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Spatial factors affecting primary succession on the Muddy River Lahar, Mount St. Helens, Washington

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Abstract Primary succession is controlled by a combination of landscape and habitat factors whose actions may be stochastic or deterministic. The 1980 eruption of Mount St. Helens, Washington spawned a massive lahar that now supports a mosaic of vegetation. Our goals were to describe vegetation patterns after 28 growing seasons, determine the factors associated with these patterns, and to contrast the effects of stochastic and deterministic processes. We described species composition and explanatory factors that included location and habitat features in one hundred and fifty one 200-m^2 plots. We classified these plots into nine community types (CTs) that were distinguished quantitatively by variations in dominant species. We used multiple regressions, redundancy analysis (RDA), and Mantel tests to compare the vegetation relationships with explanatory factors. Plots in different CTs mingled spatially and in multivariate space. Species patterns were weakly related to explanatory variables by RDA (31.6% of the species variation). RDA indicated that vegetation was most strongly related to elevation, latitude, and isolation, which are primarily landscape factors. Mantel tests confirmed that factors associated with elevation were most closely associated with vegetation. The effects of arrival order were suggested by the dominance of different colonizers in similar environment and by plots with similar vegetation found in different habitats. We concluded that species composition cannot be predicted well from the data available, suggesting that there were no prominent deterministic assembly rules.

Keywords Assembly rules · *Lupinus lepidus* · Mudflows · Priority effects · Redundancy analysis · Vegetation gradients

Introduction

Mount St. Helens is a unique setting to explore primary succession and to unravel the mechanisms that shape community assembly. We describe vegetation patterns on a lahar formed in 1980. Our goals were to provide a description of vegetation patterns, determine factors associated with these patterns, and seek evidence for priority effects. A chronosequence study would be ideal to demonstrate vegetation change (Clarkson 1998; Smits et al. 2002), but a survey of vegetation can provide insights into dynamics. There are few detailed studies of early primary succession on volcanoes (cf. Tagawa 1964). This deficiency has hampered the understanding of how species assemble (del Moral et al. 2007; Walker and del Moral in press). Appreciating early species assembly on volcanoes could help to streamline restoration on devastated landscapes (e.g., mine

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spoils) by illuminating factors that retard invasion, establishment, or development (del Moral and Walker 2007; Parsons et al. 2007; Walker et al. 2007).

Early studies on Mount St. Helens showed that barren sites need physical amelioration (Wood and del Moral 1987) before establishment can occur (Wood and Morris 1990). Colonization was affected by erratic dispersal (Walker and del Moral 2003) which permits different species to establish in similar habitats. Different arrival orders produce priority effects (D'Antonio et al. 2001) that can alter successional trajectories (Eriksson and Eriksson 1998; Wiegleb and Felinks 2001; Seabloom and van der Valk 2003). Favorable microsites improve establishment (Tsuyuzaki and Titus 1996; Titus and del Moral 1998), although pioneers may inhibit further invasion (e.g., Hooper et al. 2005). Facilitation (Bellingham et al. 2001; Gosling 2005), competition (Fraser and Keddy 2005), allelopathy (MacKenzie and DeLuca 2006), and herbivory (Bishop 2002; Fagan et al. 2005) begin early in succession and guide trajectories. While random events can dominate species assembly (cf. del Moral and Grishin 1999), more deterministic patterns may develop over time (Hodkinson et al. 2003).

We ask: are vegetation patterns linked with proximity to colonizers (landscape) or to habitat factors (surface characteristics or correlates of elevation)? If species distributions during early succession were related to isolation, we could conclude that stochastic dispersal effects are important. If habitat factors explained vegetation patterns better, then deterministic processes may have overcome stochastic dispersal effects. Determinism implies that species assembly can be predicted by rules (Holdaway and Sparrow 2006).

Methods

The study site

The 18 May 1980 eruption of Mount St. Helens created a diverse, devastated landscape (Swanson and Major 2005). Intense heat caused glaciers to melt rapidly, forming massive lahars and thick surges of debris that scoured the east flank and filled the Muddy River valley. Sand deposits about 1 m thick were mixed with boulders. Later erosion formed a new drainage (Fire Creek) near the southwestern edge of the lahar. It now joins the Muddy River near the eastern edge of the study area. Both channels eroded quickly to form wide, deep gullies. Subsequent eruptions deposited up to 0.5 m of pumice. Since pumice rocks disintegrate quickly, their cover declined gradually down the lahar as deposits became thinner and pumice size declined.

This lahar was described by Halpern and Harmon (1983) in 1981. They found that plant cover and species richness declined with distance from the forest and that nothing grew over most of the area of the present study. Our 2002 study found that isolation, later snow melt, and lower temperatures at higher elevation retarded the development of homogeneous vegetation (del Moral and Ellis 2005). Weber et al. (2006) described conifer invasion on the Lower Muddy River that was much faster than on our study area.

Plot locations

This survey covered 5.1 km^2 of the upper Muddy River lahar between 900 and 1320 m a.s.l. (Fig. 1). We excluded intact vegetation along the edges of the lahar, scoured areas on the cone, sites covered by silt

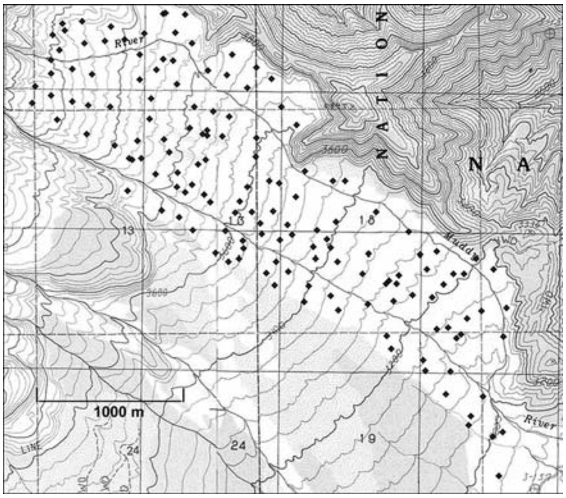

Fig. 1 Topographic map of the Muddy River lahar study area (southeast flank of Mount St. Helens), showing locations of the 151 plots. Recently scoured channels of Muddy River and Fire Creek (the southwestern drainage) are reflected by gaps in sampling. Dark gray, intact forest; light gray and stipples, open forest damaged by lahar. Contour intervals = 20 ft (6.09 m). Study was conducted between 900 and 1,320 m a.s.l. in summer 2007

in 2006, and active drainages. We determined provisional plot locations on a topographic map (National Geographic Society 2001) prior to the study to ensure adequate sampling. Five were on rises within the lahar where soil and some conifers survived. Plot positions were sometimes adjusted to avoid recent disturbances. Erosion from heavy winter 2006 rains had significantly widened creek banks, so some sites positioned in drainages were moved. Spacing between plots along transects was between 70 and 170 m (Fig. 2). We sampled 151 plots during July and August, 2007. Typical views of the lahar are shown in Figs. 3–5.

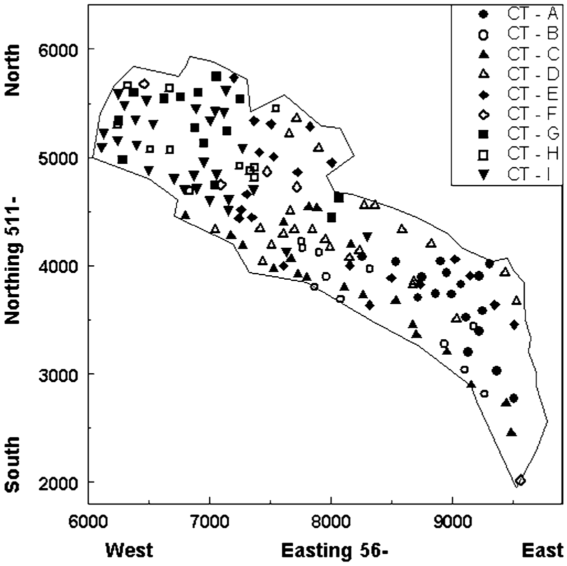

Fig. 2 Location of plots designated by nine community types (CT) revealed by agglomerative classification. Easting is in grid 10T50; Northing is in grid 511 (WGS084 datum)

Fig. 3 From the middle of the Muddy River lahar looking uphill (west-northwest), conifers are sparse with mixture of low shrubs and mosses in the foreground. Dense conifers in middle ground, right are on the "island" spared most of the devastation from the lahar

Fig. 4 From the lower Muddy River study area, near its southwestern edge, where conifers are relatively dense. Dead, standing "snags" are trees killed by the 1980 lahar

Fig. 5 From the southwestern edge of the Muddy River lahar study area, looking northeast. Conifer invasion is advanced, but trees remain scattered

Field data

Plots were 200-m^2 circles (8-m radius) within which we recorded WGS084 latitudes and longitudes and elevations. Aspect (compass bearing) was converted to a 5-point scale to reflect insolation: 1 = 330° (through 0°) to 45°; 2 = 46°–80° and 280°–329°; 3 = 81°–115° and 245°–279°; 4 = 114°–135° and 210°–244°; and 5 = 136°–209° (Whittaker 1956). Slope was determined with a clinometer. The percentage of the plot covered by lava rocks (diameter >25 cm) and the percentage of the plot covered by pumice pebbles >5 cm were estimated. The prevalence of rills (small drainages) was determined from their occurrences in quadrats: 0 = 0 rills; 1 = 1–2 with rills; 2 = 3–4 with rills; 3 = 5 with rills. Distance from intact vegetation (isolation) was determined from the map and converted to a 4-point scale that took prevailing winds into account (del Moral and Ellis 2005): 1 = <200 m from western edge; 2 = 200–400 m from western edge; 3 = 400–500 m from western edge; 4 = >500 m from western edge. These are “explanatory variables,” and are divided into landscape factors (position and isolation) and habitat factors (rocks, pumice, rills, insolation, and slope). Elevation is a complex variable that combines habitat (e.g., effective moisture and growing season) and landscape factors.

The vertical projection of plants was determined in 12 1-m^2 quadrats at 2 m intervals along each of four radii and expressed in percentage. The unsampled species within the plot were given a score of 0.1%. Mean plot cover was determined by summing the values of the species and could exceed 100%. Nomenclature was determined from the Integrated Taxonomic Information System (ITIS; http://www.itis.gov/; see the Appendix).

Statistics and data analyses

Species in each plot were counted (richness = α). Mean percent cover was used to calculate the Shannon diversity index ($H' = [-\Sigma p_i \log p_i]$) and equitability [$\mathrm{E} = H'/\ln(\alpha)$], where p_i is the proportion of the cover represented by ith species.

We classified the plots into community types (CTs) using flexible sorting and Euclidean distance. We applied multi-response permutation procedures (MRPP) to these CTs to assess the validity of differences among them (McCune and Mefford 2006). MRPP calculated a weighted mean within-group distance and a T-value determined the degree to which groups were distinct. A (0–1.0) evaluated the degree to which groups were homogeneous compared to a random classification. Total species richness of each CT (γ) was determined by inspection.

We explored the relationship between vegetation and explanatory variables with redundancy analysis (RDA; ter Braak and Šmilauer 1998). A virtue of RDA is that, unlike unimodal canonical methods (ter Braak 1986), it uses linear regressions to assess the relationship between explanatory variables and vegetation. RDA was appropriate because species turnover (β) was low, signifying that most species change linearly. The first detrended correspondence analysis axis was 2.5 half-changes (β). Whittaker’s β_w [(mean richness/total richness) − 1] was 2.9, also suggesting that linear methods were appropriate (Legendre and Anderson 1999).

The matrix of Pearson correlations (r) among variables showed that elevation and longitude were strongly correlated ($r = -0.98$), so we excluded longitude from RDA. Percent cover was square-root transformed to improve the accuracy of the assumptions of linearity, normality, and variance of homogeneity (McCune and Grace 2002). The species were first regressed to the explanatory variables by creating fitted species scores. Principal components analysis (PCA) produced plot scores in fewer dimensions. The linear equations that best specified the position of plot scores with the explanatory variables were used to create new plot scores, which are “constrained” values related to the explanatory variables. The more closely the constrained scores resemble the plot scores, the more the species variation is “explained.” The efficacy of RDA was assessed by stepwise multiple regressions of explanatory variables (Lepš and Smilauer 2003). After each step, the variance explained by a variable was compared to 2,000 permutations of the null model that they bear no relationship with plot scores. The correlation of variables to the RDA axes estimated how well each variable was related to vegetation. The residual variation implied the degree to which unmeasured variables, sampling error, and random or contingent effects were important. Finally, the importance of the regression coefficients was estimated from their t-values.

We used Mantel tests to compare a matrix of Euclidean distances of plots based on species with matrices of plots based on all explanatory data and on subsets of these data (Douglas and Endler 1982). As the similarity of two matrices converges, the difference between the observed Z (Z_{ob}, sum of the cross products of the corresponding matrix elements) and the expected Z (Z_{ex}, determined from 1,000 trials of randomized rows in the explanatory matrix) increases. The method provides a t-value and the Mantel statistic value (r).

We used Statistix® (Analytical Software 2003) to make statistical tests. These included one-way analysis of variance (ANOVA) evaluated by the Bonferroni test for differences among means and multiple regressions. Nakagawa (2004) criticized the ultra-conservative Bonferroni test because it can falsely declare no difference when differences exist. However, since we seek only to illuminate patterns and not to test hypotheses, the test is appropriate. We used MVSP® (Kovach 1999) to calculate the similarity among the quadrats of a plot.

Results

Community composition and structure

Nine CTs were identified by agglomerative clustering (Table 1) and confirmed by MRPP. The chance-corrected, within-group agreement, *A*, was 0.602 ($T = -50.6$; $\delta = 0.198$, $P < 0.00001$), indicating that group compositions differed significantly. Each comparison between groups was significant as were all individual comparisons (*T*-values from −8.8 to −28.8). The composition (Table 1) and structure (Table 2) of each CT are described in groups of increasing elevation.

CT-A (*Lupinus lepidus*–*Penstemon*–conifers–*Racomitrium*) covers much of the lower lahar. *Racomitrium* and *L. lepidus* dominated, while

Table 1 Mean percent cover of species common in the nine CTs

Community type (*N* plots in type)										
Species	A (17)	B (11)	C (20)	D (24)	E (21)	F (5)	G (14)	H (11)	I (28)	*P*-value
Lupinus lepidus	**21.70^{c}**	1.56^{a}	2.70^{ab}	8.42^{bc}	6.91^{b}	1.20^{a}	**20.32^{c}**	0.96^{a}	1.77^{a}	<0.0001
Hypochaeris radicata	0.98^{a}	0.06^{b}	0.06^{b}	0.20^{b}	0.14^{b}	0.00^{b}	0.07^{b}	0.02^{b}	0.04^{b}	<0.0001
Hieracium albiflorum	0.49	0.19	0.16	0.28	0.24	0.08	0.29	0.23	0.14	0.003
Pseudotsuga menziesii	4.28^{a}	**9.88^{b}**	2.94^{a}	2.35^{a}	2.34^{a}	0.22^{a}	0.57^{a}	0.49^{a}	0.54^{a}	<0.0001
Polytrichum juniperinum	5.87^{bc}	3.52^{ab}	1.37^{a}	1.95^{a}	1.83^{a}	**9.72^{c}**	2.16^{a}	3.46^{ab}	1.24^{a}	<0.0001
Abies procera	0.87	0.37	0.53	**2.81**	**2.92**	0.02	2.54	2.56	1.59	0.005
Tsuga mertensiana	0.20	0.23	0.08	0.13	0.11	0.00	0.19	t	0.04	ns
Salix spp.	0.20	0.50	0.15	0.54	0.68	0.02	0.78	0.19	0.26	ns
Populus balsamifera	t	0.00	t	0.05	0.07	0.00	**3.07**	0.00	0.00	ns
Chamerion angustifolium	0.02^{a}	0.05^{ab}	0.03^{a}	0.01^{a}	0.03^{a}	0.00^{a}	0.12^{b}	0.04^{a}	0.02^{a}	0.007
Racomitrium canescens	**39.94^{d}**	**29.26^{c}**	**53.19^{e}**	**32.00^{c}**	**18.46^{b}**	**9.96^{ab}**	3.78^{a}	4.15^{a}	4.32^{a}	<0.0001
Fragaria virginiana	0.12	0.56	0.23	0.10	0.32	0.06	0.04	0.26	0.03	ns
Alnus viridus	0.05	**3.07**	0.82	0.38	0.78	0.00	**3.11**	0.00	0.21	ns
Penstemon cardwellii	3.46^{a}	**14.06^{b}**	4.13^{a}	4.03^{a}	3.31^{a}	4.20^{a}	1.09^{a}	3.36^{a}	1.11^{a}	<0.0001
Castilleja miniata	0.00	0.52	t	t	0.02	0.20	t	0.17	0.21	ns
Abies lasiocarpa	0.00^{a}	0.08^{ab}	0.01^{a}	0.04^{a}	0.10^{a}	0.02^{ab}	0.24^{ab}	**3.21^{b}**	0.06^{a}	0.02
Carex rossii	0.04	0.71	0.18	0.25	0.32	**1.26**	0.29	0.76	0.73	ns
Arctostaphylos nevadensis	1.31^{b}	5.15^{b}	5.59^{b}	0.65^{b}	1.09^{b}	**49.3^{a}**	1.34^{b}	3.32^{b}	1.91^{b}	<0.0001
Pinus monticola	0.12^{a}	1.70^{b}	0.24^{a}	0.44^{a}	0.66^{ab}	0.04^{a}	0.26^{ab}	**3.66^{b}**	0.19^{ab}	0.021
Juncus parryi	0.34^{a}	0.24^{a}	0.55^{a}	1.09^{bc}	0.66^{ab}	0.24^{a}	**1.67^{bc}**	0.75^{ab}	1.24^{ab}	0.0001
Pinus contorta	0.45	2.54	2.17	0.63	0.67	0.04	0.06	**3.32**	0.34	0.01
Anaphalis margaritacea	0.10	0.35	0.58	0.32	0.24	0.26	0.30	0.44	0.39	ns
Eriogonum pyrolifolium	0.00	0.00	0.03	0.06	0.00	0.02	0.15	0.09	0.17	ns
Vaccinium membranaceum	t	0.08	0.03	0.05	0.20	0.82	0.04	0.86	**1.02**	ns
Agrostis scabra	t	t	0.02	0.03	0.08	0.00	**1.53**	0.28	0.19	ns
Agrostis pallens	0.11	0.27	0.20	0.11	0.28	1.16	0.71	**3.97**	1.44	0.005
Luetkea pectinata	0.04^{b}	0.06^{b}	0.13^{b}	0.15^{b}	0.17^{b}	0.22^{b}	1.18^{b}	**2.86^{a}**	1.13^{b}	<0.0001
Cistanthe umbellata	0.06	0.05	0.26	0.30	0.21	0.00	0.10	0.09	0.24	0.02
Lupinus latifolius	0.12^{ab}	1.55^{bc}	0.62^{ab}	0.19^{a}	0.89^{ab}	1.52^{ab}	0.29^{ab}	**3.91^{c}**	0.49^{a}	<0.0001

Species ordered by two-dimensional position in RDA reflects an elevation gradient. *Salix* rarely flowered and was difficult to ascribe to species with certainty. Bold values are species characteristic in the CT. ns, not significant; t, trace < 0.01

Note: Superscripts unite members of homogeneous groups (Bonferroni comparisons $P < 0.05$)

Table 2 Mean structure characteristics of CTs

CT	γ	α	Cover (%)	H'	E
CT-A	35	15.9^{ab}	81.4^{d}	1.414^{bc}	0.516^{b}
CT-B	38	17.9^{bc}	77.3^{cd}	1.683^{bc}	0.588^{bc}
CT-C	40	16.4^{ab}	77.7^{cd}	1.058^{a}	0.382^{a}
CT-D	51	18.3^{bc}	57.9^{bc}	1.461^{ab}	0.504^{b}
CT-E	49	19.3^{c}	44.3^{b}	1.708^{bc}	0.578^{b}
CT-F	25	13.2^{a}	80.4^{cd}	1.202^{ab}	0.473^{bc}
CT-G	46	18.7^{bc}	46.7^{b}	1.637^{b}	0.561^{b}
CT-H	34	17.4^{bc}	43.8^{b}	2.049^{c}	0.723^{c}
CT-I	46	16.5^{ab}	22.0^{a}	2.002^{c}	0.719^{c}
P		<0.0002	<0.0001	<0.0001	<0.0001

P, level of significance for the analysis of cover for the species determined by ANOVA; γ, overall species richness; α, mean per plot richness; H', diversity; E, evenness. (Sample sizes as in Table 1)

Note: Superscripts unite members of homogeneous groups (Bonferroni comparisons $P < 0.05$)

Penstemon was common. A mixed collection of conifer species was scattered throughout these plots. Cover was high, H' and E were low. The exotic species *Hypochaeris radicata* has its highest cover here. CT-B (*Pseudotsuga–Penstemon–Alnus–Racomitrium*) had the highest cover of *Pseudotsuga* and *Penstemon*, second highest *Alnus* cover, ground layer dominance by *Racomitrium,* and substantial cover by *Polytrichum*, *Arctostaphylos*, and *Pinus*. H', E, and γ, were moderate, cover was relatively high. CT-C (*Lupinus lepidus–Racomitrium*) was widespread. Prostrate woody species (e.g., *Arctostaphylos* and *Penstemon*) were common and conifers were locally abundant. Cover was moderate, while H' and E were low due to the strong dominance by mosses and shrubs.

CT-D (*Lupinus lepidus–Racomitrium*–mixed herbs) was similar to CT-A and CT-C, but with more *Juncus parryi*. Cover, H', and E were moderate, and α was relatively high. Plots occupied diverse habitats, resulting in maximum γ richness. CT-E (*Lupinus lepidus*–conifers–*Penstemon–Racomitrium*) included two sites with only moderate disturbance. They shared ground layer similarities with plots on new substrates. *Abies procera* reached its highest concentration here and surviving trees of *Pseudotsuga menziesii* were on the relicts. *Cistanthe* and *Anaphalis* were common forbs, while *L. latifolius* was locally abundant near conifers. Cover was moderate and α was the highest of any CT. CT-F (*Arctostaphylos*–mosses) occurred sporadically over the range of elevations. Three plots occurred near the relict island: one at low elevation among conifers, and two at high elevation. *L. latifolius* and *Carex* were locally abundant. Dense *Arctostaphylos* was associated with low γ, low α, H', and E, and an open overstory of conifers.

CT-G (*Lupinus lepidus–Populus–Alnus*–mixed herbs) was characterized by tall shrubs and trees. *Populus* rarely occurred elsewhere and *Salix* cover was the highest. Maximum cover of *Juncus*, *Agrostis scabra*, and *Chamerion* occurred. α, H', and E were high, and cover was moderate. CT-H (Conifers–*Agrostis pallens–Luetkea–Lupinus latifolius*) was heterogeneous (H' and E both maximal) and might be further divided if a detailed analysis were our intent. No species has developed strong dominance. Several ground layer species (e.g., *A. pallens*, *Luetkea*, and *L. latifolius*) were at their highest concentrations. CT-I (Mixed herbs–*Racomitrium*) lacked strong dominance, reflected by high H' and E and had low cover. Only *Racomitrium* and *L. lepidus* occurred consistently, but at much lower values that elsewhere. Graminoids (*Juncus, Carex*, and *Agrostis*) were widespread.

While the structure of these CTs differed significantly, there were broad overlaps in each measure (Table 2). There were 68 species in the survey. The number of species in a CT ranged from 25 to 51. Mean richness per plot varied from 13.2 to 19.3 species and decreased with elevation. Percent cover declined from 80% to 20% with elevation, reflecting declines in mosses on exposed sites and increases in conifers near forest vegetation.

Spatial and environmental patterns

Environmental factors distinguished the CTs, although weakly (Table 3, Fig. 6). The CTs were poorly distinguished by isolation, although a weak gradient of isolation existed between CTs B to C and CTs G to I. Pumice was related to elevation, so we expected segregation by pumice to be strong. Rills distinguished CT-E from CT-F and CT-H from CT-I. Rocks divided CTs A to E from CTs F, H, and I. Lava boulders were entrained in the lahar. Rocks were usually exposed on lower sites were the lahar is thinner. While each CT had a unique combination of

Table 3 Mean environmental values of CTs

CT	Long.	Lat.	Elev. (m)	Isol.	Pum (%)	Rill	Rock (%)
CT-A	9,007^{c}	3,670^{a}	977^{a}	2.35^{ab}	7.7^{a}	0.471^{ab}	34.1^{ab}
CT-B	8,371^{bc}	3,680^{a}	1,015^{ab}	1.54^{b}	26.8^{ab}	0.727^{ab}	39.1^{a}
CT-C	8,136^{b}	3,791^{a}	1,045^{ab}	1.48^{b}	33.6^{ab}	0.650^{ab}	40.2^{a}
CT-D	8,131^{b}	4,294^{ab}	1,059^{b}	2.04^{ab}	45.2^{abc}	0.500^{ab}	42.7^{a}
CT-E	8,001^{b}	4,477^{ab}	1,082^{b}	2.14^{ab}	51.1^{bc}	1.000^{b}	39.3^{a}
CT-F	7,660^{ab}	4,408^{ab}	1,113^{bc}	2.40^{ab}	57.0^{bcd}	0.000^{a}	6.40^{c}
CT-G	6,974^{a}	5,239^{b}	1,200^{c}	2.46^{ab}	79.6^{cd}	0.857^{ab}	20.0^{ab}
CT-H	6,919^{a}	5,131^{b}	1,203^{c}	2.91^{a}	91.3^{d}	0.091^{a}	14.6^{bc}
CT-I	6,846^{a}	5,020^{b}	1,209^{c}	2.81^{a}	88.3^{d}	0.786^{ab}	14.5^{bc}

Overall patterns of listed variables were significant at $P < 0.0001$, except Rills ($P < 0.01$). Aspect and slope did not differ and were excluded from this table. Long., longitude from west to east; Lat., latitude from south to north; Elev., elevation; Isol., isolation index, distance from intact vegetation; Pum, pumice

Note: Superscripts unite members of homogeneous groups (Bonferroni comparisons, $P < 0.05$)

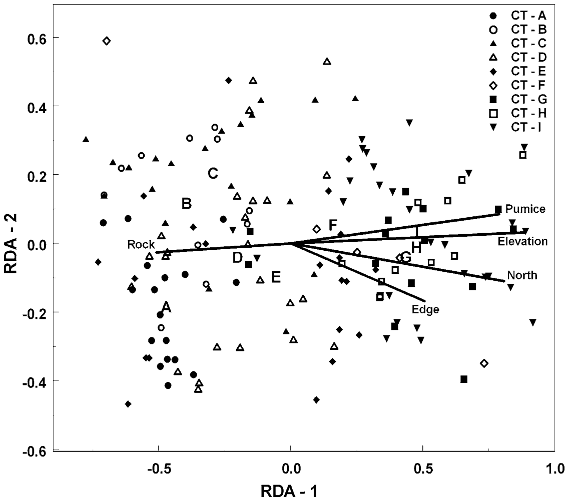

Fig. 6 Redundancy analysis bi-plot of samples and five significant explanatory variables. Lengths of the vectors indicate strength of the relationship of the variable to the RDA axis (vector lengths multiplied by two for clarity). By convention, vectors start at the center of the graph, but their tails extend an equal distance in the opposite direction. Mean position of the CTs are shown with large capital letters

features, individual plots in different CTs had similar explanatory variables.

Inspection of spatial distributions of plots within a CT suggested only weak correspondences between species patterns and landscape variables. In order to explore this relationship, we selected five sets of five proximate plots along an elevation gradient. Three different CTs occurred in each set. Within each CT, there was substantial spatial and environmental variation. Elevation differences within CTs ranged from 140 to 350 m (overall range 419 m). All CTs included plots with <10% rocks, while all but CT-F had plots with rock percentage >40%. Most CTs had several plots without rills, yet all except CT-F also had individual plots containing several rills.

We explored species responses to the explanatory variables with stepwise multiple regression. Sixteen of 39 species were related to one or more variables (Table 4), but the explained variation was low. Elevation was significant for 11 species. Six of the first seven species listed declined with increase in elevation, while the last five increased with elevation. Each species demonstrated unique responses to its location. *Lupinus lepidus* increased with isolation from the western edge. *Hypochaeris* occurred in more isolated sites. *Hieracium* responded weakly to warmer sites (insolation). *Polytrichum* was more common at higher elevations (latitude), in more isolated habitats, and on less eroded surfaces (few rills). *Abies procera* increased with latitude and decreased with isolation. *Racomitrium* increased in exposed sites, rockier locations. *Fragaria* was concentrated near forests, a common pattern for bird- and mammal dispersed species, and on gentle slopes. *Arctostaphylos* was found in dense colonies with low erosion. *Eriogonum* tended to occur on rockier sites. *Agrostis scabra* occurred on higher, gentle sites (elevation; latitude) while *A. pallens* was less common is sites with rills. *Luetkea* favored steeper slopes.

Table 4 Species with significant responses to explanatory variables determined by stepwise multiple regressions of square-root cover percentage data

Explanatory variables									
Species	Cov (%)	Adj. r^2	Elev.	Lat.	Insol.	Isol.	Rills	Rock	Slope
Lupinus lepidus	7.51	0.253	−6.35	4.14		4.37			
Hypochaeris radicata	0.19	0.237	−5.06	2.73	2.46	2.94			
Hieracium albiflorum	0.25	0.138	−3.66		2.31				
Pseudotsuga menziesii	2.49	0.336	−8.78						
Polytrichum juniperinum	2.67	0.252		−5.68		2.78	−3.78		
Abies procera	1.77	0.249	−4.56	6.51	−2.10	−1.99			
Racomitrium canescens	23.1	0.600	−9.39			−2.80		2.96	
Fragaria virginiana	0.18	0.194		−2.20		−3.99			−2.34
Penstemon cardwellii	3.75	0.301		−6.11		−2.03			
Arctostaphylos nevadensis	3.87	0.143		−3.00			−2.60	−3.78	
Juncus parryi	0.84	0.222	6.62						
Eriogonum pyrolifolium	0.07	0.188	6.04					1.98	
Agrostis scabra	0.22	0.145	4.12	−2.40					−3.16
Agrostis pallens	0.77	0.178	5.70				−1.98		
Luetkea pectinata	0.61	0.468	9.95						3.16

Cov, mean cover percentage; Adj. r^2, adjusted r^2, with only species having $r^2 > 0.10$ included. Other values are significant t-values ($P < 0.05$). Insol, insolation based on aspect. Remaining abbreviations as in Table 3. Longitude is excluded due to its strong correlation with elevation

CT-F was dominated by *Arctostaphylos*. The position and elevation of each individual plots were much more variable than any other CT. A comparison of each of these plots with four nearby plots indicated that while cover and richness were similar, *Arctostaphylos*-dominated plots had lower cover of *L. lepidus*, *Juncus*, *Luetkea*, *Racomitrium*, and conifer, and higher cover of *L. latifolius*, *Carex rossii*, and *Polytrichum*. Individual quadrats in which *Arctostaphylos* had >40% cover were compared to those in neighboring plots that lacked woody species. The associates of *Arctostaphylos* averaged 30.5% cover (predominantly mosses), while those in open plots had 48.2% cover ($P < 0.01$, t-test). There were 3.1 other species per quadrat with *Arctostaphylos*, while open plots had 4.8 species per quadrat ($P < 0.0001$ by t-test). This pattern suggests priority effects associated with shading and dense litter by this shrub.

Redundancy analysis

The first three axes accounted for 20.5%, 5.2%, and 3.7% of the species variance; the RDA of all variables explained 31.6% of the species variation. Spearman correlations between the explanatory variables and first three axes were 0.868, 0.547, and 0.533, respectively, which were associated with 65.1%, 16.6%, and 11.6% of the explained variation.

The nine CTs differed in the RDA space (Table 5). Mean positions in RDA-1 correlated strongly to

Table 5 Mean redundancy analysis axis scores of the CTs

Community	*N*	RDA-1	RDA-2	RDA-3
CT-A	17	-0.474^{a}	-0.179^{a}	0.141^{ab}
CT-B	11	-0.396^{ab}	0.123^{b}	0.001^{abcd}
CT-C	20	-0.295^{abc}	-0.199^{a}	-0.002^{bcd}
CT-D	24	-0.203^{abcd}	-0.042^{ab}	-0.086^{cd}
CT-E	21	-0.107^{bcd}	-0.092^{ab}	-0.132^{d}
CT-F	5	0.159^{de}	$0.043a^{b}$	0.279^{a}
CT-G	14	0.429^{cd}	$-0.033a^{b}$	-0.031^{bcd}
CT-H	11	0.487^{e}	0.004^{ab}	0.079^{abc}
CT-I	28	0.473^{e}	0.030^{ab}	0.023^{abcd}

ANOVA determined that means within a column were significant ($P << 0.0001$)

Note: Superscripts unite members of homogeneous groups in each column (Bonferroni comparisons, $P < 0.05$); RDA-2 and RDA-3 groups approximate due to nature of overlaps elevation. CT-B and CT-C overlapped with the latter occurring slightly higher on the lahar, and therefore occurring farther to the west, with more plots having pumice. CT-D, CT-E, and CT-F differed slightly in elevation, while CT-G, CT-H, and CT-I occurred in similar RDA-1 locations, but differed in subsequent axes (Fig. 6).

Stepwise multiple regressions of explanatory variables with plot positions established that elevation accounted for 63.3% of the explained variation (Table 6). Latitude explained 9.1% of the variation. Isolation contributed 9.1, but was significant only in RDA-2. Rock was weakly correlated to RDA-1, while rill was weakly correlated to RDA-2. Pumice did not contribute significantly. RDA-1 was an elevation gradient (low elevation, no pumice, rocky, southern sites to high elevation, relatively smooth, pumice covered, and northern sites). RDA-2 was associated with isolation (plots distant to near edge).

Mantel tests confirmed that explanatory variables were strongly correlated to the species pattern (Table 7). We explored the landscape and habitat variables separately. Landscape factors (elevation, isolation, and position) gave results that were nearly identical to the entire matrix. Habitat factors alone gave a weak relationship. Elevation is a complex variable that combines both landscape effects and habitat conditions. When it was subtracted from the landscape variables, the remaining variables yielded results virtually identical to the overall result; adding elevation to the habitat variables improved the habitat relationship greatly.

Table 7 Mantel tests

Variables	*r*	*t*	P
All variables	0.343	10.9	<<0.0001
Landscape	0.343	10.0	<<0.0001
Habitat	0.167	4.67	<0.0001
Landscape − elev.	0.342	9.98	<<0.0001
Habitat + elev.	0.335	11.33	<<0.0001
Elevation alone	0.360	11.0	<<0.0001

r, standardized Mantel statistic; *t*, estimated *t*-value; *P* is probability that there is no correlation between the matrices

Heterogeneity in vegetation composition

We used standard deviations (SD) within plot percent similarity and evenness (E) to test the hypothesis that heterogeneity differed systematically on the lahar. Based on the earlier studies, we predicted that heterogeneity would increase with elevation and with isolation. The SD was highly variable and not associated with landscape position. Evenness increased with elevation ($t = 4.25$; $P << 0.0001$), which implied greater heterogeneity, and decreased with longitude ($t = -3.41$; $P < 0.001$; adjusted $r^2 = 0.167$).

Discussion

Cutler et al. (2008) used a chronosequence approach to study the species assembly on the lavas of Mt. Hekla, Iceland. They provided evidence for the initial establishment in safe-sites (nucleation) that was followed by coalescence, and eventually by the

Table 6 Stepwise multiple regressions of explanatory variables on constrained species ordination

Variable	Regression			Inter-set correlations			Regression coefficients		
	P	*F*	Var%	Inter-1	Inter-2	Inter-3	*t*-1	*t*-2	*t*-3
Elevation	<0.001	36.9	63.3	0.851	−0.038	−0.078	5.44	3.32	ns
Latitude	<0.001	6.26	73.4	0.774	−0.142	−0.121	ns	−4.65	ns
Isolation	<0.001	5.65	82.5	0.485	−0.320	0.082	ns	−4.82	ns
Rock	<0.001	4.99	89.1	−0.489	−0.032	−0.304	−2.63	ns	−4.93
Pumice	<0.04	1.99	97.4	0.762	0.101	−0.119	ns	ns	−2.58
Rill	<0.02	2.35	94.9	0.028	−0.064	−0.319	ns	ns	−3.18

Probability less than 0.001, 0.04, and 0.02 indicates that result is due to chance (2000 random permutations); *F*, magnitude of *F*-test for each variable; Var%, cumulative percent of the explained variation (which is 31.6% of the total variation). Interset correlations between explanatory variables and RDA axes (Inter-*n*). *t*-values of the regression coefficients of the variables in the predictive equation (*t*-*n*). Values >2.0 are significant, $P < 0.05$. Variables are listed in the order they entered the regression (aspect and slope were not significant; easting excluded due to its strong correlation with elevation). ns, not statistically significant development of vegetation in response to habitat factors. After 28 seasons of primary succession on the Muddy River Lahar, colonization by conifers was underway in most sites and all sites had completed nucleation. Higher elevation sites have lower cover and have not completed coalescence. We detected no site that has reached a stage where local habitat factors have asserted control on species composition.

We recognized loose clusters of similar plots (CTs), weak correlations to spatial factors, and even weaker ones to habitat factors. Isolation has led to idiosyncratic nucleation patterns that formed mosaics within apparently homogeneous habitats. Where competitive prostrate shrubs such as *Arctostaphylos* established first, they seem to have arrested succession, suggesting that priority effects are operative. Below, we explore the evidence which suggests that assembly rules remain weak and that stochastic factors remain as the dominant controlling factors.

Vegetation and its relationship to the landscape

Although each CT was distinct, it would be possible to divide them more finely to reflect surface effects (e.g., rocks and rills) more closely. Alternatively, they could be merged to fewer types to reflect landscape patterns and to emphasize dominance. We expect that most CTs will undergo transition into different ones as conifers, *Populus,* and *Alnus* achieve local dominance (cf. del Moral 2007).

RDA identified weak, but significant relationships between the vegetation and explanatory variables, and Mantel tests corroborated these findings. Both indicated that variation in the vegetation was associated mainly with landscape factors (83%), while habitat factors had little influence. Plots from different CTs intermingled in the RDA bi-plot (Fig. 6, Table 5) because over two-thirds of the variation was not accounted for in the analysis.

The species composition of each CT overlapped. CTs either did not associate in clusters on the landscape or did when plotted in RDA space. Environmental conditions of plots in each CT overlapped with those of other CTs. These patterns suggested that the chance effects of dispersal had been extinguished neither by competitive interactions nor by responses to the environment.

The most isolated plots occupied a small part of the study area and were poorly related to other factors, yet they were classified into four CTs. This too suggested stochastic establishment. There was a gradient of decreasing vegetation development with elevation. Isolation was related to declines in percent cover and increases in diversity, which demonstrates reduced dominance. As isolation increased, the growing season decreased and stresses increased (Dlugosch and del Moral 1999). Stresses appear to have slowed succession relative to lower elevation sites such that species composition is not in equilibrium with potential explanatory variables.

Species were linked to landscape factors. The seed rain more than 50 m from mature vegetation was low (del Moral and Eckert 2005), so that initial colonization in these areas was stochastic. Under these conditions, priority effects can develop. Eventually, as conifers extend their establishment on the lahar, slowly mature, and form dense canopies, they will modify the composition of the ground layer. This will promote a transition to greater determinism in the expression of vegetation composition and structure. Our preliminary studies along the margins of this lahar suggested that species such as *Arctostaphylos*, *C. rossii*, *Achillea*, *Agrostis scabra,* and *L. lepidus* will be excluded as conifers develop in the coming decades (cf. del Moral et al. 2005). Some species may expand in more protected sites (e.g., *L. latifolius* and *Polytrichum*) or persist (e.g., *Penstemon*), despite less favorable conditions (del Moral unpublished). Others were associated with rocky gullies (e.g., *Polystichum* and *Alnus*). Thus, further vegetation changes are expected, and the potential for assembly rules to develop remains. However, the rate of these changes will be slow, hindered by the retarding effects of limited dispersal and infertile soils.

Heterogeneity

During the assembly of communities, heterogeneity often declines because nucleation foci merge and species exert dominance. Earlier studies here (del Moral and Ellis 2005) showed that heterogeneity increased as stress and isolation increased (cf. Ruprecht et al. 2007). Many authors (e.g., Anthelme et al. 2007; Janisova et al. 2007) have shown that ground layer heterogeneity is reduced by trees. Our analyses were confounded by mixtures of plots dominated by conifers and others with variable surfaces. Heterogeneity decreased within samples in more developed vegetation, but was unrelated to landscape factors. Surface variation increased vegetation heterogeneity, which is not unexpected, and which does not suggest developmental trends. Thus, while there are gradients of successional development on this lahar consistent with those documented elsewhere on Mount St. Helens (del Moral 2007), no evidence for assembly rules can as yet be deduced.

Landscape or habitat?

Our evidence suggests that this vegetation has responded more strongly to landscape effects than to habitat factors. Elevation is a complex factor that is a surrogate for both spatial (e.g., isolation) and habitat factors (e.g., pumice, moisture, and growing season), but we cannot yet appraise its components. Dispersal beyond 50 m from intact vegetation on Mount St. Helens is sparse and sporadic, so the early seed rain was spatially variable (cf. del Moral 1999; Wood and del Moral 2000; Fuller and del Moral 2003). A resonance of stochastic dispersal effects may be found in patchy dominance by *Arctostaphylos* and variable distributions of common wind dispersed species (e.g., *Hypochaeris, Chamerion*, *Anaphalis*, and *Cistanthe*). Nearly all of the 29 common species listed in Table 1 occurred in each CT, although many had significant cover differences among them. However, in some cases, habitat factors can filter the initial colonists.

Assembly rules describe filters that restrict colonists or that dictate how vegetation develops (cf. Holdaway and Sparrow 2006), for example in response to drought or soil conditions (Shiels et al. 2008). Lahar vegetation was far from equilibrium and only weakly related to explanatory factors. Most of the explained variance was due to the factors that affect dispersal and stress. Thus, assembly rules appear weak. It is premature to determine if stronger rules (e.g., about competition or safe-sites) will develop. Although deterministic mechanisms may become prominent in the coming decades, much unexplained variation should remain (cf. McCune and Allen 1985; Økland 1999).

Among less recognized sources of unexplained variation are priority effects, the "ghosts of chaos past" to paraphrase Connell (1980). Here, they are suggested by how *Arctostaphylos* suspends rules (Orr et al. 2005), at least until conifers form dense canopies. Stochastic colonization in safe-sites can also produce priority effects (Walker et al. 2006). In these montane habitats, established pioneers are likely to resist replacement. Inhibition by dense mats of *Racomitrium* and abundant *L. lepidus* are also likely to retard succession, producing a vegetation mosaic of forested and open vegetation (del Moral and Rozzell 2004).

In a study of the vegetation on the north side of Mount St. Helens (1,020–1,290 m a.s.l.), del Moral and Lacher (2005) used canonical correspondence analysis (CCA) and found only weak explanatory variables. We reanalyzed their data with RDA and obtained much improved results (RDA = 28.7% of the species variation, CCA = 13.0%). Though distinct habitats were included in that study, landscape factors, along with contrasting habitat types, dominated the explanatory variables. In neither region have habitat variables imposed structure on vegetation. Species distributions remain under the influence of stochastic factors.

Our study demonstrates that although this lahar is well vegetated, it remains in early primary succession. Stresses associated with elevation gradient control the development rate. Stochastic, not deterministic, factors are more closely associated with species patterns. Thus, significant assembly rules to form vegetation units are not yet evident. Sporadic colonization by competitive shrubs (e.g., *Arctostaphylos*) appears to preclude the establishment of other pioneering species, producing a mosaic of vegetation. Vegetation develops not from adherence to rules, but in response to dispersal limitations and the resistance of established species to invasion.

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Appendix

Species nomenclature for all species encountered in the survey. Nomenclature determined from ITIS, August 27, 2008. Growth forms are self-explanatory

Species name and authority	Growth form
Abies amabilis (Dougl. ex Loud.) Dougl. ex Forbes	Conifer
Abies lasiocarpa (Hook.) Nutt.	Conifer
Abies procera Rehd.	Conifer
Acer glabrum Torr.	Tall shrub
Achillea millefolium. var. *occidentalis* DC.	Forb, rhizomatous
Achnatherum occidentale (Thurb. ex. Wats) Barkworth	Grass
Agoseris aurantiaca (Hook.) Greene	Forb, rosette
Agrostis exarata Trin.	Grass, rosette
Agrostis pallens Trin.	Grass, rhizomatous
Agrostis scabra Willd.	Grass, rhizomatous
Alnus viridus ssp. *sinuata* (Regel) A. & D. Love	Tall shrub
Anaphalis margaritacea (L.) B. & H.	Forb, rhizomatous
Arctostaphylos nevadensis Gray	Low shrub, spreading
Arnica latifolia Bong.	Forb, rosette
Aruncus dioicus var. *vulgaris* (Maxim.) Hara	Forb, rhizomatous
Aster ledophyllus var. *ledophyllus* (Gray) Gray	Forb, rhizomatous
Athyrium distentifolium Tausch ex Opiz	Fern
Athyrium filix-femina (L.) Roth	Fern
Carex mertensii Prescott ex Bong.	Graminoid
Carex microptera MacKenzie	Graminoid
Carex rossii Boott	Graminoid
Castilleja miniata Dougl. ex Hook.	Forb, rhizomatous
Chamerion angustifolium (L.) Holub	Forb, rhizomatous
Chamerion latifolium (L.) Holub	Forb, rhizomatous
Cistanthe umbellata (Torr.) Hershkovitz	Forb, rosette
Elymus elymoides (Raf.) Swezey	Grass
Epilobium anagallidifolium Lam.	Forb
Equisetum hyemale L.	Horsetail
Eriogonum pyrolifolium Hook. var. *coryphaeum* Torr. & Gray	Low shrub, rhizomatous
Fragaria virginiana Duchesne	Forb, stoloniferous
Gaultheria ovatifolia Gray	Low shrub, rhizomatous
Hieracium albiflorum Hook.	Forb, rosette
Hieracium gracile Hook.	Forb, rosette
Hypochaeris radicata L.	Forb, rosette
Juncus parryi Engelm	Graminoid
Luetkea pectinata (Pursh.) Kuntzel	Low shrub, rhizomatous
Luina hypoleuca Benth.	Forb, rosette
Lupinus latifolius Lindl. Ex J. G. Agardh.	Forb, rosette
Lupinus lepidus Dougl. ex Lindl.	Forb, rosette
Luzula parviflora (Ehrh.) Desv.	Graminoid
Penstemon cardwellii Howell	Low shrub, spreading
Phyllodoce empetriformis (Sm.) D. Don	Low shrub, spreading
Pinus contorta var. *latifolia* Engelm. ex S. Wats.	Conifer
Pinus monticola Dougl.	Conifer
Poa secunda J. Presl.	Grass, rosette
Polygonum davisiae Brewer ex Gray	Forb, spreading
Polytrichum juniperinum Hedw.	Moss
Polystichum lonchitis (L.) Roth	Fern
Populus balsamifera ssp. *trichocarpa* (Torr. & Gray ex Hook.)	Tree, flowering
Pseudotsuga menziesii (Mirbel) Franco.	Conifer
Pteridium aquilinum (L.) Kuhn.	Fern
Racomitrium canescens (Hedw.) Brid.	Moss
Rosa nutkana K. Presl	Tall shrub
Rubus ursinus Cham. & Schlecht.	Low shrub, stoloniferous
Rumex acetosella L.	Forb
Salix sitchensis Sanson ex Bong.	Tall shrub
Saxifraga ferruginea Graham	Forb, rhizomatous
Sorbus sitchensis M. Roemer	Tall shrub
Trisetum spicatum (L.) K. Richt.	Grass, rhizomatous
Tsuga heterophylla (Raf.) Sarg.	Conifer
Tsuga mertensiana (Bong.) Carr.	Conifer
Vaccinium membranaceum Dougl. ex Torr.	Tall shrub
Vaccinium parvifolium Sm.	Tall shrub

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