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Spatial Factors Affect Primary Succession on the Muddy River Lahar, Mount St. Helens, Washington

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Abstract We surveyed vegetation 28 summers after the 1980 eruption of Mount St. Helens, Washington spawned a massive lahar. Our goals were to describe vegetation patterns early in primary succession; determine factors associated with these patterns; and seek evidence for assembly rules. We determined species composition, plot position and surface features in 151 plots. Multiple regression, redundancy analysis (RDA) of the plant to explanatory variables and Mantel tests assessed relationships between habitat and vegetation. We classified plots into nine community types (CTs). The CTs overlapped in both habitat and multivariate space. RDA accounted for only 24% of the species variation, indicating that the vegetation was not fully determined by the measured variables. Elevation and location had the strongest correlations with vegetation composition. The distribution of most species could not be predicted well with our data and appeared stochastic. Priority effects appear to have generated alternative succession trajectories. Plots with distinct composition can occupy similar environments and plots with similar vegetation occur under similar conditions. Species composition cannot be predicted closely from the data available, suggesting that assembly rules are either weak or come into play only as the vegetation matures.

Introduction

Mount St. Helens remains a unique setting to explore primary succession and to unravel mechanisms that affect community assembly. This paper describes vegetation patterns on a large lahar formed in 1980. Our goals were to provide a detailed description of vegetation patterns; determine factors associated with these patterns; and seek evidence for assembly rules. While a chronosequence study would be ideal to demonstrate floristic and vegetation change (Clarkson 1998; Smits et al. 2002; del Moral 2007), a single survey of vegetation structure can also provide insights into vegetation dynamics. There are surprisingly few detailed studies of early primary succession on volcanoes. This deficiency has hampered understanding of how species assemble (del Moral et al. 2007; Walker and del Moral 2008). Appreciating these processes will streamline the restoration of devastated landscapes (e.g. mine spoils) by illuminating factors that retard invasion, establishment or development (Walker and del Moral 2003; del Moral and Walker 2007; Parsons et al. 2007; Walker et al. 2007).

Studies on Mount St. Helens showed that barren sites need physical amelioration (Wood and del Moral 1987), good dispersal (del Moral & Eckert 2005) and establishment (Wood & Morris 1990). Establishment improves in favorable microsites (Tsuyuzaki & Titus 1996; Titus & del Moral 1998). Even early in vegetation development, biotic interactions such as facilitation (Bellingham et al. 2001; Gosling 2005; Herriquez & Lusk 2005), competition (Fraser & Keddy 2005) and herbivory (Bishop 2002; Fagan et al. 2005) can guide and deflect successional pathways. Species colonization is affected by chance, which permits different species to establish in similar habitats. The often-random order of species invasion (i.e. priority effects; D'Antonio et al. 2001) can affect succession (Wiegleb & Felinks 2001). If alien species invade preemptively, trajectories can be fundamentally altered (Eriksson & Eriksson 1998; Seabloom & van der Valk 2003; Corban & D'Antonio 2004). While random events can dominate early species assembly (cf. del Moral & Grishin 1999), more deterministic patterns can develop as a system matures (Hodkinson et al., 2003; Puyravaud et al. 2003).

Are vegetation patterns linked to spatial or to environmental factors? If species distributions during early succession were related to landscape effects, we could conclude that dispersal, which is largely stochastic, remains important. If environmental factors better explain vegetation patterns, then deterministic processes may have overcome priority effects, and assembly rules would be strong (Holdaway & Sparrow 2006).

Methods

The study site

The 18 May 1980 eruption of Mount St. Helens created a diverse, devastated landscape (Swanson & Major 2005). Heat and pyroclastic flows unleashed massive lahars by nearly instantaneously melting snow and ice that clothed the cone. The upper slopes were scoured as several thick surges of debris swept down the drainage. Deposits were comprised of unsorted sand about 1 m thick mixed with boulders. Some mature trees survived on two small rises. A new drainage (Fire Creek) formed on the southwestern side of the drainage and now joins the Muddy River near the eastern edge of the study area. Both channels eroded quickly to form broad, deep gullies. Subsequent eruptions deposited up to 0.5 m of pumice near the crater (Fig. 1). Pumice rocks decomposed slowly, so that they remained on the surface only at higher elevations.

Halpern & Harmon (1983) sampled this lahar in 1981 and found decreases in plant cover and species richness with distance from the forest edge. At that time, nothing grew over the area of the present study. Subsequent studies on this lahar found that isolation and stresses associated with higher elevation slowed succession and the development of more homogeneous vegetation (del Moral & Ellis 2004).

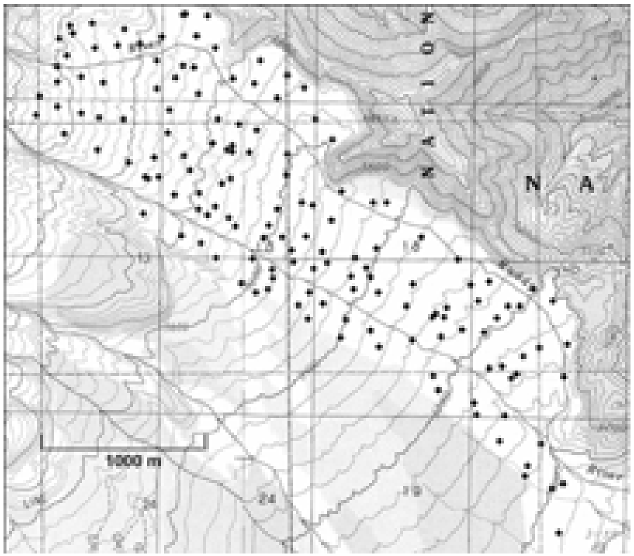

Fig. 1. Topographic map of the Muddy River lahar study area), showing locations of 151 sample plots. Dark grey = intact forest, light gray and stipples = open forest damaged by lahar. Contour intervals = 20 ft (6.09 m). Study conducted between 900 and 1320 m a.s.l.

Plot locations

This survey sampled ca. 5.1 km^2 of the upper Muddy River lahar on the east by southeast flank of the mountain. Elevation ranged from 900 m to 1320 m a.s.l. We excluded intact forest vegetation along the edges of the lahar, scoured steeper sites on the cone, lower sites covered by silt from recent floods and sites within active drainages that lacked vegetation. While elk (*Cervus elaphus roosevelti*) roam rampantly on this lahar, neither their browsing nor trampling caused us to exclude any plot (Fig. 2).

Typical views of the lahar are shown in Fig. 3-5.

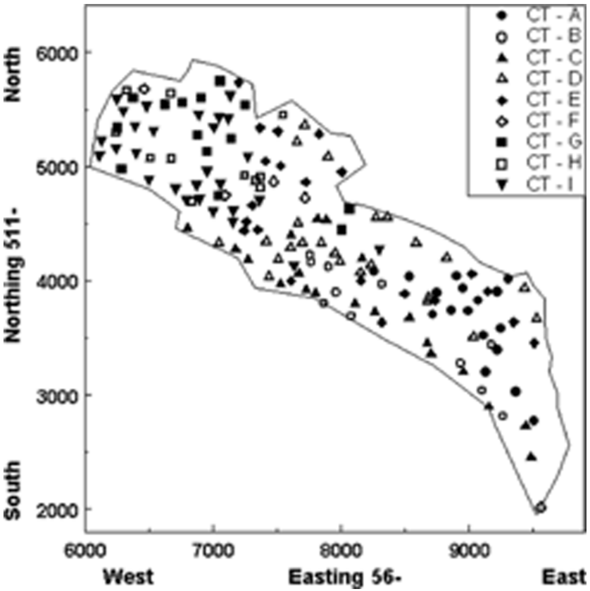

Fig. 2. Location of plots designated by nine community types (CT) revealed by agglomerative classification. Easting is in grid 10T50; Northing is in grid 511 (WGS084 datum).

Field data

Plots were 200-m^2 circles (8-m radius) within which we recorded WGS084 coordinates and elevations. We converted slope (determined with a clinometer) to a 5-point scale: 1 = 0°-3°; 2 = 4°-8°; 3 = 9°-12°; 4 = 13°-16°; and 5 ≥ 17°. Aspect was determined by compass and 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°. The percentage of the plot covered by rocks with diameter > 0.25 m was estimated and converted to a 5-point scale: 1 = 0-20%; 2 = 21-35%; 3 = 36-50%; 4 = 51-65%; and 5 ≥ 66%. Rills (small drainages) were estimated from the number of quadrats in which they occurred: 0 = no rills; 1 = 1 or 2 with rills; 2 = 3 or 4 with rills; 3 ≥ 5 with rills. We noted plots having more than 50% cover of pumice rocks ≥ 5 cm (binary parameter). Finally, proximity to intact vegetation was determined from the map and converted to a 4-point scale of increasing distance.

The percent canopy cover (vertical projection by species) of vascular plants and mosses was sampled in 12 1-m^2 quadrats at 2 m intervals along each of four radii arrayed along the cardinal directions. Quadrats were divided into 25 20 cm by 20 cm squares to promote accuracy. Unsampled species within the plot were given a score of 0.1%. Nomenclature was determined using the Integrated Taxonomic Information System (ITIS; http://www.itis.gov/) and listed in the Appendix.

Statistics and data analyses

Data were compiled to determine absolute plot cover of each species, from which the following were determined: species richness, total percent cover, Shannon-Wiener diversity index (H') and an equitability index [E = H'/ln(richness)]. H' and E were calculated from p_i, the proportion of the cover represented by i^{th} species (McCune & Grace 2002).

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.

We classified the plots into community types (CTs) by flexible sorting (β = -0.25), an agglomerative method using Euclidean distance. Multi-response permutation procedures (MRPP) were applied to these CTs to assess if differences among them were valid (McCune & Mefford 2006). MRPP calculated a weighted mean within-group distance. A ***T***-value was calculated that described the degree to which groups were distinct. ***A*** (0 to 1.0) determined the degree to which groups were homogeneous compared to a random classification.

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

We explored how spatial and environmental factors may control species patterns by both indirect and direct methods. The number of significant axes was estimated using nonmetric multidimensional scaling (McCune & Mefford 2006). We calculated species turnover with detrended correspondence analysis to determine if unimodal or linear methods of direct ordination were more appropriate. Since **β**, species turnover, was about 2.5 half-changes, linear methods would be satisfactory (ter Braak & Šmilauer 1998). Therefore, we selected redundancy analysis (RDA), a linear method of canonical analysis of relations between species and explanatory variables (Legendre & Anderson 1999). We examined the correlation matrix among these explanatory variables: Elevation, Longitude (easting), Latitude (northing), Aspect, Slope, Isolation (distance to edge), Rills, Rocks and presence of Pumice rocks. Elevation and easting were strongly correlated (r = -0.98), so easting was excluded from RDA. Percent cover was log-transformed to improve linearity. RDA standardized species and explanatory data so that differences in magnitude of the values did not affect the result. Each species was regressed with the explanatory variable to create fitted species scores. Principal components analysis (PCA) was applied to the fitted values to produce plot scores in reduced space. RDA then formed linear equations that best specify the position of samples in each dimension. Randomization tests (1000 permutations) compared these results to the null model of no correspondence between the species and explanatory data. We explored the efficacy of RDA in several ways. Stepwise multiple regression ordered the variables by their accuracy in predicting sample scores. The correlation of each variable to the RDA axes estimated how well variables were related to vegetation. The amount of species variation associated with the explanatory variables suggested the degree to which unmeasured variables, sampling error and random or contingent effects were important. The position of plots and CTs in the constrained space indicated how well this analysis captured the floristic analysis. Finally, the relative importance of the regression coefficients was suggested by their *t*-values.

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

A Mantel test related the species matrix to the matrix of explanatory data (Douglas & Endler 1982; McCune & Mefford 2006). We compared a matrix of Euclidean distances (species matrix) to a correlation matrix (explanatory data) using the Pearson correlation and a **Z** statistic (sum of cross products of the corresponding elements of the two matrices). As the similarity between matrices increases, the difference between the observed **Z** value ($\mathbf{Z}_{ob}$) and the expected **Z** ($\mathbf{Z}_{ex}$) determined from 1000 runs of randomized rows in the explanatory matrix increases. An approximate method of calculating $\mathbf{Z}_{ex}$ provided approximate *t* and *r*, the standardized Mantel statistic. We made statistical comparisons with Statistix® (Analytical Software 2003). These included one-way analysis of variance, the Bonferroni test for differences among means and multiple regressions. We used MVSP® (Kovach 1999) to calculate similarity among the quadrats of a plot.

Results

Community composition and structure

Nine CTs were identified (Table 1) and confirmed by MRPP with the 40 most common species. The chance-corrected, within-group agreement, **A**, was 0.602 (T = -50.6; δ = 0.198, P<0.00001) indicating distinct groups (McCune and Grace 2002). Each pairwise comparison was significant. The T-values of individual group comparisons ranged from –8.8 to –28.8.

Although there was substantial overlap in species composition and vegetation structure, patterns emerged. The CTs are described below, arranged by increasing mean elevation.

CT-A (*Lupinus lepidus*-*Penstemon*-mixed conifers-*Racomitrium*) covers much of the lower lahar. *Racomitrium* dominated the surface with abundant *L. lepidus* and substantial *Penstemon*. Several conifer species were scattered throughout the plots. Cover was high, while both 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 and substantial cover by *Polytrichum, Arctostaphylos* and *Pinus* species. **γ**, H' and E were each moderate, cover was relatively high. CT-C (*Lupinus lepidus*-*Racomitrium*) was widespread and dominated by *Racomitrium*, with *Lupinus* always present. Prostrate woody species (e.g. *Arctostaphylos* and *Penstemon*) were common and conifers locally abundant. Cover was moderate, while H' and E were low due to the strong dominance by mosses and the prostrate shrubs. CT-D (*Lupinus lepidus*-*Racomitrium*-mixed forbs) was similar to CT-A, but with *Abies* and *Juncus parryi* in addition to *Penstemon*. Cover, H' and E were moderate, while **α** was relatively high. The plots occupied diverse sites and had the highest **γ**. CT-E (*Lupinus lepidus*-mixed conifers-*Penstemon*-*Racomitrium*) included two sites that escaped most devastation. They were unified with primary plots by their ground layers. *Abies procera* reached its highest concentration here and surviving trees of *Pseudotsuga menziesii* were on the relict island. *Juncus*, *Cistanthe* and *Anaphalis* characterized the forbs, while *L. latifolius* was locally abundant. Cover was moderate and α was the highest of any CT. CT-F (*Arctostaphylos*-*Racomitrium*-*Polytrichum*) occurred sporadically over the range of elevations. Three plots occurred near the relict island, one at low elevation among conifers and one at high elevation. *L. latifolius* and *Carex* were locally abundant. Dense *Arctostaphylos* was associated with minimal **γ**, low **α**, H' and E and an open overstory of young conifers. CT-G

(*Lupinus lepidus*-*Populus*-*Alnus*-*mixed Forbs*) had low *Racomitrium* cover and common tall woody species. *Populus* rarely occurred elsewhere on the lahar and *Salix* was at its highest cover. Several forbs (e.g. *Juncus*, *Agrostis scabra* and *Chamerion*) also occurred at their highest levels. $\boldsymbol{\alpha}$, H' and E were high, while cover was moderate. CT-H (Conifers-*Agrostis pallens*-*Luetkea*-*Lupinus latifolius*) was floristically heterogeneous (H' and E both maximal) and could be further divided if a more detailed analysis were our intent. Cover was moderate, but no species has developed strong dominance. Several ground layer species (e.g. *A. pallens*, *Luetkea* and *L. latifolius*) are their highest concentrations. CT-I (Mixed forbs-*Racomitrium*) lacked strong dominance, reflected by high H' and E. Only *Racomitrium* and *Lupinus lepidus* occurred consistently, both much lower in cover their maximum value. *Juncus, Carex*, and both *Agrostis* species occurred widely. Cover was low.

While the structure of the nine CTs differed significantly, there were broad overlaps in each statistic employed (Table 2). There were 65 species in the survey. The number of species in a CT ($\boldsymbol{\gamma}$) ranged from 25 to 51 species. Mean richness ($\boldsymbol{\alpha}$) varied from 13.2 to 19.3 species per plot and tended to decrease with elevation. Although the elevation gradient was short, percent cover declined significantly from over 80% to about 20%. This reflected declines in mosses on exposed sites and increases in conifers at lower elevations and near surviving vegetation. H' in these plots was comparable to that of the Pumice Plains, located on the north side of Mount St. Helens (del Moral and Lacher 2005) and higher than that of the adjacent Abraham Plain (del Moral unpubl.). E was relatively low due to strong dominance in all but CT-H and CT-I.

Spatial and environmental patterns

As was the case with structure, environmental factors weakly distinguished the CTs (Table 3, Fig. 6). They fall into three broad geographic zones. CTs A to C were at low elevations, CTs D to F were intermediate and CTs G to I occurred in the highest zone. The CTs were not well distinguished based on isolation, although CTs G to I tended to be more isolated than CTs B and C. Segregation by pumice reflected the elevation gradient. Rills distinguished CT-E from CT-F and CT-H from CT-I. Large lava rocks were entrained in the lahar during deposition. Rocks were usually found on lower sites because the lahar carried them to lower elevations. Rocks divided CTs A to E from CTs F, H and I. While each CT had a unique combination of average features, individual plots in different CTs had the same environmental characteristics.

We explored the response of species to the explanatory variables with stepwise multiple regression. Fifteen of 40 common species were related to one or more variables (Table 4). Explained variation was generally low. Elevation was the predominant predictor for 10 species. *Lupinus lepidus* declined with elevation, but increased with isolation. *Hypochaeris*, a strongly wind-dispersed species, tended to occur in more exposed, isolated sites. *Hieracium* had a similar pattern, but was more widely distributed. *Pseudotsuga* and *Polytrichum* both declined with elevation. The latter often occurred beneath conifers and *Arctostaphylos*. Thus, it is more common near the forest edge and absent from rills. *Racomitrium* also declined with elevation and with proximity to edges. *Polystichum* had a strong preference for rocks in isolated moister sites. *Fragaria* was confined to sites near forests, a pattern common for bird-dispersed species, and to gentle slopes. *Juncus* was more common at higher, isolated sites. *Penstemon* increased with elevation. *Arctostaphylos* is a key species distributed by birds and found sporadically. It occurred in homogeneous, protected sites. *Juncus* increased with elevation and tended to occur on isolated sites, while *Eriogonum* was found sporadically at higher elevations. Both *Agrostis* species increased with elevation. *A. pallens* was more prominent where pumice predominated, while *A. scabra* occurred on gentle slopes. *Luetkea* increased with elevation. Finally, *Cistanthe* occurred on steeper pumice sites. These responses agree with what is known about these species on Mount St. Helens (del Moral & Lacher 2005; del Moral et al. 2005).

Significant vegetation pattern was related to these explanatory variables. The Mantel test to compare the species by plot and the explanatory variable by plot matrices was significant ($r = 0.416$; $\mathbf{Z}_{ob} = 8214$; $\mathbf{Z}_{ex} = 6608$; $t = 11.3$; $P < 0.001$). The variable matrix was reduced to spatial factors (elevation and location) and the analysis repeated with similar results ($r = 0.399$; $\mathbf{Z}_{ob} = 17010$; $\mathbf{Z}_{ex} = 13840$; $t = 11.3$; $P < 0.001$). Species do respond to explanatory variables, and that the response is primarily confined to spatial factors.

Redundancy analysis (RDA)

A virtue of RDA is that, unlike unimodal canonical methods (ter Braak 1986; ter Braak & Šmilauer 1998), it uses linear regressions to assess significance. RDA clarified which variables were related to vegetation patterns on the lahar. The first three axes accounted for 13.3%, 4.8% and 3.3% of the species variance. Spearman correlations between the explanatory variables and species axes were 0.924, 0.515 and 0.565, respectively. The RDA axes were associated with 55.4%, 16.0% and 14.5% of the species-explanatory variable variation, respectively. The complete RDA explained 24% of the species variation.

The nine CTs differed in the RDA space (Table 5). Mean positions in RDA-1 correlated strongly with elevation. CT-B and CT-C overlapped, the latter occurring slightly higher on the lahar, and therefore occurring farther to the west, with more plots having pumice. CT-G, CT-H and CT-I occur similar RDA-1 location, but differ in subsequent axes (Fig. 6).

Table 1 Mean percent cover of species common in the nine community types. Species ordered by 2-dimensional position in RDA. *Salix* rarely flowered and was difficult to ascribe with certainty). Bold values are species characteristic in the CT. ns = not significant. t=trace<0.01.

	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

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

Table 2 Mean structure characteristics of CTs. 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).

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^{bc}	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

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

Table 3 Environmental characteristics of CTs. All patterns were significant at $P < 0.0001$, except Rills ($P < 0.01$). Aspect (Asp) and Slope did not differ among the CTs. East = easting, which increases from west to east; North = northing, which increases from south to north; Elev = elevation (m); Isol = isolation, based on distance from intact vegetation; Pum = pumice (a binary variable).

	Explanatory variables								
CT	**East**	**North**	**Elev**	**Asp**	**Isol**	**Pum**	**Rill**	**Rock**	**Slope**
CT-A	9007^{c}	3670^{a}	977^{a}	3.65	2.12^{abcd}	0.000^{a}	0.471^{ab}	2.41^{b}	1.5
CT-B	8371^{bc}	3680^{a}	1015^{ab}	3.54	1.36^{ab}	0.091^{a}	0.727^{ab}	2.73^{b}	1.7
CT-C	8136^{b}	3791^{a}	1045^{ab}	3.55	1.30^{a}	0.300^{ab}	0.650^{ab}	2.60^{b}	1.8
CT-D	8131^{b}	4294^{ab}	1059^{b}	3.29	1.83^{abc}	0.417^{abc}	0.500^{ab}	2.88^{b}	1.8
CT-E	8001^{b}	4477^{ab}	1082^{b}	3.28	2.00^{abc}	0.619^{bc}	1.000^{b}	2.67^{b}	1.7
CT-F	7660^{ab}	4408^{ab}	1113^{bc}	3.20	2.60^{bcd}	0.600^{abc}	0.000^{a}	1.00^{a}	1.2
CT-G	6974^{a}	5239^{b}	1200^{c}	2.93	2.93^{d}	0.857^{bc}	0.857^{ab}	1.57^{ab}	1.6
CT-H	6919^{a}	5131^{b}	1203^{c}	3.00	2.73^{cd}	0.818^{bc}	0.091^{a}	1.09^{a}	1.6
CT-I	6846^{a}	5020^{b}	1209^{c}	3.21	2.43^{bcd}	0.929^{bc}	0.786^{ab}	1.36^{a}	1.8

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

Table 4 Species with significant responses to explanatory variables determined by stepwise multiple regressions of log-transformed cover percentage data. Values are significant t-values ($P < 0.05$). Cov = mean cover percentage; Adj. r^2 = adjusted r^2, with only species having $r^2 > 0.10$ included. Remaining abbreviations as in Table 3. Easting excluded due to its strong correlation with elevation.

	Explanatory variables									
Species	Cov	Elev	North	Asp	Isol	Pum	Rills	Rock	Slope	Adj r^2
Lupinus lepidus	7.51	-5.50	3.02		3.76					0.247
Hypochaeris radicata	0.19	-4.72		2.56	2.81					0.173
Hieracium albiflorum	0.25	-2.79		2.58						0.115
Pseudotsuga menziesii	2.49	-9.10								0.369
Polytrichum juniperinum	2.67		-5.31		3.51	-3.20	-3.73			0.331
Racomitrium canescens	23.1	-10.2			-3.17	-3.26		-2.81		0.624
Polystichum lonchitis	0.03				2.22		2.55	4.45		0.137
Fragaria virginiana	0.18				-4.25				-2.34	0.126
Penstemon cardwellii	3.75		-3.73			2.49				0.330
Arctostaphylos nevadensis	3.87			-2.11			-2.60	-3.31		0.147
Juncus parryi	0.84	4.45			2.80					0.243
Eriogonum pyrolifolium	0.07	4.24								0.102
Agrostis pallens	0.77	5.36				3.21				0.244
Agrostis scabra	0.22	3.86	-2.42						-2.36	0.116
Luetkea pectinata	0.61	10.5								0.400
Cistanthe umbellata	0.18		-2.15			3.43			3.22	0.140

Table 5 Mean redundancy analysis axis scores of the CTs. ANOVA determined that variation was significant ($P << 0.0001$).

Community	**N**	**RDA-1**	**RDA-2**	**RDA-3**
CT-A	17	-0.407^{a}	0.074^{ab}	-0.135^{c}
CT-B	11	-0.286^{ab}	0.056^{ab}	0.090^{ab}
CT-C	20	-0.188^{ab}	0.079^{ab}	0.139^{a}
CT-D	24	-0.176^{ab}	-0.093^{bc}	0.016^{abc}
CT-E	21	-0.105^{b}	-0.152^{c}	0.017^{abc}
CT-F	5	0.095^{bc}	0.241^{a}	-0.130^{c}
CT-G	14	0.345^{c}	-0.068^{bc}	-0.098^{bc}
CT-H	11	0.381^{c}	0.094^{ab}	-0.094^{bc}
CT-I	28	0.384^{c}	0.024^{ab}	0.030^{ab}

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

Table 6 Stepwise multiple regression of explanatory variables constrained species ordination: Pr=probability that result is due to chance (1000 random permutations); F=magnitude of F-test for each variable; Var%=cumulative percent of the explained variation (which is 24% of the total variation). Interset correlations between explanatory variables and RDA axes (Inter-N). T-values of the regression coefficients of the explanatory variables in the predictive equation (t-N) > 2.0 are significant, $P < 0.05$). Variables are listed in the order they entered the multiple regression (aspect and slope were not significant; easting excluded due to high correlation with elevation). ns = not statistically significant.

	Regression			**Inter-set correlations**			**Regression coefficients**		
Variable	**Pr**	**F**	**Var%**	**Inter-1**	**Inter-2**	**Inter-3**	**t-1**	**t-2**	**t-3**
Elevation	0.001	22.4	54.2	0.915	-0.060	0.014	12.8	3.64	2.62
Northing	0.001	5.71	68.9	0.790	-0.211	-0.134	-2.09	-2.26	-2.01
Isolation	0.001	3.51	79.2	0.441	-0.0471	-0.451	ns	ns	-5.37
Rock	0.002	2.59	83.3	-0.503	-0.179	-0.132	-2.14	-2.19	ns
Rill	0.011	2.32	91.2	0.051	-0.285	-0.140	ns	-2.92	ns
Pumice	0.030	1.84	95.8	0.711	-0.086	0.060	ns	ns	ns

Stepwise multiple regression of explanatory variables as predictors of the plot positions demonstrated that elevation alone accounted for 54.2% of the explained variation (Table 6). It had significant regression coefficients on each axis. The pattern for northing was similar. The remaining four variables significant variables contributed little. Isolation was significant only in RDA-3. Rock was weakly correlated to RDA-1, while rill was weakly correlated to RDA-2. Pumice, a binary variable, did not contribute significantly. RDA-1 represented an elevation gradient (low elevation, no pumice, more southerly sites to high elevation, pumice covered, northern sites). RDA-2 is associated with surface heterogeneity (rocks and rills).

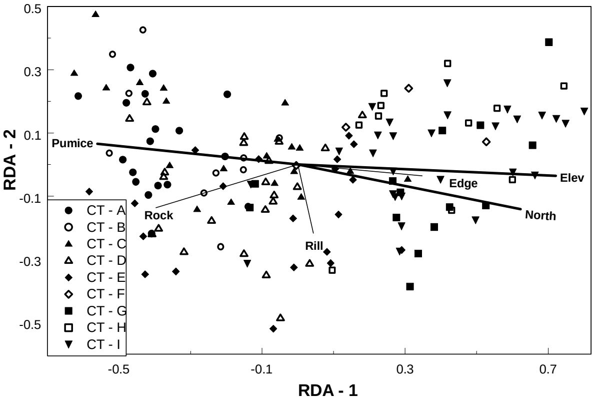

Fig. 6. Redundancy analysis bi-plot of samples and significant explanatory variables. Lengths of the vectors indicate strength of the relationship of the variable to the RDA axis. Heavy lines indicate variables correlated to vegetation plots > 0.7. Pumice vector reversed (= to no pumice variable). Elev = elevation. By convention, vectors start at the center of the graph, but their tails extend an equal distance in the opposite direction.

Heterogeneity in vegetation composition

During the assembly of communities, heterogeneity often declines as species expand and exert dominance. Earlier studies of this lahar (Dlugosch & del Moral 1999; del Moral & Ellis 2004) showed that species heterogeneity increased with increasing stress and isolation (cf. Ruprecht et al. 2007). Many authors (e.g. Anthelme et al. 2007; Janisova et al. 2007) have shown that woody plants can reduce heterogeneity and alter species composition. We used standard deviations (SD) of within plot percent similarity and evenness (E) to test the hypothesis that heterogeneity differed systematically on the lahar. We predicted that heterogeneity would increase with elevation and with isolation. The SD was highly variable and not associated with landscape position. Evenness (= more heterogeneity) increased with elevation (t = 4.25; P <<0.0000) and decreased with easting (t = -3.41; P< 0.001; adjusted r^2 = 0.167). These analyses were confounded by plots strongly dominated by conifers and those with different surfaces.

Discussion

Our goals were to describe vegetation patterns early in primary succession; to determine factors associated with these patterns; and to seek evidence for assembly rules. After 28 seasons of primary succession, the colonization by surrounding conifers was well underway. Loose aggregations of vegetation (CTs) were recognized and there were weak correlations to spatial and to environmental factors. Spatial isolation has led to stochastic dispersal patterns, while priority effects appear to have effectively precluded significant assembly rules from dictating species composition. Below we explore the evidence that suggests that assembly rules are weak and that stochastic factors remain the dominant controlling factors.

Vegetation and its relationship to the landscape

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

The random effects attributed to dispersal remained evident because CTs were fuzzy approximations of vegetation differentiated in response to environmental factors. They did not form tight spatial patterns. To demonstrate this, we selected five sets of five proximate plots in different parts of the lahar. Three CTs occurred in each set. Isolation, rills and rocks could explain why some neighboring plots were classified differently. Further, similar habitats that differed in their degree of isolation had different species compositions. Within each CT there was substantial spatial and environmental variation. Elevation differences within CTs ranged from 140 to 350 m (overall range 419 m). Each CT was composed of plots with smooth surfaces and others with rocks ranging up to 4 or 5 in most cases. Most CTs had several plots lacking rills, yet all except CT-F had plots with several rills.

While RDA identified significant relationships between the vegetation and explanatory variables, they were weak, although the Mantel test was significant. Plots from different CTs intermingled in the biplot (Fig. 6). Spatial factors accounted for 79% of the explained variance in RDA, but this represented only 24% of the overall variation. Isolation reduces the relationship between species composition and environmental factors. Plots in the most isolated sites were classified into four CTs in a spatially constrained area, suggesting stochastic establishment. Further, there is a gradient of vegetation development. Isolation was related to declines in percent cover and increases in diversity and equitability. As isolation increased, physical stresses increased. Stress has slowed succession so that species composition is not in equilibrium with potential explanatory variables.

Species patterns

RDA, multiple regressions and Mantel tests all suggested similar patterns of species distribution with respect to the explanatory variables. These approaches are complementary, but regressions provided a more clear understanding of species patterns. Species are only weakly linked to environmental factors, primarily to elevation and isolation (Table 4). Measured plot variables explain species patterns poorly. The seed rain more than 50 m is low (del Moral & Eckert 2005), so that initial colonization is stochastic. Under these conditions, priority effects can develop. Eventually, as conifers extend their establishment across and up the lahar, slowly mature and close together to form forests, they will alter the composition of the ground layer and promote a transition to greater determinism in the expression of vegetation composition and structure. This process has occurred within three decades on similar Mount St. Helens lahars adjacent to intact forests. However, on those lahars, distance alone greatly retards the process. Our preliminary studies suggested that species such as *Arctostaphylos*, *C. rossii*, *Achillea*, *Agrostis scabra* and *L. lepidus* will be excluded as conifers and *Alnus viridis* form denser cover in the coming decades (cf. del Moral et al. 2005). Other species may expand in the moister, shadier conditions (e.g. *L. latifolius*, *Polytrichum*) or persist (e.g. *Penstemon*) despite less favorable conditions (del Moral unpubl.). Still others are strongly associated with rocky gullies (e.g. *Polystichum* and *Alnus*). Thus, further changes are expected, and the potential to determine rules for assembly remains intact. However, the rate of these changes will be slow, hindered by the retarding effects of limited dispersal and infertile soils.

Heterogeneity

As vegetation developed, heterogeneity within samples declined. The relationship in this study was weaker than in an earlier study because, although internal variation differed substantially among the plots, there was no systematic pattern. The inclusion of conifers and surface differences increased heterogeneity in most sites. Thus, while there are gradients of successional development on this lahar, no evidence for assembly rules can be deduced.

RDA explained 24% of the unconstrained variation, suggesting heterogeneous vegetation loosely related to the measured variables. In a similar survey of the Pumice Plain (PP) on the northern side of the cone, del Moral & Lacher (2005) used CCA and found that explanatory variables were weak. We reanalyzed these PP data with RDA after log-transforming species data. RDA explained much more variation (23.6% vs. 13.0% in the original study). The species to environment relationships on the Pumice Plain were 0.728, 0.715 and 0.570 respectively (on the Muddy River, they were 0.924, 0.515 and 0.565). The elevation gradient on the Muddy River was strong, thus leading to a stronger pattern on the first axis. The PP data explained 23.6% of the species-environment relationship on four axes with 14 variables, while the Muddy River explained 22.0% on four axes with nine variables. These analyses suggest that both regions have developed to similar degrees. Furthermore, these results also make it clear that in comparing succession rates, methodology must be carefully considered.

Assembly rules

Assembly rules describe any filter that limits colonizing species or that dictates how vegetation develops (cf. Holdaway & Sparrow 2006). Most of the vegetation in this survey is still maturing and it remains only weakly related to explanatory factors; 76% of the species variation remained unaccounted for by RDA. Of the explained variance, 79% was due to elevation and northing, both of which affect dispersal and stress, but not establishment. Thus, any rules at this stage are weak and trivial. It is premature to determine if stronger rules (e.g. concerning specific competitive outcomes, safe-site requirements, species composition, etc.) come into play in more mature vegetation. Although it is probable that deterministic mechanisms will become more prominent in the coming decades, significant unexplained variation should remain (cf. McCune & Allen 1985; Økland 1999).

Among the sources of unexplained variation, perhaps considered as historical or contingent factors, are priority effects, the “ghosts of chaos past” to paraphrase J. H. Connell (1980). Priority effects can suspend the rules (Corbin & D’Antonio 2004; Orr et al. 2005). Until conifers form dense stands, priority effects will not be overcome. In these stressful montane to subalpine habitats, where growth is constrained, many established pioneers (e.g. *Penstemon*) will persist. Inhibition from dense mats of *Racomitrium* with periodically abundant *L. lepidus* will likely retard vegetation development for decades, leading to a persistent vegetation mosaic of forested and open vegetation (del Moral & Rozzell 2004).

Our study demonstrates that although the Muddy River Lahar is well vegetated with trees, shrubs, forbs, grasses and mosses, it remains in an early stage of succession. Development is strongly related to a gradient of environmental stress associated with elevation. Stochastic, not deterministic, factors are more closely associated with species distributions. Thus, significant assembly rules to form cohesive vegetation units are not evident and we cannot with certainty predict the future vegetation. Vegetation develops not from adherence to strict rules, but in response to dispersal limitations and the resistance of established species to invasion.

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