

Gradients in compositional variation on lahars, Mount St. Helens, Washington, USA

Roger del Moral^{1,*} and Erin E. Ellis²

¹*Department of Biology, Department of Biology-Box 355325 University of Washington 1521 NE Pacific St. Seattle, WA 98195-5325;* ²*School of Oceanography, University of Washington, Seattle, WA 98195, USA;*

**Author for correspondence (voice: (+1) 206.543.6341; facsimile: (+1) 206.685.1728; e-mail: moral@u.washington.edu)*

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Abstract

How isolation affects primary succession remains unresolved. Our hypotheses are: 1) the rate of succession is slowed within 50 m from sources and 2) dominance increases more rapidly if the growing season is longer. We sampled lahar vegetation near conifer forests on Mount St. Helens 23 years after the eruption using transects (Muddy) and grids (Butte Camp, BC). Transects were compared to isolated plots of the same age, while grids were compared to vegetation that was 400 years older. Cover declined with distance and with elevation on the Muddy due to denser seed rain near forests and shorter growing seasons at higher elevation. On BC-1, next to a forest, richness measures increased with distance, while cover decreased with elevation. On BC-2, more exposed than BC-1, mean richness and cover declined with elevation, but increased towards seed sources. Equitability increased with distance and with elevation on more stressful transects and on BC-1. Percent similarity (PS), a measure of floristic heterogeneity, declined with elevation on Muddy-SW. BC-1 PS decreased with both distance and elevation. Data from grids collected since 1987 showed that both sites became more homogeneous through time. Directional changes on BC-1 were greater than on BC-2, while annual variation of DCA scores declined only on BC-2. These differences are related to conifer dominance patterns. Succession is influenced by isolation, which controls the seed rain, and by stress, which controls establishment, the rate of biomass accumulation, and the spread of immigrants. Although community development is governed by environmental factors, this study shows that the effects of dispersal that result from distance factors can persist and may be a source of unexplained variation in mature communities.

Introduction

This study describes our space-for-time substitutions to explore how communities form. While vegetation variation declines during succession, structural heterogeneity often persists (Fridriksson and Magnusson 1992; Davey and Rothery 1993; Kazmierczak et al. 1995; Frelich et al. 1998; Hubbell et al. 1999). While vegetation heterogeneity declines over time (del Moral and Jones 2002), it never disappears (Matlack

1994a). Communities of similar age may have different structures if subjected to different levels of stress.

Proximity to intact vegetation shapes community structure during succession. Vegetation near potential colonists is more homogeneous than is isolated vegetation (Tagawa 1992) because chance increases with distance (del Moral 1999). Homogeneity, percent cover, and species richness usually decline with isolation (Halpern and Harmon 1983; Primack and Miao 1992; Brunet and von Oheimb 1998; Butaye et al. 2001; Foster and Tilman 2003).

Table 1. Designation, sample size, sample design, elevation, and coordinates of each study area. N = the number of 100 m² plots. Muddy = Muddy River lahar, BC = Butte Camp lahars. Coordinates are near the center of the site in question.

Designation	N	Sample Design	Elevation (m)	Latitude	Longitude
Muddy-SE	32	4 transects	985–1110	46°10'44" N	122°07'10" W
Muddy-NW	23	3 transects	1050–1150	46°10'40" N	122°07'25" W
Muddy-Control	42	6 by 7 grid	1210–1240	46°11'16" N	122°08'13" W
BC-1	40	10 by 20 grid, selection	1424–1439	46°10'33" N	122°13'32" W
BC-2	61	16 by 20 grid, selection	1431–1448	46°10'55" N	122°13'42" W
BC-Control	33	10 by 20 grid, selection	1385–1390	46°11'16" N	122°08'13" W

Volcanic landscapes provide many examples of how differential isolation affects vegetation composition and heterogeneity. Fuller and del Moral (2003; del Moral and Grishin 1999) demonstrated floristic gradients on pumice near remnant vegetation. Isolated habitats elsewhere are less diverse, and vegetation in habitats of similar size and environment differ significantly (Borgegård 1990; Matlack 1994b; Fastie 1995; Verheyen et al. 2003). Isolation affects composition because stochastic factors can lead to alternative species assemblies (Tilman 1997).

The pace of succession is also affected by the length of the growing season. The growing season shrinks with elevation, so species expansion slows, and seedling survival drops (Dlugosch and del Moral 1999). With time, the homogeneity of vegetation increases as species establish and expand. The invasion of woody species may then decrease homogeneity by creating environmental mosaics (Aarssen and Epp 1990) and the woody species create a mosaic of environmental and competitive habitats. When these species achieve complete dominance, the vegetation again becomes more homogeneous.

The 1980 lateral blast of the Mount St. Helens volcano produced many lahars (mudflows) that created barren sites next to intact vegetation. The transition from intact vegetation to barren surfaces formed strong gradients of species invasion. Our first hypothesis is that even isolation by a few meters retards the rate of succession (see del Moral and Eckert 2004). The second is that the development of dominance is controlled by the length of the growing season. These hypotheses were tested by exploring community structure and floristic heterogeneity along several distance gradients. We predicted that richness and cover would decline, but that equitability would increase with distance from colonists and with shorter growing seasons (Glenn-Lewin 1980; Savage et al. 2000; Walker and del Moral 2003). Equitability should be higher because several species occur, but

none is common at first. At even short distances, all sites are effectively equidistant from a source of propagules, so no spatially related pattern is expected within isolated samples.

Methods

Study Sites

Most sampling was conducted on lahars deposited during the eruption of Mount St. Helens on May 18, 1980 (Foxworthy and Hill 1982; Dale et al. 2004; Table 1). Rapidly melting ice spawned the very large Muddy River Lahar (henceforth 'Muddy'). The deposit was over 20 m deep at its maximum and was at least 1 km wide in the study area.

We established transects from both edges of the Muddy at several elevations. Along the Southwest-facing (SW) edge, forest vegetation was dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Pinus contorta* var. *latifolia*, and *Pinus monticola*. Here, transects started 40 m from the forest with plots established at 40 m intervals. Transect elevations were 985 m (SW-1), 1025 m (SW-2), 1075 (SW-3), and 1105 m (SW-4). The Northeast-facing (NE) edge was ragged. Dominance was similar to that described above, but *Abies amabilis* was also common. Conifers alleviated drought by reducing wind and creating shade, so woody plant establishment was substantial. The lahar edge was also thinner and there were islands of surviving vegetation near the transects. Therefore, the transects were started farther from intact vegetation. The NE transects were at 1050 m (NE-1), 120 m from forest vegetation, 1100 m (NE-2), 140 m from the edge, and 1155 m (NE-3), 280 m from surviving vegetation. NE-3 was also isolated by a deep ravine. The nearest vegetation near NE-3 was dominated by *Abies lasiocarpa* and shrubs.

Several smaller lahars were spawned near Butte Camp (BC). Lahar BC-1 terminated near a level area. An intact forest dominated by *Abies lasiocarpa* and *Pinus contorta* survived along its eastern edge, where the lahar is 1 to 2 m deep. The distance from forest to a sample along this edge varied from 4 to 15 m. The sample plots started 60 m above the lahar terminus. Lahar BC-2 is larger, deeper, and more isolated. The nearest conifers are 80 m downhill in a forest that was damaged by the lahar, so pools of most species were several hundred meters distant. These lahars were sampled on grids monitored since 1987. Each consisted of contiguous 10 by 10 m plots (BC-1, 175 plots; BC-2, 317 plots). The intensely sampled plots were separated by at least 10 m ($n = 40$ on BC-1; $n = 61$ on BC-2).

Vegetation structure was sampled at two other locations in 2003 to serve as baselines. A grid 120 m by 210 m was located 900 m uphill from transects on the Muddy, isolated from surviving vegetation. Here, 42 plots were sampled 30 m between nearest neighbors. At Butte Camp, 33 plots were sampled on a 400-year old lahar within an area 120 by 400 m, within 400 m of the grids. There was 30 m between samples. This site had recovered from a deposit of 30 cm of fine pumice (tephra) in 1980 and supports dry meadow vegetation.

Nomenclature

Nomenclature was determined from the Integrated Taxonomic Information System at http://www.itis.usda.gov/advanced_search.html on September 10, 2003. A complete list of species names used in this study, and earlier names used in our previous studies of Mount St. Helens vegetation can be found at <http://protist.biology.washington.edu/delmoral/>.

Sampling

Each plot was sampled by 25 1-m² quadrats placed so that none was within 1 m of another. The cover of each species in each quadrat was determined to the nearest 1%. Mosses, especially *Racomitrium canescens*, have excellent dispersal ability. They were so common that they obscured patterns found when only seed plants were analyzed. Therefore, they were excluded from the analysis of Muddy plots. Plots were arrayed either on transects (Muddy) or in grids (BC). Plots were separated by a minimum of 40 m on transects or 10 m on the grids.

To assess the development of homogeneity, data from BC-1 and BC-2 from 1987 to the most recent sampling dates were gathered from the same plots as sampled in 2002. Grid sampling used this index (see Wood and del Moral 1988): 1 = one to five plants; 2 = six to 20 plants; 3 = > 20 plants or 0.25 to 0.5% cover; 4 = > 0.5% to 1%; 5 = > 1% to 2%; 6 = > 2% to 4%; 7 = > 4% to 8%; 8 = > 8% to 16%; 9 = > 16% to 32% and 10 = > 32%. Therefore, similarity values are not comparable to those of the intensive 2002 sampling. Ten sets of data on each grid, collected between 1987 and 2002, were analyzed to determine changes in structure and the percent similarity among the plots in each year.

Data summary. For each plot, these parameters were calculated (McCune and Mefford 1999): richness (number of species), mean richness per quadrat, total cover, mean species cover, and the standard deviation of species cover in the plot. Three measure of community structure were used to describe a plot: Simpson's diversity index, $S [1 - \sum(P_i * P_i)]$, evenness, $E_{plot} [H'/\ln(\text{Richness})]$, and Shannon's diversity index, $H'_{plot} [-\sum(P_i + \ln P_i)]$, where P_i is the proportion of a species in a plot. E and H' were also calculated for each quadrat of a plot and the means determined (E_{quad} and H'_{quad}). All indices increase as the species become more equitably distributed.

Heterogeneity. The variation of species composition within a plot may be affected by surface characteristics, but it also responds to proximity to colonists. Floristic similarity was calculated among all pair-wise combinations of the 25 quadrats of a plot. We predicted that similarity would decline with distance and with elevation if samples were initiated near sources of colonists, which should have higher levels of similarity than isolated plots. However, moderately isolated plots should have similar levels of floristic variation. In contrast, mature surfaces should have high similarity relative to otherwise similar younger surfaces.

Percent similarity (PS) was calculated from pair-wise comparisons (within-plot similarity) and between the plots of a sample using mean species cover (among-plot similarity) as follows: $PS_{ij} = 200 \sum \min(X_{ik}, X_{jk}) / \sum (X_{ik} + X_{jk})$, where i and j are two quadrats, there are k species, X is percent cover, and \min is the lower value (Kovach 1998). Mean similarities were compared along transects and within an entire data set.

Statistical Analyses. Within each set of data, the relationship between structural variables such as per-

Table 2. Mean cover percent of common species in the six study areas. Designations given in Table 1. SW = the southwest facing edge; NE = the northeast facing edge. Species listed average > 0.2% cover at one or more sites. Column headings defined in Table 1.

Species	Muddy-SW	Muddy-NE	Muddy-Control	BC-1	BC-2	BC-Control
Trees						
<i>Abies</i> spp.	1.34	0.65	1.41	14.1	1.65	0.11
<i>Pinus contorta</i>	0.10	1.12	0.02	7.81	0.71	1.65
<i>Pinus monticola</i>	0.06	0.46	0.01	0	0	0
<i>Populus balsamifera</i>	0.02	0.35	> 0.01	0	0	0
<i>Pseudotsuga menziesii</i>	1.36	1.63	0.2	0	0	0
Shrubs						
<i>Alnus dioica</i>	0.25	0.84	0	0	0	0
<i>Arctostaphylos nevadensis</i>	1.82	1.52	0.59	0	0	> 0.01
<i>Penstemon cardwellii</i>	2.68	4.78	2.03	0.45	2.66	> 0.01
<i>Salix commutata</i>	0.41	0.22	0.20	0.01	0.03	0.01
<i>Vaccinium membranaceum</i>	0	0.14	0.32	0.01	0	0.01
Herbs						
<i>Achnatherum occidentale</i>	0	0	0.02	0	0.07	0.59
<i>Agrostis pallens</i>	0.08	0.42	1.13	0.59	0.56	13.5
<i>Anaphalis margaritacea</i>	0.75	0.59	0.63	0.17	0.27	> 0.01
<i>Aster ledophyllus</i>	0	0	> 0.01	0	0.09	0.33
<i>Carex microptera</i>	0.08	0.62	> 0.01	0	0.01	> 0.01
<i>Carex rossii</i>	0.05	0.09	0.18	0.06	0.12	1.83
<i>Cistanthe umbellata</i>	0.48	0.53	0.17	0.41	0.84	0.22
<i>Elymus elymoides</i>	0	0.04	0.03	0	0.11	0.71
<i>Eriogonum pyrolifolium</i>	0.04	0.03	> 0.01	0.31	2.43	1.65
<i>Hieracium albiflorum</i>	0.47	0.10	0.39	0.08	0.18	> 0.01
<i>Hypochaeris radicata</i>	0.45	0.02	0.28	0.01	0.02	> 0.01
<i>Juncus parryi</i>	1.60	0.80	1.10	1.38	0.98	0.78
<i>Lomatium martindalei</i>	0	0	0	0.35	0.26	1.70
<i>Luetkea pectinata</i>	0.20	0.16	2.05	2.48	0.87	0
<i>Lupinus latifolius</i>	0.81	2.19	1.06	0	0.56	> 0.01
<i>Lupinus lepidus</i>	11.21	0.67	1.05	1.15	4.29	1.70
<i>Polygonum davisiae</i>	0	0	0	1.53	3.21	1.23

cent cover and a measure of distance was calculated. For the transects, the coordinates (X meters from the edge; Y meters elevation) were used in multiple regression. Linear regression of one variable was also used if the other variable was not significant. On the grids, the plot coordinates were used, first in multiple regressions, then in linear regression. These measures were used in regression analyses with the several structural variables (Analytical Software 2001). The PS of the Butte Camp grids though time was compared for each sample date by t-test. Detrended correspondence analysis (McCune and Mefford 1999) was used to determine changes in floristic composition and variation of plots on BC-1 and BC-2 from 1987 to 2003. Graphs were visualized using AXUM 7 (Mathsoft 2001).

Results

Species composition

In most sites, trees were sparse, but on BC-1 *Abies* and *Pinus* dominated near the lower western edges (Table 2). Tall shrubs were sparse, while *Penstemon cardwellii* was common on young surfaces. *Arctostaphylos nevadensis* was common on the Muddy. Herb composition varied among and within sites. Muddy-SW was dominated by *Lupinus lepidus*, *Juncus parryi*, and *Anaphalis margaritacea*. Muddy-NE had conifers, *Alnus dioica*, *Lupinus latifolius*, *L. lepidus*, *Juncus*, and *Cistanthe umbellata*. BC-1 was dominated by conifers, with *Eriogonum pyrolifolium*, *Luetkea pectinata*, *Lupinus lepidus*, *Polygonum davisiae*, *Cistanthe*, and *Juncus*. Conifers were sparser on BC-2. *Penstemon*, *L. lepidus*, *Polygonum*, *Cistanthe*, and *Eriogonum* were common, while *Luetkea pectinata* was less abundant on BC-2. The old BC surface

Table 3. Relationship between richness per plot, mean richness, plot cover, mean species cover, and variation of species cover (SD) with 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		Plot Cover		Species Cover		SD of Species Cover	
	r^2	P <	r^2	P <	r^2	P <	r^2	P <	r^2	P <
Muddy-SE (n = 32)		NS	0.26	0.04(-)	0.72	0.001(-)	0.29	0.02(-)	0.31	0.005
Distance		NS	0.19	0.02(-)	0.65	0.001(-)		NS		NS
Elevation		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(-)		NS		NS	0.59	0.05
Transect 2 (n = 7)		NS	0.58	0.04(-)	0.62	0.04(-)		NS		NS
Transect 3 (n = 9)		NS	0.60	0.03(-)	0.50	0.04(-)	0.51	0.03(-)		NS
Transect 4 (n = 10)	0.54	0.02(-)		NS		NS	0.48	0.03(-)		NS
Muddy-NW (n = 23)		NS		NS	0.34	0.01(-)	0.37	0.01(-)	0.45	0.003(-)
Distance		NS		NS	0.22	0.03(-)	0.25	0.02(-)	0.38	0.002(-)
Elevation		NS		NS	0.29	0.008(-)	0.32	0.005(-)	0.33	0.004(-)
Transect 1 (n = 6)		NS		NS		NS		NS	0.70	0.02
Transect 2 (n = 12)		NS		NS		NS		NS		NS
Transect 3 (n = 5)		NS		NS		NS		NS	0.78	0.03
BC-1 (n = 40)	0.37	0.001	0.66	0.001	0.56	0.001(-)	0.61	0.001(-)	0.37	0.001(-)
Distance	0.21	0.004	0.51	0.001		NS	0.16	0.01(-)		NS
Elevation	0.16	0.04(-)	0.17	0.008(-)	0.50	0.001(-)	0.46	0.001(-)	0.33	0.001(-)
BC-2 (n = 61)	0.42	0.001	0.43	0.001	0.53	0.001	0.32	0.001	0.32	0.001
Distance	0.25		0.24	0.001	0.25	0.001	0.13	0.004	0.08	0.04
Elevation	0.16	0.001	0.18	0.001(-)	0.26	0.001(-)	0.18	0.001(-)	0.24	0.001(-)

Table 4. Mean values of structural parameters among transects on the Muddy River. 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	SE-2	SE-3	SE-4	NW-1	NW-2	NW-3
	(n = 6)	(n = 7)	(n = 9)	(n = 10)	(n = 6)	(n = 12)	(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
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
Simpson's Index (S)	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

was dominated by graminoids (*Agrostis pallens*, *Carex rossii*, *Elymus elymoides*, *Achnatherum occidentale*, and *Juncus*), along with *Lomatium martindalei* and *Aster ledophyllus*.

Structure

Richness. Each study area was examined for patterns in total number of species per plot and the mean quadrat richness. Quadrat richness on Muddy-SW de-

clined with distance (Table 3), while both plot and mean richness declined on SW-1 due to strong *Lupinus lepidus* dominance on more distant plots. Mean quadrat richness also declined on SW-2 and SW-3. Mean quadrat richness of Muddy-SW was greater than that of Muddy-NE (Table 5).

Both plot richness and mean richness on BC-1 increased significantly with distance from the edge and with elevation (Table 3). Elevation correlated with greater exposure and deeper lahar deposits that

Table 5. Overall means of structural values at each study site. The same superscript among the muddy samples and among the BC samples = samples that are not significantly different ($P < 0.05$; one-way ANOVA, followed by Bonferroni test.) No superscript = no significant difference among values of a row.

Parameter	Muddy-SE	Muddy-NW	Muddy-Control	P <	BC-1 (n = 40)	BC-2 (n = 61)	Control (n = 33)	P <
Richness (n)	14.3	14.9	15.7	NS	15.5	16.4	16.8	NS
Mean richness (n)	4.31 ^a	3.69 ^b	4.20 ^{ab}	0.03	4.69 ^a	5.49 ^b	8.32 ^c	0.001
Cover (%)	24.7 ^a	16.7 ^b	13.3 ^b	0.002	32.1 ^a	21.5 ^b	35.1 ^a	0.001
Mean species cover (%)	1.93 ^a	1.14 ^{ab}	0.85 ^b	0.002	2.20 ^a	1.29 ^b	2.09 ^a	0.001
Species variation (%)	2.30	2.24	1.73	NS	2.92 ^a	1.84 ^b	2.02 ^b	0.001
Simpson's Index (S)	0.520	0.538	0.565	NS	0.509 ^a	0.648 ^b	0.692 ^b	0.001
E – quadrats	0.710 ^a	0.766 ^b	0.772 ^b	0.01	0.660 ^a	0.796 ^c	0.748 ^b	0.001
E – plots	0.656 ^a	0.752 ^b	0.774 ^b	0.001	0.588 ^a	0.745 ^b	0.840 ^c	0.001
H' – quadrats	1.01	1.00	1.09	NS	1.014 ^a	1.319 ^b	1.569 ^c	0.001
H' – plots	1.65 ^a	2.01 ^b	2.13 ^b	0.001	1.640 ^a	2.072 ^b	2.010 ^b	0.001

Table 6. Relationships between community structure, distance, and elevation. r^2 and P determined from multiple or simple regressions. Signs show 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	Simpson (S)		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

reduced conifer dominance. Mean plot richness and mean quadrat richness was higher than on BC-1. Richness declined uphill, and increased from east to west (Table 3). Mean quadrat richness changed in a similar way to mean plot richness. The control grid demonstrated no spatial patterns, though there were significant variations among the plots. Mean species richness per quadrat was much greater than the grid plots (Table 6).

Cover: Vegetation cover best represents site development. Plot cover on the Muddy-SW transects de-

clined with increasing distance and with elevation (Table 3). Cover declined with distance along SW-2 and SW-3. Mean species cover declined along SW-3 and SW-4, but the variation among species increased only on SW-1 (Table 3). When considering all transects, mean plot cover, mean species cover, and variation of species cover all declined with elevation (Table 4). There were only minor spatially related declines in mean plot cover, mean species cover, and variation of species cover with distance and elevation along the Muddy-NE transects (Table 3, Table 4).

Variation was large and sample size small. However, species variation did increase on both NE-1 and NE-3. There were no spatial patterns on the Muddy Control grid in cover related variables, where plot cover was similar to the NE transects and lower than the SW transects. Mean species cover was lower than that of both transects due to higher elevation.

On BC-1, plot cover declined up the lahar due to changes in conifers. Mean species cover was higher than on the other primary surface. The higher values were concentrated near the forest. The mean species cover declined with distance and elevation, and the variation of this cover declined up hill (Table 3). Mean plot cover on BC-2 was lower than on either BC-1 or the control. BC-2 also had lower mean species cover and the lowest variation of cover (Table 5). Cover declined with elevation, but increased from east to west (Table 3). The BC-control was well vegetated. Plant cover in adjacent plots has varied in response to seasonal factors since 1984 (del Moral 2000). 2003 was a dry year and cover was 6 to 10% lower than in 2002. Control cover was the highest of any site. Both mean species cover and cover standard deviation were intermediate to BC-1 and BC-2. These variables were not related to spatial factors, though there were significant differences among the plots.

Hierarchical structure. S increased with elevation on the Muddy-SW plots (Table 4), but only SW-3 showed lower S with distance. Both E_{quad} and E_{plot} on Muddy-SW increased with elevation, but not with distance (Table 4, Table 6). Changes in H' reflect dominance changes because richness values varied little. Mean values of H'_{quad} were similar on all transects (Table 4). H'_{quad} of SW-3 decreased with distance, but H'_{plot} increased with elevation and along SW-4 (Table 6).

On the Muddy-NE samples, S increased with distance and elevation, reflecting reduced dominance. NE-3, with little woody vegetation, was the only transect to show increased equitability with distance from the edge. Combining all NE plots revealed that E_{quad} increased with distance, but also with elevation (Table 6). E_{plot} responded primarily to elevation. H'_{quad} and H'_{plot} presented similar patterns. Both increased between the transects, reflecting reduced dominance with elevation. Distance was not consistently related to H'_{plot} .

Muddy-control lacked spatially consistent difference in any structural parameter. Both evenness measures were higher on Muddy-NE than Muddy-SW, while Muddy-control was similar to Muddy-NE.

H'_{plot} was higher on Muddy-NE and the control than on Muddy-SW.

The BC lahars are physically similar except for their degree of isolation. Spatially related structural patterns were more common on BC-1. S , E_{quad} , E_{plot} and H'_{plot} increased with distance from the forest edge and with elevation (Table 6). On BC-2, E_{quad} declined with distance and increased with elevation. E_{plot} declined only with distance.

The hierarchical structure on the Butte Camp grids differed significantly (Table 5). BC-1 vegetation consistently expressed significantly lower S , E and H' values than did BC-2. BC-2 was similar to BC-control in S and H'_{plot} , but less diverse than the control in E_{plot} and H'_{quad} .

Heterogeneity

Percent similarity (PS) measures floristic overlap in two samples of vegetation. The mean PS of the Muddy-SW transects declined from 57.4% on the lowest transect to 30.0% on the highest (Table 7). While there were similarity differences among the plots (ANOVA), linear regressions of PS vs. distance were not significant (Figure 1A). The PS of Muddy-SW plots declined with elevation (Table 7). The among-plot PS was intermediate between the Muddy-NE transects and the controls. Spatial heterogeneity increased with elevation.

Muddy-NE transects started farther from the forest edge than did the east transects. The mean among-plot PS of transects was similar (Table 7). NE-1 PS increased with distance as tree density declined. NE-3 PS declined with distance, as predicted (Table 7; Figure 1B). Among-plot PS were not different and were similar to those of the lower SW transects. Mean within-plot PS of Muddy-control plots was the lowest of the Muddy sets, but there were no internal spatial patterns. The among-plot PS was higher than the transect plots.

Vegetation on BC-1 responded to distance from colonists. Within-plot PS declined both with elevation and distance from the forest (Table 7). However, there were no spatial patterns on either BC-2 or the control. Within-plot PS were highest in the control and the variation was least. However, the mean was low, suggesting that substantial residual floristic variation. The PS of BC-2 was higher than that of BC-1, even though cover was greater on the latter.

Among-plot PS was lowest on BC-1, and its variation was the highest. Among-plot PS on the mature

Table 7. Within plot percent similarity (PS) and SD (standard deviation). Regressions are of similarity with distance and elevation. Within a column, between lines, lower case superscripts indicate membership in homogeneous groups, $P < 0.01$, Bonferroni test). E = regression significant with elevation; D = regression significant with distance from edge. Upper case superscripts indicate comparisons between all plots in a study area.

SITE	WITHIN PLOTS			AMONG PLOTS	
	PS	SD	Regression	PS	SD
Muddy-SE	39.1 ^A	± 13.5	E: $r^2 = 0.67$; $P < 0.001(-)$	52.3 ^B	± 15.8
SE-1 (n = 6)	57.4 ^a	± 4.5	NS	71.2 ^a	± 9.9
SE-2 (n = 7)	52.1 ^a	± 4.1	NS	62.6 ^{ab}	± 13.8
SE-3 (n = 9)	30.1 ^b	± 6.8	NS	49.5 ^{bc}	± 17.4
SE-4 (n = 10)	30.0 ^b	± 9.8	NS	45.4 ^c	± 19.0
Muddy-NW	29.4 ^B	± 6.5	NS	48.0 ^A	± 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: $r^2 = 0.50$; $P < 0.001(-)$ E: $r^2 = 0.34$; $P < 0.001(-)$ D: $r^2 = 0.17$; $P < 0.007(-)$	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

BC-control was higher than either BC-1 or BC-2. This suggests that control plots have undergone substantial, though incomplete convergence. Considerable patchiness remains and some locally dominant species remain absent from some plots.

Development of vegetation

Because the BC grids have been sampled since 1987, we could select those plots sampled in 2002 to follow structure and similarity changes. Each structural measure changed on both lahars (Figure 2). Richness (Figure 2a) increased through 1996, but then declined gradually, particularly on BC-1 where the increase in conifers has eliminated some species. Cover increased on both lahars (Figure 2b), and cover on BC-1 remains greater than on BC-2. H' increased through the mid-1990s, but on BC-1 it subsequently declined. On BC-2, there was little change after 1996. H' on BC-1 was significantly lower than on BC-2 (Figure 2c). S initially increased on BC-1 with richness, but after 1990, S declined. In contrast the lack of strong dominants on BC-2 permitted S to increase until 1996 (Figure 2d). E has declined steadily on BC-1 as conifers increased, but it has remained nearly constant on BC-2 until a decline in 2002 (Figure 2d).

Mean similarity increased from the early samples (Figure 3). On BC-1, PS increased until 1990. Thereafter, similarity changed. BC-2 was very heteroge-

neous in 1987, but PS became comparable to those of BC-1. The developing conifers have created heterogeneity on BC-1 resulting in a decline in PS after 1998. The mean PS of the two lahars differed for each comparison (e.g., seventh sample year vs. seventh year) except in 1989 (t-test, $P < 0.001$).

Species composition of each year was analyzed by DCA to assess directionality and variation changes of the mean positions (Figure 4). BC-1 changed more than BC-2, due to conifers, *Lomatium martindalei*, *Luetkea pectinata*, *Luzula parviflora*, *Penstemon cardwellii*, and *Polygonum davisiae*. Changes on BC-2 were due to slower accumulations of graminoids. On BC-2, species have accumulated, but there have been few major changes in structure or composition. The DCA scores on each of the first three axes of both BC-1 and BC-2 changed directionally (Figure 4a, b; ANOVA, $P < 0.001$ in both cases). For BC-1, the regression of standard error (SE) vs. years was not significant on axes DCA-1 and DCA-3, but on DCA-2 SE declined from 3.14 to 2.26 ($r^2 = 0.61$, $P < 0.008$). The SE of all BC-2 axes declined (DCA-1, $r^2 = 0.82$, $P < 0.003$; DCA-2, $r^2 = 0.69$, $P < 0.003$; and DCA-3, $r^2 = 0.86$, $P < 0.001$), indicating increased homogeneity. Thus, directional changes have been greater on BC-1 than on BC-2, but the latter has converged to a greater degree.

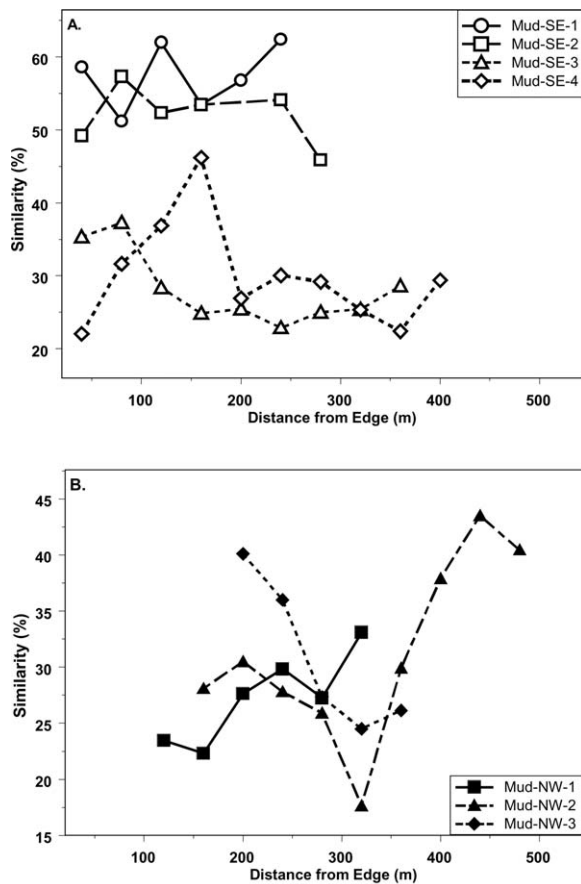


Figure 1. Percent Similarity (PS) along transects on the Muddy Lahar as a function of distance from the nearest forest edge: A = Muddy-SE; B = Muddy-NW (See Table 7 for statistical details).

Discussion

This study explored how distance from sources of colonists and environmental stress relate to the rate of succession measured by vegetation structure and heterogeneity. We predicted that within-plot heterogeneity and equitability would increase with distance from sources. Because the seed rain becomes diffuse within a few meters (Wood and del Moral 2000) and stochastic factors affect dispersal, the first colonists will be diverse, sparse, and spatially dispersed. As these colonists expand and competition creates dominance hierarchies, the vegetation becomes more homogeneous. Consequently, community structure should approach that of mature vegetation, but not necessarily with same species composition (Tofts and Silvertown 2002; Kahmen and Poschod 2004). The

rate at which development occurs is a function of the environmental stress.

Structure

Several studies have shown how spatial effects, even over short distances, influence species composition and succession (Tagawa 1992; Martínez et al. 2001). This study extends the effects to smaller scales and to other aspects of vegetation structure.

Community structure was related to distance on transects. On Muddy-SW, cover, mean richness, and mean species cover all decreased with distance. Species variation increased, which is a consequence of less predictable invasion. Plot cover, mean species cover, and species variation all declined with elevation, suggesting that community development is indeed slowed by a shorter growing season. S, E, and H' all increased with elevation, suggesting that the development of dominance is retarded as the length of the growing season decline.

The Muddy-NE transects were more complicated due to the invasion of woody species. These transects revealed few trends in structure. However, cover and its correlates declined with distance, and cover and mean species cover declined with elevation, consistent with the predictions. Equitability also increased along these transects and with elevation. These patterns also support the hypotheses that distance and growing season length affect succession rates.

The Muddy-control plots were sufficiently isolated from sources of colonists that each was effectively at the same dispersal distance. They demonstrated no spatial patterns. They did demonstrate reduced cover and mean species cover and greater evenness when compared to the Muddy-SW transects, which is consistent with the hypotheses stated above.

The Muddy lahar transect data support the hypothesis that primary succession is constrained by dispersal and that development rates are related to the length of the growing season. The degree of isolation required for significant dispersal effects is on the order of tens of meters.

The BC grids sampled a smaller area than did the Muddy transects; yet several parameters were influenced by position. This occurred because plots of BC-1 were as near as 5 m from the woodland. Total conifer cover declined with distance from the edge and with elevation. The gradients of conifer cover appear directly related to the patterns shown in Table

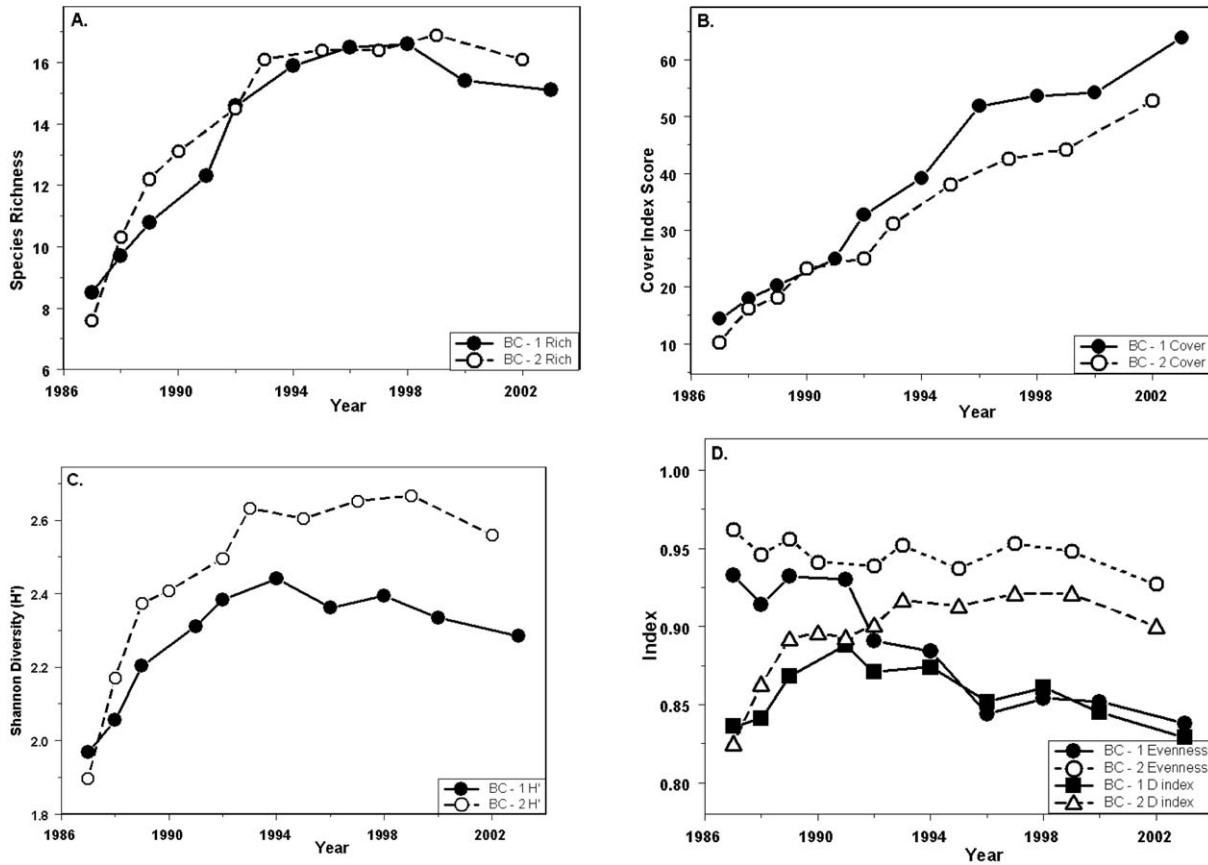


Figure 2. Structural changes on Butte Camp (BC) lahars since 1987: A. Species Richness; B. Total Cover Index; C. Diversity Index (H'); D. Evenness (E) and Simpson's Index (S).

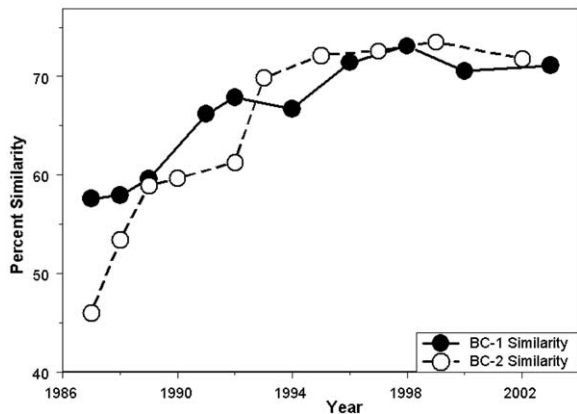


Figure 3. Changing percent similarity on BC-1 and BC-2 since 1987.

3, Table 6. All equitability measures increased with distance and elevation, variables that were correlated with the reduction of conifer cover.

In contrast, the few spatial trends revealed on BC-2 were less pronounced than on BC-1 and were related to exposure, not to isolation. All plots were similarly isolated, since the minimum distance to woodland vegetation was over 80 m. This sparse woodland was below the grid and only has a remnant understory. Lower plots were less stressful than upper ones because topography protected them from desiccation. Longer distances from the base point are associated with greater wind exposure, both with elevation and towards the west. Richness increases to the west may have resulted from a denser seed rain due to up-valley winds.

The control grid was on a 400 year-old lahar, near intact forest. This site was impacted by tephra in 1980, but recovered fully within four years (del Moral 1993). No spatial patterns in any parameter were found. The age of the control surface has expunged most effects of differential dispersal, yet substantial compositional variation remained. Even within a

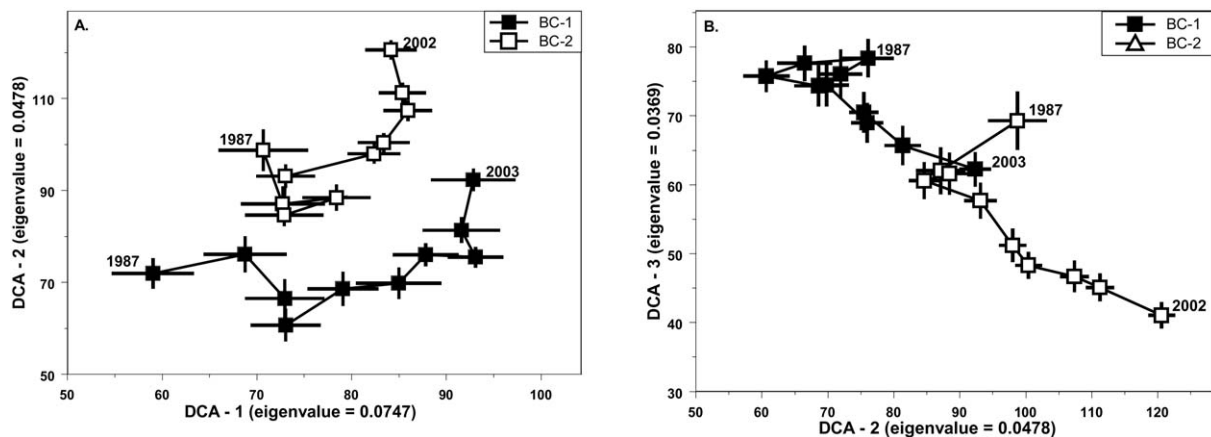


Figure 4. Mean DCA positions on BC-1 and BC-2 since 1987: A. BC-1 vs. BC-2, Axis 1 vs. Axis 2; B. BC-1 vs. BC-2, Axis 2 vs. Axis 3. Horizontal and vertical lines are standard errors (SE) of the DCA scores in each year on two axes.

small area on a homogeneous substrate, the vegetation has remained heterogeneous.

Similarity

We predicted that within plot similarity, which estimates floristic heterogeneity, should decline with distance from sources and with environmental stress. Contingency effects cap expected similarity values (McCune and Allen 1985; Bunting and Warner 1998), even if assembly rules lead to communities of similar growth forms (Weither and Keddy 1999). Priority effects, common when dispersal rates are low, can lead to unique trajectories (Malanson and Butler 1991; Inouye and Tilman 1995). Under extreme conditions, priority effects (Eriksson and Eriksson 1998) may produce novel species assemblages (cf. Roozen and Westhoff 1985; Facelli and D'Anela 1990; del Moral and Wood 1993; Ward and Thornton 2000).

Within-plot similarity does indeed decline with distance from sources and with elevation. This effect recalls long-term studies of small islands in a Swedish lake (Rydin and Borgegård 1991), where similarity increased over time, but where further development appeared arrested because dominant trees have failed to reach the islands. Convergence to a 'climax' community has been arrested by the failure of certain dominances to invade (Belyea and Lancaster 1999).

On the Muddy transects, there was a decline of within-plot similarity with distance from the forest and with elevation, including the low values found on the isolated controls located at higher elevations. Muddy-NE, at intermediate elevations, with patches of woody species, had similarities lower than the

lower Muddy-SW transects, but were less heterogeneous than high elevation plots. The invasion of trees and shrubs on the Muddy-NE created substantial within-plot variation that should diminish as conifers exert greater dominance. Between plot similarity on the Muddy confirmed the prediction that plots become more variable with elevation.

At Butte Camp, substrates were homogeneous and mean within plot similarities were higher than most transects and the controls on the Muddy. On BC-1, mean within plot similarity declined with distance from conifers. In contrast, there were no spatial patterns among the isolated plots of BC-2 or when sufficient time had occurred to permit greater convergence (BC-control). However, the floristic variation among BC-control plots suggested that random establishment patterns have persisted and combined with subtle habitat differences to preserve considerable variation within this subalpine meadow.

Time

Our hypotheses lead to predictions concerning the development of between plot similarity on BC-1 and BC-2. Similarity should increase early in primary succession during which time plots that receive a dense seed rain will develop more quickly than isolated sites. The differential invasion of conifers on BC-1 should lead to lower mean similarity among the plots and greater floristic variation.

Structure developed quickly on both lahars when compared to pyroclastic and pumice sites on Mount St. Helens (del Moral 1998). Most species occupy both lahars, but composition differed (PS = 35%).

Species rank abundances were correlated (Spearman $r = 0.70$, $P < 0.001$). The differences were due to the proximity of woodlands that contributed differentially to the vegetation of BC-1. Conifers reduced the number of species per plot by altering conditions from meadow to woodland. As a result, richness was slightly lower, and declining. H' , which was initially comparable to that of BC-2, did not increase after 1994 and began to decline thereafter. E and S demonstrated similar contrasts between BC-1 and BC-2 through time. These contrasts resulted from the differential proximity to conifers. While conifers declined with distance and elevation on BC-1, the proportion of common meadow species increased.

DCA demonstrated directional change on both lahars. There was greater turnover on BC-1 because of the greater degree of conifer development and correlated increases in some herb species. Initially, both samples had low conifer density, but conifers became dominant on most plots of BC-1. Spatial variations in conifer distribution also precluded reductions in DCA score variation with time. In contrast, BC-2 lacked a strong conifer gradient, so that directional change was smaller and variation decreased significantly. This demonstrates how transitional sites can remain heterogeneous until all plots have been saturated with invading species. A failure of vegetation to converge or to become homogenous may be due to initial dispersal gradients. Such gradients may contribute to the regularly low degree of predictability observed in studies relating species composition to environmental factors (McCune 1992).

Through time, the plots became more similar, as would be expected. However, significant compositional differences initiated by events early in this process rather than from environmental differences may persist even if trees dominate the entire site (del Moral et al. 2004). Just as control meadow vegetation remains variable, woodland vegetation may retain vestiges of its early development that preclude complete homogeneity. The similarity in a small woodland sample adjacent to BC-1 was 60%, reflecting the presence of residual meadow species.

The present study confirmed predictions based on the influence of isolation solely by distance. Cover declined while equitability and floristic heterogeneity increased with increasing isolation. Secondary dispersal from early colonists appears to be of minor importance. It also confirmed the prediction that the rate of community development is related to the growing season. Less mature vegetation found at

higher elevations was more variable and exhibited less dominance than more mature vegetation. Samples within the seed shadow, where the seed rain is denser, developed stronger dominance more quickly than did distant samples.

Restoration ecologists are aware of the importance of dispersal limitations in rehabilitating forests and recommendations to augment species diversity by the introduction of seeds of infrequent species are increasingly common (Makana and Thomas 2004). Our data demonstrated that colonization may be limited over even shorter distances than is often assumed.

Vegetation is molded both by environmental and biological factors, but the initial conditions upon which these factors work are created by landscape effects and chance (del Moral and Wood 1988). The pace of early succession is governed by the rate of dispersal, which is dictated by proximity, and 'relative succession rates.' Relative succession rates were described on long-term chronosequences in Hawaii, in terms of soil development and species turnover (Kitayama and Mueller-Dombois 1995), and on a 121-year chronosequence in Dutch dunes (De Kovel et al. 2000). Development on slack dune vegetation is also governed in large part by the accumulation of biomass, which is controlled by local hydrological patterns (Sekora et al. 2004). Here we show that the effect is present at the onset of succession.

This study showed that the proximity effect is rapidly attenuated and that dispersal limitation effects can occur even within 40 m (del Moral and Eckert 2004). Small differences in growing season retard succession as evidenced by reduced cover and increased heterogeneity with increased elevation. As succession unfolds, species occupy the landscape and dominance patterns develop. Spatial variation and equitability decline, but there is a limit to the degree of homogeneity that can develop. Vegetation can retain a residual of unexplainable variation that is linked to the types of landscape effects demonstrated in this study. Historical accidents (contingencies) and stochastic invasion patterns that can produce priority effects that alter dominance patterns also will affect the ultimate species composition in mature vegetation.

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