Succession and local species turnover on Mount St. Helens, Washington

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Abstract

The 1980 eruption of Mount St. Helens provided a singular chance to study community assembly. Permanent plots were used to monitor species richness, cover and evenness. Structure stabilized quickly on mildly impacted sites, but secondary and primary successional sites continued to develop. Annual DCA score increments changed least on tephra and most on primary sites. Vegetation changed more rapidly soon after impact, more slowly recently. Net plot displacement after 18 seasons was 0.4 half-change (HC) on tephra, 1.0 HC on secondary sites and 1.1 HC on primary sites. Colonization and extinction percentages in 0.25-m^2 quadrats were estimated for three intervals. The extinction percentages declined from recovered to primary sites, while the colonization percentages were similar in all. The proportion of extinction events to colonization events declined sharply. These results support the carousel model at an intermediate spatial scale, even during succession. Degree of site isolation, stress and impact intensity combined to form a mosaic of recovering vegetation that remains dynamic. Each community had unique structure, developmental sequences and local population dynamics.

Keywords: Carousel model; Local colonization; Local extinction; Primary succession; Secondary succession; Volcano.

Abbreviations: ANOVA = Analysis of variance; CV = Coefficient of variation; DCA = Detrended Correspondence Analysis; HC = Half-change.

Nomenclature: Titus et al. (1998).

Introduction

The lateral eruption of Mount St. Helens on 18 May 1980 destroyed the northern half of its cone. This blast seared ridges while pyroclastic flows, pumice deposits and lahars created a new landscape (Foxworthy & Hill 1982). I established sets of permanent plots starting in 1980 to monitor vegetation establishment and recovery. This paper describes development on new surfaces (primary succession), intensely damaged habitats (secondary succession) and sites that recovered quickly. These patterns are interpreted in terms of impact intensity and site isolation. Trends were described using detrended correspondence analysis, while I compared local colonization and extinction percentages to determine the degree of local population dynamics.

Study area

Mount St. Helens is centred at 46° 20' N, 122° 18' W, with an elevation of 2549 m. This study included 10 sites. At each, permanent plots that represent different combinations of impact intensity (Table 1) were monitored with permanent plots. Del Moral & Bliss (1993) provided a map and site descriptions.

Recovered sites were impacted by air-fall deposits of coarse pumice (tephra) that buried vegetation on the southern slopes of the cone up to 20 cm. Coarse texture, shallow depth and erosion permitted significant survival and rapid recovery (del Moral 1983). Three sites (Tephra A, B and C) had fully recovered by 1983.

Secondary succession sites received a variety of impacts. Blast A is on the west side of the cone at the edge of the directed blast that killed woody plants. Some dormant herbs survived. Rapid snow-melt formed lahars (cold slurries of mud and rocks) that scoured canyons and ridges before forming deposits at lower elevations (del Moral & Wood 1988). A lower site on an east slope ridge (Scour A) is within 100 m of surviving vegetation, while a nearby upper site (Scour B) is more isolated. Lahars on

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Acta Phytogeogr. Suec. 85: 51-60. ISBN 91-7210-085-0.

Table 1. Summary of characteristics of the ten study areas.

Site	Location	Impact type	Elevation (m)	Isolation	Succession type
Tephra A	South Flats	Tephra	1370	None	Recovered
Tephra B	South Flank	Tephra	1525	None	Recovered
Tephra C	South Flank	Tephra	1600-1680	None	Recovered
Scour A	East Ridge	Light scour	1370	Low	Secondary
Blast A	West Ridge	Blast edge	1280-1340	Intermediate	Secondary
Scour B	East Ridge	Moderate scour	1510	High	Secondary
Scour C	South Ridge	Intense scour	1580-1710	Low	Secondary
Lahar	South Flank	Lahar	1320-1350	Low	Primary
Blast B	Northwest Ridge	Direct blast	1200-1310	High	Primary
Pumice	North Flats	Pumice deposit	1220-1280	High	Primary

the south side scoured high elevation sites, permitting little survival (Scour C).

Three types of primary succession habitats were sampled. Lahars formed on meadows on the south slope. Proximity to intact vegetation permitted rapid establishment. Blast B, on a northwestern ridge, was severely impacted by the lateral blast. All vegetation was killed and most soil was removed (del Moral 1993). The Pumice site, on the lower north slope (del Moral et al. 1995; del Moral & Wood 1993), was seared by the blast, and then covered by pumice.

Methods

Sampling

The 10 sites were sampled using permanently marked plots to permit accurate repeated sampling. Species cover was recorded at 1-m intervals on four radii in 0.25 m^2 quadrats. Repeat non-destructive measures permit direct interpretations of colonization and extinction at this scale (Austin 1980). The design is 10 sites characterized by a variable number of permanent 250 m^2 plots that were sampled using 24 0.25 m^2 quadrats each.

Statistics

Species richness (R), mean cover (C) and evenness (E) were calculated for each plot. $E = H'/\ln R$, where H' is the Shannon index. Changes in these measures were tested for significance by ANOVA, followed by between-mean comparisons with the Bonferroni statistic. Pooled plots may differ markedly due to different successional rates. The resultant high variance between samples of a given year often obscured trends. Therefore, linear regressions between year and observations of individual plots on each variable were conducted (Anon. 1994).

Detrended Correspondence Analysis (DCA) was performed with PC-ORD (McCune & Mefford 1997). This program corrects problems associated with input order (cf. Tausch et al. 1995; Oksanen & Minchin 1997; Podani 1997). Detrending was effected in 26 segments. Species with fewer than five occurrences and plots with only one species were removed. Rare species were downweighted.

Turnover

Colonization and extinction percentages were calculated from 0.25-m^2 quadrats during three overlapping intervals. In most cases, comparisons were from 1986 to 1991, 1989 to 1994 and 1991 to 1997. Pumice sampling started in 1989, so comparisons were 1989 to 1992, 1991 to 1995 and 1992 to 1997. Blast A was not sampled between 1988 and 1993. Comparisons were 1986 to 1994, 1987 to 1995 and 1994 to 1997. These analyses permit three independent turnover estimates.

The extinction rate of a species was calculated by modification of the method of Fröborg & Eriksson (1997). Their method is sensitive to the usual preponderance of empty quadrats and to different numbers of quadrats among the sites. Therefore, the index was expressed as a percentage of the number of sampled quadrats (see del Moral 2000 for details): The number of quadrats occupied at $Time_0$ that are empty at $Time_1$, divided by the total number of quadrats times 100% estimates the extinction percent. The colonization rate is the number of quadrats empty at T_0 that are occupied at T_1 divided by the total number of quadrats times 100%.

Results

Community structure

Table 2 summarizes community structure at each site after 18 seasons. Data for these analyses may be viewed at: http://www.biology.washington.edu/delmoral/. Tephra A had the highest cover and high richness. Strong dominance by *Agrostis pallens*, *Lupinus lepidus* and *Pinus contorta* saplings produced low evenness. Tephra B was similar, but dominance was less pronounced. Tephra C is more stressful, reducing richness and cover. Persistent forbs such as *Eriogonum pyrolifolium*, *Penstemon cardwellii* and *Phlox diffusa*, rather than graminoids, dominated this higher elevation habitat.

Cover of secondary successional sites continued to increase and to accrue species. Evenness is higher than in recovered plots. Scour A developed cover close to that of recovered plots, though mosses that were scarce on tephra contributed significantly. Some expected species, such as *Calyptridium umbellatum*, *Hieracium albiflorum*, and *Achnantherum occidentale*, were absent or rare, while *Agrostis pallens*, *Luetkea pectinata* and *Lupinus lepidus* dominated. Many plants survived at Blast A and most expected species occurred. *A. pallens*, *L. lepidus*, *Polygonum newberryi*, *Eriogonum pyrolifolium*, *Achillea millefolium* and *Fragaria virginiana* were common. *Agrostis*, *Luetkea*, *Penstemon* and *Eriogonum* dominated scour B, but richness was low. Common subalpine plants such as *Luetkea* and *Calyptridium umbellatum* dominated scour C. Cover was low on these exposed ridges, but richness was comparable to other secondary sites and the nearby Tephra C.

Primary successional plots had low cover and high evenness. The lahar plots had richness comparable to adjacent tephra, but lower cover. *Abies lasiocarpa* and *Pinus contorta* dominated the plots near forest, while *L. lepidus*, *Penstemon* and *Calyptridium* dominated more isolated ones. Blast B plots were on more protected sites where large populations of *L. lepidus* had established, leading to high cover. *Agrostis* was the only other species with high cover. Pumice plots were the least developed, showing very low cover and very high evenness. *Agrostis scabra* and *L. lepidus* dominated these plots.

Fig. 1 summarizes the changes in richness. Richness increased quickly, then stabilized in recovered plots (Fig. 1a). Secondary plots recovered rapidly by 1983, then gradually accumulated species (Fig. 1b). The lowest richness occurred at Scour B, where colonization requires uphill migration. The primary sites lacked species in 1980 (Fig. 1c). Lahar plots were established in 1982, Blast B plots in 1984 and Pumice plots in 1989. The first plants near the Pumice plots were noted in 1984 (Wood & del Moral 1988). Once establishment started, richness increased steadily.

Table 2. Community structure 18 seasons after the eruption. Plots summarized are those used in DCA and turnover studies. Richness is the mean number of plant species in *N* 250-m^2 plots. Cover is the mean percent cover in 24 0.25-m^2 quadrats in each of *N* plots. Evenness is the mean from the *N* plots.

Study site	N	Richness	Cover (%)	Evenness
Recovered sites				
Tephra A	3	21.3	57.3	0.419
Tephra B	4	22.8	52.7	0.611
Tephra C	4	17.5	30.1	0.710
Secondary succession				
Scour A	4	19.5	49.7	0.569
Blast A	5	18.8	25.8	0.642
Scour B	4	11.8	21.7	0.652
Scour C	5	17.4	13.6	0.644
Primary succession				
Lahar	4	20.2	14.5	0.656
Blast B	6	16.3	19.7	0.650
Pumice	5	15.8	3.8	0.833

Cover responded to weather variation in recovered plots (del Moral & Bliss 1993; Fig. 2a). Tephra A cover increased dramatically in 1981 due to *Agrostis* and *Lupinus* then fluctuated greatly. Tephra B still may be developing since peaks in 1982, 1990, and 1997 were successively higher. Tephra C appears to be stable. Cover in secondary plots continues to increase (Fig. 2b). Fluctuations in Scour A were due to fluctuations in *L. lepidus*. Primary site cover continues to increase (Fig. 2c). Blast B demonstrated large fluctuations in *L. lepidus* cover. While lower elevation plots may be at equilibrium, plots higher on this ridge have low cover. The Pumice site is stressful and establishment was confined to favourable microsites (del Moral 1993). Cover expansion was limited by low nutrients and drought (del Moral & Bliss 1993).

No evenness trends were observed on recovered or secondary sites other than Scour B, where evenness declined as dominance developed. Evenness on primary sites declined as species established, except on Blast B. Here, strong *L. lepidus* dominance yielded low evenness. As other species invaded, evenness similar to that of other primary sites developed.

ANOVA, followed by means-difference tests, were conducted for richness, cover and evenness. Table 3 shows the number of significantly different groups identified by Bonferroni comparisons, with a value of "1" indicating no differences among groups. An asterisk indicates groups that are not sequentially related and not due to succession.

Richness at Tephra B was the only case where structure at a recovered site changed with time. Secondary sites demonstrated significant increases in richness and cover, but evenness declined significantly only on Scour B. Primary sites demonstrated significant responses in most cases, even though among-plot differences obscured patterns. Lahar and Pumice plots each had several clusters of means.

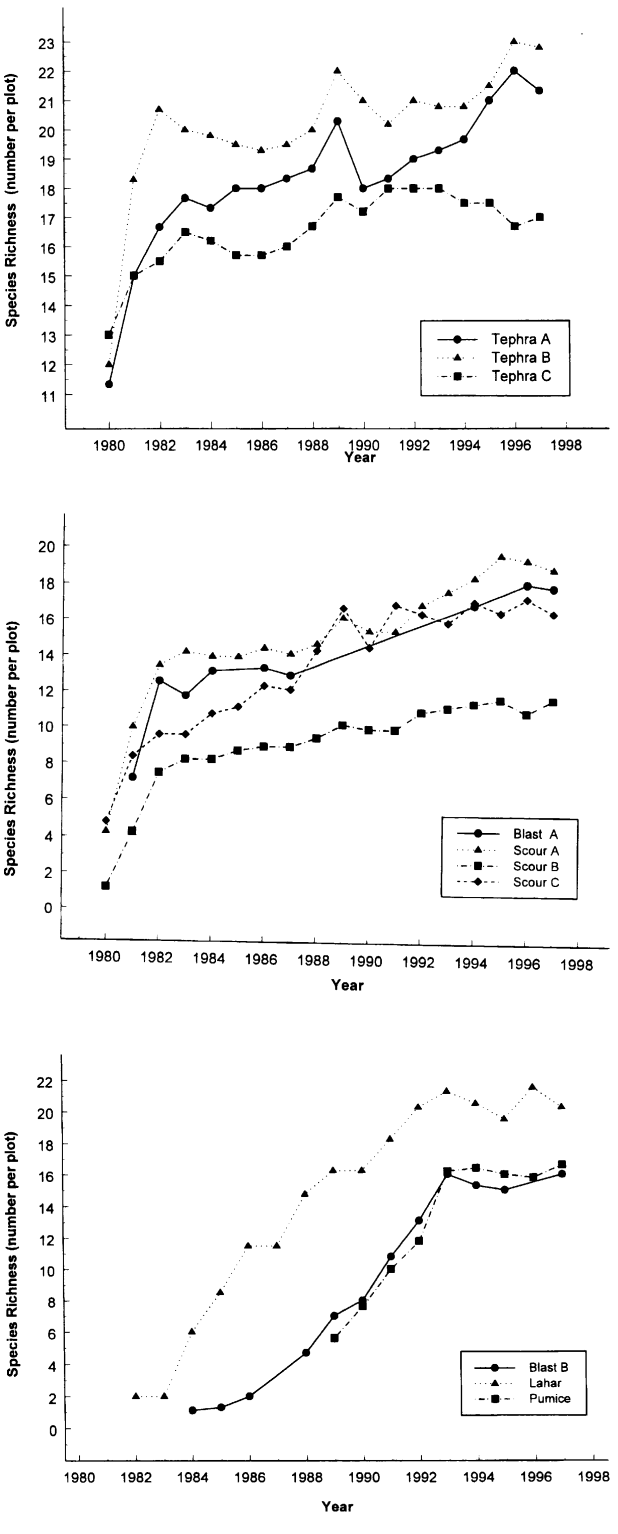

Fig. 1. Changes in richness (mean number of species per 250 m^2 quadrat) in permanent plots; a. recovered sites; b. secondary successional; c. primary successional sites.

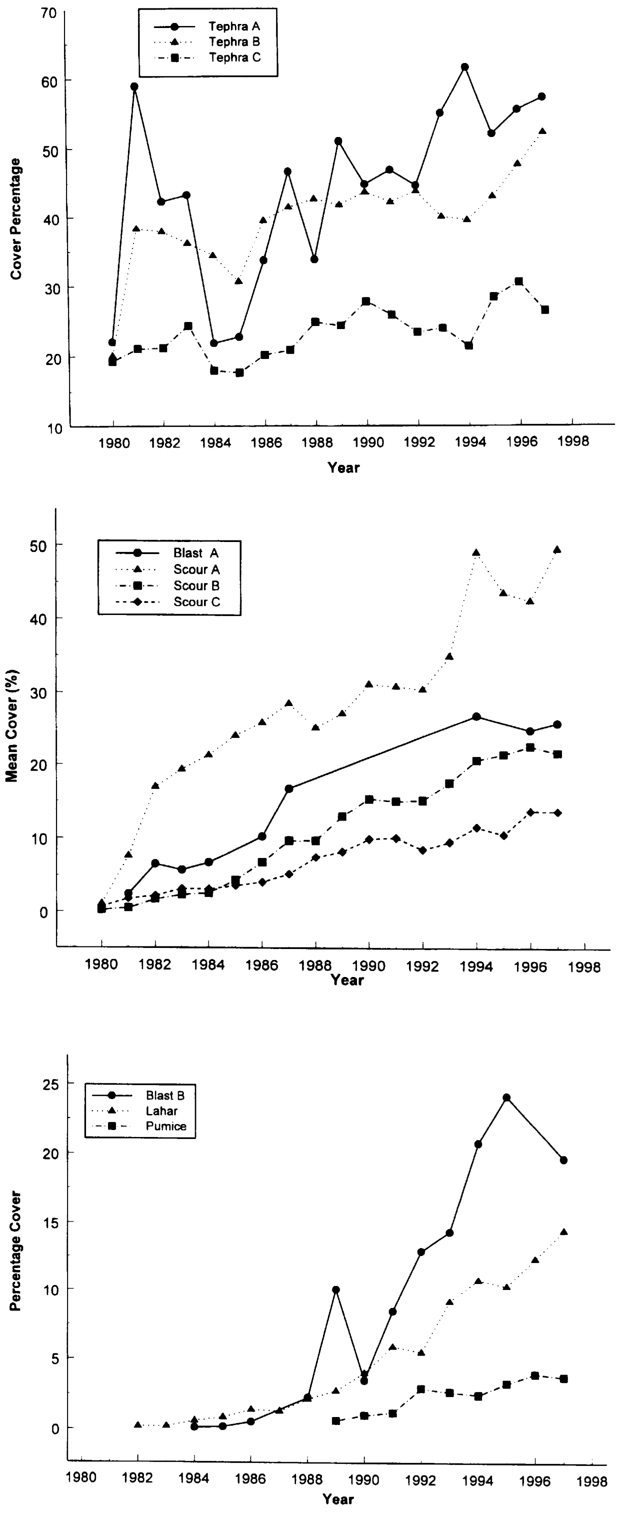

Fig. 2. Changes in cover percentage (mean per 250 m^2 quadrat) in permanent plots; a. recovered sites; b. secondary successional; c. primary successional sites.

Table 3. Number of groups resulting from ANOVA followed by Bonferroni comparisons of the means of richness, cover, and evenness (see Table 2 for definition). Each group consists of means not significantly different ($P < 0.05$) for the structural variable. An * indicates significant differences that were not sequential in time, indicating only response to climatic variation.

Site	Richness	Cover	Evenness
Recovered sites			
Tephra A	3*	4*	2*
Tephra B	3	2*	1
Tephra C	1	1	1
Secondary sites			
Scour A	2	5	2*
Blast A	2	3	1
Scour B	3	3	3
Scour C	2	1	1
Primary sites			
Lahar	6	5	5
Blast B	5	1	1
Pumice	3	3	4

Table 4. Regression index at each site. Richness, cover and evenness as described in Table 2.

Site	Richness	# $P < 0.01$	Cover	# $P < 0.01$	Evenness	# $P < 0.01$
Recovered sites						
Tephra A ($n=3$)	2.33	3	0.67	1	0	0
Tephra B ($n=4$)	2.25	3	2.33	1	0	0
Tephra C ($n=4$)	0.5	1	0	0	2.75	3
Secondary sites						
Scour A ($n=4$)	3.75	4	5.0	4	0.5	1
Blast A ($n=5$)	1.4	2	4.1	5	0.8	1
Scour B ($n=4$)	4.75	4	5.0	4	3.75	4
Scour C ($n=5$)	3.0	3	5.0	5	2.4	3
Primary sites						
Lahar ($n=4$)	5.0	4	5.0	4	4.75	4
Blast B ($n=6$)	5.0	6	3.0	6	1.67	3
Pumice ($n=5$)	2.2	5	2.0	3	0.6	2

Differences between successive years may fall within Bonferroni limits because the combined plots were not replicates. Therefore, linear regressions between year and each parameter were calculated for each plot. A weighted average summarized these regressions (Table 4). The index was derived as follows: A linear regression at $P < 0.01 = 1$; $P < 0.005 = 2$; $< 0.001 = 3$; $P < 0.0005 = 4$; $P < 0.0001 = 5$. The weights were added and divided by the number of regressions to yield the index. This arbitrary index provides a descriptive comparison among the sites and is not intended to test statistical differences.

The number and strength of time-related relationships increased from recovered to primary sites. Cover increased significantly in two of 11 recovered plots, all secondary plots, and all but two primary plots. Pumice showed fewer cover trends because annual fluctuations were large and the recovery small.

Vegetation change

Directional vegetation change was explored by DCA. All data were analysed together to permit direct comparisons of species change. DCA used 58 species in 613 samples. The first three eigenvalues were 0.492, 0.391 and 0.289. The X-axis spanned 3.95 HC, while the Y-axis spanned 3.32 HC. Along X, high values were associated with *Lupinus latifolius*, *Luetkea pectinata* and *Luzula parviflora*. These were species common in late snowmelt habitats. The middle of X included samples from nearly all sites. Between X-values 191 and 199, only the Blast B and Pumice samples did not occur. Primary succession plots dominated the low end of X. Plots with low DCA scores were characterized by sparse cover and dominated by *Anaphalis margaritacea*, *Epilobium angustifolium*, *Hypochaeris radicata*, *Saxifraga ferruginea*, *Juncus mertensianus*, *Carex microptera* and rock crevice ferns (e.g. *Cryptogramma cascadensis*). They also included more widely distributed species such as *Agrostis pallens* and *Lupinus lepidus*.

Sites with very high Y-axis scores were dominated by *Saxifraga ferruginea*, *Polygonum newberryi* and *Carex mertensii*. All Scour C#4 plots had extreme values. Plots missing from the middle were Pumice, Blast B and early lahars, which dominated the low values. The species concentrated with low Y-scores included *L. lepidus*, *A. pallens*, *A. scabra*, *H. radicata* and *Lomatium martindalei*.

Table 5 shows the mean annual Euclidean distance change along DCA X and Y for each plot and the CV of these changes. The mean increment measures the magnitude of annual change, while the CV measures the steadiness of change. Changes are not always unidirectional, as a sample can fluctuate about a mean.

The first two increments where cover was more than 0.3% were compared with the last two increments to determine rates of change (Table 6). This table also shows the net change from first to last samples to indicate overall compositional change.

Mean annual change of Tephra plots was low, despite initially large changes. These sites vary around 0.15 HC/yr; CV was ca. 60%. Early samples changed more than late samples. The directional change ranged from about 0.2 to 0.5 HC in X and from 0.2 to 0.3 HC in Y. Euclidean change ranged from 0.3 to 0.5 HC. Changes in Tephra A plots were associated with the increasing dominance of *Agrostis pallens*, decline of *Eriogonum pyrolifolium* and fluctuations in *Lupinus lepidus* and *Lomatium martindalei*. Changes in Tephra B involved less dramatic increases in *Agrostis*, development of *Danthonia intermedia* and a decline in *Lomatium* and *Lupinus*. Tephra C changes were associated with development of grasses, *Juncus parviflora* and *Penstemon cardwellii*, while *Lupinus* and *Calyptridium* fluctuated.

Table 5. Floristic changes (Euclidean distance) in DCA space; excludes samples with cover less than 0.4%. Units are HC (× 100). Δ_n is the mean annual DCA increment for an individual plot. CV is the coefficient of variation of the increments.

Study Site	Mean D_1	Mean D_2	Mean D_3	Mean D_4	Mean D_5	Mean D_6	Grand Mean
Tephra A	16.0	12.6	12.3	-	-	-	13.6
CV	66.9	60.0	47.6				58.2
Tephra B	13.0	14.5	18.0	14.5	-	-	15.0
CV	55.6	72.1	64.3	33.3			56.3
Tephra C	14.6	10.8	11.1	10.3	-	-	15.1
CV	46.5	55.3	57.6	93.5			63.2
Scour A	11.6	18.5	39.5	17.8	-	-	21.9
CV	99.0	82.6	104.4	89.0			73.7
Blast A	43.2	28.4	41.5	17.9	42.8	-	34.9
CV	78.0	70.8.0	100.2	100.9	115.0		92.8
Scour B	27.2	28.4	17.8	19.6	-	-	23.3
CV	84.9	76.9	92.9	71.6			81.6
Scour C	14.8	43.1	29.3	28.2	15.6	-	26.2
CV	69.5	51.3	125.5	84.7	74.8		81.2
Lahar	31.9	32.7	21.5	40.7	-	-	31.7
CV	112.9	56.2	65.6	82.7			79.4
Blast B	19.3	28.0	42.8	44.6	43.4	51.4	38.3
CV	58.1	146.6	276.2	117.9	120.3	166.2	147.6
Pumice	33.7	28.8	38.1	33.6	27.7	-	32.4
CV	54.1	68.2	40.9	60.5	52.2		55.2

Secondary sites showed substantial mean increment change and all had CVs larger than CVs on tephra. (The increment between 1987 and 1994 in Blast A was excluded from the calculation.) Early recovery substantially exceeded recent changes. Directional change was large, ranging from 0.5 to 1 HC in X and 0.5 to 0.7 HC in Y. Euclidean change ranged from 0.8 to 1.2 HC.

Scour A changes with the increase in *Agrostis*, *Lupinus lepidus*, *Luetkea pectinata*, *Penstemon* and mosses. Several species of *Carex* tended to increase. Blast A changed with the development of *Agrostis*, *Achillea millefolium*, *Castilleja miniata*, *Lomatium*, *Penstemon* and *Racomitrium canescens*, the decline of *Lupinus latifolius* and variation in *L. lepidus*. Scour B also changed with the development of *Agrostis*, *Eriogonum*, *Penstemon* and mosses. Scour C changed primarily with the development of *Carex mertensii*, *Eriogonum*, *Penstemon* and *Polygonum*.

The primary sites had lower cover than other plots, yet their mean annual change was higher than all but Blast A. The contrast between initial and recent changes varied. Initial changes were high, similar to secondary plots. Recent increments were much higher than on recovered sites, and, except for the lahar, higher than secondary plots. Directional X change varied from 0.4 to 0.9 HC, while that of Y was from 0.4 to 1.3 HC. Euclidean change ranged from 0.9 to 1.5 HC. The Lahar changed in response to the development of *Abies*, *Pinus*, *Juncus*, *Luetkea*, *Penstemon*, *Calyptridium*, mosses and several grasses. Blast B fluctuated substantially due to large changes in *L. lepidus*. Directional change occurred in response to the development of *Agrostis*, *Anaphalis*, *Penstemon* and mosses. The Pumice plots have changed in response to *Agrostis scabra*, *Penstemon*, *Calyptridium* and mosses.

Table 6. Floristic changes (two-dimensional Euclidean distance) in DCA space comparing first two annual increments with last two increments. Δ Early is the mean difference between first two increments; Δ Late is mean of the last two increments. DXY is overall mean change in plots during study. Mean ΔX, ΔY and ΔXY are the mean of the extreme values of samples in the ordination space. [Units are HC × 100.]

Study Site	Δ Early	Δ Late	Early/Late Ratio	Mean ΔX	Mean ΔY	Mean ΔXY
Tephra A	17.8	9.5	1.87	45.3	31.8	48.5
Tephra B	15.9	9.9	1.61	28.3	14.5	32.1
Tephra C	12.9	11.3	1.14	20.5	20.0	29.7
Scour A	52.1	11.4	4.56	63.8	61.0	97.1
Blast A	54.3	19.9	2.73	98.2	56.4	118.8
Scour B	35.6	15.9	2.24	62.0	63.0	94.9
Scour C	47.5	15.0	3.17	54	60.8	85.3
Lahar	61.5	14.6	4.21	43.0	123.0	142.1
Blast B	52.9	25.3	2.09	88.2	46.0	101.3
Pumice	41.9	28.9	1.45	63.8	48.2	88.2

Turnover

Table 7 summarizes extinction and colonization percentages for three several-year intervals in each habitat. By 1997, richness was similar among most plots (Fig. 1), but successional plots had lower cover than did recovered ones. There were always more colonization than extinction events, reflected by E/C ratios less than 1.0 in each case.

Extinction percentages were high on tephra (4.6 to 12.3% of total quadrats), moderate on secondary sites (1.2 to 4.9% of quadrats) and low on primary sites (0.6 to 5.2%). Colonization percentages demonstrated no pattern. Tephra sites varied from 3.9 to 17.0 % of the quadrats, secondary sites varied from 5.8 to 15.3% of the quadrat, and primary sites varied from 3.9 to 15.9% of the quadrats. The disparity between these two processes is reflected by the ratio of extinctions to colonizations. These ratios approach 0.9 on recovered sites, vary from 0.26 to 0.45 on secondary sites and from 0.19 to 0.26 on primary sites.

Discussion

Community structure

The degree of development reached by 1997 resulted from combinations of factors. Tephra plots recovered quickly from disturbance. While many plants died, there was no evidence that any vascular plant species was eliminated. Cover doubled in Tephra A within two years, possibly the result of a pulse of nutrients released by decomposing plants (del Moral 1983) and reduced evaporation. Tephra sites differed in elevation and exposure, resulting in different rates of productivity. Cover fluctuated in response to the amount and distribution of summer rain (Pfitsch & Bliss 1988), while evenness increased due to decreasing grass dominance. Changes after 1982 were associated with secular fluctuations in summer precipitation, so there were no meaningful correlations between structure and year.

Secondary successional sites suffered different impacts, but each lost species and was isolated from potential colonists to different degrees. Blast A lost its forest cover, some soil and species with exposed parts. The substrate was unstable, and the site was exposed to drought, high temperatures and wind. Therefore, recovery has been slower than at other sites. Richness continued to increase. Cover remained incomplete. As competitive dominance by species such as *Agrostis*, *Lupinus lepidus* and *Penstemon* continues to be asserted, evenness should decline.

The scours offer direct contrasts of isolation and impact effects. Scour A was close to intact understorey vegetation. Scouring was incomplete and burial shallow (del Moral 1983). This site developed rapidly and now resembles tephra sites. Scour B lost most vegetation (del Moral 1981). Isolation, exposure and the modest dispersal ability of most colonists (Wood & del Moral 1987), have limited species richness. Cover continues to increase, but was half that of Scour A. Scant soil, strong winds and shorter growing season reduced the development rate. Scour C was intensely impacted. It is at high elevation and drought stressed. Because it is near intact vegetation, it has 2/3 more species than Scour B, but only 2/3 as much cover. Changes on secondary sites were time-correlated, despite substantial variation in response to weather patterns. The number of significant cover groups was correlated to the initial impact intensity.

Each primary successional site has developed under unique circumstances. The lahars consist of reworked volcanic material with more nutrients than new substrates (del Moral & Clampitt 1985). They were deposited next to intact vegetation. Rapid dispersal produced richness comparable to that of recovered sites, though the species composition is dramatically different (del Moral 1998). Though not recovered, cover was similar to more extreme secondary sites. Evenness was typical of the open communities studied. Blast B was exposed and continued to receive propagules from up-valley winds. *Epilobium* spp., *Asteraceae*, ferns and mosses were common. Species richness was greater than that of Scour B and cover was high due to *Lupinus lepidus*. This short-lived, nitrogen-

Table 7. Mean extinction and colonization percentages. The extinction to colonization ratio was calculated from the mean percentages. I, II and III represent three comparison periods.

	Recovered			Secondary sites				Primary sites		
Property	Tephra A	Tephra B	Tephra C	Scour A	Blast A	Scour B	Scour C	Lahar	Blast B	Pumice
Extinction Percent I	5.3	4.7	4.6	2.6	1.8	2.5	2.0	0.9	1.8	0.7
Extinction Percent II	12.3	6.3	4.8	2.8	4.9	3.3	1.2	0.9	0.6	1.5
Extinction Percent III	9.1	6.8	6.5	3.7	4.7	4.7	2.5	5.2	4.7	1.8
Mean Extinction %	8.9	5.9	5.3	3.0	3.8	3.5	1.9	2.3	2.3	1.3
Colonization Percent I	17.0	6.5	6.2	5.8	13.2	12.0	5.8	6.2	13.2	3.9
Colonization Percent II	6.1	3.9	7.1	7.6	15.3	8.3	6.8	12.4	15.9	6.1
Colonization Percent III	6.2	10.3	9.3	6.8	6.5	8.7	9.5	7.9	6.5	6.7
Mean Colonization %	9.8	6.9	7.5	6.7	11.7	9.7	7.4	8.8	11.9	5.6
Extinction/Colonization	0.91	0.86	0.71	0.45	0.32	0.36	0.26	0.26	0.19	0.23

fixing species fluctuates significantly over a 4- to 5-yr period (Bishop & Schemske 1998). As a result of its facilitative effect, cover was enhanced on some plots on this ridge. Blast B retains older substrates and protected microsites that enhance the recovery rate. Pumice consists of newly formed material, is isolated, nutrient poor and lacks significant ameliorative features (Wood & del Moral 1988; del Moral 1993). Though species richness was moderate, cover was the least of any in this study. There were few species interactions and evenness was very high. All primary sites showed rapid richness increases, which suggested that richness accumulates more quickly than other aspects of structure. Lahar and pumice sites have demonstrated significant cover and evenness changes. Blast B lacks significant cover and evenness groups, an artifact of large fluctuations in *L. lepidus*.

Regressions of the structural values of individual plots through time eliminated the pseudoreplication problem. Significant ($P < 0.05$) richness increases occurred in all but two Tephra sites and one Blast A plot. The strength of these relationships varied with impact intensity. Cover relationships were moderate on secondary sites, which started with low cover but have gradually accumulated biomass. Low cover on Pumice and extreme *L. lepidus* variation on Blast B obscured cover relationships on primary sites.

Evenness is sensitive to changes in both cover and richness. Declining evenness indicates the development of a dominance hierarchy. This pattern is best revealed on scours and the lahar where initial cover was very low and different species developed differentially. Evenness remains high on most pumice plots. Evenness of Blast B plots varied with *L. lepidus* fluctuations.

Detrended Correspondence Analysis

DCA permits direct comparison of the rates and direction of vegetation change in permanent plots through time. This study confirmed that responses to disturbance are related to impact intensity and isolation. Equally isolated sites developed differently in response to local factors, such as soil fertility.

Annual change (Δ), net change and fluctuation (CV) were small in recovered plots. These measures form a baseline of normal variation. Annual changes on secondary sites were large and moderately directional. The recent rate of change of Scour A was similar to that of tephra, its annual change was the lowest of successional sites and its CV was the least of the moderately vegetated sites. Two-dimensional movement that is about three times that of tephra reveals its successional status. Blast A changed substantially between years. The annual increment was high because, in addition to the increase of species adapted to open conditions, there was a marked decline of *Lupinus latifolius*. Thus, the net change was the highest among secondary sites. The other scours experienced moderate annual change, were highly variable and changed substantially at first, less so more recently. The net change of secondary sites was three times that of the tephra sites.

All primary sites changed significantly between years. Lahar variation was comparable to that of secondary sites, but low cover on Pumice led to low annual variation. In contrast, Blast B had very high annual variation, due to *L. lepidus* variation. Net change on Pumice was low, but recent changes were the highest of any site. The rate of development on Blast B was accelerating in more exposed plots.

DCA permitted a direct comparison among the sites. It demonstrated that each had a unique response to the disturbance regime. The details of the numerical response are affected by richness and cover, but the analysis is robust, and readily revealed patterns. These results support the finding of Myster & Pickett (1994) that early change is usually more rapid than later change.

Turnover

The concept of local species turnover is embedded in the lottery model (Lavorel & Lebreton 1992; Laurie & Cowling 1995), the carousel model (van der Maarel & Sykes 1993), mass effect (Shmida & Ellner 1984), the hierarchical continuum concept (Hoagland & Collins 1997) and the core and satellite hypothesis (Hanski 1982; Collins et al. 1993). The turnover rate at small scales in stable meadows is high (Herben et al. 1997). Tsuyuzaki (1991) found turnover early in volcanic succession to be dominated by colonization, with few extinction events in large quadrats. Fröborg & Eriksson (1997) showed that local colonization and extinction in a stable forest understory at a scale of 100 m^2 were high, and that some of this effect was correlated to seed weight and dispersal types. Van der Maarel et al. (1995) suggested that there was little evidence for niche structure on a small scale, indirectly supporting a carousel model (but see Kikvidze 1993). Van der Maarel & Sykes (1997) quantified the rate of local mobility among species and found it much larger than generally recognized.

The present study indicates that species do have high local mobility. It differs from previous studies of local turnover in two ways: it explores an intermediate scale and it investigates the process against a successional background. Species present in 1986 may have survived the 1980 impacts, arrived by long-distance dispersal or grown into the quadrat. Once present, a plant may be lost by senescence (e.g. *Lupinus lepidus*, *Hypochaeris radicata* or *Hieracium gracile*), disturbance (e.g. elk or gopher), dieback or competitive displacement.

Extinction percentages declined from recovered to primary sites as expected. The decline occurred because there were fewer quadrats with species at risk in primary sites than in stable ones. Colonization events were more numerous than extinction events and colonization percentages were high. Empty quadrats are colonized at similar rates on all sites. No trends were evident. However, the ratio of extinction percentage to colonization percentage provides a basis for comparison. In recovered sites, extinction events are nearly as frequent as colonization events. In secondary sites, they are only one-third as common and on primary sites they are one-fourth as common. All habitats are dynamic at this scale.

Small-scale extinction and colonization appear to be based on life histories, dispersal ability and proximity to seed sources. Some deterministic extinction may have occurred, but rates were high in open quadrats. Colonization percentages were no lower in recovered sites than the others, suggesting that the presence of less open vegetation does not inhibit invasion. Stochastic extinction and colonization appear to dominate local population dynamics in most cases.

This study examined succession in permanent plots from three perspectives and provided insights into mechanisms of community assembly. Each site has a different combination of impact intensity and type (Walker 1999), biological legacies (Franklin et al. 1985) and isolation (del Moral 1993). Isolation creates a selective filter that limits colonization rates. Isolated sites have a species composition distinct from similar sites near sources of colonists. Site stress affects cover strongly and has some impact on species composition. The principal site factor is substrate age. New surfaces (pumice, pyroclastic materials) had the least cover. Old devastated surfaces (blasted ridges, scours) may develop more quickly, but the details depend on stress factors. Reworked old substrates (lahars) can support many species and moderate cover, but isolation effects have been noted on some lahars (del Moral 1998).

The developing meadow vegetation of Mount St. Helens demonstrates high rates of local colonization and extinction. Successional status affects these rates, but the composition of each site is dynamic. These results, obtained in recovered and successional sites with diverse traits, support the carousel model. The species in these habitats do not have narrow, discrete niches. Therefore, they may coexist or they may replace one another in a non-deterministic way.

Acknowledgements

National Science Foundation Grants BSR-89-06544 and DEB-94-06987 provided funds for this study. The Mount St. Helens National Volcanic Monument staff facilitated this study. I am particularly grateful to Helen de la Hunt, Katrina Dlugosch, Roger Fuller, Richard Robham, Jon Titus and David Wood, who all made significant contributions to data collection. The manuscript was improved by valuable input to the manuscript from Beth Brosseau, Roger Fuller, Chad Jones and Dennis Riege, as well as by two anonymous reviewers. Perceptive papers by Prof. Eddy van der Maarel stimulated this study.

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