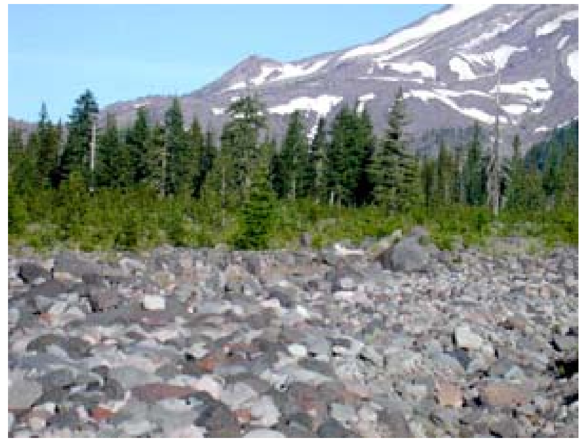
Transition



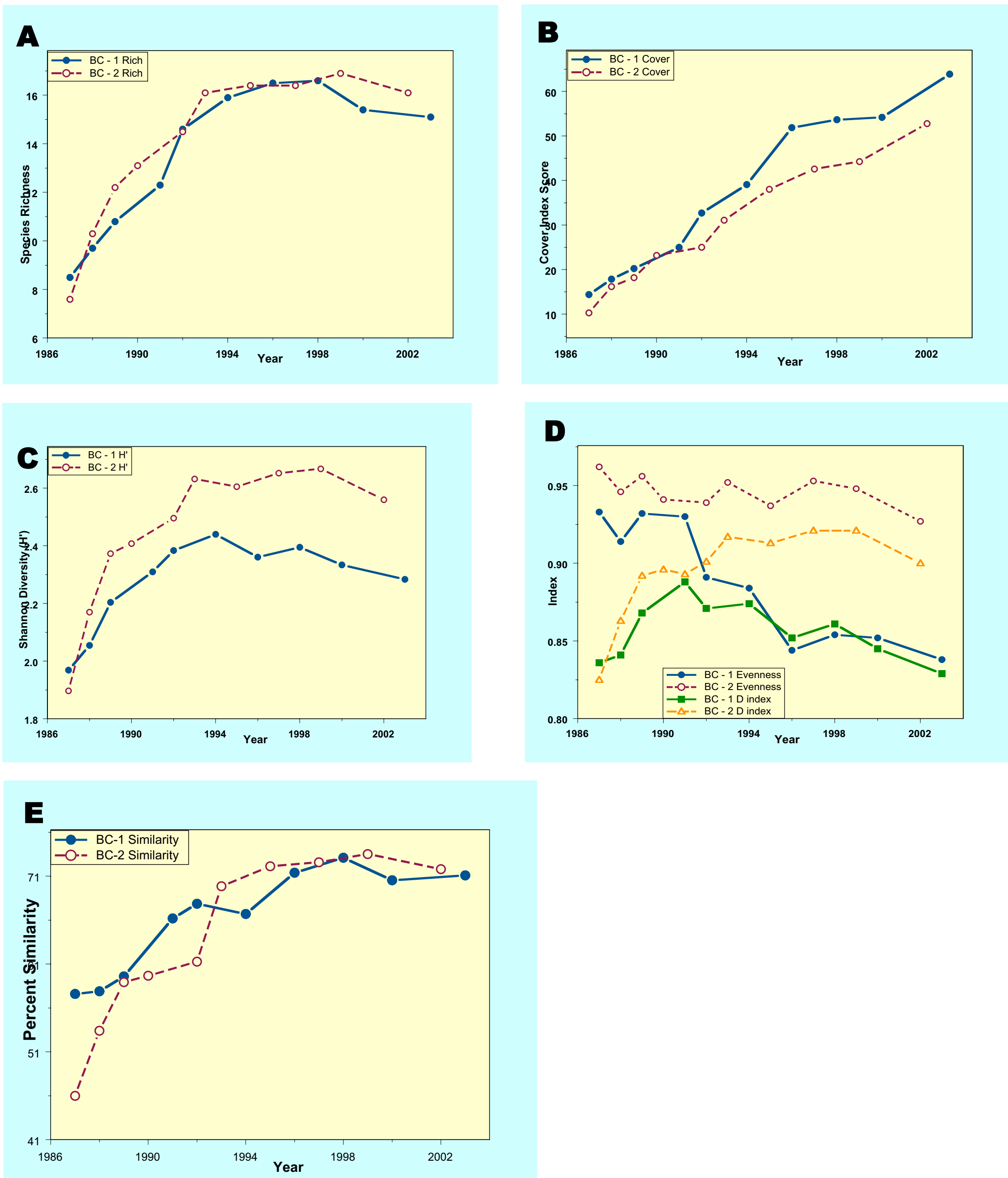
Selected plots (based on a companion study) were analyzed from 1987 to the present, in order to compare Lahar 1 and Lahar 2 in terms of structural changes through time and to determine if either is converging to a single vegetation type. Lahar 1 has a relatively dense invasion of Abies and Pinus saplings whose size and density diminishes with distance from the intact forest. Lahar 2 (Butte Camp), much more distant from conifer seed sources, supports a much less dense invasion. The effect of conifers on understory species composition was investigated by selecting 40 (Lahar 1) and 61 (Lahar 2) plots by a stratified system such that a) the entire grid was represented and b) no two plots were contiguous. These data were analyzed by detrended correspondence analysis and by similarity analyses. Structure through time and the variation of among DCA values through time were calculated.

Development of vegetation

The temporal analysis the lahars permits a direct evaluation structure and similarity development (Fig. 1). Structure developed quickly on both lahars compared to pyroclastic and pumice sites on Mount St. Helens. All structural measures changed significantly on both lahars. Though most species occur on both lahars, composition differs (PS between lahar vegetation= 35%) though the dominance hierarchies are similar (Spearman rank correlation = 0.70, $P < 0.001$). These differences are traced to the proximity of woodlands that contributed strongly, but differentially to the vegetation of Lahar 1. Richness (Fig. 1a) increased through 1996, but has since declined gradually, more so on Lahar 1. This appears due to the increase in conifers that have eliminated some species. As a result, richness was slightly lower, and seems to be declining. Cover continues to increase on both lahars (Fig. 1b), and cover on Lahar 1 remains consistently greater than on Lahar 2. H' increased through the mid-1990s. On Lahar 1, it appears to be declining, but thereafter it has declined. On Lahar 2, there has been little change after 1996. H' on Lahar 1 is significantly lower than on Lahar 1 (Fig. 1c) and appears to be declining. D increased on Lahar 1 as richness expanded, but after 1990, D has declined. In contrast, the lack of any strong dominants permitted D to increase on Lahar 2 until 1996 before leveling off. E has declined steadily with conifer increases on Lahar 1, while it has remained nearly constant until declining in 2003 (Fig. 1d) on Lahar 2. Evenness and D demonstrated similar developmental contrasts between Lahar 1 and Lahar 2. This contrasts result primarily from the differential proximity to conifers. While conifers declined with distance and elevation, common meadow species increased their share of the community, leading to lower dominance.

Similarity increased strongly on Lahar 1 until 1990, after which it increased unevenly. Lahar 2 was very heterogeneous in 1987, but it has reached levels similar to those of Lahar 1. The developing conifers have created heterogeneity on Lahar 1 so that there was a small decline in the similarities within plots after 1998. The similarities of the two lahars were significantly different for each comparison except 1989 (t-test, $P < 0.001$). Lahar 1 was less similar during 1994-1998 when conifer dominance was most pronounced.

Fig. 1. Changes in structural parameters on two lahars at Butte Camp. Values are the means from the same plots used in the study of similarity patterns. A. Richness. B. Cover Index. C. Shannon diversity (H'); D. Evenness and Dominance Index; E. Percent Similarity.



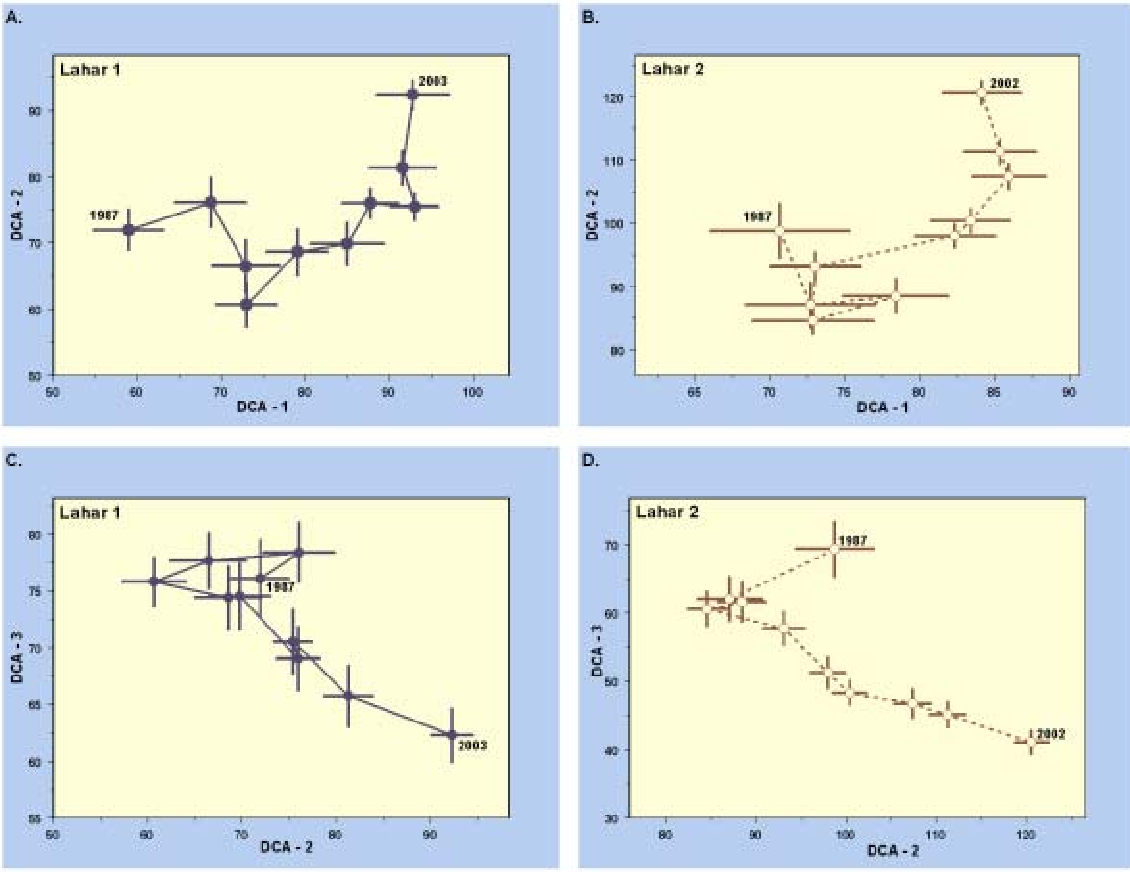
Mean species composition in the each sample was analyzed by DCA to assess variation changes and directionality of trends. Lahar 1 changed substantially more than Lahar 2, a function of the accumulation of conifers, *Lomatium martindalei, Luetkea pectinata, Luzula parviflora*, *Penstemon cardwellii*, *Polygonum davisiae*, and mosses. Changes on Lahar 2 were due to graminoids, but the changes were less pronounced. On Lahar 2, common species have expanded and more species that are rare have accumulated, but there have been few major changes in structure or composition.

Fig. 2a-d demonstrates the changes in species composition on both grids. DCA scores on each of the first three axes of Lahar 1 changed significantly (ANOVA, $P < 0.001$), and were directional. Lahar 2 experienced significant directional changes on each axis, most strongly on DCA-3. The regression of SE vs. years was not significant DCA-1 and DCA-3, but on DCA-2 SE declined from 3.14 to 2.26 ($P < 0.008$). Of more interest is that the SE of the DCA scores all declined significantly ($P < 0.001$ in each case), indicating increased homogeneity. However, by this measure, Lahar 2 became less heterogeneous than did Lahar 1.

DCA demonstrated directional change on both lahars, but Lahar 1 changed to a greater degree, again because of the gradient in conifer development. Note that the variation declines with age of the site. This gradient also precluded reductions in variation in two axes. In contrast, Lahar 2 lacked the strong conifer gradient, so that directional change was smaller and variation decreased significantly on all axes. The result demonstrates how sites on ecotones can remain heterogeneous until all plots have been saturated with invading species. Failures for vegetation to converge or to become strongly homogenous may be due to dispersal gradients present early in the development of the vegetation that are not appreciated in mature vegetation. Such gradients may contribute to regularly low degree of predictability found in studies relating species composition to environmental factors.

Through time, the plots became more similar (percent similarity), as would be expected. Stronger dominance along the ecotone may reverse the trend towards homogenization as trees begin to dominate. Significant compositional differences, initiated by events early in the process rather than from environmental differences, may persist even if trees dominate the entire site.

Fig. 2. A. Lahar 1, Axis 1 vs. 2; B. Lahar 2, Axis 1 vs. 2; C. Lahar 1, Axis 2 vs. 3; D. Lahar 2, Axis 2 vs. 3. Horizontal and vertical lines are SE of the plot scores in each year.



Distance Effects

Methods

Two related questions were addressed by sampling 100 m^2 plots intensively on three lahars. In 2002, Lahar 1 had a relatively dense invasion of *Abies* and *Pinus* saplings whose size and density diminish with distance from the intact forest. Lahar 2 (Butte Camp), more distant from conifer seed sources, supports a less dense invasion. The effect of conifers on understory species composition was investigated on these two lahars by selecting 40 (Lahar 1) and 61 (Lahar 2) plots by a stratified system such that a) the entire grid was represented and b) no two plots were contiguous. Within each plot, 25 1-m^2 quadrats were established on a grid system such than none was contiguous with any other. On the Muddy River lahar, 10 by 10 m plots were established at 40 m intervals from both edges of the lahar between elevations of 980 and 1l50 m. A total of 60 plots were sampled as above.

In 2003, two sets of control plots were sampled to provide baselines. At Butte Camp, 33 plots were sampled in a meadow that developed on a lahar deposited about 400 years ago. Distances between plots were similar to those of the lahars. On the Muddy River, 42 plots were sampled in sites higher and more isolated than any transects, but of the same age.

Various structural features (richness, cover, diversity) were determined for each plot. Distance from the edge of intact vegetation was used as the independent variable in regression analyses to determine if distance affected these factors. Internal similarity and similarity between plots were also determined to test the hypothesis that heterogeneity will increase with distance and elevation.

Results

Recent studies of primary succession suggest that even short distances from pools of colonists affect species composition, diversity, and heterogeneity. Understanding how plant communities assemble after major disturbances in fragmented landscapes has practical ramifications for ecosystem restoration. This study uses new data and mines data collected since 1987 to investigate how landscape features affect community structure during primary succession.

Since distance affects the local seed rain, vegetation that is isolated from sources is initially heterogeneous. Heterogeneity persists until colonists expand or sufficient time elapses to saturate the habitat with propagules. Over time, heterogeneity of a site declines, but is never eliminated. Lahars created sharp transitions from intact vegetation to new surfaces.

Succession proceeds at different rates in response to local growing season conditions. As the growing season shrinks, species grow more slowly and seedling survival is lower. At any given time, random effects are more prominent at higher elevations, leading to greater heterogeneity. Distance also retards succession simply because dispersal is restricted. Therefore, early in succession, compositional changes along transects away from sources of colonists are expected. As more species establish and populations become denser, the vegetation becomes more homogeneous. Changes in homogeneity are expected along gradients that affect either the rate of vegetation development or the invasion rate. The invasion of woody species near the edges of lahars alters community structure. Many herbaceous species are suppressed, while the establishment of others may be facilitated. Thus, when taller growth forms invade a site, heterogeneity increases until these species achieve complete dominance.

The study is focused on three 23-year old lahars. We predicted that richness and vegetation cover would decline, while measures of dominance would increase with distance from sources of colonists. A community is initially dominated by relatively few species, but heterogeneity is large due to strong stochastic elements inherent in dispersal. At a surprisingly short distance, all sites are effectively equidistant from a source (see Relict studies), so no spatially related pattern is expected when comparing isolated samples.

Structure

On the Muddy Lahar, plot structure and heterogeneity measures were analyzed by one-way ANOVA with respect to position on each transect. In addition, both sets of transects were analyzed with respect to distance from the edge and elevation. The patterns of spatial variation on plots of the Muddy were assessed using distance from the edge and elevation in a multiple regression. The overall patterns of the two grids at Butte Camp and the control grids at Butte Camp and the Muddy River were assessed using multiple regressions of their spatial coordinates.

Richness. Each site was examined for patterns in total number of species per plot and the mean richness in 25 quadrats. There were few significant patterns with plot richness On Muddy-SE, mean quadrat richness declined with distance (Table 1). The transect plot and quadrat richness values did not differ significantly (Table 2). There was only a trend for increased quadrat richness with elevation on the Muddy-NW transects (Table 1). There were no spatial gradients in either plot or quadrat richness of the control plots. The mean quadrat richness of Muddy-SE was significantly greater than that of Muddy-NW, with Muddy-Control being intermediate (Table 3).

Plot richness on BC-1 (Lahar 1) increased with distance from the forest edge and varied from 8.0 to 22 species per plot, with a mean of 15.5. This result is due to the influence of conifers that reduced the number of species near the forest. Richness increased significantly with distance from the forest edge and with elevation (Table 1). Elevation changes correlated with greater exposure and deeper lahar deposits that reduce conifer dominance. Mean richness (5.49 species) also increased with distance, ranging from 2.2 to 7.0 species. The regression was highly significant and due to both distance and elevation.

On grid BC-2, all plots are in effect similarly isolated from intact vegetation, so distance is of limited importance. From east to west, plots may receive more species from up-valley winds. Lower elevation plots are more protected by topography from desiccation and late afternoon sun than are higher elevation sites.

Table 1. Relationship between richness, cover, and frequency and distance and elevation. r^2 and P were determined from multiple or simple regressions. Minus signs indicate a negative relationship. No spatially consistent pattern was found in the Muddy or the BC controls, so these are omitted. NS = not significant.

Location	**Richness**		**Mean Richness**		**Mean Species Frequency**		**Plot Cover**		**Species Cover**		**Species Standard Dev.**	
	r^2	**P <**	**r^2**	**P <**	**r^2**	**P <**	**r^2**	**P <**	**r^2**	**P <**	**r^2**	**P <**
Muddy-SE (n=32)		NS	0.26	-0.04	0.21	-0.04	0.72	-0.001	0.29	-0.02	0.31	0.005
Distance		NS	0.19	-0.02	0.18	-0.02	0.65	-0.001		NS		NS
Elevation		NS		NS		NS	0.24	-0.005	0.28	-0.02	0.30	-0.001
Transect 1 (n=6)	0.69	-0.04	0.60	-0.04	0.63	0.05		NS		NS	0.59	0.05
Transect 2 (n=7)		NS	0.58	-0.04		NS	0.62	-0.04		NS		NS
Transect 3 (n=9)		NS	0.60	-0.03	0.44	-0.05	0.50	-0.04	0.51	-0.03		NS
Transect 4 (n=10)	0.54	-0.02		NS		NS		NS	0.48	-0.03		NS
Muddy-NW (n=23)		NS		NS		NS	0.34	-0.01	0.37	-0.01	0.45	-0.003
Distance		NS		NS		NS	0.22	-0.03	0.25	-0.02	0.38	-0.002
Elevation		NS		NS		NS	0.29	-0.008	0.32	-0.005	0.33	-0.004
Transect 1 (n=6)		NS		NS		NS		NS		NS	0.70	0.02
Transect 2 (n=12)		NS		NS		NS		NS		NS		NS
Transect 3 (n=5)		NS		NS	0.77	0.05		NS		NS	0.78	0.03
BC-1 (n=40)	0.37	0.001	0.66	0.001	0.44	0.001	0.56	-0.001	0.61	-0.001	0.37	-0.001
Distance	0.21	0.004	0.51	0.001	0.39	0.001		NS	0.16	-0.01		NS
Elevation	0.16	-0.04	0.17	-0.008		NS	0.50	-0.001	0.46	-0.001	0.33	-0.001
BC-2 (n=61)	0.42	0.001	0.43	0.001		NS	0.53	0.001	0.32	0.001	0.32	0.001
Distance	0.25	0.001	0.24	0.001		NS	0.25	0.001	0.13	0.004	0.08	0.04
Elevation	0.16	-0.001	0.18	-0.001		NS	0.26	-0.001	0.18	-0.001	0.24	-0.001

Plot richness was 16.4 species, while the mean number of species per quadrat was 5.49, more than BC-1, less than the control (Table 4). Richness declined significantly uphill, and increased from east to west (Table 1), though there is much variation. Mean richness per quadrat increased in a similar way. It was significantly greater than BC-1.

The control grid demonstrated no significant spatial patterns, though there was substantial variation among the plots. Mean plot richness was slightly higher than either lahar, and more species occurred per m^2 (Table 4).

Cover. Vegetation cover best represents the degree to which a site has matured. Plot cover declined significantly, primarily with increasing distance, but also with elevation on the Muddy-SE transects (Table 1). Each transect demonstrated declines with distance, but only the declines of SE-2 and SE-3 were significant. Mean cover among these transects declined strongly (Table 2), demonstrating the general effect of shorter growing seasons. The mean species cover also declined significantly with elevation. SE-3 and SE-4 mean species cover declined with distance, but the variation among species only increased significantly on SE-1 (Table 1). Cover, mean species cover, and variation of species cover all declined significantly with elevation (Table 2). These correlated measures suggest that community development is retarded with elevation.

The Muddy-NW transects demonstrated moderate spatially related declines in mean plot cover, mean species cover, and variation of species cover (Table 1; Table 2). All values declined with elevation and *with* distance from the edge. Variation was large and sample size too small for many significant responses with respect to distance along (individual transects) to be manifested. However, species variation did increase significantly on both NW-1 and NW-3. The Muddy Control grid demonstrated no spatial patterns in cover-related variables, but there were differences when compared to transect data (Table 3).

Cover on BC-1 was higher than the means on any other primary surface, and ranged from 12.0% to 63.8%. The higher values were concentrated near surviving forests. Cover declined with elevation on the lahar, as plots were increasingly isolated from the edge, a function of decreasing conifer density (Table 1). The cover of the mean species (2.20%) declined significantly with distance and elevation, while and the variation of this cover (2.92%) declined with elevation. Cover on BC-2 (21.5%) was significantly lower than on either BC-1 or on the control. It had significantly lower mean cover (1.29%) and lowest variation of cover (1.85%; Table 4). Cover declined with elevation on BC-2, but increased from east to west (Table 1). BC-control grid was well vegetated. Plant cover in the immediate vicinity of this site has varied in response to seasonal factors since 1984. The year 2003 was dry and cover of three nearby plots was 6 to 10% lower than in 2002. Even so, cover was the highest of any sample (35.1%), consistent with its age. Both mean species cover and cover standard deviation were intermediate to BC-1 and BC-2. None of these variables was related to spatial factors, though there were significant differences among the plots.

Distance clearly affects community structure. After 23 growing seasons, mean richness, cover and mean species cover decreased with distance from sources on Muddy-SE. Overall, there were weak reductions in mean richness and frequency and strong declines in cover. Species variation also increased with distance. Cover, species cover and species variation all declined with elevation.

The Muddy-NW transect patterns are complicated due to the invasion of woody species. The nearby intact forest not only provided ample seed sources, but also protected invading species from desiccation by blocking wind and providing shade. These transects demonstrated few trends in structure. Overall, cover and its correlates declined, while richness measures were variable. Elevation changes affected cover and mean species cover more than did distance. Individual transects demonstrated few significant patterns.

The 42 plots of the control grid were sufficiently isolated from sources of colonists that each was effectively at the same dispersal distance. They did not demonstrate any spatial patterns. Taken together, these plots are an extension of the Muddy-SE sample, being at higher elevation and greater isolation. As expected, they demonstrated reduced cover and mean species cover. Together, the results from the Muddy lahar support the hypothesis that early primary succession, even short distances from sources of colonists, is constrained by dispersal.

Table 2. Comparison of structural parameters among transect means on the Muddy Lahar. The superscripts = samples that are not different (P < 0.05; one-way ANOVA, followed by Bonferroni test.) SE=transects from the southeast facing edge; NW=transects from the northwest facing edge.

Parameter	MUDDY-SE				MUDDY-NW		
	SE-1 (n=6)	SE-2 (n=7)	SE-3 (n=9)	S2-4 (n=10)	NW-1 (n=6)	NW-2 (n=12)	NW-3 (n=5)
Richness (n)	15.3	15.7	13.3	13.3	14.0	15.8	13.8
Mean richness (n)	4.55	5.01	4.04	3.90	3.42	3.72	3.96
Frequency (%)	30.9	32.8	30.4	27.9	24.5	24.4	28.8
Vegetation Cover (%)	49.5^{a}	29.7^{b}	16.0^{b}	14.3^{c}	28.8^{a}	14.2^{b}	8.3^{c}
Mean species cover (%)	4.28^{a}	1.98^{ab}	1.78^{b}	1.15^{c}	2.10^{a}	0.89^{b}	0.60^{b}
Species variation (%)	3.82^{a}	2.14^{ab}	1.97^{ab}	1.80^{b}	4.03^{a}	1.79^{b}	1.16^{b}
Dominance	0.424^{a}	0.522^{a}	0.557^{ab}	0.544^{b}	0.447^{a}	0.555^{ab}	0.605^{b}
E – quadrats	0.569^{a}	0.662^{b}	0.733^{b}	0.780^{b}	0.668^{a}	0.671^{a}	0.836^{b}
E – plots	0.495^{a}	0.582^{a}	0.733^{b}	0.735^{b}	0.663^{a}	0.761^{a}	0.836^{b}
H' – quadrats	0.83	1.06	1.03	1.06	0.81^{a}	1.02^{ab}	1.14^{b}
H'– plots	1.09^{a}	1.57^{ab}	1.86^{b}	1.87^{b}	1.75^{a}	2.06^{b}	2.20^{b}

Table 3. Comparison of structural values on each Muddy sample. Superscripts = samples are not different (P < 0.05; one-way ANOVA, followed by Bonferroni test.)

Parameter	Muddy-SE	Muddy-NW	Muddy-Control	P <
Richness (n)	14.3	14.9	15.7	NS
Mean richness (n)	4.31^{a}	3.69^{b}	4.20^{ab}	0.03
Frequency (%)	30.1^{a}	25.3^{b}	26.8^{b}	0.001
Cover (%)	24.7^{a}	16.7^{b}	13.3^{b}	0.002
Mean species cover (%)	1.93^{a}	1.14^{ab}	0.85^{b}	0.002
Species variation (%)	2.30	2.24	1.73	NS
Dominance	0.520	0.538	0.565	NS
E – quadrats	0.710^{a}	0.766^{b}	0.772^{b}	0.01
E – plots	0.656^{a}	0.752^{b}	0.774^{b}	0.001
H' – quadrats	1.01	1.00	1.09	NS
H' – plots	1.65^{a}	2.01^{b}	2.13^{b}	0.001

The Butte Camp lahars study areas were much smaller than the Muddy lahar yet several parameters were influenced by position. This resulted from the close proximity (5 to 25 m) of the nearest plots along the edge of BC-1 to the adjacent woodland. Total conifer cover declined sharply with both distance from the edge and elevation, as did *Abies lasiocarpa* cover (P< -0.001

in both cases). These gradients of conifer cover are the primary cause of the patterns shown in Table 1 and Table 4. Measures of diversity all indicated increased equitability as a function of distance and elevation, correlated with the reduction of conifer cover.

In stark contrast, BC-2 demonstrated few spatial trends. What weak trends did occur were not pronounced and appear to be related to exposure, not isolation. Effectively, all plots were similarly isolated, since the minimum distance to woodland vegetation was over 100 m. This woodland is located below the grid, sparsely wooded, with a damaged understory. Greater distances from the base point are associated with greater wind exposure, either with elevation or towards the west.

The control grid is located on an old lahar deposited at least 400 years ago, and is near intact forest. This site was impacted by tephra in 1980, but recovered fully within 5 years. No spatial patterns in any measure of structure were found. The age of the control surface is sufficient to expunge any effects of differential dispersal, though significant compositional variation remains.

Table 4. Comparison of structural values among the composite samples at Butte Camp (BC). Superscripts = samples are not different ($P < 0.05$; one-way ANOVA, followed by Bonferroni test.)

Parameter	BC-1 (n=40)	BC-2 (n=61)	Control (n=33)	P <
Richness (n)	15.5	16.4	16.8	NS
Mean richness (n)	4.69^a	5.49^b	8.32^c	0.001
Frequency (%)	30.1^a	33.6^b	49.5^c	0.001
Cover (%)	32.1^a	21.5^b	35.1^a	0.001
Mean species cover (%)	2.20^a	1.29^b	2.09^a	0.001
Species variation (%)	2.92^a	1.84^b	2.02^b	0.001
Dominance	0.509^a	0.648^b	0.692^b	0.001
E – quadrats	0.660^a	0.796^c	0.748^b	0.001
E – plots	0.588^a	0.745^b	0.840^c	0.001
H' – quadrats	1.014^a	1.319^b	1.569^c	0.001
H' – plots	1.640^a	2.072^b	2.010^b	0.001

Hierarchical structure

We used three common structural indices to estimate dominance patterns, all reported in Table 4. All increase as the species are more evenly distributed. D was calculated only for quadrats and compares the degree to which species occupy a sample. E and H' were calculated both from quadrats and from the plot means to provide complementary views of structure at two scales.

The Muddy-SE plots showed a weak increase in D with elevation (Table 3), but only SE-3 showed reduced D with distance from the edge. Both quadrat and plot evenness on Muddy-SE increased with elevation, but not with distance. Both measures of evenness did decline with proximity to the edge, but local heterogeneity prevented patterns to emerge along an individual transect.

Changes in H' primarily reflect dominance changes because richness values changed only slightly. Overall, H'_{quad} did not vary spatially due to high variation among quadrats of a plot. Mean values increased slightly with elevation (Table 3). Only SE-3 increased significantly with distance. In contrast, H'_{plot} increased significantly with elevation and along SE-4.

Transects on the northwest side of the Muddy lahar are less stressful than the opposing side due to greater shade and protection from wind. This side of the lahar also contains several forested relict islands and the deposits are less deep. As a result, woody species have invaded to a substantial degree.

Overall, D increased with both distance and elevation. NW-3, with the least woody vegetation, was the only individual transect to demonstrate a significant increase with distance from the edge. E_{quad} increased with distance, but to a greater degree with elevation. This increase was due primarily to NW-3, in which woody plants were rare. E_{plot} responded primarily to elevation, with a small component of variation related to distance from the margin. The three transects were substantially different. None of the transects demonstrated significant variation associated with distance. H'_{quad} and H'_{plot} presented similar patterns. Both values increased significantly between the transects. There were significant spatial effects for both parameters, but distance did not affect H'_{plot}.

Muddy-control demonstrated no spatially consistent difference in any structural parameter, as would be expected in this isolated site.

The lahar grids differ in degree of isolation, but are otherwise similar. Spatially related structural patterns are more prominent on BC-1. Here, D increased strongly both with distance from the forest edge and with elevation (Table 5). E_{quad} increased with both, though more strongly with elevation, and E_{plot} increased strongly with both parameters. Variation in H'_{quad} was too great for patterns to emerge, but H'_{plot} increased strongly with both dimensions.

Table 5. Relationship between community structure and distance and elevation. r^2 and P were determined from multiple or simple regressions. Signs indicate the direction of the relationship. No spatially consistent pattern was found in the Muddy or the BC controls, so these are omitted. NS = not significant.

Location	**Dominance**		**Evenness-Quadrats**		**Evenness-Plots**		**Shannon-Quadrats**		**Shannon-Plots**	
	r^2	**P <**	**r^2**	**P <**	**r^2**	**P <**	**r^2**	**P <**	**r^2**	**P <**
Muddy SE	0.25	0.02	0.61	0.001	0.49	0.001		NS	0.37	0.002
Distance		NS		NS		NS		NS		NS
Elevation	0.20	0.02	0.60	0.001	0.47	0.001		NS	0.34	0.001
SE - 1		NS		NS		NS		NS		NS
SE - 2		NS		NS		NS		NS		NS
SE - 3	0.79	-0.002		NS		NS	0.60	-0.02		NS
SE - 4		NS		NS		NS		NS	0.51	0.02
Muddy NW	0.31	0.03	0.27	0.05	0.51	0.001	0.30	0.03	0.45	0.003
Distance	0.24	0.02	0.18	0.05	0.18	0.05	0.24	0.02		NS
Elevation	0.23	0.02	0.24	0.02	0.51	0.001	0.23	0.03	0.45	0.001
NW - 1		NS		NS		NS		NS		NS
NW - 2		NS		NS		NS		NS		NS
NW - 3	0.84	0.03		NS		NS		NS		NS
BC 1 (n=40)	0.75	0.001	0.61	0.001	0.71	0.001		NS	0.75	0.001

Distance	0.40	0.001	0.28	0.001	0.38	0.001		NS	0.39	0.001
Elevation	0.36	0.001	0.39	0.001	0.35	0.001		NS	0.38	0.001
BC 2 (n=61)		NS	0.31	0.001	0.13	-0.02		NS		NS
Distance		NS	0.07	-0.04	0.13	-0.01		NS		NS
Elevation		NS	0.23	0.001		NS		NS		NS

On BC-2, measures of structure are weakly related to space. E_{quad} declined with distance and increased with elevation, but both effects were weak. E_{plot} declined with distance.

There are clear differences among the three grids (Table 4). BC-1 vegetation consistently expressed significantly lower D, E and H' values than BC-2. BC-2 was similar to BC-control in D and H'_{plot}. BC-2 was less diverse than the control in E_{plot} and H'_{quad}.

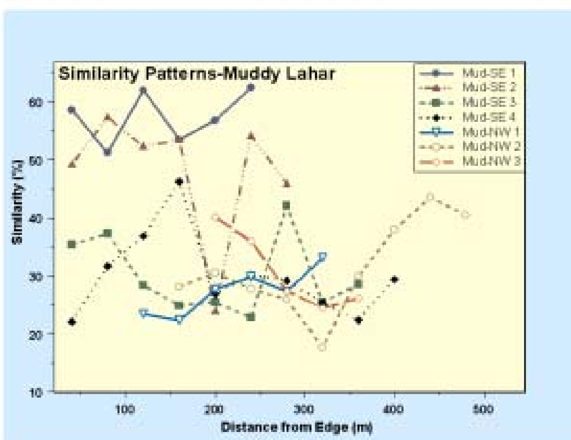
Diversity measures demonstrated no clear pattern with distance. On the scale of this study, local factors were more important than distance in determining dominance relationships. D, E and H' all increased strongly with elevation, reflecting reduced dominance of common species. Elevation is a surrogate that measures the length and quality of the growing season, so this pattern would be expected if dispersal becomes increasingly limited as the pace of succession runs more slowly.

Taken together, this portion of the study confirms that isolation will have impacts on the structure of vegetation and that the succession clock runs at a rate controlled by the growing season.

Heterogeneity Patterns

Percent similarity (PS) measures the degree of compositional overlap in two samples of vegetation. The overall mean of the Muddy-SE plots was 39.1%. Similarity of the four transects declined significantly, from 57.4% on the lowest transect to 30.0% on the highest one (Table 1). Fig. 1 summarizes the changes of within plot similarity in the Muddy transects. While there were statistically significant differences among the plots (ANOVA), linear regressions of PS vs. distance were not significant. Local conditions often override the effects of distance from the edge when one transect was considered. When all Muddy-SE plots are considered together, only elevation provides a significant correlation; distance effects are not significant. The means for these transects declined significantly. The overall similarity among plots was 52.3%, intermediate to the NW transects and the controls. The similarity among plots declined strongly with elevation, indicating that spatial heterogeneity increased with elevation.

Fig. 1. Percent similarity changes on Muddy River.



Muddy-NW transects started farther from the forest edge than the east transects due to conifer dominance near the edge. Within plot similarity averaged < 29.4% and ranged from 17 to 43%. The mean PS of transects did not differ significantly (Table 6). NW-1 similarity increased with distance, apparently because tree density declined. NW-2 similarities declined, but not significantly (P < 0.09) as they are quite variable. NW-3 similarity declined with distance, as predicted (Table 6; Fig. 7). Between plot similarities were not significantly different and similar to those of the lower SE transects.

Mean within plot similarity of Muddy-control plots was the lowest of the Muddy sets. There were no internal spatial patterns even though distances between plots were similar to those of a transect. The sample area was relatively homogeneous, and the PS between plots was 56.7%, higher than the transect sites which extended over a much larger area.

The BC-1 lahar demonstrated a response to distance from colonists. BC-1 similarities varied from 12% to 63% (mean = 35.3). Within-plot similarities declined with both elevation and distance from the forest (Table 6). Within plot similarities were highest in the control (57.1%), while BC-2 similarity was significantly higher than that of BC-1, even though cover was greater on the latter. The range of similarities was from 26 to 67% (mean = 42.4%). There were no spatial patterns on either BC-2.

Table 1. Within plot percent similarity (PS) regressions of similarity with distance and elevation; and between plot similarities at each study area. SD = standard deviation. Between lines, within a column, lower case superscripts indicate membership in homogeneous groups, p < 0.01, Bonferroni test). Upper case superscripts indicate comparisons between all plots in a sample.

	WITHIN PLOTS			BETWEEN PLOTS	
SITE	**PS**	**SD**	**Regression**	**PS**	**SD**
Muddy-SE	39.1^{A}	± 13.5	Elevation: r^2=0.67; P < -0.001	52.3^{B}	± 15.8
SE-1 (n=6)	57.4^{a}	± 4.5	NS	71.2^{a}	± 9.9
SE-2 (n=7)	48.0^{b}	± 11.2	NS	59.6^{ab}	± 13.8
SE-3 (n=9)	30.1^{c}	± 6.6	NS	49.5^{bc}	± 17.4
SE-4 (n=10)	30.0^{c}	± 7.1	NS	45.4^{c}	± 19.0
Muddy-NW	29.4^{B}	± 6.5	NS	48.0	± 22.7
NW-1 (n=6)	27.3	± 4.0	r^2=0.70; P < 0.04	61.6	± 11.6
NW-2 (n=12)	29.8	± 7.8	NS	57.3	± 22.4
NW-3 (n=5)	30.8	± 6.8	r^2=0.85; P < -0.03	59.5	± 10.3
Muddy-Control (n=42)	26.4^{C}	± 5.6	NS	56.7^{C}	± 11.7
BC-1 (n=40)	35.3^{A}	± 12.0	Total: r^2=0.50; P < -0.001 Elevation: r^2=0.34; P < -0.001 Distance: r^2=0.17; P < -0.007	52.1^{A}	± 16.6
BC-2 (n=61)	42.4^{B}	± 8.2	NS	53.6^{B}	± 13.4
BC-Control (n=33)	57.1^{C}	± 5.6	NS	64.7^{C}	± 12.0

Between plot similarities were lowest on BC-1 (52.1%), and the variation between plots was the highest, even though distances on BC-2 were longer. Between plot similarities on the mature meadow of BC-control were substantially higher than either.

BC-control had the highest mean similarity and least variation. However, the mean of 57.1% implies that substantial floristic variation remains within plots. There were no spatially relevant patterns. The similarity among the plots (64.7%) indicates substantial convergence, even though patchiness remains and some locally dominant species are absent from some plots.

Early in primary succession, plots that receive a dense seed rain will develop more quickly than more isolated sites, so that early in the process, within plot similarity should decline with distance. Simple isolation delays the homogenization of vegetation. The highest similarity occurs on Muddy-SE, which has plots at lower elevations than the others. The lowest similarities are for plots at the highest elevation and the Muddy controls. Muddy-NW, at intermediate elevations and including patchy woody species populations, has intermediate similarities. The presence of substantial invasions on the Muddy-NW creates substantial within plot variation that will diminish as conifers exert greater dominance.

The BC grids were both more exposed and at higher elevations than the Muddy, so vegetation development was retarded. Only on BC-1, where there was a strong gradient of conifer density did mean similarity decline with respect to spatial factors. Where all plots were isolated (BC-2) or where sufficient time has occurred to permit homogenization (BC-control), there were no spatial patterns. However, the variation in BC-control suggests that chance establishment patterns persist and combine with subtle habitat differences to preserve substantial variation within a dry subalpine meadow.

This study of heterogeneity along spatial and temporal gradients demonstrates the importance of distance alone in determining both species composition, community structure, and heterogeneity. It also shows that the rate of community development is affected by growing season length. Less mature vegetation (e.g. that found at higher elevations) is more variable and exhibits less dominance than more mature vegetation. Samples within the seed shadow, where the seed rain is denser, develop greater dominance more quickly than more distant samples.

Isolation and “relative succession rates” affect practical efforts to restore habitats. This study demonstrated that distance alone can impede recruitment and that stress slows the rate of species turnover. In addition to habitat amelioration common in restoration, natural recruitment can be facilitated by promoting dispersal vectors and by providing suitable sites for establishment by naturally dispersing species. Restoration targets should be more general, for example in terms of plant functional types and alternative communities. The desired conditions of the ecosystem (e.g., plant biomass, cover, and soil organic matter) should be of greater importance than any particular community.

Vegetation is molded by environmental and biological factors, but the initial conditions upon which these factors work are created by landscape effects and chance. The pace of early succession is governed by the rate of dispersal and is dictated by proximity. This study showed that the proximity effect is rapidly attenuated and that short distances effectively limit dispersal. The effects of differential dispersal can persist indefinitely and may be one source of persistent, unexplained variation in vegetation. As succession unfolds, species fill in the landscape, and spatial variation in vegetation typically declines. There is a limit to developing homogeneity because local differences can persist due to inhibitory effects of the founding species. Mature communities will retain a residual of unexplainable variation linked to historical accidents (contingencies), stochastic invasion patterns, and landscape effects.