

Limits to convergence of vegetation during early primary succession

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Abstract

Questions: Primary succession, measured by changes in species composition, is slow, usually forcing a chronosequence approach. A unique data set is used to explore spatial and temporal changes in vegetation structure after a 1980 volcanic eruption. On the basis of data from a transect of 20 permanent plots with an altitudinal range of 250 m sampled through 2005, two questions are asked: Do changes along the transect recapitulate succession? Do plots converge to similar composition over time?

Location: A ridge between 1218 and 1468 m on Mount St. Helens, Washington, USA.

Methods: Repeat sampling of plots for species cover along a 1-km transect. Floristic changes were characterized by techniques including DCA, clustering and similarity.

Results: Species richness and cover increased with time at rates that decreased with increasing elevation. The establishment of *Lupinus lepidus* accelerated the rate of succession and may control its trajectory. Diversity (H') at first increased with richness, then declined as dominance hierarchies developed. Primary succession was characterized by overlapping phases of species assembly (richness), vegetation maturation (diversity peaks, cover expands) and inhibition (diversity declines). Each plot passed through several community classes, but by 2005, only four classes persisted. Succession trajectories (measured by DCA) became shorter with elevation. Similarity between groups of plots defined by their classification in 2005 did not increase with time. Similarity within plot groups converged slightly at the lower elevations. Despite similarities between temporal and spatial trends in composition, trajectories of higher plots do not recapitulate those of lower plots, apparently because *Lupinus* was not an early colonist. Any vegetation convergence has been limited to plots that are in close proximity.

Keywords: Ecoinformatics; Long-term permanent plot; Mount St. Helens; Primary succession; Succession trajectory; Vegetation structure.

Abbreviations: AG = Amalgamated group; CC = community class; DCA = Detrended Correspondence Analysis; MRPP = Multiple response permutation procedure; PS = Percent similarity; SD = Standard deviation.

Nomenclature: A list of species used in this study is at <http://protist.biology.washington.edu/~delmoral/>. Nomenclature follows the Integrated Taxonomic Information System: http://www.itis.usda.gov/advanced_search.html.

Introduction

The cataclysmic 18 May 1980 lateral eruption of Mount St. Helens, Washington provided a unique chance to explore primary succession (del Moral et al. 2005). In 1984, a transect of permanent plots up a devastated ridge was established to initiate one of the longest continuous records of early volcanic primary succession (cf. Magnússon & Ólafsson 2003; Weber et al. 2006).

Permanent plot studies have a long history and are an elegant alternative to chronosequence studies because they eliminate assumptions based on space-for-time substitutions (Austin 1981). The Buell secondary succession study (Bartha et al. 2003) clarified aspects of community dynamics and restoration (Pickett et al. 2001). Dutch ecologists have used permanent plots for decades to show cyclical and directional vegetation dynamics (Leendertse et al. 1997; Smits et al. 2002). Permanent plots are useful in studies of climate change (Petriccione 2005), and in field experiments (Brys et al. 2005) and restoration (Bekker et al. 1999; Grootjans et al. 2001; Bernhart & Koch 2003; Kiehl & Wagner 2006). Despite their advantages, permanent plots are rarely used to study primary succession because vegetation changes slowly (del Moral & Grishin 1999), but the 25-year period of this study was sufficiently long to reveal patterns.

Measuring sequential percent cover and species composition in permanent plots allows the trajectory of vegetation change to be quantified by multivariate methods and similarity measures (Philippi et al. 1998). If two sites become floristically more similar over time, their trajectories are convergent (Baer et al. 2005). Whether or not vegetation converges to a single community is a critical theme in studies of primary succession (Fukami et al. 2005). The tendency for vegetation samples to approach a 'target' or to become more similar to each other has been noted where biotic interactions are strong (Weiher & Keddy (1999; del Moral et al. 2007). However, failure to converge can result from several factors (Capers et al. 2005; McEwan & Muller 2006). Early in primary succession, biotic interactions are weak (Callaway & Walker 1997), so landscape (Belyea & Lancaster 1999) or priority effects can alter establishment success (Drake 1991; Inouye & Tilman 1995; Temperton & Zirr 2004) and preclude convergence. Differing environmental

conditions among plots also may reduce convergence.

Species assembly and vegetation maturation dominate early succession as populations increase in response to abiotic factors (Walker & del Moral 2003). After most available species have established and expanded their dominance, inhibition can exclude rare species, leading to turnover and lower richness (del Moral & Ellis 2004).

Here, changes in vegetation structure (i.e. richness, cover, diversity) are described on a volcanic ridge between 1984 and 2005, with increasing elevation to compare rates of succession. Floristic trajectories and transitions among 'community classes' (CCs) are followed. Note that CCs are not formal associations. Trajectories of high elevation plots could be seen as a recapitulation of those followed by lower plots delayed by environmental stress (see del Moral & Ellis 2004). However, this view assumes that surfaces are similar, that landscape factors are irrelevant and that priority effects are unimportant. Higher plots are slightly steeper, with less soil, and *Lupinus lepidus* has not yet formed dense populations. I will investigate if vegetation samples converge over time and discuss factors that may preclude convergence.

Methods

Several complementary approaches are used to address questions about succession rates and convergence. Regression analyses of time was used as a predictor of descriptors of plant structure to document temporal and spatial changes. Community classes were developed to enhance visualization of overall changes in vegetation in time and space. Detrended Correspondence Analysis (DCA) of these data and percent similarity (PS) was used to compare rates of floristic change and to explore trajectory patterns.

Location

Studebaker Ridge is on the northwest flank of Mount St. Helens, Washington, USA. During the eruption, the direct lateral blast removed all vegetation and most soil (Dale et al. 2005). I established a transect between 1218 m and 1480 m, centered at 46°13'52" N, 122°11'39" W. Plot SR-1 is 3.9 km from the focus of the 1980 eruption (i.e. the first dome), while SR-20 is 2.9 km distant. Structural data of these plots through 2002 were presented earlier (del Moral et al. 2005), but floristic patterns have not been presented.

Sampling

Circular plots (250 m²) were established up the ridge at 50 m intervals. The first ten were established in 1984; in 1989, ten more plots were added uphill. The center of each plot and the ends of four 9-m radii were marked. Slopes range between 9 and 15°. More soil survived in SR-1 to SR-8 (except at SR-5) than higher plots. Species % cover was measured annually in 0.25-m² quadrats arrayed at 1-m intervals along each radius ($n = 24$). Species within the plot but not in any quadrat were given cover of 0.1%. In 1983 no plants were found above 1200 m. A few plants may have established by 1988 on plots first sampled in 1989. Other than *Salix* spp., all taxa were identified to species. Data were posted on the H. T. Andrews LTER web site <http://www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=TV070&topnav=97>.

Pattern descriptions

For each plot, I calculated the number of species (richness), percent cover and the Shannon-Wiener index ($H' = [-S(P_i \ln P_i)]$), where P_i is the proportion of total plot cover of a species. Graphs were produced using AXUM 7 (Mathsoft, Anon. 2001). The % cover data for each plot in each year were classified into provisional community classes using agglomerative sorting with absolute Euclidean distance and flexible sorting ($\beta = -0.25$). The validity of the ten CCs formed was assessed by multi-response permutation procedures (MRPP; McCune & Mefford 2002) that use Sørensen's distance to compare the within- with between-group distances.

Trajectories

β diversity is compositional change in space or time (Carey et al. 2006). DCA with Hill's scaling (McCune & Mefford 2002) was used to describe composition changes (species with < 30 occurrences removed). DCA axes are expressed in standard deviation units (SD), so that a typical species enters and leaves along the axis in ca. 4 SD. So measured, distance in DCA ordination-space estimates β diversity such that about 1.3 SD is one half-change (two samples have 50% compositional similarity). DCA was used despite its well-known disadvantages (Minchin 1987), because it is robust with low β -diversity and it is suited to estimating gradient lengths (Legendre & Anderson 1999). Non-metric multidimensional scaling (McCune & Mefford 2002) showed that only one axis was significant, so only DCA-1 was used.

Four analyses were conducted using data from 1989 to 2005: 1. Individual plots – cover percentage; DCA axis reflects both changes in cover and shifts in species composition. 2. Individual plots – cover values trans-

formed to proportion of species maximum in the data set; DCA axis reflects changes in species composition. 3. Amalgamated groups (AG) – cover percentage; formed by assignment of plots to one of four groups based on its community class in 2005. AG-J consisted of plots SR-1 to 4; AG-I was divided into lower (AG-IL, SR-6 to 10) and upper (AG-IU, SR-11 to 15) plot groups; and AG-H consisted of SR-16 to 20. The anomalous SR-5 was omitted. D. AG as in (3) but cover values transformed as in (B). Two-way indicator species analysis (McCune & Mefford 2002) was used to obtain a reasonable order for species.

Convergence

Convergence was assessed by evaluating changes in the SD of DCA scores of plots that were in the same CC at the last (2005) census (based on absolute and relative cover). Changes in DCA scores were compared for each of the four plot groups using absolute and relative cover.

A complementary approach uses *PS* for pair-wise comparisons:

$$PS_{ij} = 200 \frac{\sum_{k=1}^n \min(x_{ik}, x_{jk})}{\sum_{k=1}^n \min(x_{ik} + x_{jk})} \tag{1}$$

where *i* and *j* are two samples, there are *n* species, *x_{ik}* and *x_{jk}* are the percent cover of species *k* in samples *i* and *j* and *min* is the lower value (Kovach 1999). *PS* values were calculated among plots of each plot group over time.

Statistics

Statistical analyses and summaries were conducted with Statistix 8 (Anon. 2003). The simultaneous analysis of temporal changes in plots without replication and along environmental gradients is problematic. Lack of independence and pseudoreplication preclude using these data to test hypotheses, but one can illustrate patterns, seek trends and generate hypotheses. Changes in structure were assessed by multiple regressions with elevation and time as independent variables. The number of years it took DCA scores of a plot to reach a benchmark DCA score was compared using Spearman’s rank order correlations (*S_r*). DCA scores generally declined with age, so the benchmarks were 0.25, 0.5, 1.0 and 1.5 SD. Lower plots would reach each value sooner than higher plots, so the regression was between plot number (1 to 20) and number of years for each plot to reach each benchmark.

Linear regression of DCA scores vs. time were used to assess trends. I assessed changes in similarity within and between groups over time with one-way ANOVA. Comparisons among groups were based on the conservative Bonferroni statistic.

Results

Vegetation structure

Each measure of structure changed significantly over time in each plot and between plots (Table 1). *Lupinus lepidus* was often the first species to arrive, followed closely by *Anaphalis margaritacea*. The remaining early colonizers were wind-dispersed species (e.g., *Chamerion angustifolium*, *Hieracium albiflorum* and *Hypochaeris radicata*; Fuller & del Moral 2003). Although cover of *Lupinus* increased progressively up the ridge, it was not among the pioneers at the higher plots.

I noted 48 species, many of them uncommon, or, like ferns, confined to gullies. Initially, richness increased in each plot (Fig. 1), then after about 2001 it declined. Mean richness increased from 1.5 species per plot in 1984 to 19 species per plot in 2001 (*P* < 0.0001 by ANOVA). Only time (*P* < 0.0001; *r*² = 0.68) predicted species richness in a regression of richness vs. time and elevation.

Percent cover increased with time, but it decreased with elevation in any particular year. Using cover derived from the 24 individual quadrats per plot permitted a statistical test of differences in cover between years and between plots within each year (Fig. 2). Cover increases of each plot over time were significant (*P* < 0.0001).

Total percent cover increased progressively with age from negligible values in each plot (*P* < 0.0001; Table 1). Changes in cover over elevation and time were visualized in a 3-dimensional plot (Fig. 3). Cover increased with time and decreased with elevation. The rate of cover increase was decreased with elevation. Cover of SR-1 increased most quickly, with rates decreasing sequentially for higher plots. Mean cover over all years decreased from 48.1% in SR-1 to < 3% in higher plots (ANOVA, *P* < 0.0001). At lower elevations, peak values were due to a pulse of *Lupinus*, followed by its decline and increases in other species. At higher elevations, grasses and mosses became more important. Coinciden-

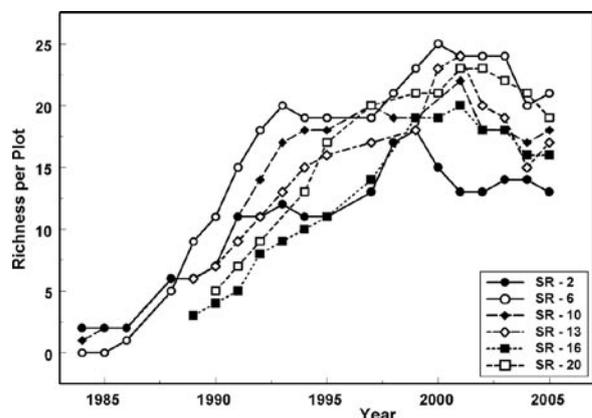


Fig. 1. Species richness changes over time in selected plots.

Table 1. Summary of structural characteristics. Superscripts indicate group membership determined after ANOVA by Bonferroni comparisons ($P < 0.05$). Left side of table: N_p is number of plots in a year, values are means for all plots in the year; right side of table: N_y is number of sample years for each plot, values are means of the plot across all sampled years. Richness = mean number of species per plot; Cover = mean percent cover in plots; H' is mean Shannon-Wiener diversity, excluding plots with no species. N.B. Cover in 1998 is skewed upward because the sparsely vegetated plots SR-11 to SR-20 were not sampled. Groups defined by Bonferroni comparisons are for illustrative purposes only.

Year	N_p	Richness	Cover	H'	Plot	N_y	Richness	Cover (%)	H'
1984	4	1.5 ^a	0.07 ^a	0.277 ^a	SR-1	20	12.6 ^{ab}	48.1 ^a	1.063 ^{ef}
1985	5	1.6 ^a	0.09 ^a	0.554 ^{bcd}	SR-2	20	10.5 ^{ab}	31.7 ^b	1.15 ^{def}
1986	7	2.0 ^a	0.28 ^a	0.553 ^{ab}	SR-3	20	13.2 ^{ab}	23.0 ^b	1.34 ^{cdef}
1988	9	4.0 ^a	1.4 ^a	1.10 ^{abcd}	SR-4	20	8.30 ^{ab}	24.2 ^b	0.89 ^f
1989	19	4.95 ^a	3.3 ^a	1.35 ^{abcd}	SR-5	16	10.4 ^{ab}	4.3 ^{de}	1.63 ^{bdef}
1990	20	6.25 ^{ab}	1.4 ^a	2.26 ^{cd}	SR-6	20	15.9 ^{ab}	19.2 ^b	1.86 ^{bdef}
1991	20	8.3 ^{bc}	3.1 ^{ab}	1.79 ^{abcd}	SR-7	16	12.5 ^{ab}	4.2 ^e	1.82 ^{bdef}
1992	20	11.2 ^{cd}	4.7 ^{ab}	2.09 ^{bcd}	SR-8	18	13.1 ^{ab}	8.2 ^{cd}	1.76 ^{bdef}
1993	16	13.4 ^{de}	6.4 ^{bc}	2.12 ^{cd}	SR-9	20	12.9 ^{ab}	6.5 ^{de}	1.73 ^{bdef}
1994	20	13.1 ^{de}	7.4 ^{bc}	2.11 ^{cd}	SR-10	19	13.3 ^{ab}	5.9 ^{de}	1.86 ^{bdef}
1995	20	14.7 ^{ef}	7.7 ^{bc}	2.28 ^d	SR-11	15	16.1 ^a	6.4 ^{de}	2.09 ^{bcd}
1997	20	15.9 ^{efg}	10.3 ^{bc}	2.23 ^{cd}	SR-12	15	14.2 ^{ab}	8.3 ^{cd}	1.96 ^{bdef}
1998	10	16.7 ^{efg}	18.6 ^{bcd}	1.87 ^{abcd}	SR-13	15	15.3 ^{ab}	7.9 ^{cd}	2.04 ^{bcd}
1999	20	18.1 ^g	15.9 ^{bcd}	2.07 ^{cd}	SR-14	15	13.8 ^{ab}	3.5 ^{de}	2.00 ^{bcd}
2000	17	19.0 ^g	21.2 ^{de}	1.94 ^{abcd}	SR-15	15	12.6 ^{ab}	3.3 ^{de}	2.02 ^{bcd}
2001	20	19.0 ^g	19.7 ^{cde}	1.93 ^{abcd}	SR-16	15	12.7 ^{ab}	2.0 ^e	2.21 ^{abc}
2002	20	17.9 ^g	22.5 ^{de}	1.85 ^{abcd}	SR-17	14	14.2 ^{ab}	1.9 ^e	3.30 ^a
2003	20	18.5 ^g	22.4 ^{de}	1.81 ^{abcd}	SR-18	14	15.9 ^{ab}	2.1 ^e	2.47 ^{ab}
2004	20	17.3 ^{fg}	27.1 ^e	1.67 ^{abcd}	SR-19	14	12.6 ^{ab}	1.8 ^e	2.19 ^{abcd}
2005	20	16.9 ^{fg}	21.3 ^{de}	1.71 ^{abcd}	SR-20	13	17.0 ^a	2.7 ^{de}	2.50 ^{ab}

tally, time and elevation contributes nearly equally to cover predictions ($r^2 = 0.53$; $t_{\text{plot}} = -16.2$; $t_{\text{year}} = 14.7$; $P < 0.0001$). This relationship will change. The regression lines of cover vs. time of the lower 10 plots declined with elevation from 4.03 to 0.96 ($P < 0.0001$); the slopes of this regression for the upper 10 plots decreased from 1.3 to 0.18 ($P < 0.0001$).

Plot diversity (H') variation in time and elevation was complex (Table 1). Both time ($P < 0.0001$, $t_{\text{year}} = 11.8$) and elevation ($P < 0.0002$, $t_{\text{plot}} = 3.81$) were significant predictors (combined $r^2 = 0.25$), but non-linear responses were evident. Adding quadratic functions improved the fit such that for time, $r^2 = 0.42$, while elevation had little

power ($r^2 = 0.04$). Mean H' was least at lower elevations due to the dominance of *Lupinus*. High elevation plots had similar richness, but little dominance, producing an increase in H' through time. There was a universal increase in H' over time, but as dominance was asserted in later years, diversity declined from peaks in the middle of the time sequence. Non-linear regressions for each plot with time were all significant.

Community classes

Ten classes resulted from agglomerative clustering of all plots in all years. MRPP demonstrated that they were significantly different. The chance-corrected within-

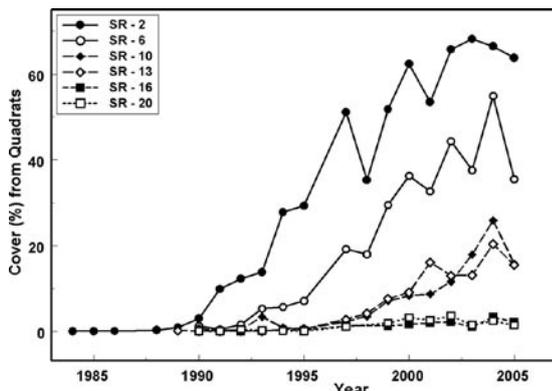


Fig. 2. Percentage cover changes over time in selected plots of Studebaker Ridge, determined from individual quadrats, which permitted significant changes in a plot to be determined by ANOVA.

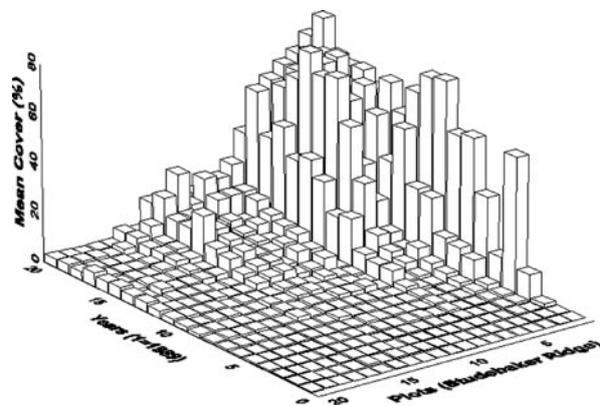


Fig. 3. Percent cover changes in each plot for each of the 20 sample years.

Table 2. Community class of each plot in each year for plot numbers S1 - 20. Types described in Table 3.

Year	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
1984	A	A							A	A										
1985	A	A	A						A	A										
1986	F	A	A			A		A	A	A										
1988	J	F	D		B	A	B	C	A	D										
1989	J	F	D	D	B	D	C	D	C	D	C	A	C	C	C	B	B	B	A	
1990	J	F	F	D	B	D	C	C	C	C	C	A	D	D	C	C	C	B	C	D
1991	J	J	F	D	B	D	D	D	D	C	E	F	D	D	C	C	D	D	F	D
1992	J	J	F	D	E	G	D	D	D	E	E	E	E	F	E	C	F	D	F	E
1993	J	J	G	G	E	G	D	H	F	E	E	E	E	F	E	C	C	D	F	E
1994	J	J	G	I	E	G	D	H	F	E	G	G	E	F	E	C	C	D	F	E
1995	J	J	G	I	E	G	H	H	F	E	H	G	E	E	E	C	H	E	E	E
1997	J	J	G	I	G	I	H	I	F	H	I	G	H	E	E	H	H	E	E	H
1998	J	J	I	J	G	I	H	I	I	H	I	G	I	G	G	H	H	H	E	H
1999	J	J	I	J	G	I	H	I	I	I	I	I	I	G	G	H	H	H	E	H
2000	J	J	J	J	G	I	I	I	I	I	I	I	I	G	G	H	H	H	E	H
2001	J	J	J	J	G	I	I	I	I	I	I	I	I	I	I	H	H	H	H	H
2002	J	J	J	J	G	I	I	I	I	I	I	I	I	I	I	H	H	H	H	H
2003	J	J	J	J	G	I	I	I	I	I	I	I	I	I	I	H	H	H	H	H
2004	J	J	J	J	G	I	I	I	I	I	I	I	I	I	I	H	H	H	H	H
2005	J	J	J	J	G	I	I	I	I	I	I	I	I	I	I	H	H	H	H	H

group agreement compared to a random expectation, was high (0.44; $P < 0.0001$).

Each plot changed through several CCs (Table 2) reflecting accumulation of species and increases in cover. Plots reached their 2005 class by 2001. Transitions through CCs reflected increasing dominance by persistent species (Table 3). Cover increased progressively in SR-1 to SR-4, which stabilized as CC-J. Although initially dominated by *Lupinus*, they now have substantial concentrations of *Penstemon*, *Agrostis* and mosses. The anomalous SR-5 is exposed, barren and rockier than other plots and was arrested in CC-G and lacks dominance by *Lupinus* or mosses. Plots SR-6 to SR-15 stabilized as CC-I, although at different times and by different trajectories. CC-I had less cover than CC-J and was dominated by *Agrostis pallens* and mosses, with some *Lupinus*. I divided plots in CC-I into lower and upper sub-classes

for studies described below. Plots SR-16 to SR-20 were sparsely populated and diverse. They stabilized at CC-H, characterized by *Agrostis pallens*, *Cistanthe* and low cover by mosses and *Lupinus*.

The relative importance of *Lupinus lepidus* declined over time in many plots. I calculated relative *Lupinus* cover for each plot over time. When I correlated relative *Lupinus* cover with year, there were significant negative correlations in SR-1 to SR-3, SR-13 and SR-14 and SR-19. *Lupinus* was dominant in these plots. In contrast, SR-5 and SR-20 had positive relationships.

Trajectories

I conducted DCA to compare vegetation change over space and time. DCA scores over time for individual plots form succession vectors (i.e. trajectories) because they are

Table 3. Mean percent cover of species common in 10 community classes. Species ordered by two-way indicator species analysis. *Salix* rarely flowered and is difficult to ascribe with certainty. Bold values are species characteristic in the AG.

Species	Community class									
	A	B	C	D	E	F	G	H	I	J
Occurrences	20	9	24	31	35	20	29	53	78	45
<i>Carex mertensii</i>	0.01		0.01	0.03	0.05	0.04	0.10	0.10	0.12	0.02
<i>Cistanthe umbellata</i>	0.01	0.02	0.02		0.11	0.05	0.19	0.17	0.07	0.02
<i>Luetkea pectinata</i>		0.02	0.04	0.02	0.07	0.04	0.09	0.12	0.08	0.01
<i>Agrostis pallens</i>	0.01		0.08	0.04	0.09	0.07	1.15	0.34	4.46	4.18
<i>Agrostis scabra</i>					0.06	0.05	0.21	0.13	0.22	0.33
<i>Salix</i> spp.				0.01	0.04	0.05	0.16	0.08	0.30	0.11
<i>Hieracium albiflorum</i>		0.01	0.07	0.11	0.11	0.08	0.11	0.12	0.13	0.42
<i>Hypochaeris radicata</i>		0.02	0.10	0.09	0.10	0.10	0.21	0.14	0.19	0.74
<i>Anaphalis margaritacea</i>	0.04	0.09	0.10	0.11	0.13	0.13	0.28	0.16	0.34	0.18
<i>Chamerion angustifolium</i>	0.01	0.06	0.10	0.10	0.11	10.0	0.08	0.09	0.09	0.01
<i>Penstemon cardwellii</i>				0.02	0.02	0.06	0.29	0.08	0.37	2.08
<i>Polytrichum juniperinum</i>			0.01	0.01	0.03	0.02	0.28	0.18	0.50	3.06
<i>Achillea millefolium</i>					0.02	0.01	0.04	0.02	0.03	0.38
<i>Lupinus lepidus</i>	0.11		0.10	0.09	0.15	1.05	1.96	0.47	1.76	15.5
<i>Racomitrium canescens</i>				0.03	0.11	0.07	2.43	0.29	6.38	25.9

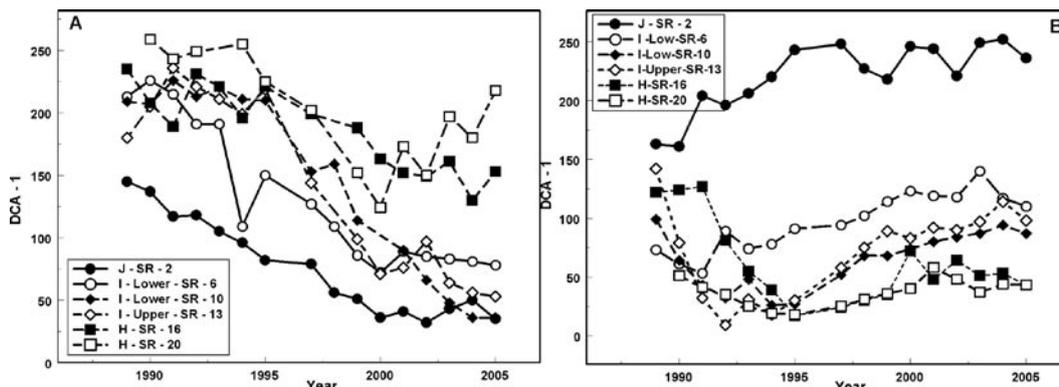


Fig. 4. DCA trajectories of six selected plots. A. Absolute cover; B. Relative cover.

directional and species composition at the end of the study differs systematically from the first samples.

Mean DCA scores (absolute cover, plots) changed through time ($r^2 = 0.27$; $P < 0.0001$); axis 1 extended for 2.97 SD, with 25% of the total variance. DCA scores of representative plots over time demonstrate this pattern (Fig. 4A). The change of DCA scores was large in low elevation plots and small in higher elevation plots. High DCA scores occurred in early years and in high elevation plots dominated by *Chamerion*, *Cistanthe*, *Anaphalis* and *Luetkea*. Low scores reflected dominance by *Lupinus*, *Penstemon*, *Agrostis pallens*, *Salix* and mosses.

DCA scores declined with time since disturbance, so I noted the first year in which a plot reached a benchmark score in this analysis to estimate succession rate. The order in which plots reached a benchmark can estimate succession rate. Spearman's rank correlations (S_r) between plots and the year that a benchmark was reached demonstrated that lower plots reached each benchmark more quickly ($S_r 0.25 = 0.851$, $P < 0.002$; $S_r 0.50 = 0.808$, $P < 0.002$; $S_r 1.00 = 0.740$, $P < 0.005$; and $S_r 1.50 = 0.848$, $P < 0.0001$).

DCA scores of plots based on relative cover changed

little with time ($r^2 = 0.03$, $P < 0.004$). The first axis was 2.49 SD long and had 17% of the variance (Fig. 4B). Annual changes slowed after initial changes. DCA scores of lower sites diverged from those of higher ones between 1989 and 1995, reflecting disproportionate increases in *Lupinus*, *Penstemon* and mosses.

The mean DCA scores (absolute cover) of each amalgamated group (AG; each yearly sample of those plot in community class in 2005) declined with time (Fig. 5A). AG-J changed 1.5 SD ($P < 0.0001$, slope = -9.3); AG-IL shifted over 1.5 SD ($P < 0.0002$, slope = -11.4); AG-IU declined 1.1 SD ($P < 0.0001$, slope = -9.5); and AG-H changed 0.3 SD ($P < 0.0001$, slope = -4.2). Each regression was significantly different from the other, although those of the AG-I subgroups were barely distinct. When the mean DCA scores (relative cover) of the AGs were regressed with time, patterns were subtler than with absolute cover (Fig. 5B). AG-J increased 1.6 SD ($P < 0.0001$, slope = 5.4); AG-IL increased 0.6 SD ($P < 0.0001$, slope = 3.0); AG-IU increased 0.7 SD ($P < 0.0001$, slope = 2.9); and AG-H decreased 0.6 SD ($P < 0.007$, slope = -1.9). The slopes of the AG-I subgroups did not differ.

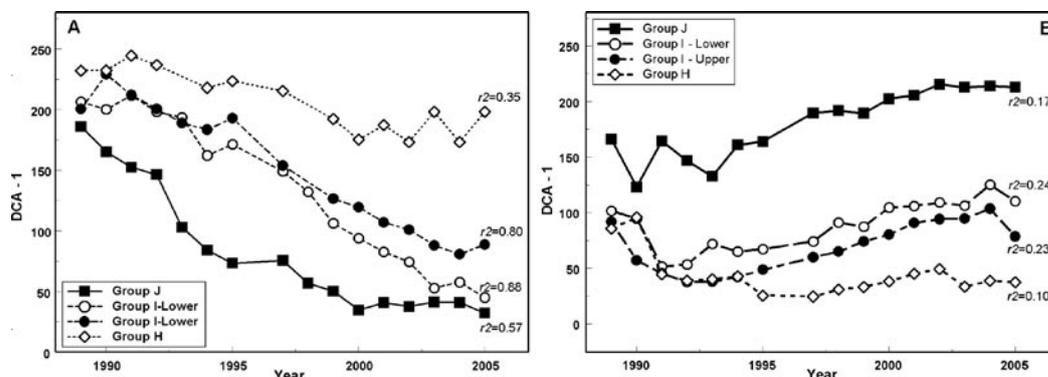


Fig. 5. Mean DCA scores of amalgamated groups recognized by their 2005 classification. r^2 based on regression of DCA-1 vs. year. A. Absolute cover; B. Relative cover.

Convergence

Reduced variation in DCA scores (SD) of plots within each amalgamated group over time would suggest convergence. This was rarely the case. This regression showed a significant decline only in AG-J ($t = -2.53$, $P < 0.03$, $r^2 = 0.31$), and SD in 2005 remained large (0.4 SD). With DCA scores based on relative cover, the SD of AG-J declined ($t = -2.26$, $P < 0.04$, $r^2 = 0.27$), while the initially heterogeneous AG-H declined more steeply ($t = -4.24$, $P < 0.001$, $r^2 = 0.57$). In 2005, SD in AG-J was 0.96, compared to 0.23 in AG-IL, 0.19 in AG-IU and 0.14 in AG-H.

I calculated linear regressions of the mean PS within an amalgamated group vs. time (Table 4). The plots in AG-J converged significantly ($P < 0.0001$) as the mean similarity increased from 20 to 70%. There were no linear trends for plots within AG-IL. The similarities were always high (60 to 70%). A quadratic regression fit the trend of increasing similarities as species assembled, followed by decreasing similarities as dominance hierarchies formed at different rates ($r^2 = 0.66$; $P < 0.002$; $t = 4.22$). There were no trends in AG-IU, where similarities ranged from 51 to 61%. The trend among plots of AG-H was weakly positive ($P < 0.0003$). However, after 1991, when all plots had plants, there was no trend, with PS varying around 65%.

I used linear regressions of between-amalgamated group similarity to determine if there was convergence at larger scales. There were six annual pair-wise comparisons. The increase in similarity between AG-J and both AG-I sub-classes was significant (Table 4), although final values were lower than PS between the two AG-I sub-classes. There were no significant changes between AG-J and AG-H, because PS remained very low. The similarity between each AG-I set and AG-H decreased over time, indicating divergence.

Discussion

Questions about patterns of structure, rates of vegetation development, trajectory convergence and transitions from assembly to inhibition phases are addressed. Consistent changes in structure (richness, diversity, percent cover) among the plots were found, but rates of change depended on elevation. Despite these changes, little evidence was found for floristic convergence.

Structure

After 26 growing seasons, the vegetation on Studebaker Ridge retains steep compositional gradients over elevation, but community composition is changing only slowly as each plot has remained in its CC for several years. Richness stabilized by 2001 in all plots, similar to other Mount St. Helens sites (del Moral 2000). Although many plots were still quite barren, richness subsequently declined. Species that disappeared were short-lived species (e.g. *Polygonum*) or present only as seedlings (e.g. *Abies* and *Cistanthe*). Most species on this ridge are wind-dispersed, yet *Lupinus lepidus*, dispersed by ants, plays a major role in many plots (Bishop et al. 2005). *Lupinus* increases soil nitrogen and appears to have promoted grasses and mosses. Plots yet to experience dense *Lupinus* populations may take much longer to reach levels of vegetation cover found in community class J and may undergo distinct trajectories. The early establishment of *Lupinus* is the most important example of priority effect on this transect. Based on the pattern of development at lower elevation (cf. del Moral & Rozzell 2005), the development of dense populations of *Lupinus* will almost surely govern both subsequent rates and trajectories.

Cover had stabilized only in the lowest plots where conditions are less severe (cf. del Moral & Lacher 2005), while limited soil, lower nutrients and greater exposure seem to inhibit cover accumulation at higher elevations. This occurred after species richness stabilized (see also Wiegleb &

Table 4. Changes in percent similarity (PS) within and among amalgamated groups (AG) in each year of the study. ‘Early’ is the mean PS of 1989-1991. ‘Mean’ is the mean PS between 1989 and 2005. ‘Late’ is the mean PS of 2003-2005. Positive slope indicates increasing PS over time, negative slope indicates decreasing PS over time. Classes listed from lowest to highest elevation. Probability (P) determined from linear regression of the similarities.

Comparison	Early (%)	Mean (%)	Late (%)	Slope	$P <$	r^2
AG-J internal	17.7	42.1	69.5	+3.28	0.0001	0.47
AG-IL internal	64.3	56.1	68.9	+0.28	ns	ns
AG-IU internal	57.2	57.3	61.8	+0.19	ns	ns
AG-H internal	50.1	61.0	63.1	+0.86	0.0003	0.09
AG-J to AG-IL	13.8	28.1	49.8	+2.61	0.0001	0.812
AG-J to AG-IU	12.5	19.3	29.9	+1.38	0.0004	0.639
AG-J to AG-H	8.2	7.4	7.0	-0.06	ns	ns
AG-IL to AG-IU	68.5	66.3	65.5	-0.12	ns	ns
AG-IL to AG-H	55.6	40.2	19.8	-2.82	0.0001	0.820
AG-IU to AG-H	60.9	52.2	32.0	-2.36	0.0001	0.695

Felinks 2001). Eventually, seedlings of conifers, which now occur sporadically, will establish and permit shade-tolerant species to establish. Though cover remained low at higher elevations, it too is increasing while richness has declined. Most common species present on the transect occur near all plots, most are wind-dispersed and all species found can occur above 1500 m (del Moral & Eckert 2005), so the pool of species on the transect is similar throughout. However, increasing environmental stress is likely to restrict cover below values obtained at lower elevations on the transect.

Diversity (H') is likely to continue the decline noted for each plot because dominance hierarchies will intensify and uncommon species will be eliminated. Grasses, *Penstemon*, *Salix*, mosses and perhaps *Lupinus* should become dominant if patterns reflect those of lower elevation (del Moral & Lacher 2005). If conifers become dominants, diversity should decline further (cf. del Moral & Ellis 2004) because, in this flora, fewer species thrive beneath conifers compared to meadows (del Moral 2000).

Richness, cover and diversity combine to describe overlapping assembly, maturation and inhibition phases in early primary succession. Assembly continues until all probable colonists have established (cf. del Moral & Jones 2002). Maturation occurs as vegetation cover expands in the plot. During this phase, facilitation may permit the establishment of additional species (del Moral & Wood 1993). Diversity peaks at the end of assembly, then declines with differential cover expansion. While vegetation continues maturing, facilitation of some species may continue, but the inhibition phase commences when restricted seedling establishment causes further declines of diversity, while cover remains stable (cf. Walker & del Moral 2003).

Rates

Succession rates are critical measures of the community, reflecting species turnover and changes in dominance hierarchy (Brown et al. 2006). Cover, generally reflecting recovery from disturbance, is here a measure of successional rate since the system started on barren surfaces, but species composition based ordination provides a more comprehensive estimate of successional rates.

The slopes of richness vs. time for each plot were similar, indicating that elevation had a small effect in slowing establishment. In contrast, the accumulation of cover was substantially retarded at higher elevations evidenced by sharply declining slopes of cover vs. time with increasing elevation. Within an elevation range of only 260 m, the rate of succession differs due to a shorter growing season and increased environmental stress. In the 25 years encompassed by this study, the effects of increasing elevation were qualitatively similar to effects of reduced successional time-span. Although this relationship will change substantially,

it confirms that succession was delayed progressively up the slope.

DCA scores of lower plots changed more than higher ones. Mean annual DCA shifts in plots in AG-J were large until 2000, but AG-I continued directional change to 2004, while AG-H changed little. The rate at which DCA scores of plots reached specific benchmarks declined with elevation, additional evidence that the development of high elevation vegetation was retarded at least by the shorter growing seasons (del Moral & Ellis 2004).

The classification produced clear patterns. Each plot developed sequentially, but at different rates. All initial CCs transitioned often and assembly and vegetation maturation were consistent across plots (Table 2). By 2005, there was a regular progression of classes (excluding CC-G) with the most mature (CC-J) found in the lowest plots, and the immature CC-H in the highest plots. Lower plots had developed through more CCs than had upper ones.

These alternative ways to assess succession rates confirm that rates declined with elevation. At least some individuals of most species can establish as soon as there are suitable safe-sites, so richness patterns are similar throughout the transect. In contrast, vegetation development is slowed by limited soil and less favorable conditions at higher elevations. Thus, negative species interactions, now intense at lower elevations, have scarcely commenced in the higher plots.

Convergence

The pattern of species establishment was similar at each plot, except that *Lupinus* was the first colonist at lower elevations, but was sparse in higher elevation plots. Trajectories differed depending on early establishment of *Lupinus*. As in other habitats on Mount St. Helens (del Moral et al. 2005), mosses were not pioneers. Mosses require facilitation, after which they may form dense mats that preclude seedling establishment (del Moral & Rozzell 2005). In SR-8 to SR-13, a weak *Lupinus* invasion occurred in the mid-1990s, but dense vegetation has yet to form. Thus, the degree to which the relatively poorly dispersed *Lupinus lepidus* has established is a determinant of the degree to which vegetation will converge.

Trajectories described by DCA exhibited several patterns. The likelihood of convergence decreased as distance between samples increased. When amalgamated groups were analysed using absolute cover, there was some evidence for convergence between AG-J and AG-IL, but AG-IU diverged from both, and AG-H, once similar to the others, also diverged. When relative cover was used to emphasize floristics, convergence was not found. The lack of *Lupinus* at higher elevation could lead to alternative trajectories. Thus, given the rapid decline of similarity with distance, any convergence on this transect should occur only within

short distances (del Moral 1998; del Moral & Ellis 2004), and divergence is possible.

Plots within a community class were spatially proximate and there was weak evidence for convergence within a CC. The SD of DCA scores for plots within amalgamated groups declined in AG-J and AG-H, but remained very high in the lower plots, indicating that these plots retained large floristic differences. The PS within AGs increased in AG-J, and slightly in AG-H, but they remained relatively low. There was no directional change in either AG-I subclass, which suggests that trajectories of individual plots were changing in parallel, not converging. The PS between AGs weakly suggested incipient convergence, but the similarities between them were low. AG-J has very low similarity to the distant AG-H, while AG-IL is diverging from AG-H. Spatial effects alone will limit convergence between these AGs, and even convergence among plots within AGs will be partial, at most.

None of the approaches used in this study demonstrated either that vegetation within classes will become more homogeneous or that the classes will tend to merge as they mature. Limited convergence may occur within closely spaced samples (< 250 m), but even if such processes as priority effects were overcome, the environmental gradient and local variations would appear to preclude tight convergence.

Permanent plot studies can be used to explore assembly rules, but thus far, the time is too short to test specific predictions based on rules. However, this study does offer clues. Each plot has passed through a consistent sequence that demonstrated a network of trajectories with elements of convergence and divergence. Three initial CCs existed at the first sampling. A network of transitions followed to form different CCs that were sorted by elevation. Establishment started sooner and vegetation grew more quickly at lower elevations than at higher elevations. If higher plots were to recapitulate the trajectories of lower ones, then CC-H would eventually develop into CC-J. However, dense populations of *Lupinus* have directed trajectories at lower elevation, so it is equally likely that trajectories will differ because *Lupinus* may never become common at high elevation on this ridge. Local environmental conditions and priority effects also may prevent the occurrence of similar vegetation along this transect.

This study suggests that forces that may produce vegetation convergence early in primary succession are weak, while those that promote divergence (e.g. priority effects and intrinsic environmental differences) are strong. Trajectories of plots at higher elevations do not closely recapitulate those of lower ones, emphasizing that environmental severity affects trajectories. Weak evidence for convergence exists, but only among plots located in close proximity. Common space-for-time substitution methods used in toposequence studies may

be even more suspect than commonly acknowledged.

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