns on Surtsey and Mount St. Helens were similar despite the context differences. Isolation and stress combined to constrain establishment for several years. On Mount St. Helens it took about 10 years to reach 50% of the current richness, and on Surtsey it took about 25 years to reach this point. Clearly, isolation and the late colonization by sea-birds retarded the plant colonization of Surtsey. Arrival does not guarantee persistence. On Surtsey, only 72% of species found in 2008 have viable populations. On Mount St. Helens, about 1/3 of the species are sporadic. These examples emphasize the importance of isolation in driving succession. They suggest that restoration projects cannot depend on spontaneous establishment to provide desirable vegetation and that reintroduction of desirable species is often required.

Safe sites

Safe sites were crucial to early development on Mount St. Helens. On old lava sites, plants established in crevices, while on new surfaces, erosion created favorable microsites and larger rocks offered protection. On Surtsey, upland colonization also appears to have been in cracks in the lava (Fig. 5), while the coarse surfaces on the beach offered refuge to seeds washed ashore. That such different volcanoes offer similar conclusions about establishment emphasizes that restoration plans should pay heed to seedling establishment conditions.

Facilitation

Without facilitation, both Surtsey and Mount St. Helens would have scarcely developed. Seabirds deposit nutrients in and around their colonies (Fig. 6). Wind carries in organic matter to Mount St. Helens and now birds and large mammals contribute nutrients. However, winds reaching Surtsey carry much lower nutrient loads and Surtsey also lacks vascular plants that can fix nitrogen. On Mount St. Helens, two *Lupinus* species and *Alnus* contribute to improving fertility. Both volcanoes demonstrate the importance of soil fertility to the rate of succession. However, where nitrogen is concentrated, as in the gull colonies, dominance by a few nitrophilous species is promoted (Magnússon & Magnússon, 2008). Nitrogen levels remain generally low on Mount St. Helens, so that intense competition has not occurred. Restoration scientists who wish to develop diverse communities must control fertility.

Plants on both volcanoes can act as "nurse plants", sheltering seedlings until they can become established (Fig. 7). Erosion acts to facilitate succession on both volcanoes. On Mount St. Helens, tephra and mud were removed to reveal old surfaces, pumice rocks were fractured by frost and water channels were formed to support seedling establishment. On Surtsey, wind has moved sand over lava, allowing the invasion of *Leymus* and other species.

Permanent plots

Long-term studies of succession are few (Svavarsdóttir & Walker 2008). Permanent plot studies of succession avoid most problems associated with "chronosequence" studies. They allow us to track internal dynamics (e.g. expansion of species, local extinction, etc.) and climate effects. Studies on Surtsey, where human disturbances are regulated, promise to provide a clear record of succession under several stressful conditions, including how birds influence the pattern and whether succession on lava will result in significant species turnover. Because of its isolation and legal protection, Surtsey will offer ecologists important lessons for decades.

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Table 1. Total number of species, stable species, sporadic species and species not found for at least three years after last occurrence in each data set. (Plots were 250 m^2 circles, all species recorded).

Site	**Total**	**Stable**	**Sporadic**	**“Extinct”**
Pumice—Low	32	21	11	3
Pumice—High	37	25	12	2
Ridge—Low	41	21	20	9
Ridge—Mid Low	34	20	14	9
Ridge—Mid High	37	26	11	8
Ridge—High	34	25	9	6

Note: Pumice plots consist of six plots each, Ridge plots

Table 2. Structural differences between plots dominated by conifers (cover $> 30\%$) and sparse conifer plots (cover $< 20\%$). (Dense, $n=14$; Sparse, $n=22$; comparisons significant, Wilcoxon rank sum test , $P \ll 0.05$).

Parameter	**Conifers Included**		**Conifers Excluded**	
Parameter	*Conifers Dense*	*Conifers Sparse*	*Conifers Dense*	*Conifers Sparse*
Richness	13.8	17.5	11.8	15.5
Cover (index)	51.3	21.5	5.7	9.9
H'	1.059	1.845	1.813	2.186

Fig. 1. Lupine patch facilitates vegetation (2007).

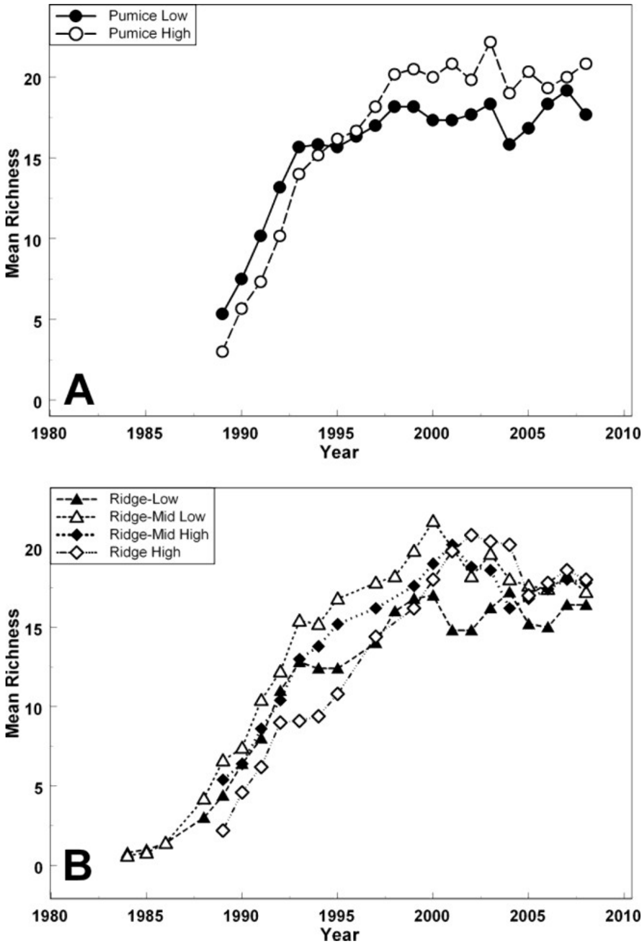

Fig. 2. Species richness in permanent plots. A. Pumice; B. Ridge.

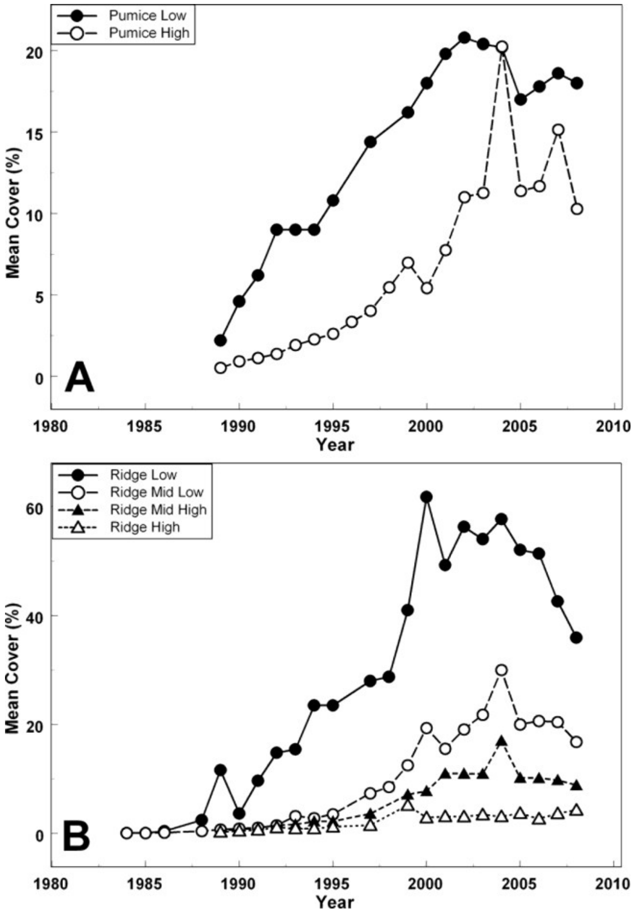

Fig. 3. Percent cover in permanent plots. A. Pumice; B. Ridge.

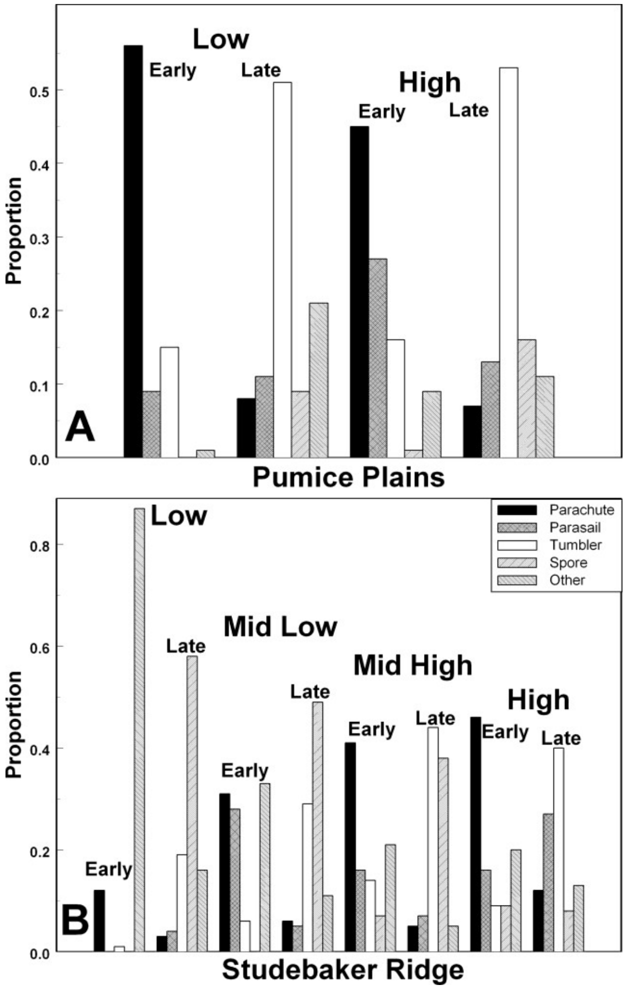

Fig. 4. Dispersal spectra early (first four years) and late (last four years). A. Pumice; B. Ridge.

Fig. 6. Gull colony demonstrates the importance of facilitation.

Fig. 5. *Cochlearia officinalis* in lava cracks.

Fig. 7 *Honckenya peploides* acts as nurse plant for *Cakile arctica*.